FACULDADE DE BIOCIÊNCIAS

PROGRAMA DE PÓS-GRADUAÇÃO EM ZOOLOGIA

ANÁLISE FILOGENÉTICA DE DORADIDAE (PISCES, SILURIFORMES)

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Resumo

Doradidae é uma família monofilética endêmica da América do Sul diagnosticada por uma única sinapomorfia entre os bagres e reconhecida por uma combinação de características morfológicas. Espécies da família possuem um escudo infranuchal, que é uma placa óssea superficial formada pela fusão dos ossículos expandidos da linha lateral e um ligamento ossificado que se estende desde a placa nucal posterior ate a ponta da primeira costela. A maioria das espécies são caracterizadas por ter uma placa cefálica bem desenvolvida, boca subterminal, processo poscleitral largamente exposto, acúleo peitoral e dorsal serrilhados e o corpo achatados dorsoventralmente (Sabaj, 2002). É uma família diversificada com 92 espécies, das quais uma é fóssil, agrupadas em 32 gêneros.

Os estudos filogenéticos dos Doradidae têm sido tradicionalmente baseados em caracteres morfológicos e apenas um trabalho foi baseado em caracteres moleculares, os resultados desse trabalho são conflitantes com os resultados morfológicos.

O objetivo principal deste estudo foi recuperar relações filogenéticas de Doradidae a traves da análise simultânea de todos os conjuntos de dados previamente disponíveis para a família Doradidae alem de dados morfológicos e moleculares propostos neste estudo. 200 caracteres, utilizados por outros autores, referentes à morfologia externa, osteologia, gônadas e bexiga natatória foram revisados. 91 caracteres miológicos foram analisados e propostos aqui pela primeira vez num contexto filogenético. 3011 caracteres moleculares foram obtidos de dois genes mitocondriais (*16s* e *co1*) e um gene nuclear (*rag1*). Foram compilados um total de 3302 caracteres para 94 espécies.

Para atingir o objetivo principal estudos moleculares e anatômicos foram realizados por separado. Uma análise apenas molecular foi realizado com 77 espécies descritas e seis espécies não descritas. A análise foi baseada em fragmentos dos genes mitocondriais *16s* e *co1* e um gene nuclear *rag1*. Foi obtido um alinhamento de 3011 pares de bases para 146 espécimes de Doradidae e o grupo externo Auchenipteridae e Aspredinidae. Os dados foram analisados usando máxima parcimônia, máxima verossimilhança, e análises Bayesianas. Um estudo anatômico foi também desenvolvido e é apresentado como um manuscrito descritivo da musculatura peitoral e cranial de Doradidae. 61 espécies de Doradidae foram examinados incluindo representantes de todos os gêneros. 22 músculos foram descritos referindo-se a sua origem ontogenética, função, áreas de origem e de inserção, e porções, em alguns casos aspectos chave de cada músculo foram descritos.

A análise simultânea de todos os dados disponíveis revelou interessantes hipóteses de relacionamentos. Astrodoradinae é recuperado como o clado mais basal da família. Os gêneros monotípicos *Wertheimeria*, *Franciscodoras* e *Kalyptodoras*, endémicos das drenagens da costa leste do Brasil, são recuperados como um clado. Os gêneros monotípicos *Doraops* e *Centrochir*, endêmicos das drenagens transandinas, são recuperados como grupo irmão dos gêneros amplamente distribuídos, *Pterodoras* e *Platydoras* respectivamente. Os gêneros de Doradidae com barbilhões ramificados e *Oxydoras*, são recuperados como um grupo monofilético. O gênero *Ossancora*, recentemente descrito, não e recuperado como um um grupo monofilético

Abstract

Doradidae is a monophyletic family endemic to South America diagnosed by a unique synapomorphy among catfish and recognized by a combination of morphological characteristics. Species of the family posses a infranuchal scute which is a superficial plate-like bone co-formed by the fusion of an expanded ossicle of the lateral line canal and an ossified ligament extending from beneath the posterior nuchal plate to the tip of the first rib. Most species are characterized by a well-developed cephalic shield, subterminal mouth, large exposed postcleithral process, sturdy serrated pectoral- and dorsal-fin spines, and dorsoventrally flattened bodies (Sabaj, 2002). It is a diverse family with 92 extant and one fossil species grouped into 32 genera.

Phylogenetic studies of doradids have traditionally been based on morphological characters and only one work has been based on molecular characters, which conflicts with previous morphological results.

The main goal of this study was to recover phylogenetic relationships of the entire Doradidae by the analysis of all the previously available data for Doradidae and newly gathered morphological and molecular data. 200 characters referring to external morphology, osteology, gonads, and swimbladder were reviewed from previous authors. 91 myological characters were analyzed and proposed here for the first time in a phylogenetic context. 3011 molecular characters were gathered correspondent to two mitochondrial genes (*16s* and *co1*) and one nuclear gene (*rag1*). Compiling a total of 3302 characters for 94 species.

In order to achieve the main goal molecular and anatomical studies were performed separated. An only molecular analysis was carried out including 77 described and six undescribed species. The analysis was base on fragments of the mitochondrial *16s* and *co1* and the nuclear *rag1*. It was obtained an aligment of 3011 base pairs for 146 specimens of Doradidae and the outgroup Auchenipteridae and Aspredinidae. Data were analyzed using Maximum Parsimony, Maximum Likelihood, and Bayesian analyses. An anatomical study was also developed and is presented as a descriptive manuscript of the cranial and pectoral musculature of Doradidae. 61 species of Doradidae were examined including representatives of all the genera. 22 muscles were described referring to their ontogenetic origin, function, area of origin and insertion, and portions; in certain cases key aspect of each muscle were described.

The analysis of the all the data together uncovered newly hypothesized relationships. Astrodoradinae is recovered as the most basal clade of the family. The monotypic *Wertheimeria*, *Franciscodoras*, and *Kalyptodoras*, endemic to the east-coast drainages of Brazil, are recovered as a clade. The monotypic *Doraops* and *Centrochir*, endemic to TransAndean drainages, are recovered as sister to widely distributed *Pterodoras* and *Platydoras* respectively. The Doradidae with fimbriate barbels and *Oxydoras* are recovered as a monophyletic group. The recently described *Ossancora* is not recovered as a monophyletic group.

Sumário

ANÁLISE FILOGENÉTICA DE DORADIDAE (PISCES, SILURIFORMES)

Introdução geral a Doradidae

Siluriformes compreende os peixes mais diversos e amplamente distribuídos do grupo Ostariophysi, com 36 famílias, 478 gêneros e aproximadamente 3100 espécies (Ferraris, 2007). Dentro dessa ordem a superfamília Doradoidea, considerada monofilética (sensu de Pinna, 1998: 306), está representada em América do Sul pelas famílias Doradidae e Auchenipteridae, e por Mochokidae na África (Ferraris, 2003).

Doradidae é reconhecida por três sinapomorfias: escudos ósseos laterais, formados a partir dos túbulos da linha lateral; ligamento entre o ramo de Müller e a linha lateral; e ligamento ossificado entre a primeira costela e a placa nucal posterior (Birindelli, 2010). A maioria das espécies tem uma placa cefálica bem desenvolvida, boca subterminal, processo umeral largamente exposto, espinhos dorsais e pectorais serreados e o corpo deprimido.

As espécies da família se distribuem na América do Sul, chegando a altitudes de 1000 m nos Andes de Peru e Venezuela (Burgess, 1989). As espécies de Doradidae predominam na bacia Amazônica (~55 espécies), mas também se distribuem nas bacias do Magdalena (uma espécie), Maracaibo (duas espécies), Orinoco (~21 espécies), Essequibo (~15 espécies), Guiana (quatro espécies), Tocantins (sete espécies), Paraná (oito espécies), São Francisco (uma espécie), Paraguassú (uma espécie) e Jequitinhonha (uma espécie).

A biologia do grupo tem sido estudada para algumas espécies por diversos autores como D´Orbigny (1846, apud. Veitenheimer & Mansur, 1975), Miranda Ribeiro (1911); Starks (1913), Eigenmann (1925), Ihering & Azevedo (1934), Schultz (1944), Menezes & Menezes (1948), Menezes (1949), Goulding (1979 e 1980), Hahn, Fugi & Andrian (1991), Ferriz et al. (2000), e Fugi, Agostinho & Hahn (2001). O estudo mais completo até hoje foi desenvolvido por Carvajal (2005) que analisou 31 espécies da família na Venezuela, dividindo-as de acordo com os hábitos em onívoras (sete espécies), insetívoras (21 espécies), herbívoras (duas espécies) e malacófagas (uma espécie).

Pouco se conhece sobre a biologia reprodutiva da família, Burgess (1989) reportou a construção de ninhos, enquanto que Goulding (1979 e 1980) descreveu hábitos migratórios para espécies como *Pterodoras granulosus* (Valenciennes), *Lithodoras dorsalis* (Valenciennes), e *Megalodoras uranoscopus* (Eigenmann & Eigenmann). Rapp Py-Daniel & Cox Fernandes

(2005), em um trabalho sobre os aspectos reprodutivos de espécies amazônicas, mostraram que a família pode desenvolver dimorfismo sexual apresentando alterações nos filamentos da nadadeira dorsal de machos maduros de *Nemadoras humeralis* (Kner).

Taxonomia e estudos filogenéticos

O estudo taxonômico da família começou com Linnaeus (1758 e 1766) que descreveu três espécies em *Silurus*. Em 1771, Catesby propôs o gênero *Cataphractus* para *Silurus cataphractus* (espécie proposta por Linnaeus). Em 1803, La Cépède descreveu o gênero *Doras* que incluía *Silurus carinatus* e *Silurus costatus*. A partir daí, todas as espécies pertencentes à família Doradidae foram descritas neste gênero até que, em 1855, Kner descreveu, além de 18 espécies novas, o subgênero *Oxydoras*. Bleeker (1858, 1862, 1863a, 1863b e 1864) descreveu outros gêneros como *Acanthodoras*, *Astrodoras*, *Amblydoras*, *Hemidoras*, *Lithodoras*, *Platydoras*, *Pseudodoras*, *Pterodoras* e *Rhinodoras*. O mesmo autor em 1863b propôs as tribos Doradini, Pseudoauchenipterini e Auchenipterini as quais foram agrupadas por Günther (1864) no grupo Doradina. No fim do século XIX, mais alguns gêneros foram descritos por Cope (1872 e 1878), Eigenmann & Eigenmann (1888) e Boulenger (1896). Eigenmann & Eigenmann (1890) estabeleceram várias subfamílias de Siluriformes, entre as quais se encontra Doradinae, mas foi somente Miranda Ribeiro (1911) quem elevou o grupo à categoria de família e propôs pela primeira vez *Weirtheimeria* Steindachner, 1877 como parte de Doradidae.

Em 1925, Eigenmann fez a única revisão taxonômica completa de Doradidae, agrupando as 68 espécies em 26 gêneros e definindo a família com base em caracteres anatômicos relativamente bem detalhados, além de ter publicado a primeira chave existente para a família. Poucos trabalhos foram realizados depois desta data, sendo a literatura subsequente composta por descrições de espécies e gêneros (e.g. Myers, 1927; Fowler, 1941; Schultz, 1944). Em 1968, Fernandez-Yepez publicou uma revisão dos Doradidae da Venezuela descrevendo alguns gêneros e espécies que posteriormente foram sinonimizados.

Somente em 1992 Higuchi realizou a primeira tentativa de conhecer as relações filogenéticas da família em sua tese de doutorado, o trabalho do Higuchi foi compilado e publicado por de Pinna (1998). Higuchi fez uma analise cladística de caracteres morfológicos propondo a filogenia de toda a família, ele estabeleceu o gênero monotípico *Wertheimeria* como o mais “basal”. Confirmou a monofilia da família e estabeleceu três subfamílias:

Astrodoradinae, Platydoradinae e Doradinae (Fig. 1). A única subfamília estabelecida nominalmente é Astrodoradinae (Higuchi et. al., 2007).

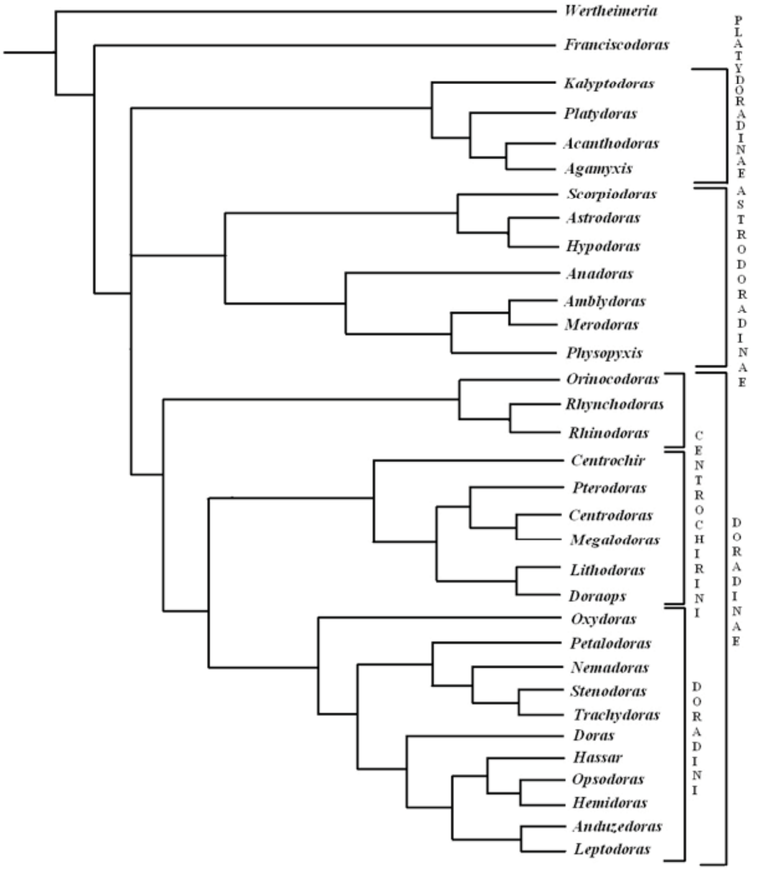

Figura 1. Filogenia de Doradidae proposta por Higuchi (1992) com base em dados morfológicos.

Sabaj (2002) fez uma lista taxonômica comentada que foi posteriormente publicada (Sabaj & Ferraris, 2003) e estabeleceu as relações filogenéticas das espécies do gênero *Leptodoras* (Boulenger) usando como grupo externo *Doras* (La Cépède), *Anduzedoras* (Fernandez-Yépez), *Hassar* (Eigenmann & Eigenmann) e *Hemidoras* (Bleeker).

Moyer *et al.* (2004) usou dados moleculares (genes 12s e 16s do rRNA mitocondrial e o gene nuclear elongation factor-1 alpha) propondo uma filogenia para 23 gêneros de Doradidae (Fig. 2), no entanto o seu estudo não incluiu os táxons mais basais (*Wertheimeria* e *Franciscodoras*) prospostos na analise de Higuchi.

A analise filogenética de Moyer *et al.* (2004) corroborou a monofilia da família e da subfamília Astrodoradinae, mas ainda assim mostrou muitas incongruências com o resultado de Higuchi. Por exemplo, a falta de suporte para a subfamília Platydoradinae e as tribos Centrochirini e Doradini. Baseado em uma reavaliação parcial dos dados de Higuchi, Moyer *et al*. concluíram que vários dos caracteres de Higuchi foram incorretamente polarizados e os estados estabelecidos para vários táxons são incorretos.

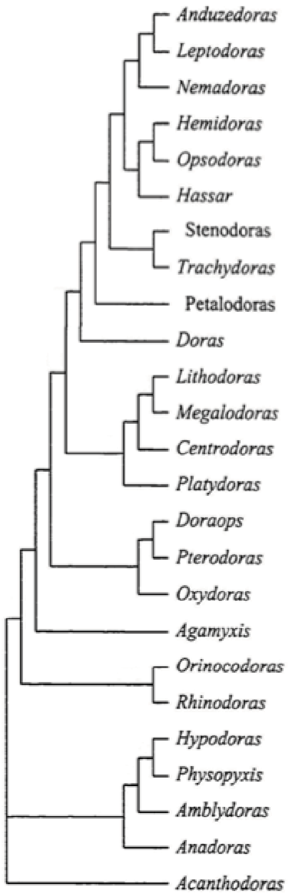

Figura 2. Filogenia de Doradidae proposta por Moyer *et al.* (2004) com base em dados moleculares.

Birindelli (2006) completou a revisão taxonômica de três gêneros na tribo Rhinodoradini e uma analise filogenética que incluiu 46 espécies de Doradidae, a maioria pertencentes à subfamília “Doradinae” (Fig. 3).

Birindelli encontrou o gênero monotípico *Kalyptodoras bahiensis* numa tritomia basal com

Wertheimeria, e um clado com os outros doradídeos. Ele rejeitou as sinapomorfias de Higuchi para as tribos Centrochirini e Doradini e estabeleceu como grupos irmãos Astrodoradinae e Doradinae baseado em um caráter apenas.

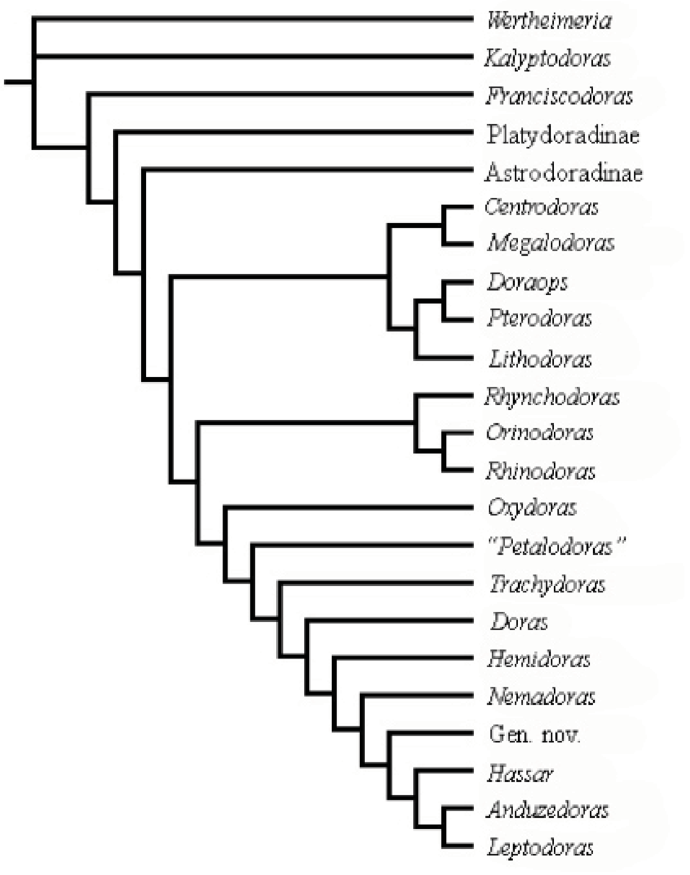

Figura 3. Filogenia de Doradidae proposta por Birindelli (2006) com base em dados morfológicos.

Birindelli (2010) estudou as relações do superfamília Doradoidea com ênfase em Doradidae. Ele incluiu 27 gêneros representados em 55 espécies e seus resultados foram similares a aqueles de 2006. Birindelli encontrou o clado *Wertheimeria* + *Kalyptodoras* como grupo irmão do restante da família. Ele propôs duas subfamílias: Platydoradinae e Doradidinae e três tribos dentro de Doradinae: Pterodoradini, Rhinodoradini e Doradini (Fig. 4).

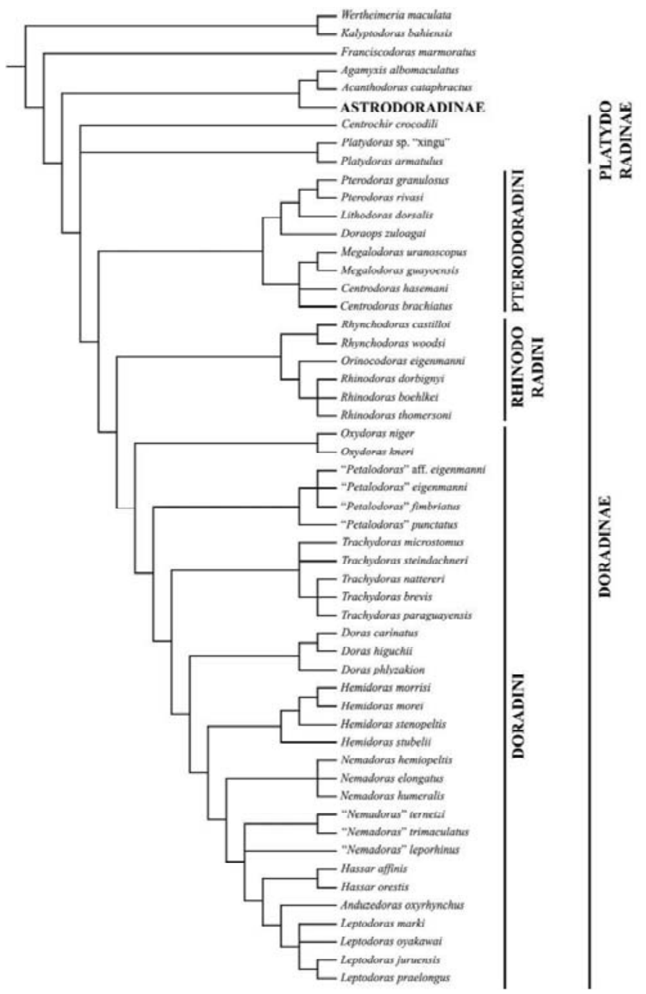

Figura 4. Filogenia de Doradidae proposta por Birindelli (2010) com base em dados morfológicos.

Sousa (2010) fez uma revisão taxonômica e estabeleceu as relações filogenéticas das espécies da subfamília Astrodoradinae incluíndo os gêneros *Acanthodoras* e *Agamyxis* (Fig. 5). Ele propôs a sinonimização de *Physopyxis* e *Merodoras* ao gênero *Amblydoras*.

Figura 5. Filogenia de Doradidae proposta por Sousa (2010) com base em dados morfológicos.

Nos últimos anos vários estudos taxonômicos tem sido publicados, como a revisão de *Leptodoras* (Sabaj, 2005) e *Physopyxis* (Sousa & Rapp-Py Daniel, 2005), descrições de novas espécies de *Rhinodoras* (Sabaj et al., 2006, Sabaj *et al*., 2008), *Rhynchodoras* (Birindelli *et al.,* 2007), *Doras* (Sabaj Pérez *et al.,* 2007; Sabaj Pérez & Birindelli 2008), *Platydoras* (Piorski *et al*. 2008) e *Leptodoras* (Birindelli *et al*. 2008, Birindelli & Sousa 2010), a descrição de um novo gênero *Ossancora*, com uma nova espécie *Ossancora asterophysa* (Birindelli & Sabaj-Pérez, 2011), e a descrição de um novo gênero e espécie *Merodoras nheco* (Higuchi *et al*. 2007).

Analise filogenética de Doradidae

O objetivo principal deste estudo foi reconstruir as relações filogenéticas das espécies da família Doradidae, baseada na análise conjunta de sequências de DNA mitocondrial e nuclear, e caracteres morfológicos em uma análise de evidência total para todos os táxons da família.

Até hoje somente Higuchi (1992), Moyer *et al*. (2004) e Birindelli (2006 & 2010) tentaram estabelecer as relações filogenéticas das espécies de Doradidae utilizando metodologias diferentes, mas cada um deles encontrou relações de parentesco diferentes entre os gêneros. Os dados morfológicos existentes eram caracteres de morfologia externa, osteologia, gônadas e bexiga natatória e os dados moleculares correspondiam a 23 gêneros para os quais foram sequenciados os genes 12s, 16s e elongation factor 1 alpha.

O presente estudo compilou e completou a informação existente sobre a morfologia além de agregar um novo conjunto de evidencia morfológica referente a caracteres da miologia da família assim como evidencia molecular usando os genes *16s*, *cytochrome c oxidase subunit 1* (*co1*) e *recombination activating subunit 1 gene* (*rag1*).

O trabalho foi desenvolvido em grande parte no Laboratório de Sistemática de Vertebrados da PUCRS com material próprio da coleção do Museu de Ciências e Tecnologia e exemplares emprestados do Museu de Zoologia da Universidade de São Paulo, Instituto Nacional de Pesquisa da Amazônia e Academy of Natural Sciences of Philadelphia. O trabalho molecular foi desenvolvido nos laboratórios moleculares da Academy of Natural Sciences of Philadelphia. Como resultado do estudo foram produzidos três artigos ainda não submetidos.

1. Cranial, ventral, and pectoral musculature of thorny catfishes (Siluriformes: Doradidae)

Este artigo constitui um texto descritivo sobre a musculatura cefálica, ventral e peitoral dos representantes da família Doradidae. Foram estudadas 61 espécies de Doradidae pertencentes a todos os gêneros da família. Foram descritos e ilustrados um total de 22 músculos fazendo referencia a informações sobre origem ontogenética, função, áreas de origem, inserção e divisões do músculo e foram registradas observações especificas a cada músculo.

O trabalho pretende complementar a escassa informação disponível sobre musculatura em Siluriformes e especificamente em Doradidae. Dentro dos Siluriformes alguns trabalhos no contexto de morfologia funcional tem sido publicados (Alexander, 1965; Gosline, 1989; Schaefer & Lauder, 1986 e Adriaens *et al.*,2001) assim como estudos referentes à ontogenia (Adriaens & Verraes, 1996 & 1997; e Adriaens, 1998). Recentemente, vários trabalhos sobre a musculatura esquelética de Siluriformes têm sido publicados por Rui Diogo: *e.g.* Diogo & Chardon (2000a, b); Diogo *et al.* (1999, 2000, 2001, 2002, 2003a, b, c, d, 2004a, b, c, d, 2006a, b) mas somente um deles aborda informações referentes à Doradidae (Diogo *et al.*, 2004b). Diogo *et al.* (2004b) realizam algumas inferências filogenéticas com base em poucos exemplares, razão pela qual as observações são tratadas com cautela e algumas discordâncias com os autores são assinaladas no artigo.

O manuscrito será submetido para publicação na Neotropical Ichthyology, revista da Sociedade Brasileira de Ictiologia.

2. Molecular phylogeny of thorny catfishes (Teleostei: Siluriformes: Doradidae)

Este artigo apresenta os resultados das análises dos dados moleculares. Foram compiladas um total de 3011 pares de bases provenientes dos genes mitocondriais (*16s*, *cytochrome c oxidase subunit 1*) e um gene nuclear (*recombination activating subunit 1 gene*). Foram sequenciados 146 terminais que incluem 32 gêneros de Doradidae e 10 espécies do grupo externo.

O trabalho pretende estabelecer relações filogenéticas baseadas em dados moleculares. O único trabalho prévio sobre filogenia molecular foi publicado por Moyer *et al.* (2004) no qual não foram incluídos todos os gêneros da família. Neste artigo foi completada a amostragem taxonômica e foram usados genes comuns em estudos filogenéticos recentes fazendo o estudo comparável com outros.

Três tipos de análises de inferência filogenética foram empregadas (Máxima Parcimônia, Máxima Verossimilhança e Analise Bayesiana) para abordar os diferentes critérios de otimização e fazer uma completa exploração dos dados. Além disso, cada gene foi analisado separadamente com a finalidade de entender qual informação cada um está fornecendo para a reconstrução filogenética.

O manuscrito será submetido para publicação na revista Molecular Phylogenetics and Evolution.

3. Total evidence analysis of the Doradidae

Este artigo apresenta a reconstrução de hipóteses filogenéticas com base na análise simultânea de todos os conjuntos de dados disponíveis para a família Doradidae. No trabalho foram revisados caracteres morfológicos utilizados por outros autores referentes à morfologia externa, osteologia, gônadas e bexiga natatória (totalizando 200 caracteres); assim como aqueles referentes à musculatura que são propostos no artigo pela primeira vez dentro do contexto filogenético (91 caracteres). Além disso foram incluídos caracteres moleculares de dois genes mitocondriais (*16s*, *cytochrome c oxidase subunit 1*) e um gene nuclear (*recombination activating subunitn 1 gene*). O estudo reúne um total de 3302 caracteres para 92 espécies, e no corpo do trabalho são comparados e discutidos os resultados da filogenia morfológica com os resultados obtidos pela evidência total.

Para esta análise somente a máxima parcimônia foi utilizada pois até o momento apenas este critério de otimização está disponível e implementado nos softwares existentes.

O trabalho reune toda a informação filogenética disponível para Doradidae até o momento. Uma nova classificação para a família assim como mudanças taxonômicas não são apresentadas, no entanto, pois novos dados moleculares continuam sendo obtidos e deverão refinar ainda mais a filogenia proposta muito em breve.

O manuscrito será submetido para publicação na revista Zoological Journal of the Linnean Society.

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CRANIAL AND PECTORAL MUSCULATURE OF THORNY CATFISH (SILURIFORMES: DORADIDAE)

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ABSTRACT

This paper constitutes a descriptive text about cephalic, ventral, and pectoral musculature of Doradidae. 61 species of Doradidae were examined including representatives of all the genera.

22 muscles were described referring to their ontogenetic origin, function, area of origin and insertion, and portions; in certain cases key aspect of each muscle were described. Nine muscles of the cranial region were described: *adductor mandibulae*, *retractor tentaculi*, *extensor tentaculi*, *levator arcus palatini*, *dilatator operculi*, *levator operculi*, *adductor operculi*, and *adductor arcus palatini*. Six muscles of the ventral region were described: *intermandibularis*, *protractor hyoides*, *hyohyoides inferioris*, *hyohyidei abductores*, *hyohyoidei adductores*, and *sternohyoideus*. Seven muscles move the pectoral fin of Doradidae: *adductor superficialis*, *adductor profundus*, *abductor superficialis*, *abductor profundus*, *arrector ventralis*, *arrector dorsalis*, and *abductor rotator*.

Analysis and comparisons between Doradidae and other catfish families (*e.g.* Auchenipteridae, Aspredinidae) were performed in order to get a better understanding of function, position, shape, and development of muscular system. Homologies were established after the careful observation of all the specimens available. Most of the nomenclature follows Winterbotton (1974). A muscle not previously identified for the pectoral fin of catfishes is described and named *abductor rotator*.

KEY WORDS

Myology, catfish, anatomy, *adductor mandibulae*, *protractor hyoidei*, functional morphology.

INTRODUCTION

Doradidae is diagnosed by a unique synapomorphy among catfish and recognized by a combination of morphological characteristics. Species of the family posses a infranuchal scute which is a superficial plate-like bone co-formed by the fusion of an expanded ossicle of the lateral line canal and an ossified ligament extending from beneath the posterior nuchal plate to the tip of the first rib. Most species are characterized by a well-developed cephalic shield, subterminal mouth, large exposed postcleithral process, sturdy serrated pectoral- and dorsal-fin spines, and dorsoventrally flattened bodies (Sabaj, 2002). It is a diverse family with 92 extant and one fossil species grouped into 32 genera.

Species of Doradidae are widely distributed in South America and commonly found in lowlands in the Amazon basin. Species of the family can also be found in the Magdalena, Maracaibo, Orinoco, Essequibo, Guiana, Tocantins, Paraná, São Francisco, Paraguassú, and Jequitinhonha.

Information about the anatomy of the Doradidae are restricted to the phylogenetic studies of previous years (Higuchi, 1992; Sabaj, 2002; Birindelli, 2006 & 2010; Sousa, 2010). Little research has been done in muscular anatomy of the species of Doradidae. The previous studies analyzed morphological characters related to the external morphology, osteology, gonads, and gasbladder.

In general, studies about the anatomy of Siluriformes are restricted to the skeletal system and no other alternative system are approached. There are some studies referring to functional morphology such us: Alexander, 1965; Gosline, 1989; Schaefer & Lauder, 1986; and Adriaens et al., 2001. Also, some efforts in the field of ontogeny have being made by Adriaens & Verraes, 1996 & 1997; and Adriaens, 1998. More recently, several studies approaching the muscular system have been published by Rui Diogo: e.g. Diogo & Chardon (2000a, b); Diogo (2003); Diogo et al. (1999, 2000a, b, 2001, 2002, 2003a, b, c, d, 2004a, b, c, d, 2006a, b. Only one of Diogo's papers (Diogo et al, 2004a) referred to musculature of three species of Doradidae.

This paper carried out an exhaustive study of the cranial and pectoral musculature of Doradidae. Several specimens of 61 species representing the 32 genera of Doradidae were dissected and compared with each other and with species of Auchenipteridae, Aspredinidae and Dyplomystidae. As a result, this paper presents the description of 22 muscles of Doradidae with annotations on function, form, origin, insertion, and any key aspect that was consider relevant.

MATERIALS AND METHODS

Anatomical nomenclature

Most of the myological nomenclature follows Winterbottom (1974). Winterbottom does not include a lot of information for Siluriformes but his work presents the most appropriate standardization of the muscle names of the teleostei. Diogo & Chardon (2000a) proposed a new nomenclature for the *adductor mandibulae,* and the same authors (2000b) described four new muscles related with the movement of mental barbels. Diogo *et al* (2004) implemented those names in a detailed study of osteology and myology of the cephalic region of *Franciscodoras marmoratus*. The revision of the musculature of *Franciscodoras,* as well as 61 other species of Doradidae, resulted in some discrepancies (see discussion) with the findings of Diogo & Chardon (2000a, 2000b).

In this study there are two cases in which Winterbottom (1974) nomenclature does not apply. There is a muscle on the pectoral fin of Doradidae that was not listed under Winterbottom's study. This muscle will be referred as *abductor rotator*. McMurrich (1884) was followed for the nomenclature of the *adductor profundus* because it more closely resembles my observations. Winterbottom (1974) described the insertion of the *adductor profundus* as follows: "…insertion is tendinous on the postero-ventral flanges at the bases of all the fin rays except the marginal (first)". I found the *adductor profundus* inserting on the pectoral spine as stated by McMurrich (1884): "…inserted into the base of the semi-circular process of the first ray ".

Anatomical preparations

The protocol developed by Datovo & Bockmann (2010) was used to stain the cartilage and bones of the specimens. They proposed a methodology for staining specimens based on the original protocol for clearing and staining proposed by Taylor & van Dyke (1985), with some modifications made by Springer & Johnson (2004).

The staining was a multi-step process that took around three days. First, cartilage was stained using an alternate Alcian Blue 8GX solution (with 80 parts of 95% ethanol and 20 parts of glacial acetic acid). Then the specimens were transferred to a sodium borate-based neutralization solution for 12 to 24 hours. Finally, the specimens were placed into an ethanol-based solution of Alizarin Red-S for 3 to 6 hours in order to stain the bones. Specimens were maintained in 70% ethanol.

Once the specimens were stained they were ready for dissection. First, skin and any fat deposits were removed in the anterior half of the body. This allowed the examination of the origin and insertion of all the superficial musculature. The left side was left intact for posterior observations and all the subsequent dissections were performed on the right side of the body.

Next, some bony structures and muscles were removed, which allowed the examination of the origin and insertion of deeper muscles and confirm previous observations of the superficial muscles. On the lateral surface, the suspensorium was removed with all the muscles attached to it. On the ventral surface, the *protractor hyoide* was separated from the origin and the *hyohyoideus inferioris* and *hyohyoides abdutores* were cut along the medial aponeurosis.

For observations of deep muscles of the pectoral fin, it was necessary to pull out the pectoral gridle and peel the cleithrum off. Because this process partially destroyed the specimens, it was only performed on *Acanthodoras spinosissimus*, *Anadoras weddellii*, *Nemadoras ternetzi, Platydoras* sp*, Rhinodoras dorbignyi*, *Trachydoras steindachneri*, and *Wertheimeria*,.

Anatomical descriptions.

Information was gathered from 61 species belonging to all the genera of Doradidae. When the observed species of the same genus were found to have a common characteristic, the statements about the muscles were made at a generic level. When the characteristic was not common to all the observed species, the statements were made at a specific level.

All of the muscles are described following the same format. First, the ontogenetic origin and function are established. Second, the area of origin and insertion of the muscle are described.

Third, the shape, size, and portions are discussed. Lastly, any key aspects of the muscle are described.

Bones corresponding to origin and insertion of the ten most variable muscles of the cranial and pectoral areas are listed in the appendix 1.

Material examined

Museum abbreviations follow Sabaj Pérez (2010). The standard length (mm) is presented in parenthesis.

Doradidae: *Acanthodoras cataphractus*; ANSP 179854 (69.0), MCP 33158 (52.21). *Acanthodoras spinosissimus*; MCP 37476. *Agamyxis albomaculatus*; ANSP 153646 (97.8). *Agamyxis pectinifrons*; MCP 33150 (51.2). *Amblydoras affinis*; ANSP 179797 (67.4). *Amblydoras nauticus*; ANSP 178207 (60.9). *Anadoras grypus*; MCP 26187 (51.6), MCP 29527 (78.5). *Anadoras weddellii*; AUM 45441 (2) (60.3). *Anduzedoras oxyrhynchus*; MZUSP 45553. *Astrodoras asterinifrons*; MCP 33218 (61.2). *Centrochir crocodili*; CU 47930 (157.2). *Centrodoras brachiatus*; ANSP 181021 (108.4), MCP 26443 (146.7). *Doras carinatus*; ANSP 177276 (137.4). *Doras higuchi*; ANSP 10359 (139.9). *Doras phlyzakion*; MZUSP 82294 (145.58). *Franciscodoras marmoratus*; MCP 14115 (174.8). *Hassar affinis*; MCP 45010 (106.9), MCP 22526 (41.00). *Hassar orestis*; MCP 29721 (176.0). *Hassar wilderi*; INPA 5299 (170.7). *Hemidoras morrisi*; MCP 24078 (82.5), MCP 44320 (120.7). *Hemidoras stenopeltis*; MCP 24295 (67.8), MCP 29887 (88.3). *Hypodoras forficulatus*; ANSP 182517 (100.6). *Kalyptodoras bahiensis*; MCP 45009 (141,5 & aprox. 180.0). *Leptodoras cataniai*; ANSP 191822, MCP 29659 (65.8 & 146.1). *Leptodoras hasemani*; INPA 17705 (103.6). *Leptodoras juruensis*; MCP 24603 (2) (109.3 & 94.5). *Leptodoras linelli*; ANSP 180817, MCP 39806 (88.8 & 149.8). *Leptodoras oyakawai*; MZUSP 94141 (70.1). *Leptodoras praelongus*; INPA 21428 (169.6). *Lithodoras dorsalis*, ANSP 181024 (163.4), MZUSP 52585. *Megalodoras guayoensis*; MHNLS 20354 (135.8). *Megalodoras uranoscopus*; ANSP 181184 (131.0). *Merodoras nheco*; MCP 45548 (2) (41.9 & 56.1). *Nemadoras elongatus*; MCP 24579 (74.9). *Nemadoras humeralis*; MCP 24426 (64.9), MCP 44318 (84.7). *Nemadoras leporhinus*; ANSP 179585 (148.12), MZUSP 95617 (127.9). *Nemadoras trimaculatus*; INPA 18063, MZUSP 55774 (63.0 & 68.5). *Opsodoras morei*; MZUSP 32526 (134.4). *Opsodoras ternetzi*; ANSP 182874 (2)

(87,9 & 72.3). MCP 24607 (76.0). *Orinocodoras eigenmanni*; ANSP 180891 (121.1). *Oxydoras niger*; MCP 20951 (158.7). *Oxydoras sifontesi*; ANSP 181069 (137.9); MCP 19921 (136.2). *Ossancora eigenmanni*; ANSP 182612, MCP 24575, MCP 29658 (55,6 & 55,4 & 71,4). *Ossancora asterophysa*; MZUSP 7838, ANSP 182612, MCP 25590 (71.9 & 71.6). *Ossancora fimbriata*; MCP 32951, MCP 32952 (50.8 & 74.1 & 66.9). *Ossancora punctata*; MCP 26181, MCP 29663 (62.4 & 63.7 & 38,5). *Physopyxis ananas*; MCP 36418 (3) (18.7 & 16.7 & 18.6). *Physopyxis lyra*; MCP 36430 (23.4). *Platydoras armatulus*; MCP 15359 MCP 44317 (64.7). *Platydoras hancocki*; ANSP 162763 (177.0). *Platydoras* sp; MCP 22532. *Pterodoras granulosus*; MCP 24599, MCP 26275 (88.05 & 62.25). *Rhinodoras boehlkei*; SIUC 39703 (110.0). *Rhinodoras dorbignyi*; MCP 13067 (134.6). *Rhynchodoras woodsi*; ANSP 181042 (67.5). *Scorpiodoras heckelii*; MCP 15271 (71.5). *Trachydoras brevis*; MCP 36417 (59.45). *Trachydoras microstomus*; MCP 36423 (35.1). *Trachydoras nattereri*; ANSP 182454 (76.7), MCP 29390 (90.4). *Trachydoras paraguayensis*; INPA 634 (112.9), MZUSP 21109 (78.7). *Trachydoras steindachneri*; ANSP 183076 (58.8 & 59.5), MCP 24370 (71,2), MCP 24627, MCP 44319 (66.8). Wertheimeria *maculata*; MCP 34689 (157.7), MCP 43855 (98.2).

Auchenipteridae: *Ageneiosus inermis*, ANSP 162406 (270.0). *Ageneiosus ucayalensis*; MCP 32832 (224.0). *Auchenipterus nigripinnis*; MCP 17601 (153.5). *Centromochlus heckelii*; ANSP 178331 (77.4). *Glanidium leopardum*; MZUSP 64256 (103.1). *Liosomadoras oncinus*; MCP 45029 (51.68). *Trachelyopterus galeatus*; ANSP 182244 (126.2).

Aspredinidae: *Aspredo aspredo*; ANSP 191477 (289.0). *Bunocephalus verrucosus*; ANSP 177200 (57.3).

Diplomystidae: *Diplomystes sp* MCP 18595 (127.8).

RESULTS

In this chapter is described the morphology of all the muscles observed in this study. For detailed information about the origin and insertion of *adductor mandibulae*, *retractor tentaculi*, *extensor tentaculi*, *adductor arcus palatini*, *levator arcus palatini*, *dilatator operculi*, *levator operculi*, *adductor operculi*, and *protractor hyoidei*, see appendix 1.

Anatomical descriptions of the muscles on the lateral surface of the head

Adductor mandibulae

The *adductor mandibulae* develops from the ventral division of the masticatory muscle plate (Winterbottom, 1974) and closes the mouth (Gosline 1989).

The muscle always originates on the preopercle and hyomandibula. Fibers at the origin can also rise from the quadrate and metapterygoid. The insertion is mainly on the anguloarticular, although in *Centrodoras, Lithodoras, N. humeralis,* and *Rhinodoras,* the dentary is also involved. The muscle arises from the sphenotic in *Kalyptodoras*, *Orinocodoras*, and *Wertheimeria.*

It is the most conspicuous muscle in the cheek with a variable shape that ranges from a kidney-like shape like in *Kalyptodoras* (Fig. 1A**)** to a lenticular shape like in *Anduzedoras* (Fig. 1B).

The size and robustness of the muscle are related to the elongation of the snout and by the area of origin on the preopercle. In genera with a short snout, the muscle originates on almost the entire length of the preopercle, is robust, and covers other muscles on the cheek (Fig. 1A). In genera with long snout, the muscle originates in the ventral-most part of the preopercle, is more laminar, and does not cover other muscles of the cheek (Fig. 1B).

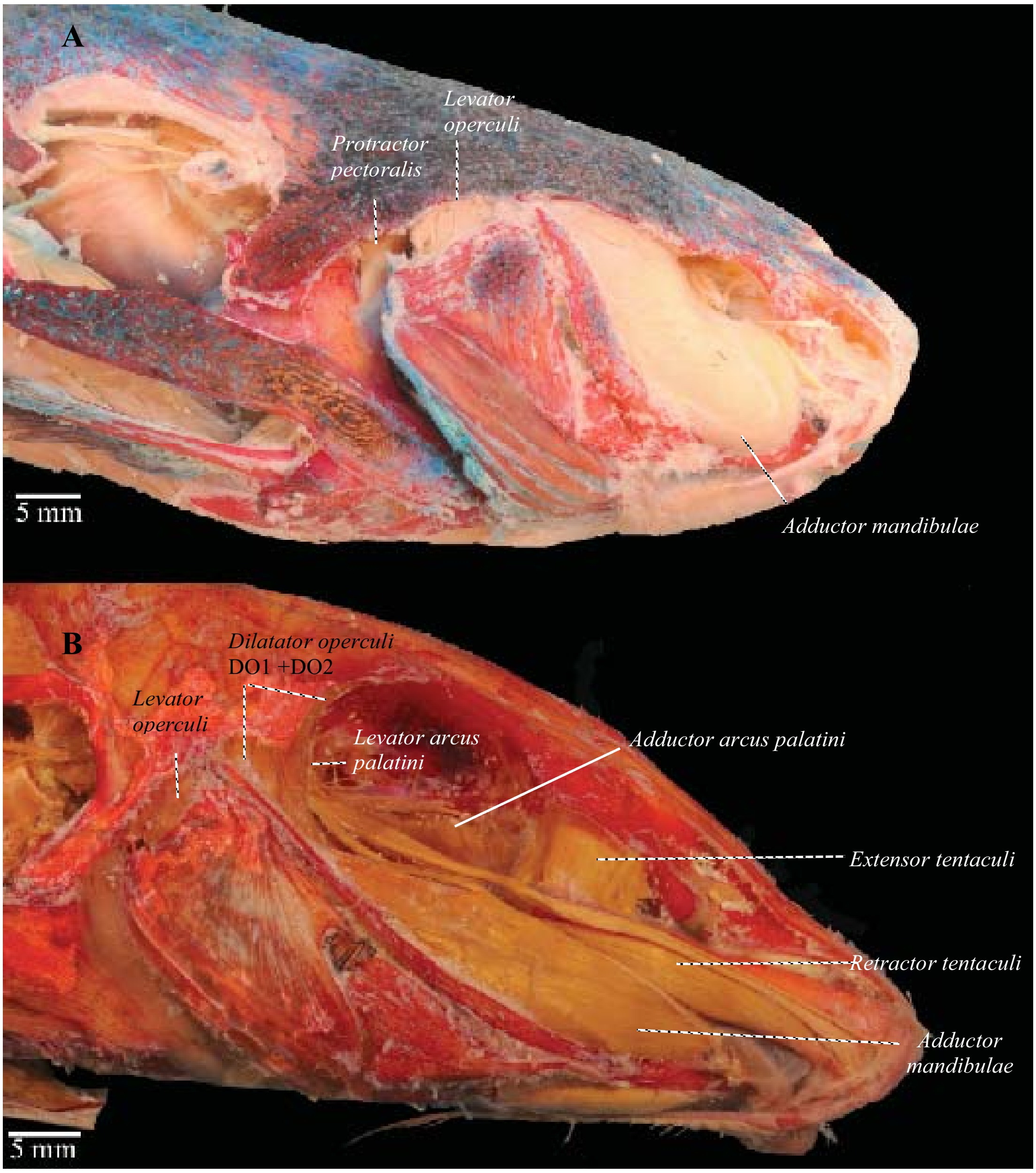

Figure 1. Lateral view of the head of *Kalyptodoras bahiensis* MCP 45009 (A) and *Anduzedoras oxyrhynchus* MZUSP 45553 (B). The two species represent ranges of variation in size and shape of the *adductor mandibulae.*

The *adductor mandibulae* in Doradidae has two main facial subdivisions, a lateral A2 and a medial A3. The fibers of the portions could appear separated, partially separated, or mixed. On *Hassar, Platydoras,* and *Wertheimeria,* the muscle is conspicuously separated on A2 and A3 portions for the entire length of the muscle. On *Anduzedoras*, *Centrochir*, *Doraops*, *Doras*, *Franciscodoras*, *Leptodoras* (except *L. juruensis*), *Lithodoras*, *Merodoras*, *Nemadoras* (except *N. humeralis*), *Pterodoras*, and *Scorpiodoras* the muscle is separated at its origin and the fibers get fused toward the insertion (Fig. 2). On the remaining genera of the family there is not evident separation of the muscle. It appears as a single mass (A2A3), with some internal tendinous fibers as a remnant of separation.

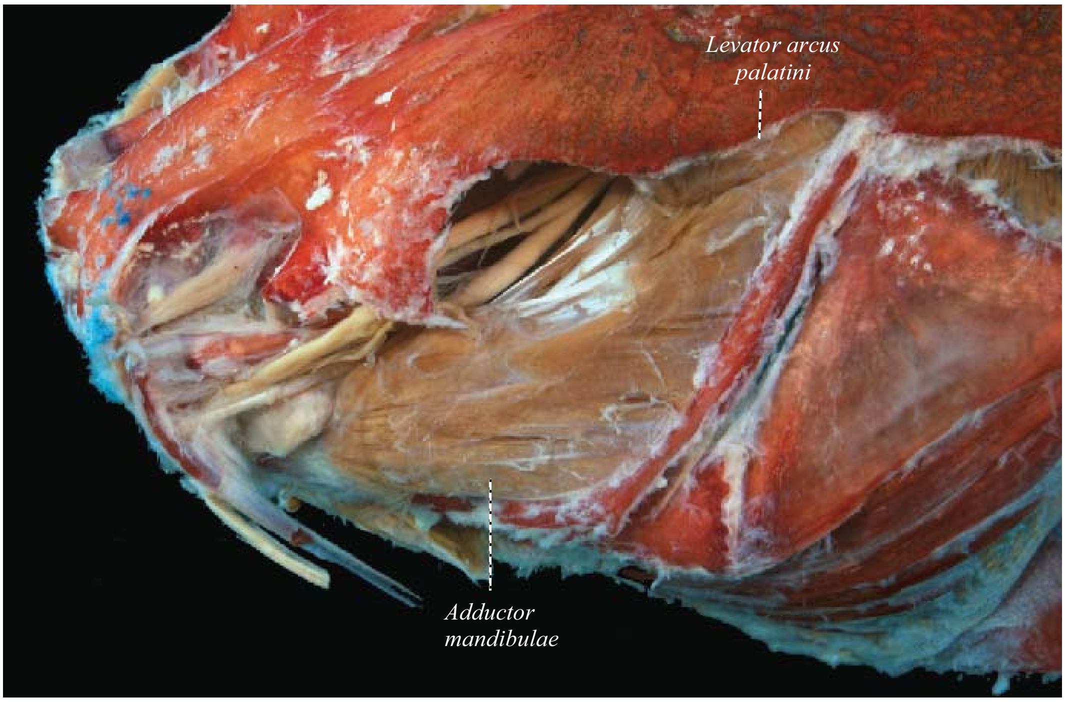

Figure 2. Lateral view of the head of *Franciscodoras marmoratus* (MCP 14115) showing the origin of the *adductor mandibulae* separated only by the insertion of the *levator arcus palatini.* Fibers at the insertion are mixed together.

A unique condition is found for *Rhynchodoras,* were the external A2 portion is divided into a ventral A2' and a dorsal A2'' (Fig. 3).

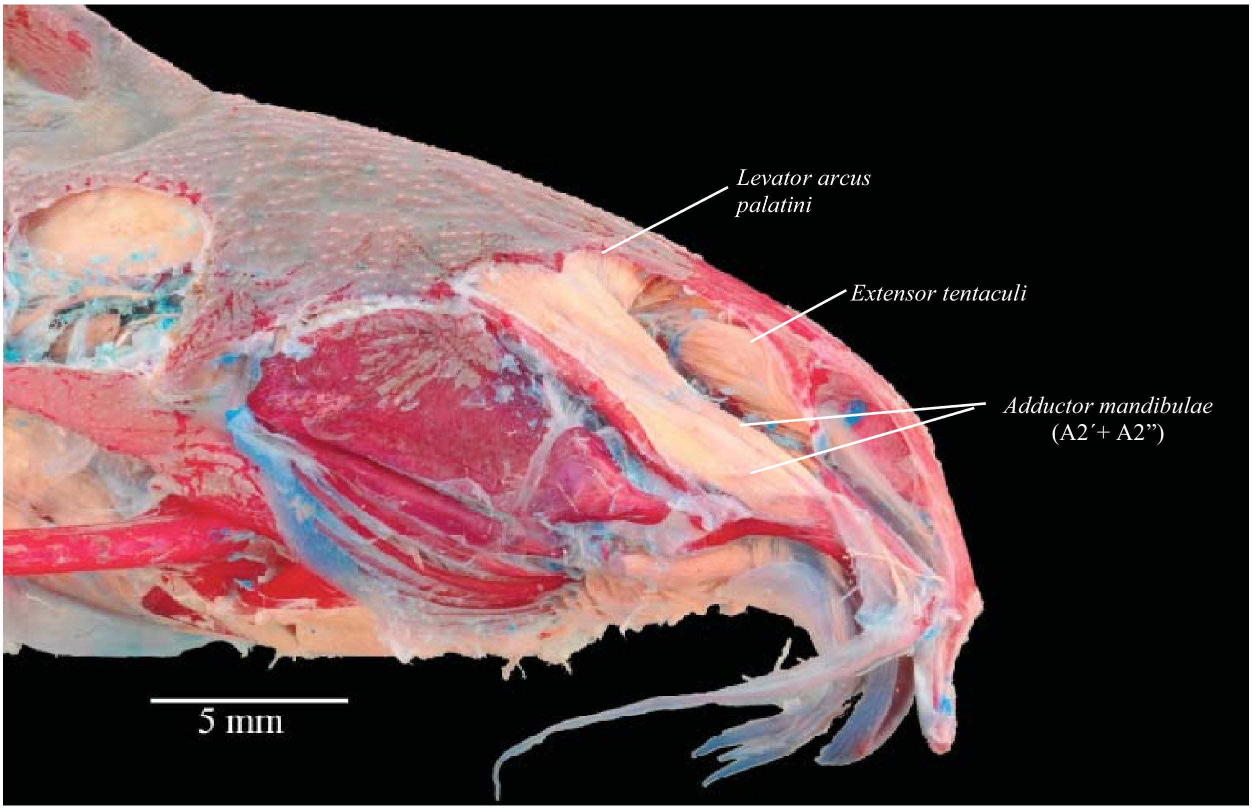

Figure 3. Lateral view of the head of *Rhynchodoras woodsi* (ANSP 181042). The *adductor mandibulae* is divided in ventral (A2´) and dorsal (A2") portions.

Retractor tentaculi

The *retractor tentaculi* derives from the dorsal portion of the A3 muscle of the *adductor mandibulae* complex (Adriaens & Verraes, 1997) and it retracts the maxillary barbel.

The origin of the muscle on the hyomandibula is always clearly differentiated from the *adductor mandibulae* origin. Fiber origin can be located in one of two different positions. They either originate medial to the *levator arcus palatini* such as in *Acanthodoras*, *Agamyxis*, *Amblydoras*, *Anadoras*, *Centrochir*, *Centrodoras*, *Doraops*, *Franciscodoras*, *Hypodoras*, *Kalyptodoras*, *Lithodoras*, *Merodoras*, *Orinocodoras*, *Physopyxis*, *Pterodoras*, *Rhinodoras*, *Rhynchodoras*, *Scorpiodoras*, and *Wertheimeria* (Fig. 4A**)** or ventral (Fig. 4B) to the insertion of the *levator arcus palatini* in the remaining genera.

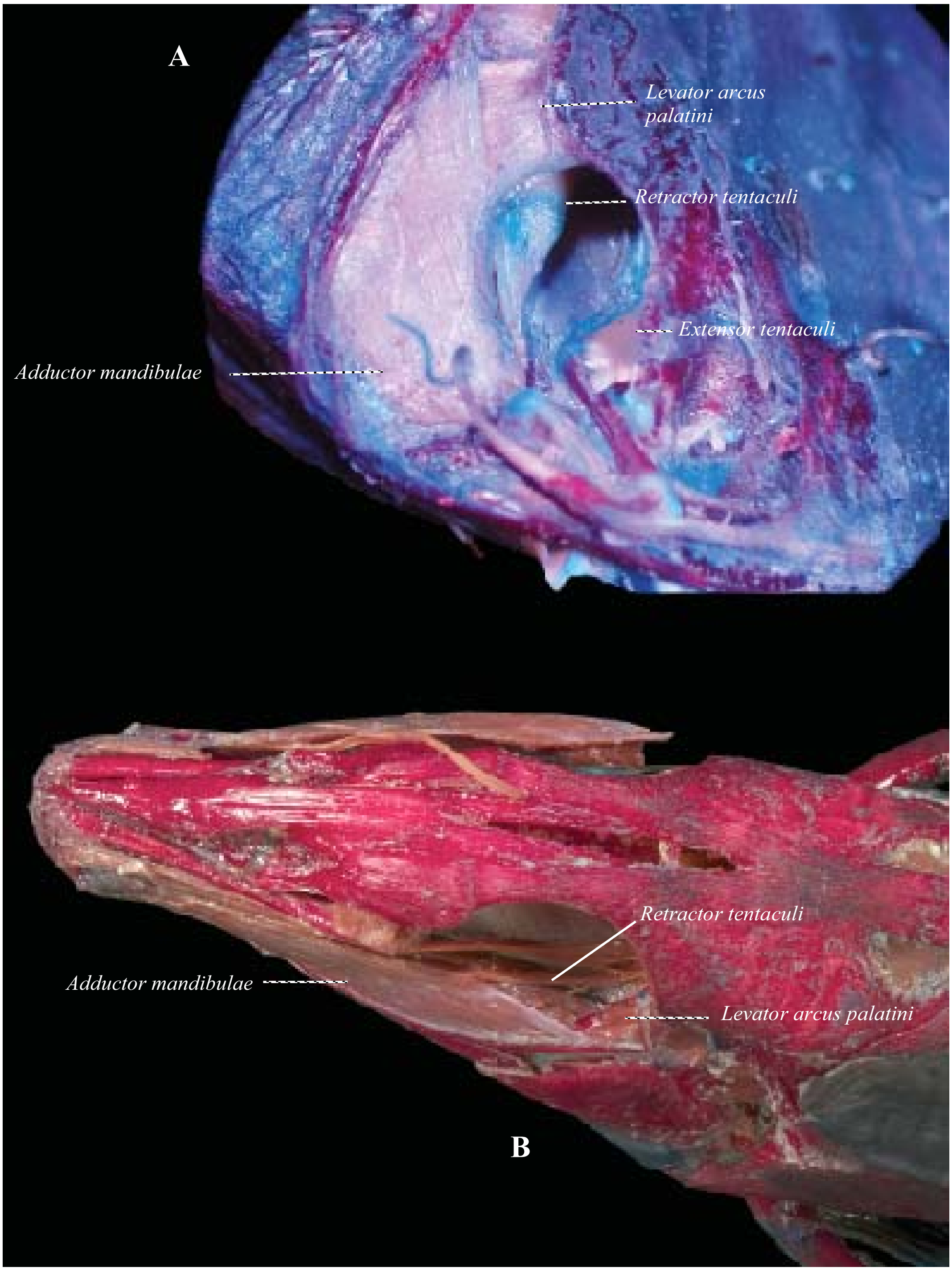

Figure 4. Dorso-lateral view of *Anadoras grypus* MCP29527(A) and *Hassar orestis* MCP 29721 (B). The figure ilustrates the mesial (A) and ventral (B) position of the *retractor tentaculi* in relation to the *levator arcus palatini.*

Insertion of the *retractor tentaculi* is variable; the fibers can insert only on the dentary, the dentary and the maxilla, only in the maxilla, or in the buccopalatal membrane. In *Acanthodoras, Hypodoras, Merodoras,* and *Physopyxis*, the attachment is only on the dentary. In *Agamyxis*, *Centrodoras*, *Doraops*, *Franciscodoras*, *Kalyptodoras*, *Lithodoras*, *Megalodoras*, *Rhinodoras*, and *Wertheimeria* the fibers are connected to the lower jaw and the maxilla. In *Amblydoras* and *Astrodoras* the fibers reach the bucopalatal membrane. In *Anduzedoras*, *Centrochir*, *Doras*, *Hassar*, *Hemidoras*, *Leptodoras*, *Nemadoras*, *Opsodoras*, *Orinocodoras*, *Ossancora*, *Platydoras*, *Pterodoras*, *Rhynchodoras*, and *Trachydoras,* the insertion is only in the maxilla.

The muscle has a conical shape tapering towards the insertion. In *Acanthodoras, Amblydoras, Anadoras, Astrodoras, Hypodoras*, *Kalyptodoras*, *Merodoras*, *Physopyxis*, *Scorpiodoras*, the fibers of the *retractor tentaculi* are fused with those of the *adductor mandibulae* towards the insertion.

Extensor tentaculi

The *extensor tentaculi* is derived from the *adductor arcus palatini,* and forms the antagonist of the *retractor tentaculi* in Siluriformes (Winterbottom, 1974).

The origin of the muscle is on the ventral surface of the lateral ethmoid and the insertion is on the distal end of the autopalatine.

The muscle is a quadrangular mass with the origin slightly wider than the insertion. In *Amblydoras, Centrochir, Hypodoras*, *Kalyptodoras*, *Merodoras*, *Physopyxis*, and *Rhinodoras*, the muscle is not divided. In all the other Doradidae genera the muscle is divided into an outer and inner portion with a narrow slit between them. The fibers of the outer portion run transversally from the lateral ethmoid to the autopalatine. The posterior fibers of the inner portion run transversally from the origin to the insertion. Anterior fibers run tilted posterior from the origin to the insertion. Fibers of the inner portion are visible anterior to the outer portion (Fig. 5).

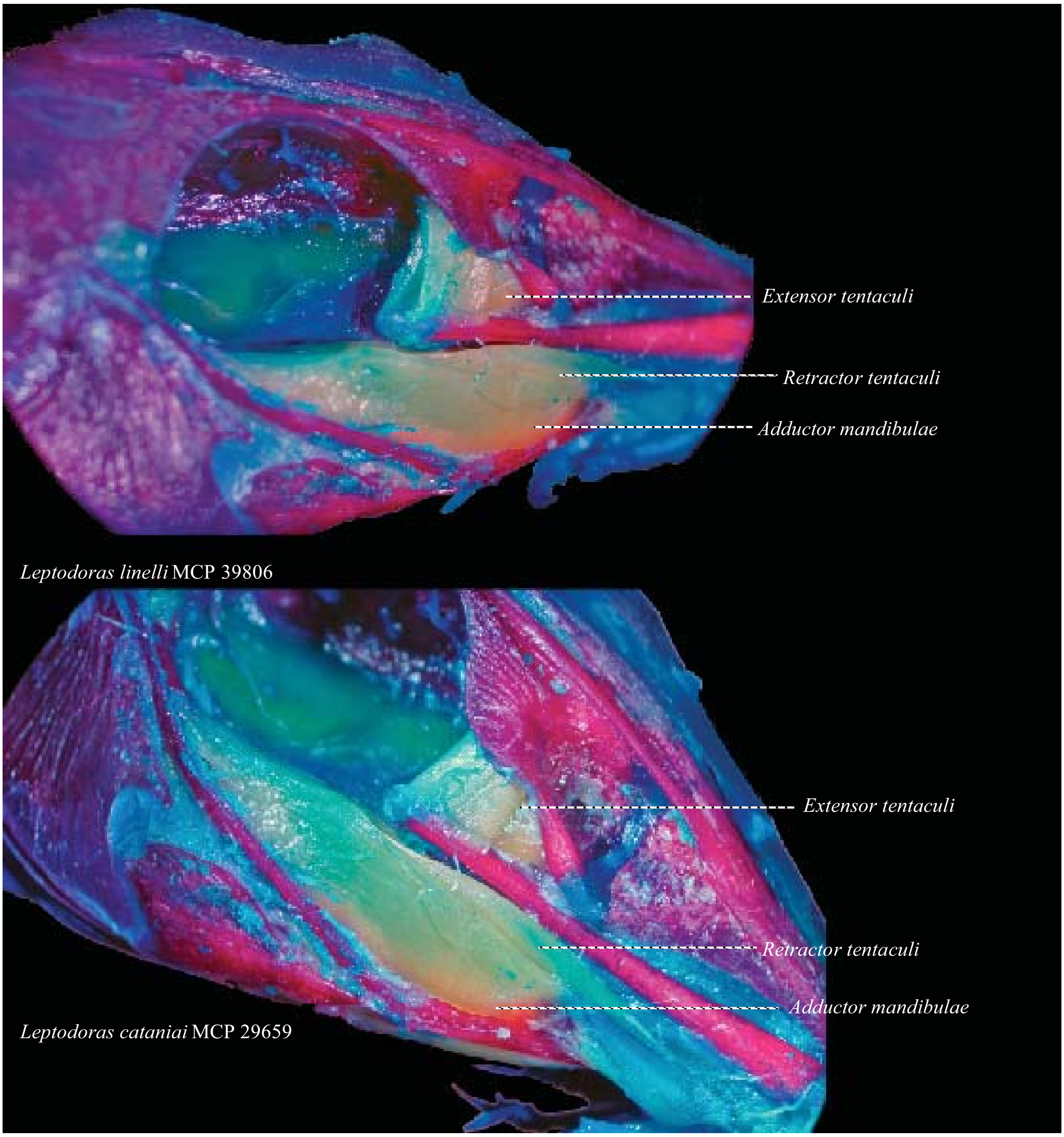

Figure 5. Lateral view of the head of *Leptodoras linelli* and *L. cataniai* showing the inner and outer portions of the extensor tentaculi.

The clade formed by *Orinocodoras*, *Rhinodoras* and *Rhynchodoras* present a unique characteristic in which the insertion of the fibers into the autopalatine is ventral (Fig. 3, 6)

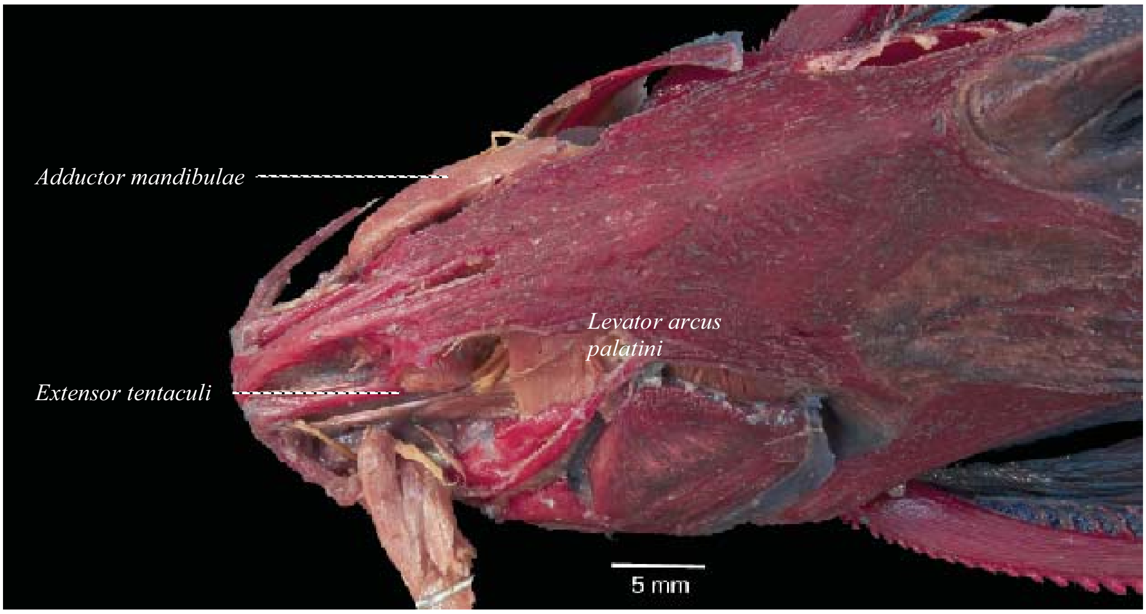

Figure 6. Dorso-lateral view of the head of *Rhinodoras boehlkei* (SIUC 39703). Ventral insertion of the *extensor tentaculi* on the autopalatine is evident in the picture

Levator Arcus Palatini

The *levator arcus palatini* develops from the anterior part of the *constrictor dorsalis* plate (Adriaens, 1998) and is active during the inspiratory phase of aquatic respiration, producing the abduction of the suspensorium (Osse, 1969).

The origin of the muscle is mainly from the sphenotic with a few exceptions. In *Acanthodoras*, *Agamyxis*, *Anadoras*, *Centrodoras*, *Doraops*, *Franciscodoras*, *Kalyptodoras*, *Orinocodoras*, *Pterodoras*, *Rhinodoras*, *Rhynchodoras*, and *Wertheimeria,* the muscular fibers can also reach the frontal.

The insertion is always on the dorsal surface of the hyomandibula. Fibers at the insertion can be interdigitating the origin of the *adductor mandibulae* and *retractor tentaculi* or the fibers can be located dorsally to those muscles.

The *levator arcus palatini* occupies the area at the rear of the orbit between the skull and the palatal arch. Based on the way the fibers are disposed, the muscle could be flat and rest on the hyomandibula (Figs. 1A, 4B) or the muscle can be laminar and protrude from the hyomandibula

(Figs. 2, 3, 4A, 6). When the muscle is flat, its origin is restricted to the ventral process of the sphenotic. The fibers are twisted anterior to insert transversally on the entire width of the hyomandibula. The muscular fibers are mixed with some tendinous fibers and they touch slightly against the *adductor mandibulae* and *retractor tentaculi.*

When the muscle is laminar the origin and insertion of the muscle are parallel to the body axis and the fibers interdigitate with those of the *adductor mandibulae* and *retractor tentaculi.*

Dilatator Operculi

The *dilatator operculi* develops from the posterior part of the constrictor dorsalis plate (Adriaens, 1998) and serves to lift the operculum and to widen the opercular opening (Datta Munshi, 1960).

The origin of the muscle may be located on undersurfaces of the frontal, sphenotic, lateral ethmoid, orbitosphenoid, and hyomandibula. The insertion, through a mixture of tendinous and muscular fibers, is on the dorsal most margin of the opercle.

The muscle has a conical shape and lies posterior and medial to the *levator arcus palatini.* It connects the neurocranium with the opercle. The anterior most fibers are longitudinal to the body axis while the posterior most fibers are perpendicular to it.

Three divisions are recognized in the *dilatator operculi* in Doradidae and are named here as DO1, DO2, and DO3. Each portion has a different origin but the insertion remains the same.

The DO1 is the biggest of the three portions and exhibits fibers that are longitudinal and perpendicular to the body axis. Its origin is anterior and medial to the *levator arcus palatini.* The fibers always rise from the ventral surface of frontals, but may also be attach to the sphenotic, lateral ethmoid and orbitosphenoid. Fibers are attached to the sphenotic in *Amblydoras*, *Anadoras weddellii*, *Anduzedoras*, *Astrodoras*, *Centrochir*, *Centrodoras*, *Doras*, *Hassar*, *Hemidoras*, *Leptodoras*, *Nemadoras, Opsodoras ternetzi*, *Ossancora*, *Scorpiodoras*, and *Trachydoras.* Fibers attached to the sphenotic and lateral ethmoid in *Agamyxis*, *Anadoras* *grypus*, *Doraops*, *Franciscodoras*, *Hypodoras*, and *Pterodoras*. Fibers attached to the orbitosphenoid in *Kalyptodoras*, *Merodoras*, *Opsodoras*, *Oxydoras*, *Platydoras armatulus*, *Rhynchodoras*, and *Wertheimeria.* And attached to the orbitosphenoid and lateral ethmoid in *Lithodoras*, *Megalodoras*, *Orinocodoras*, and *Rhinodoras*.

The DO2 exhibits fibers that are directed slightly posterior. It lies behind the *levator arcus palatini,* originating from the sphenotic. Its insertion is located dorsally to DO1.

The DO3 is constituted by short fibers that originate on the hyomandibula. The muscle portion is located under fibers of the DO1 at the insertion.

Levator Operculi

The *levator operculi* develops from the *constrictor hyoideus dorsalis*, a division of the hyoid muscle plate and contraction result in the rotation, elevation of the opercle and depression of the lower jaw (Adriaens, 1998).

The origin of the muscle is on the pterotic, supracleithrum, or in both. The insertion is on the posterodorsal margin of the opercle.

The muscle is quadrangular with tilted fibers. The fibers are directed anteriorly from its origin to its insertion on *Anduzedoras*, *Doras*, *Hemidoras*, *Kalytodoras*, *Leptodoras praelongus*, *Nemadoras*, *Opsodoras*, *Orinocodoras*, *Ossancora* (except *O. asterophysa*), *Oxydoras*, *Pterodoras*, *Rhinodoras*, *Rhynchodoras*, and *Trachydoras.* The fibers are transverse to the body axis in *Amblydoras nauticus*, *Astrodoras*, *Centrodoras*, *Franciscodoras*, *Hypodoras*, *Leptodoras hasemani*, *L. linelli*, *Merodoras, Ossancora asterophysa*, and *Platydoras armatulus.* In all the other species the fibers run posterior.

Adductor operculi

The *adductor operculi* also develops from the *constrictor hyoideus dorsali* (Adriaens, 1998) and its contraction result on the adduction of the opercle (Osse, 1969)

The origin on the muscle is on the ventral surface of the pterotic and the insertion on the medial posterodorsal surface of the opercle.

The *adductor operculi* has the same shape and occupies the same area as the *levator* operculi but is located medially to the latter and is not visible superficially. Fibers can be slightly inclined, usually in the opposite direction of the *levator.*

Adductor Arcus Palatini

The *adductor arcus palatini* develops from the constrictor hyoideus dorsalis of the hyoid muscle plate (Adriaens, 1998). It controls the lateral movement of the pterygo-palatine arch (Datta Munshi, 1960).

The muscle originates through muscular fibers in the ventral surfaces of the lateral ethmoid, orbitosphenoid, pterosphenoid and parasphenoid. Fibers at the insertion, in most of the genera, connect to the hyomandibula, metapterygoid and mesopterygoid. The insertion is muscular posteriorly becoming more membranous anteriorly. In *Agamyxis*, *Amblydoras*, *Anadoras*, and *Astrodoras* the insertion is restricted to the hyomandibula and metapterygoid. In *Nemadoras elongatus* and *Anduzedoras oxyrhynchus* the insertion is on hyomandibula and mesopterygoid.

The muscle is laminar and is constituted as an extensive muscle mass filling the space between the cranium and the suspensorium elements

Protractor pectoralis

The *protractor pectoralis* apparently develops from the posterior edge of the *levator arcuum branchialum* (Winterbottom, 1974).

The origin is on the exoccipital-pterotic region of the skull and the insertion is on the dorsal process of the cleithrum.

Fibers run transversal to the body axis from the origin to the insertion. The muscle is a strong, thick, single mass visible on lateral view on most of the genera. In *Hassar*, *Kalyptodoras*, *Merodoras*, *Oxydoras*, *Rhynchodoras*, *Scorpiodoras*, and *Trachydoras* (except *T. nattereri*), the muscle is shorter and is totally concealed by the supracleithrum.

Anatomical descriptions of the muscles on the ventral surface of the head

Intermandibularis

The *intermandibularis* develops from the ventral intermandibular muscle plate (Adriaens & Verraes, 1996) and it narrows the angle between the two halves of the lower jaw, during the expiration phase (Osse, 1969).

The fibers stretch transversally between the anterior-most region of the dentary.

The muscle is small and located anterior on the body. Its shape is variable according to the way the fibers are disposed. In genera with simple barbel (except in *Rhynchodoras*) the muscle is a sub triangular mass, visible when the skin is removed (Fig. 7). In Doradidae with fimbriate barbels, the muscle develops as series of transverse fibers joining the two sides of the dentary. It is not visible when the skin is removed because the muscle is ventrally covered by the connective tissue that forms the oral hood.

The *intermandibularis* is not visible in *Rhynchodoras* due to the modifications on the lower jaw.

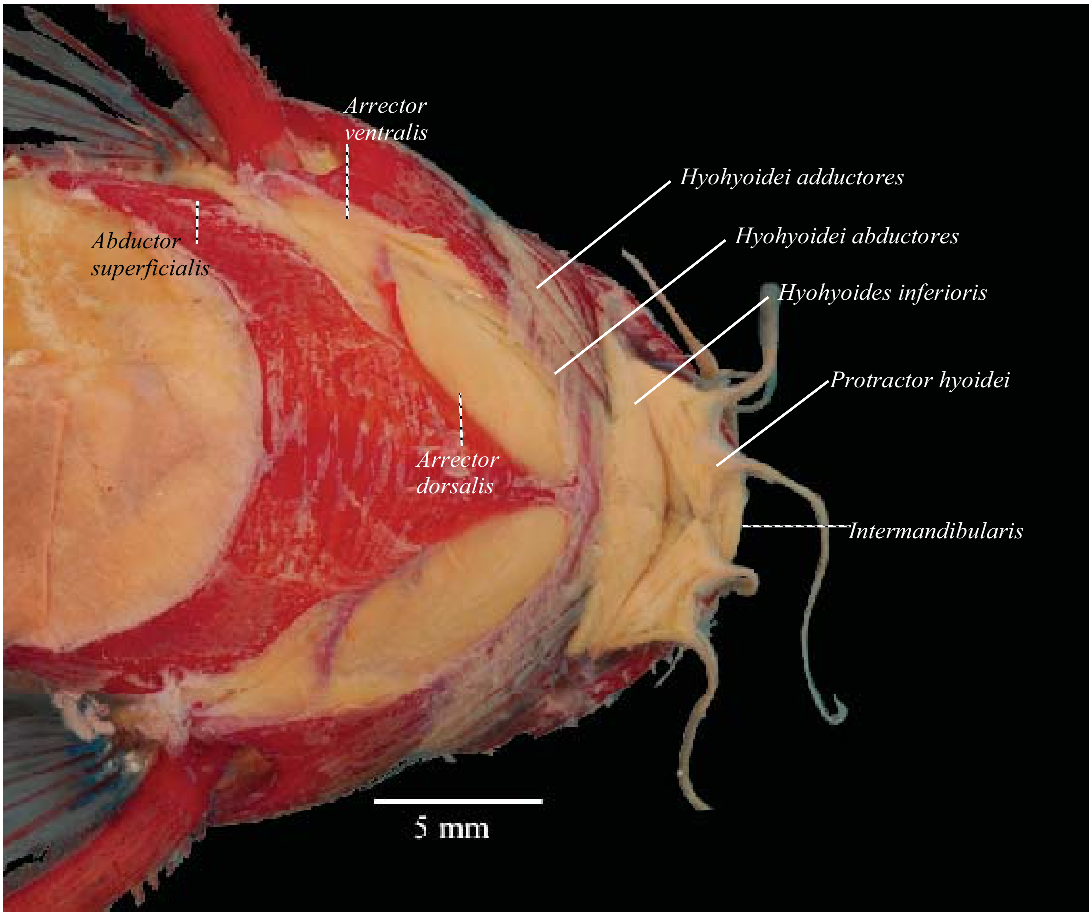

Figure 7. Ventral view of the head of *Anadoras weddellii* AUM 45441. The *intermandibularis* is a sub-triangular mass in the anterior-most portion of the head.

Protractor hyoidei

The *protractor hyoidei* develops from the fusion of two subdivisions of the muscle plate of the hyoid arch, the *intermandibularis posterior*, and the *interhyoides anterior* (Adraiens, 1998). The muscle is related to the contraction of the hyoid arch during quiet respiration (Winterbottom, 1974) and also in Siluriformes it control the movement of the cartilage associated with mental barbels (Diogo & Chardon, 2000a).

The origin is located on different parts of the dentary and in a medial aponeurosis. The insertion is on the anterior and posterior ceratohyal. In *Doras*, *Hassar*, *Hemidoras*, and *Leptodoras* a specific keel on the bone is developed for the insertion of the *protractor*.

The muscle occupies almost all the ventral area of the head; its fibers are directed longitudinally and are incompletely divided in portions not completely isolated from one another. In some genera, it is possible to observe three portions comparable to those of Diogo & Chardon (2000a) and Datta Munshi (1960). However, their terminology will not be used due to some discrepancies within these studies (see discussion).

In genera with simple barbel (except *Oxydoras*) there are three portions: one dorsal (PH1), one ventral external (PH2), and one ventral internal (PH3). PH1 is the largest and the most robust of the portions. PH2 is subdivided in three bundles that support the cartilage structures related to mental barbels: an anterior bundle, from the dentary to the base of inner most barbel (PH2a), a middle bundle that goes from the base of the inner barbel to the base of the outer barbel (PH2b), and a posterior bundle from the base of the outer barbel to the ceratohyal (PH2c). PH3 meets its counterpart on a raphe and attaches to the dentary anteriorly through muscular or tendinous fibers that surround the *intermandibularis* (Fig. 8).

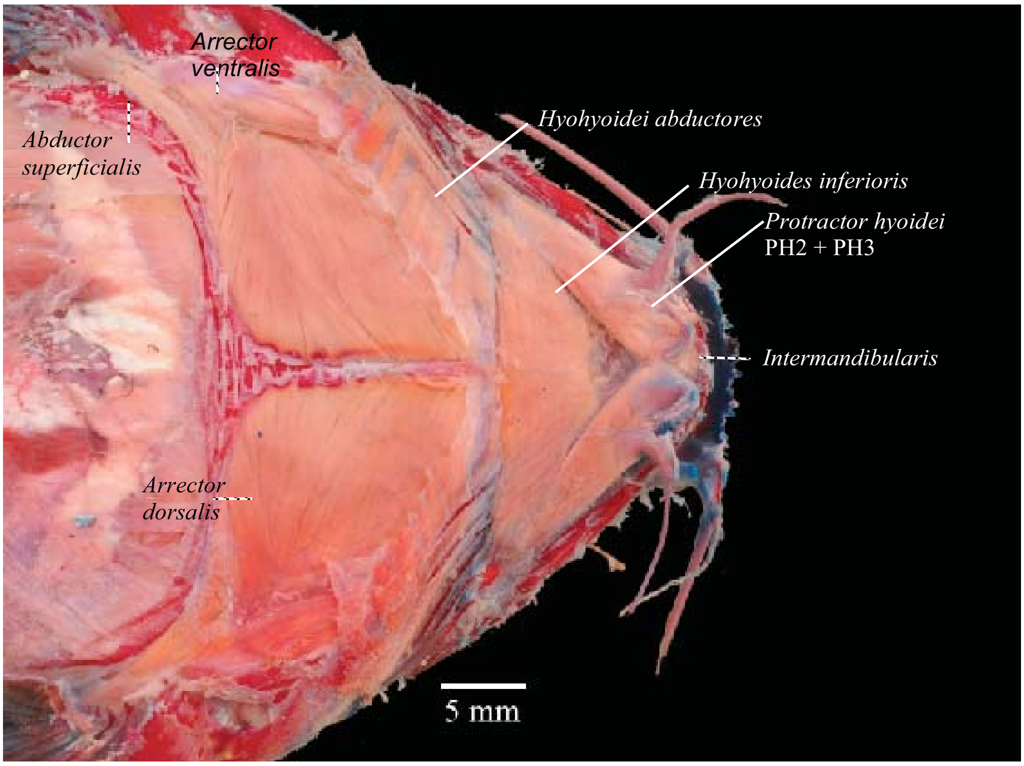

Figure 8. Ventral view of the head of *Megalodoras uranoscopus* (ANSP 181184). PH2 and PH3 are visible, PH3 surrounds the *intermandibularis* to attach to the dentary.

In genera with fimbriate barbels and *Oxydoras* there are two or three portions of the *protractor hyoide,* dependent on the genera. There are two portions of the *protractor hyoidei* on *Anduzedoras*, *Hassar*, *Hemidoras*, *Leptodoras*, *Nemadoras humeralis*, *Opsodoras*, *Ossancora*, *Oxydoras*, and *Trachydoras.* A most external dorsal portion (PH1) originates on a tendon on the lateral area of the dentary. A ventral portion (PH2PH3) originates on a pair of tendons that lay ventrally to the *intermandibularis* and meets to constitute a middle raphe. PH2PH3 supports the structures related with the oral hood and mental barbel. (Figs. 9, 12). There are three portions in *Doras*, *Nemadoras elongatus*, *N. leporhinus*, and *N. trimaculatus*: PH1, PH2, and PH3. In this genera the fibers of the PH2 and PH3 are intertwined towards the insertion. Each ventral portion supports one barbel (Fig. 10**).**

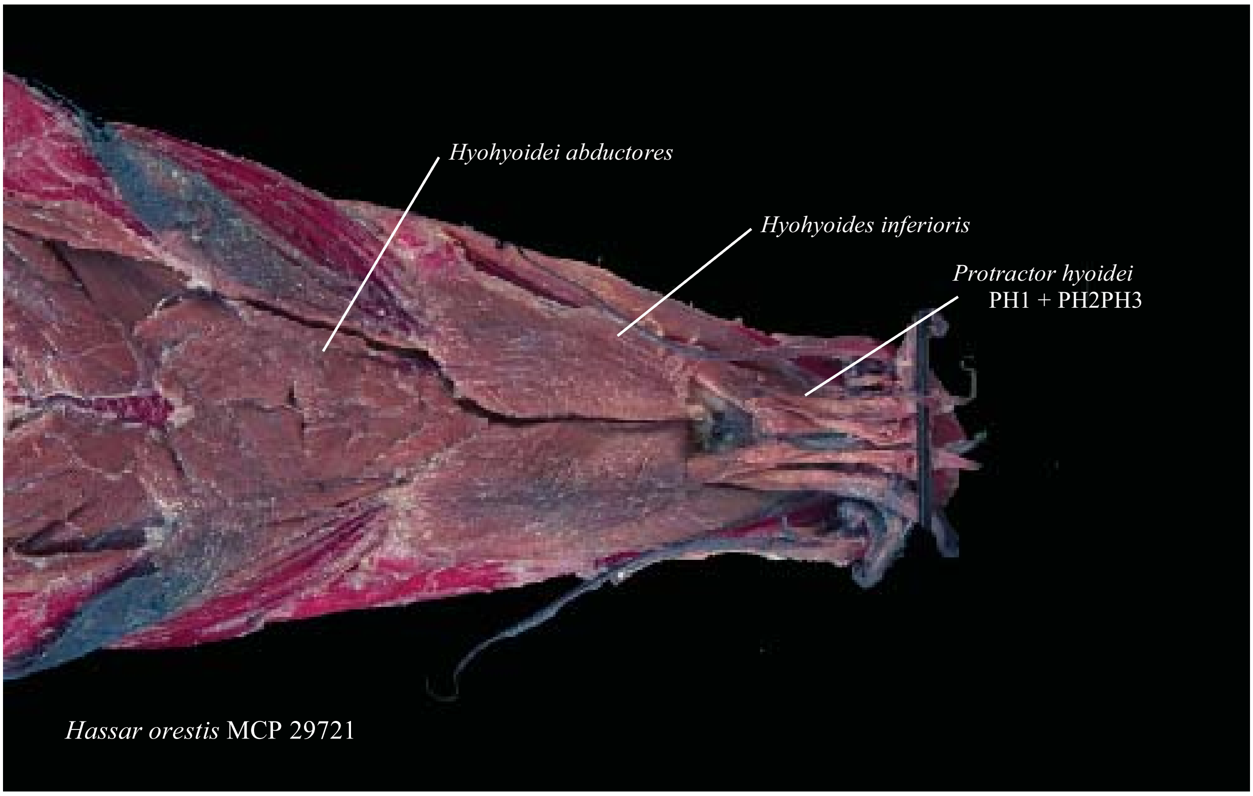

Figure 9. Ventral view of the head of *Hassar orestis.* The two divisions of the *protractor hyoidei* are visible.

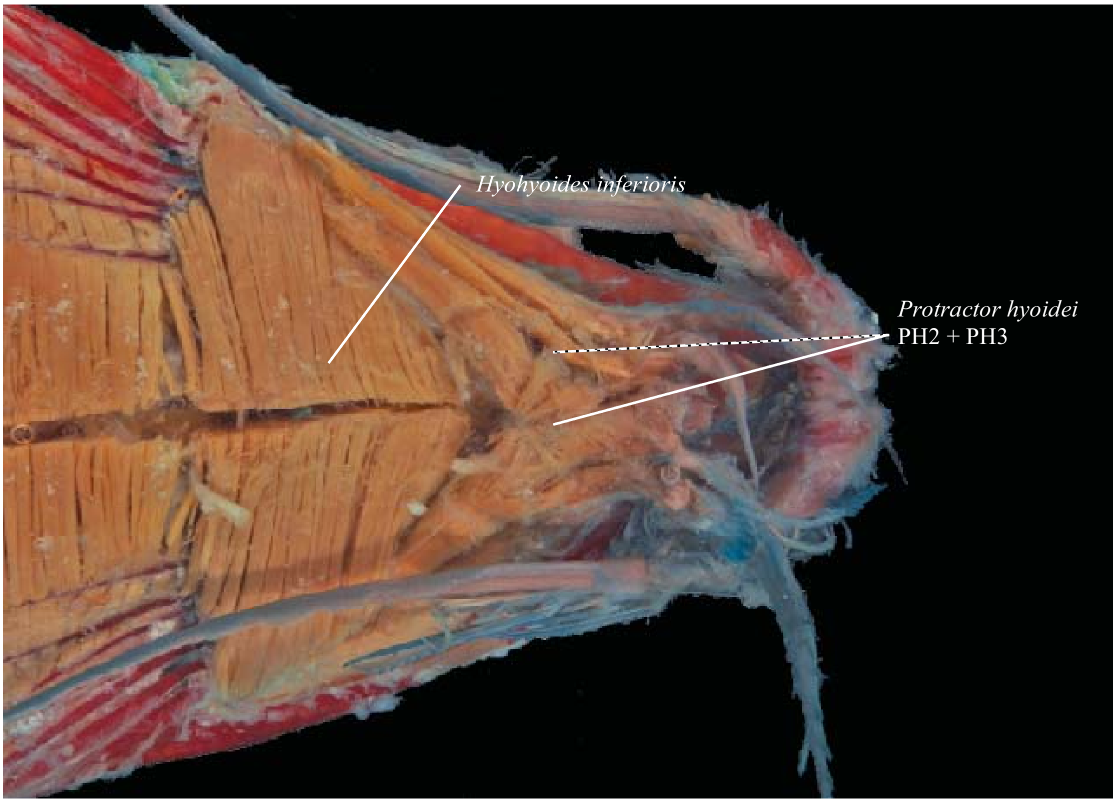

Figure 10. Ventral view of the head of *Nemadoras leporhinus* (ANSP 179585). Fibers of PH2 and PH3 intertwined towards the insertion.

Hyohyoides inferioris

The *hyohyoides inferioris* develops from the *interhyoideus posterior.* Its contraction results in the expansion of the branchiostegal membrane (Adriaens, 1998).

The origin is from a ventral midline raphe and the insertion is generally on the anterior and posterior ceratohyal. In *Acanthodoras*, *Agamyxis*, *Amblydoras*, *Anadoras*, *Anduzedoras*, *Astrodoras*, *Centrochir*, *Centrodoras*, *Hassar*, *Hemidoras stenopeltis*, *Leptodoras juruensis*, *Nemadoras elongatus*, *N. leporhinus*, *N. trimaculatus*, *Opsodoras morei*, *O. ternetzi*, and *Pterodoras granulosus* the insertion is only on the anterior ceratohyal.

The muscle is located posterior to the *protractor hyoidei* and its fibers run either transversally or obliquely to the longitudinal body axis. In *Anduzedoras*, *Doras*, *Hassar*, *Hemidoras*, *Leptodoras*, *Nemadoras*, *Opsodoras* except *O. ternetzi*, and *Trachydoras* the *hyohyoides inferioris* is disposed obliquely (Figs. 9, 11). In the remaining genera, the fibers of the muscle are disposed transversally (Figs. 7, 8, 10).

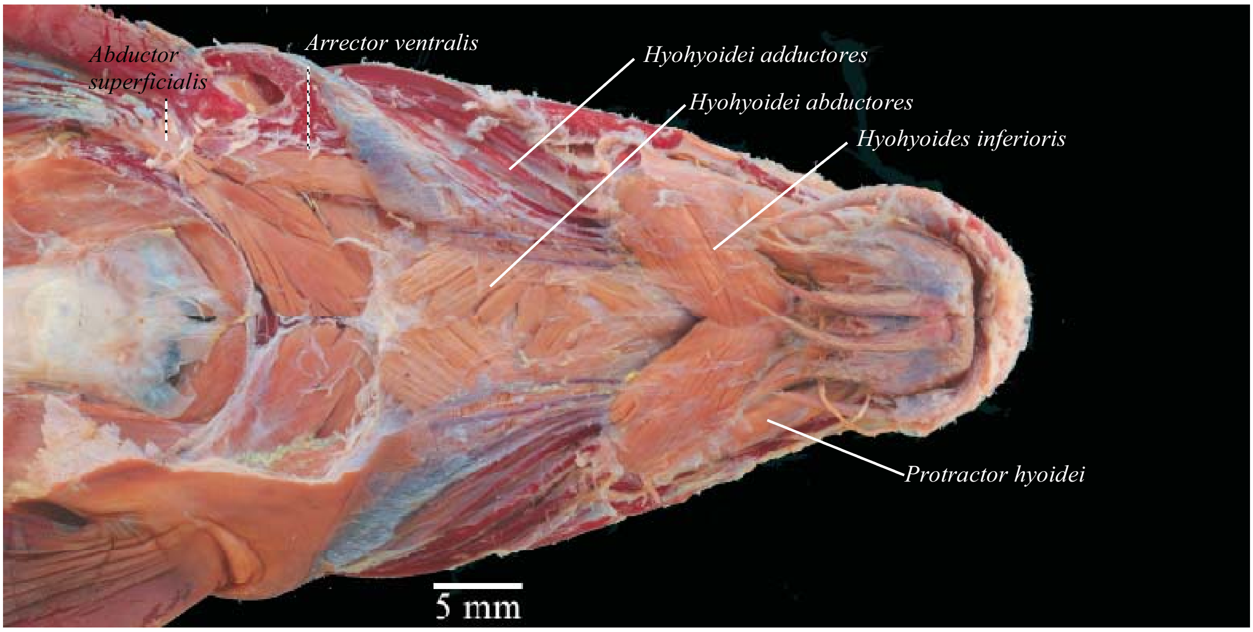

Figure 11. Ventral view of *Doras carinatus* (ANSP 177276). *Hyohyoides inferioris* disposed obliquely.

A pair of tendons raising from the middle raphe and attaching anterior to ventral hypohyal are present in all genera except in *Acanthodoras.* In *Agamyxis*, *Astrodoras*, *Centrochir*, *Centrodoras*, *Franciscodoras*, *Hassar*, *Hypodoras*, *Hemidoras*, *Kalyptodoras*, *Lithodoras*, *Merodoras*, *Opsodoras*, *Ossancora fimbriata*, *O. asterophysa*, *Physopyxis*, *Platydoras,* and *Wertheimeria* the tendons cross over the muscle forming a Y shape. In all the other genera the tendons are developed in the anteriormost region of the muscle and cover the outline of the muscle forming either a V or a U shape.

Hyohyoidei abductores

The *hyohyoidei abductores* also develops from the *interhyoideus posterior* (Adriaens, 1998). Its contraction results in the expansion of the branchiostegal rays and membrane in order to enlarge the opercular cavity (Osse, 1969).

The origin is on a middle raphe and the insertion is on the anteriormost branchiostegal ray.

Fibers of the muscle run mainly transverse to the body axis but the way they meet their equivalent counterpart may vary. In *Acanthodoras*, *Agamyxis*, *Centrochir*, *Doraops*, *Franciscodoras*, *Hypodoras*, *Kalyptodoras*, *Lithodoras*, *Megalodoras*, *Merodoras*, *Platydoras*, and *Scorpiodoras* the left and right *hyohyoidei* are connected by a membrane (Fig. 8). In *Amblydoras*, *Anadoras*, *Astrodoras*, *Centrodoras*, *Hemidoras*, *Leptodoras*, *Nemadoras*, *Opsodoras*, *Orinocodoras*, *Ossancora*, *Oxydoras*, *Rhinodoras*, *Trachydoras*, and *Wertheimeria* the anteriomost fibers of the muscle are in direct contact with its homologous antimere (Fig. 12). In *Nemadoras leporhinus* the muscular fibers of the left and right side are connected along the majority of the length of the branquiostegal ray and are slightly attached to the suture of the coracoids (Fig. 13). In *Anduzedoras*, *Doras*, and *Hassar* the fibers of both sides are interdigitated along the length of the muscle and are attached to the pectoral girdle (Fig. 11, 14). Due to the poor preservation of the specimens of *Rhynchodoras*, *Pterodoras*, *Leptodoras juruensis*, and *Nemadoras elongatus*, it was not possible to identify the type of connection for the *hyohyoides abductor* on this species.

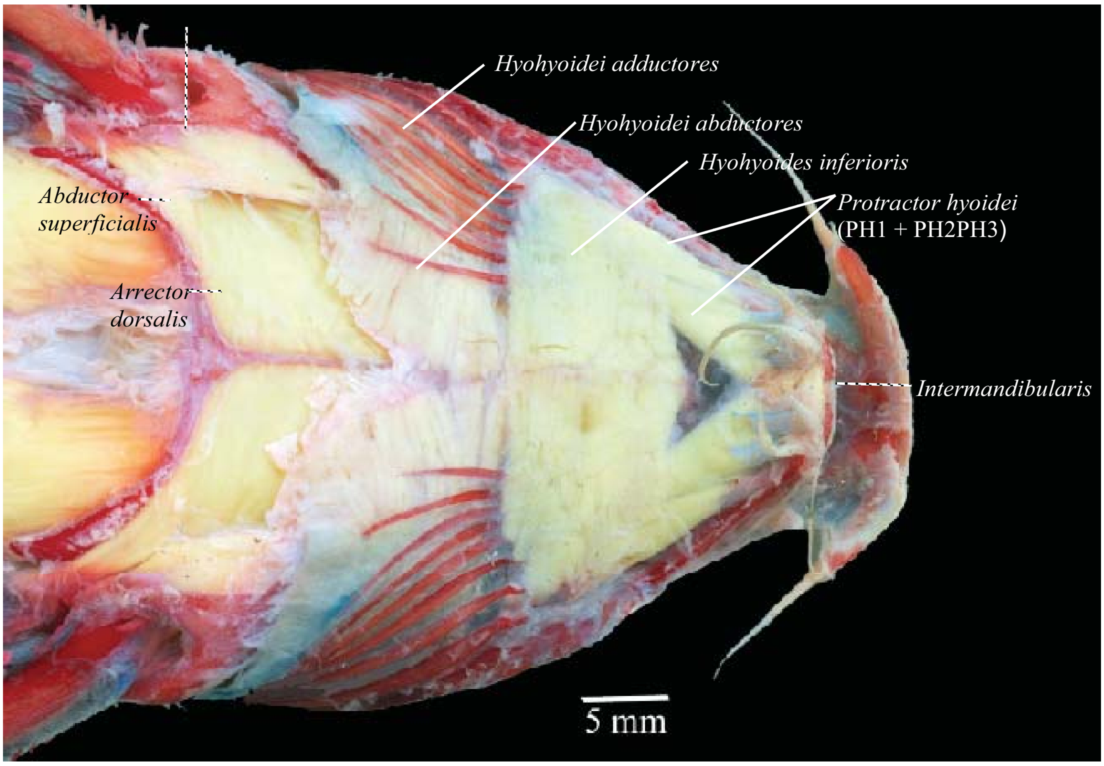

Figure 12. Ventral view of *Oxydoras sifontesi* (ANSP 181069). Anteriomost fibers of *hyohyoides inferioris* are in direct contact with its homologous antimere.

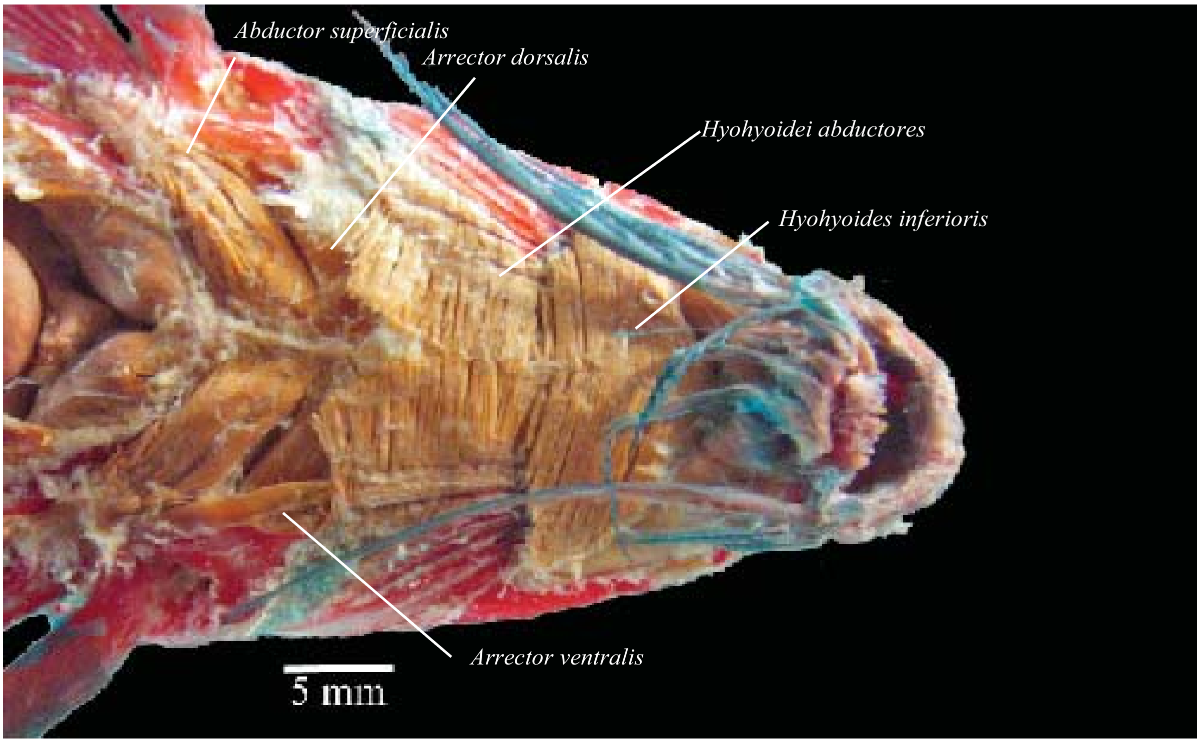

Figure 13. Ventral view of *Nemadoras leporhinus* (ANSP 179585). Fibers of left and right side of *hyohyoides inferioris* are connected along the majority of the length of the branquiostegal ray.

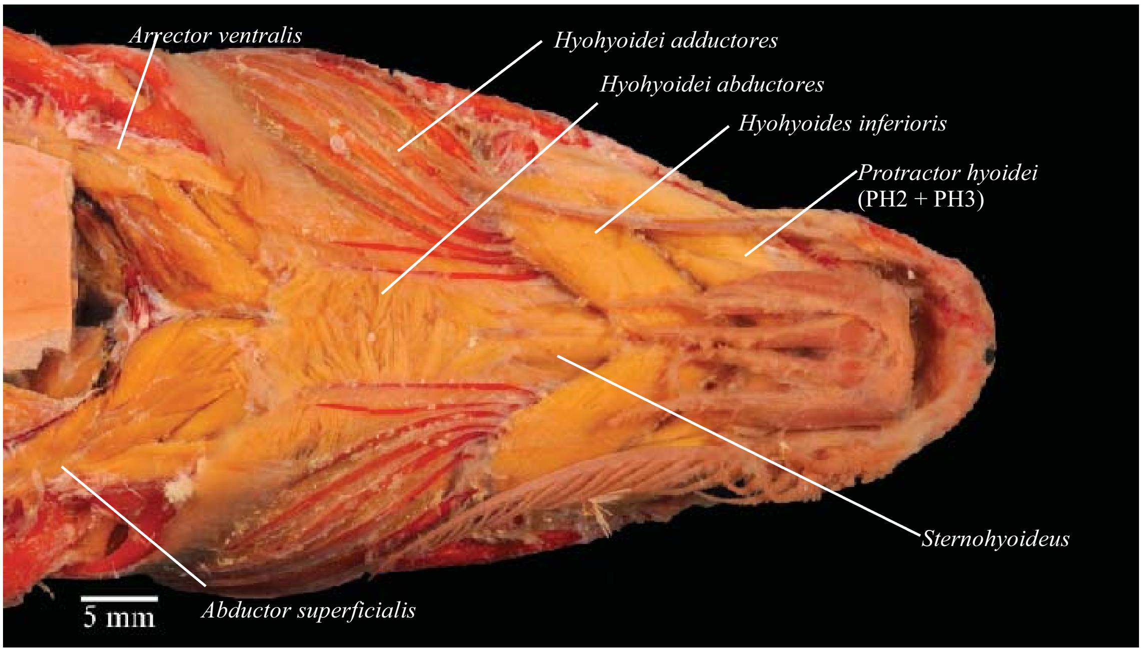

Figure 14. Ventral view of *Anduzedoras oxyrhynchus* (MZUSP 45553). Fibers of the left and right sides of *hyohyoides inferioris* interdigitated along the length of the muscle.

Hyohyoidei adductores

The *hyohyoidei adductores* develops from the *interhyioideus posterior*. It is the muscle that constricts the branchiostegal membrane (Adriaens, 1998).

It is spread between the branchiostegal rays to the medial face of the opercle as a continuous sheet of fibers.

The muscle is a continuation of the *hyohyoidei abductores* fibers. The fibers can be slightly grouped in bundles or exposed as simple fibers.

There was no major variation in the area of origin and insertion, size, and shape of the *hyohyoidei adductores* between the genera of Doradidae.

Sternohyoideus

The *sternohyoideus* differentes from the hypobranchial muscle plate of the first spinal myomeres (Adriaens, 1998). The muscle participates in the retraction of the hyoid arch as well as in the depression of the lower jaw (Osse, 1969).

The origin is on anterior most portion of the cleithrum, although the most posterior dorsal fibers can also attach to the coracoid. The insertion is on the posterior portion of the urohyal.

The muscle is dorsal to the *hyohyoides inferioris* and *hyohyoidei abductor* and usually is not exposed when the skin is removed. In *Anduzedoras*, *Hemidoras*, *Leptodoras*, and *Opsodoras* portions of the muscle are exposed in ventral view (Fig. 14**).**

The muscle is divided in *Agamyxis albomaculatus*, *Amblydoras affinis*, *Anadoras*, *Anduzedoras*, *Centrochir*, *Doras*, *Hassar*, *Hypodoras*, *Leptodoras*, *Megalodoras*, *Merodoras*, *Platydoras*, *Pterodoras*, *Rhynchodoras*, *Scorpiodoras*, and *Trachydoras nattereri.* In the remaining genera of Doradidae the muscle is a single mass.

Muscles of the pectoral fin

Abductor superficialis

The *abductor superficialis* abducts and separates the fin rays (McMurrich, 1884).

The origin of the muscle is mainly on a ventral keel developed on the coracoid and adjacent areas of the bone. The keel is present in all the genera except *Rhynchodoras*, *Amblydoras*, *Merodoras*, and *Physopyxis*. The insertion is on the ventral bases of the branched fin rays.

In most genera, the muscle is visible when the skin is removed and is located on the posterior external end of the pectoral girdle. In *Amblydoras,* the muscle is partially covered by the expanded bone of the coracoid, and is located on the anterior most part of the pectoral girdle (Fig. 15).

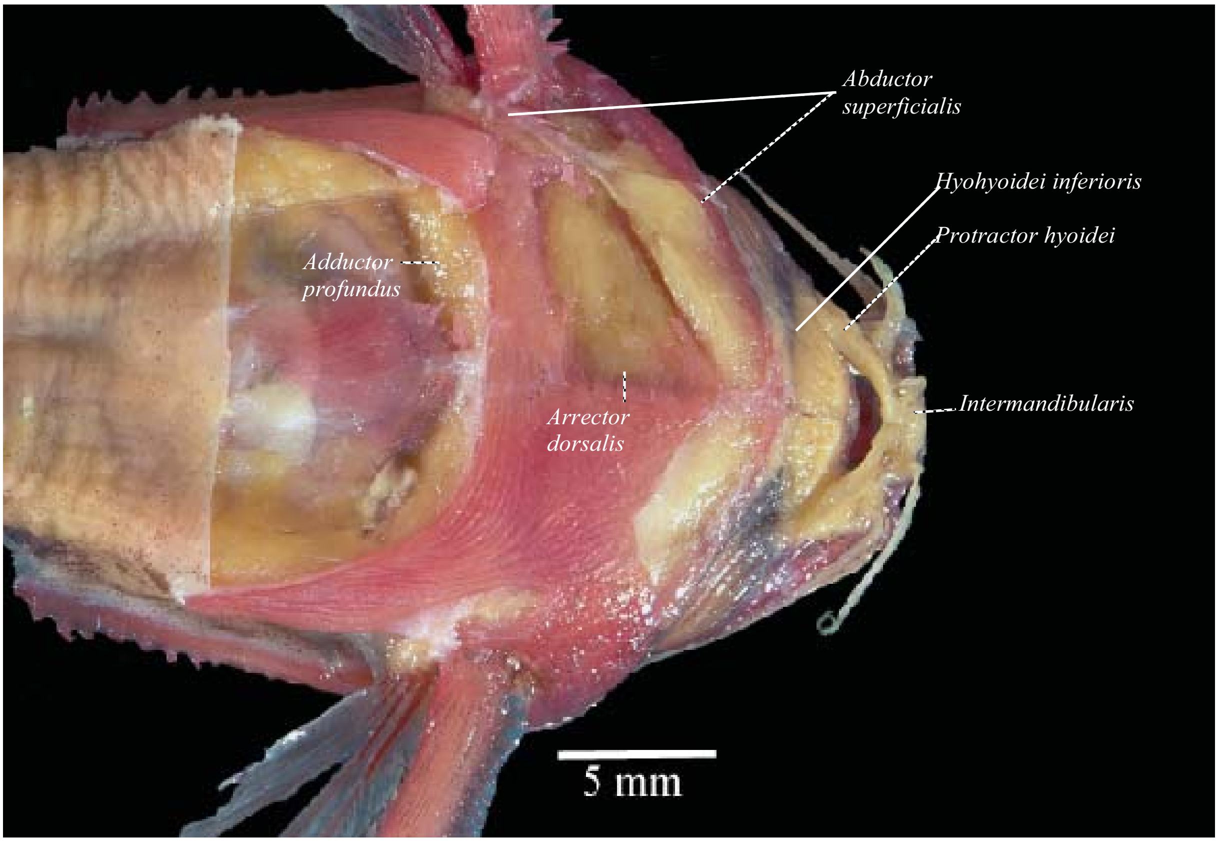

Figure 15. Ventral view of *Amblydoras nauticus* (ANSP 178207). Muscles of the pectoral fin are mostly covered by bone, At the right side of the specimens bone was removed for detailed observations.

Variation of the size and robustness of the muscle in Doradidae are determined by differences in the area of origin. In *Physopyxis* and *Merodoras*, the origin of the *abductor superficialis* is restricted to the external lateral portion of the posterior process of coracoid (Fig. 16). In *Acanthodoras*, *Agamyxis*, *Anadoras*, *Astrodoras*, *Centrochir*, *Centrodoras*, *Doraops*, *Franciscodoras*, *Hypodoras*, *Lithodoras*, *Megalodoras*, *Orinocodoras*, *Ossancora*, *Oxydoras*, *Platydoras*, *Rhinodoras*, and *Scorpiodoras* the muscle originates mainly from the keel and the posterior ventral surface of the coracoid (Fig. 17). In *Anduzedoras*, *Doras*, *Hassar*, *Hemidoras*, *Kalyptodoras*, *Leptodoras*, *Nemadoras*, *Opsodoras*, *Rhynchodoras*, *Trachydoras*, and *Werthemeria* the muscle originates from the keel and the posterior ventral surface of the coracoid but fibers attach to the suture area between left and right portion of the coracoid (Fig. 18)

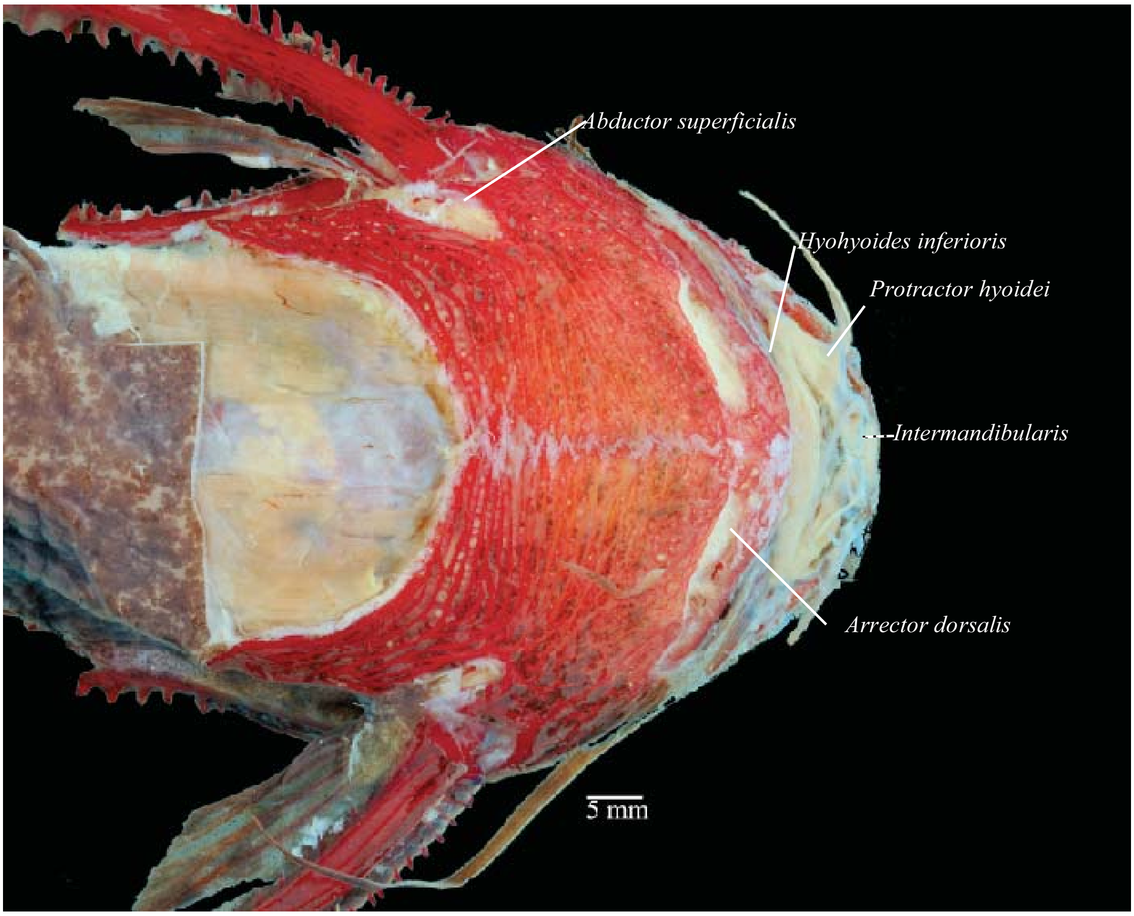

Figure 16. Ventral view of *Merodoras nheco* (MCP 45548). The *abductor superficialis* is restricted to the external lateral portion of the posterior process of coracoid

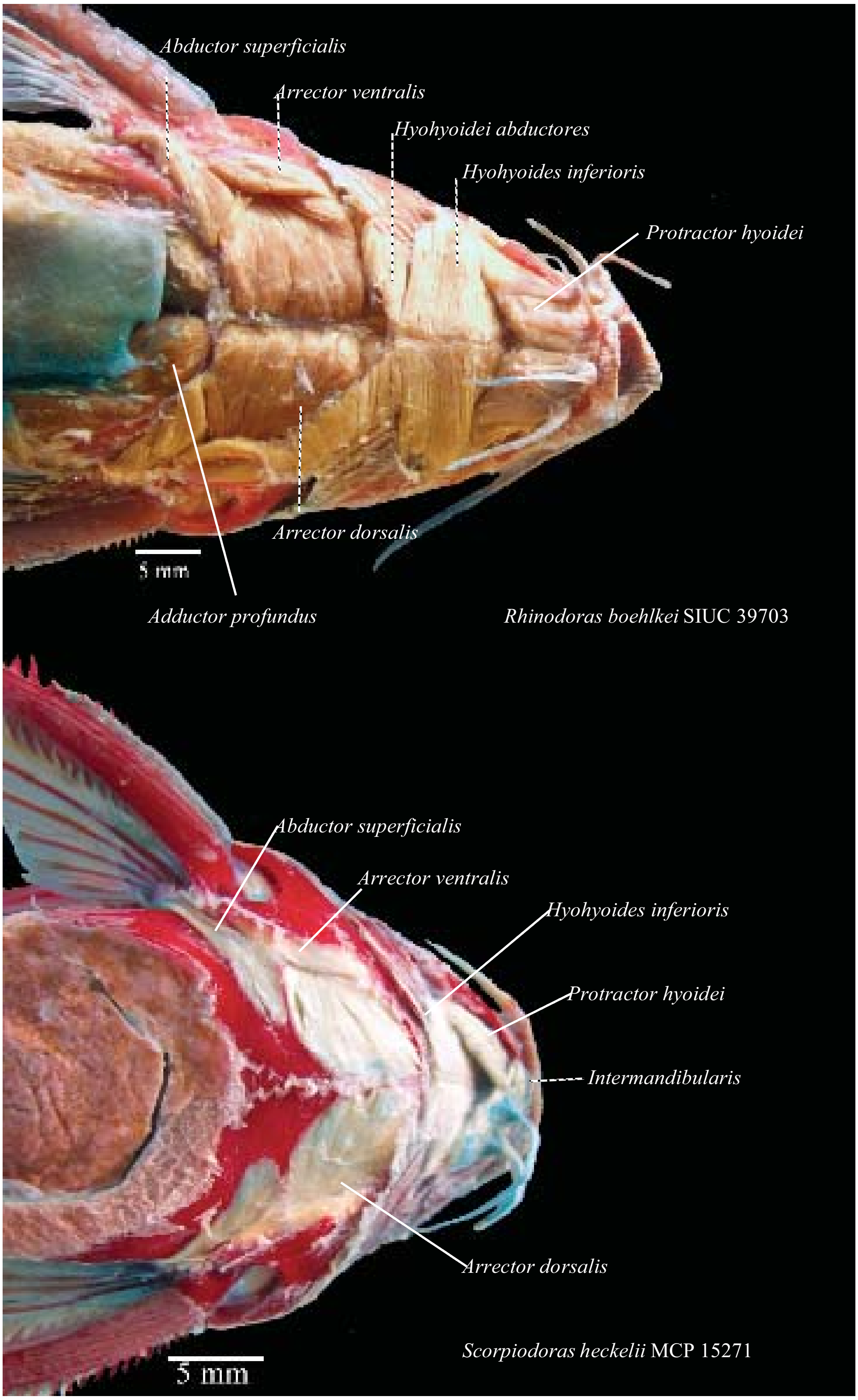

Figure 17. Ventral view of *Rhinodoras boehlkei* and *Scorpiodoras heckelii.* The *abductor superficialis* originates mainly from the keel and the posterior ventral surface of the coracoid.

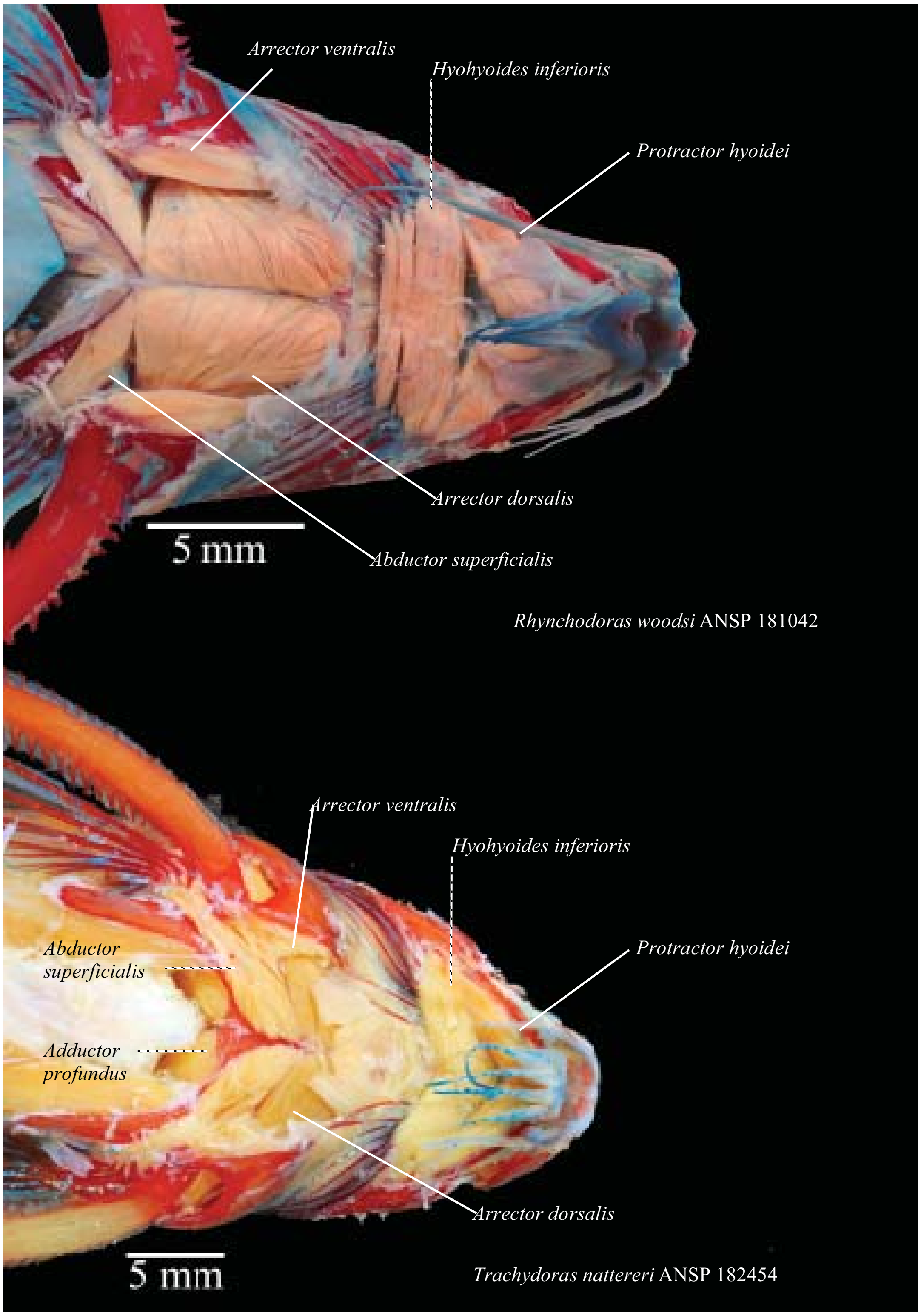

Figure 18. Ventral view of *Rhynchodoras woodsi* and *Trachydoras nattereri.* The *abductor superficialis* originates from the keel and the posterior ventral surface of the coracoid, fibers attach to the suture area between left and right portion of the coracoid.

Abductor profundus

The *abductor profundus* develops on the medial side of the lateral muscle mass serving the pectoral fin (Winterbottom, 1974) and it assists in the abduction of the pectoral fin (McMurrich, 1884).

The origin is on dorsolateral anterior most surface of the posterior process of the coracoid. Some inner fibers also arise from the radials. The insertion is on the posteroventral flanges of all the branched fin rays.

The muscle is smaller than and lays dorsally to the *abductor superficialis*.

There was no major variation in the area of origin and insertion, size, and shape of the *abductor profundus* between the genera of Doradidae.

Arrector ventralis

The *arrector ventralis* is the first to separate out from the lateral pectoral fin muscle 'anlage' (Winterbottom, 1974). It rotates the first ray allowing it to complete its abduction and fixation (McMurrich, 1884).

The origin is on the internal margin of the ventrolateral surfaces of the cleithrum and coracoid. The insertion is tendinous, on the distal end of the ventral process of the pectoral spine.

This muscle lies laterally to the cleithrum-coracoid bridge and is flat, short, and lenticular. In all the genera, except in *Physopyxis* and *Amblydoras*, it is visible when the skin is removed.

Variation trough the Doradidae refers to variation on the inner margin of the muscle. In *Hemidoras*, *Hypodoras*, *Megalodoras*, *Opsodoras morei*, *Ossancora*, *Platydoras*, *Pterodoras*, *Scorpiodoras*, and *Trachydoras* the internal most fibers of the muscle reach the keel of the coracoid and the internal margin appears divided (Figs. 17-*Scorpiodoras*, 18-*Trachydoras*). In all the other genera the internal margin is straight (Figs. 17-*Rhinodoras*, 18-*Rhynchodoras*)

Adductor superficialis

The *adductor superficialis* represent the dorsomedial component of the muscle mass located on the medial face of the pectoral girdle (Winterbottom, 1974). It adducts the fin, and when the fin is abducted this muscle works together with the abductors to produce the ondulatory movement of the fin (McMurrich, 1884)

The muscle is divided in two portions. The origin of the external portion is on the inner surface of the ascending process of the cleithrum. The origin of the internal portion is on the dorsomedial anterior most surface of the posterior process of the coracoid. The insertion is on the anterior and posterior dorsal faces of the branched pectoral fin rays.

The external portion is laminar and lies between the *adductor profundus* and the cleithrum. It is the larger of the two and the variation in size depends on the area of insertion. In *Doras*, *Hassar*, *Kalyptodoras*, *Leptodoras*, *Nemadoras*, *Opsodoras*, *Ossancodoras puntatus*, *Rhynchodoras woodsi*, and *Trachydoras* the origin is more dorsal, reaching farther on the dorsal process of the cleithrum. The muscle almost completely surrounds the *adductor profundus.*

The internal portion is shorter and attaches slightly to the dorsal face of the proximal radialis. No variation was observed for this portion.

Adductor profundus

The *adductor profundus* adduct the pectoral spine, when the fin is abducted it acts obliquely on its point of insertion and accordingly gives the rotation necessary to release the spine from its locking (McMurrich, 1884).

The origin is on the posteroventral margin lamina of the coracoid and the insertion is on the posterior medial margin of the dorsal process of the pectoral spine via strong tendon.

This muscle is a bulky mass that lies under the *hypaxialis*, and embraces the dorsal process of the cleitrhum. The *adductor* is most of the times visible after removing the ventral musculature. It is posterior to the posterior margin of the coracoid and never reaches farther than the posterior process of it.

Arrector dorsalis

The *arrector dorsalis* is the first muscle to separate off from the dorsomedial ‘anlage’ of the pectoral fin musculature (Winterbottom, 1974). It works together with the *arrector ventralis* to abduct the pectoral spine.

The muscle is divided in two portions, a dorsal and a ventral. The origin of the dorsal portion is on the dorsal surfaces of the coracoid. Fibers are in contact with the ventral muscles related to the gill arches and with the posteriormost fibers of the *sternohyoideus.* The origin of the ventral portion is on the ventral surface the cleithrum and the anteroventral surface of the coracoid.

The insertion of both portions is on the anterior fossa of the pectoral spine. The dorsal portion passes under the dorsal shelf of the cleithrum to reach the fossa dorsally. The ventral portion goes beneath the cleithrum coracoid bridge to insert, via a strong tendon, on the ventral face of the anterior fossa.

This muscle occupies the biggest area of the pectoral girdle and is exposed ventrally on most of the genera, except in *Amblydoras* and *Merodoras* **(**Figs. 17, 18**)**.

No variation was found for the dorsal portion of the *arrector dorsalis.* The only variation found in the ventral portion is related to the size of the muscle origin.

Abductor rotator (New muscle)

This muscle is apparently involved in the abduction of the pectoral spine, creating a little rotation to help on the binding step of the locking mechanism.

The origin is on the undersurface of the dorsal shelf of cleitrum. The fibers slightly twisted to the insertion on the proximal tubercle of the pectoral spine (Fig. 19).

This muscle lies dorsally to the fibers of the dorsal portion of the *arrector dorsalis* and is always covered by the bone on the "shoulder" of the cleithrum. No variation was found for this muscle.

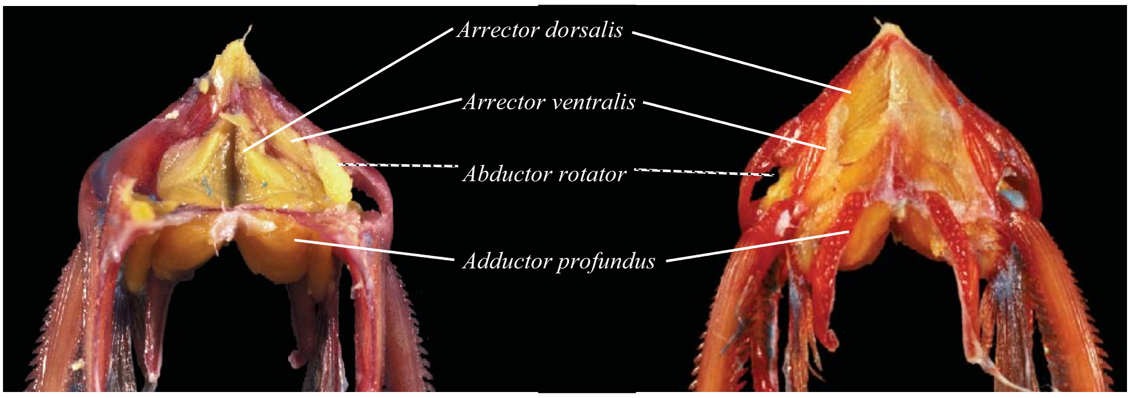

Figure 19. Ventral and dorsal view of the pectoral girdle of *Trachydoras steindachneri* ANSP 183076. Bones on the right side of the fish were removed to allow observation of the *abductor rotator.*

DISCUSSION

Comparison with previous studies of doradidae

Discrepancies were found when comparing my results with previous studies on the musculature of Doradidae. Diogo *et al* (2004) reviewed the cephalic musculature of *Franciscodoras marmoratus* and compared it with the cephalic muscles in *Anadoras weddellii*, *Acanthodoras cataphractus*, and *Ossancora fimbriata.* Based on those four genera they made statements about the myology of the Doradidae. I found differences in the descriptions of the *adductor mandibulae*, *retractor tentaculi*, *extensor tentaculi*, *dilatator operculi*, *hyohyoidei abductores*, and *abductor profundus.*

1. *Adductor mandibulae:*

Doradidae has an *adductor mandibulae* divided in two portions, which contradicts the findings of previous studies. Diogo *et al* (2004) examined the muscles of *Acanthodoras cataphractus*, *Anadoras weddellii*, *Ossancora punctata*, and *Franciscodoras marmoratus* and they found the *adductor mandibulae* to be divided on A1ost, A2, A3'd and A3v. When examined the species studied by Diogo *et al* (2004) only *Franciscodoras* displays a separation of the *adductor.* The *levator arcus palatini* inserts on the hyomandibula splitting the fibers at the origin of the *adductor.* In *Acanthodoras cataphractus*, *Anadoras weddellii*, and *Ossancora punctata* the *adductor* is a single mass (A2A3) where the fibers are completely mixed.

Contrary to previous studies, there is no strong attachment of the *adductor mandibulae* to the sphenotic or pterotic in any of the Doradidae examined. Diogo *et al* (2004) described that in *Franciscodoras marmoratus* a portion of the *adductor mandibulae* (their A2) originates from the sphenotic and pterotic. My observations established that the origin of the *adductor mandibulae* in *F. marmoratus* is restricted superficially only to the preopercle (Fig. 2). In *Kalyptodoras*, *Orinocodoras*, and *Wertheimeria*, as well as in some Auchenipteridae (e.g. *Glanidium* and *Trachelyopterus*), I observed a connection of the A2A3 with the sphenotic (Fig 1A, 20, 21). In those species some connective tissue or tendinous fibers give origin to the muscular fibers of the *adductor.* These tendinous fibers originate weakly from the sphenotic. In Doradidae the only case of strong attachment of the *adductor mandibulae* to the sphenotic is observed in *Rhynchodoras* (Fig. 3).

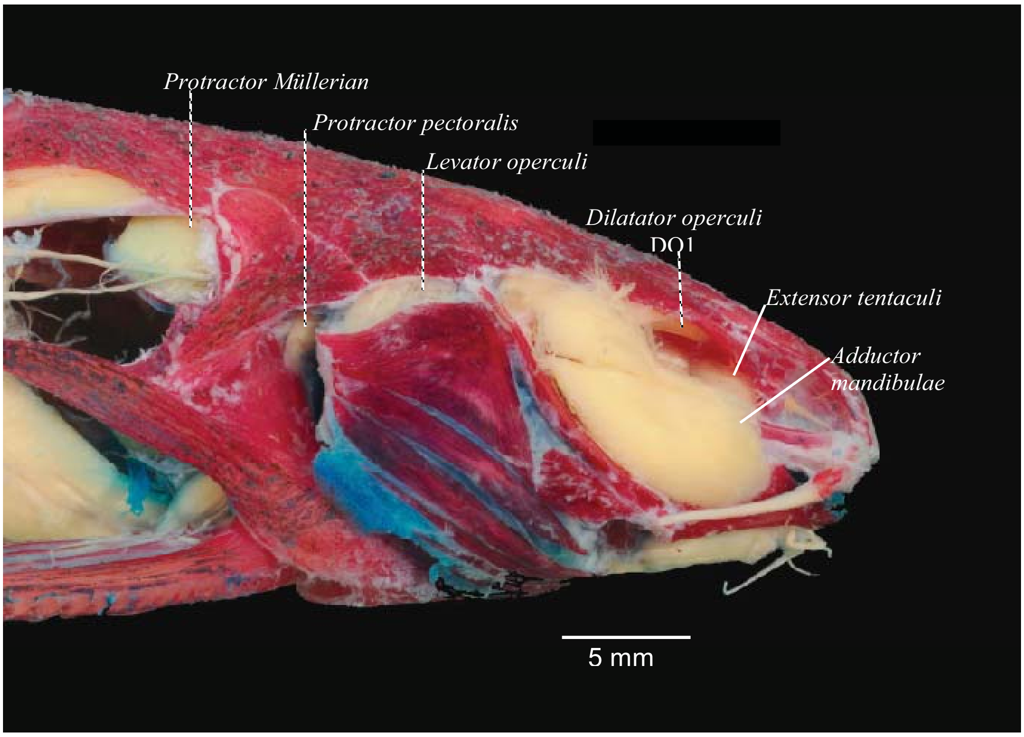

Figure 20. Lateral view of the head of Wertheimeria *maculata* MCP 34689. Fibers of the *adductor mandibulae* reaching the sphenotic.

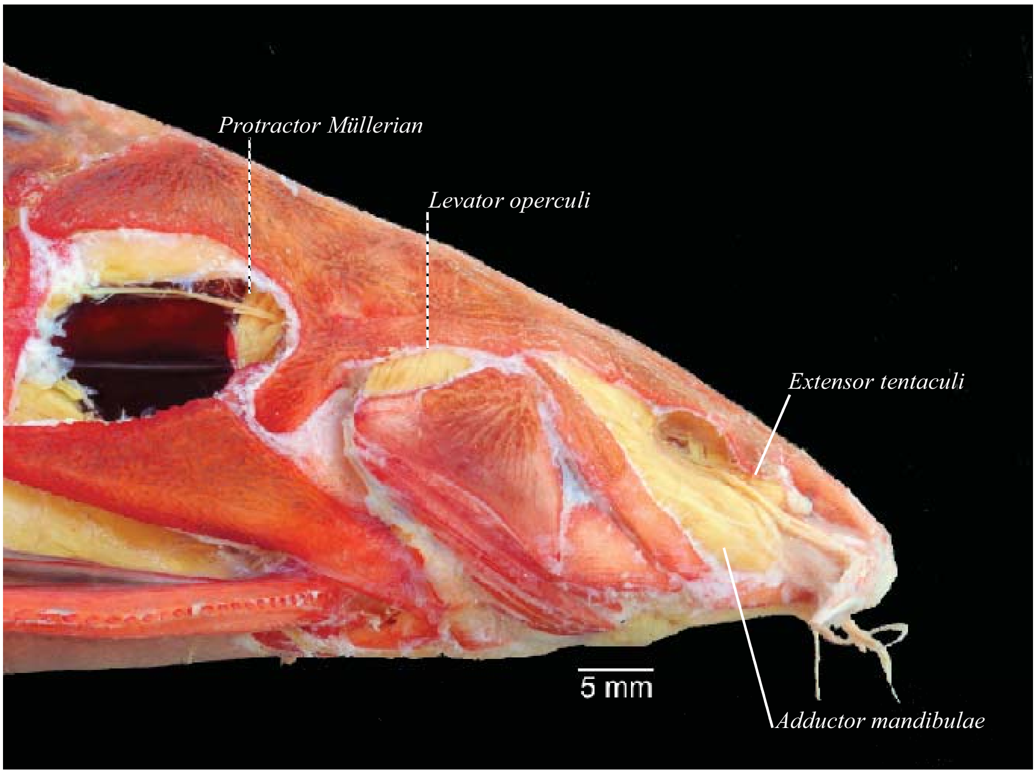

Figure 21. Lateral view of the head of *Orinocodoras eigenmanni* (ANSP 180891). Fibers of the *adductor mandibulae* reaching the sphenotic.

Observations of *Franciscodoras marmoratus,* along with comparisons with the illustration in Diogo *et al* (2004), suggest that the muscle named as A2 actually correspond to the *levator arcus palatini* (Fig. 22**).** Diogo *et al* (2004) present an illustration of the main cranial muscles on lateral view and their illustration shows a strong muscle mass leaving the neurocranium. They identified this muscle as a part of the *adductor mandibulae* (their A2).

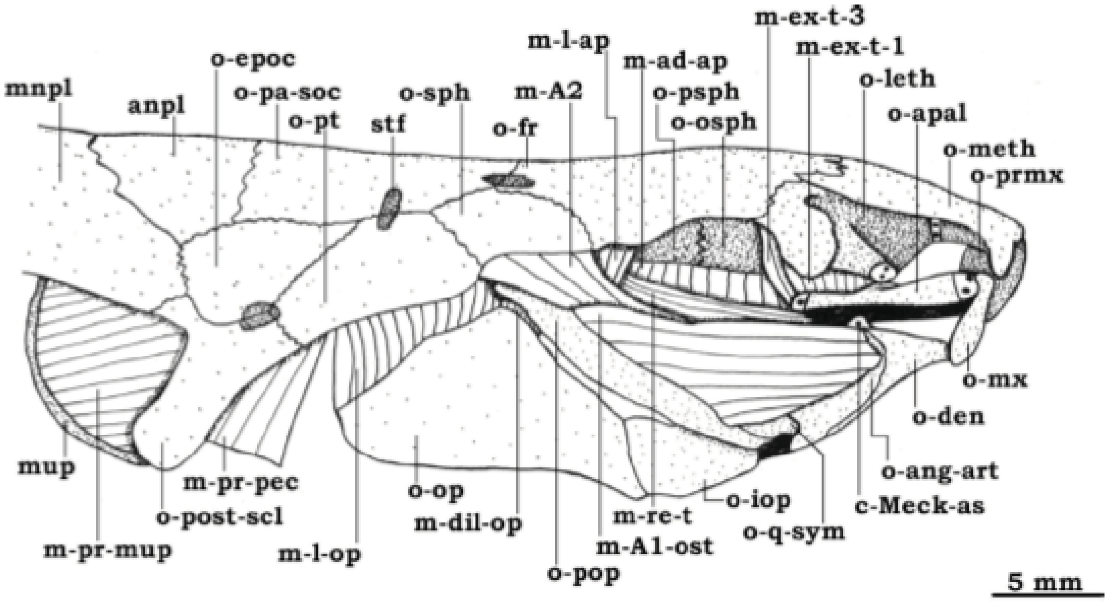

Figure 22. Illustration of cephalic musculature of *Franciscodoras marmoratus* in Diogo et al (2004a)

2. <u>*Retractor tentaculi*</u>

In *Franciscodoras marmoratus* the *retractor tentaculi* is connected to the maxilla and to the lower jaw and not only to the maxilla. Diogo *et al* (2004) recorded that in *F. marmoratus* the insertion of the *retractor* is only at the maxilla. Careful dissections revealed that in this species the *retractor* has a distal tendon that divides in three branches. The ventral-most branch attaches to the dentary and the other two branches attach to the maxilla dorsally and ventrally.

In *Anadoras weddellii* and *Acanthodoras cataphractus* the *retractor* is present and connected only to the lower jaw an. Diogo *et al* (2004) considered the *retractor* as a muscle connected to the maxilla. I consider the most medial muscle associated with the retraction of the maxillary barbel to be the *retractor tentaculi* independently of its insertion. The *retractor* is present in all the species of Doradidae. In *Ossancora punctata*, the *retractor tentaculi* is present and is connected to the maxilla. Diogo *et al* (2004) stated that the muscle is absent in *Ossancora punctata.* I observed three specimens of *Ossancora punctata* and eight specimens that belong to other species in the same genus. In all the species of *Ossancora* the *retractor tentaculi* develop a distal tendon that inserts ventrally and dorsally to the maxilla.

3. Extensor tentaculi

The *extensor tentaculi* in Doradidae is either a single muscle mass or divided in two portions. Observations of Diogo *et al* (2004) denote the presence of three bundles for this muscle in *Franciscodoras.*

The superficial observation of some specimens may mislead to the identification of three bundles due to the position of the portions' origin. The medial most portion usually has a wider origin than the external one. The origin of the medial portion is somehow shifted making it visible in lateral view (Fig. 5**)**. The careful examination of the fibers allows me to establish the presence of only two bundles.

4. Dilatator operculi

My observation of the origin of dilatator operculi differs from previous works. In Doradidae, the DO1 and DO2 portions of the *dilatator* originate from the frontal, sphenotic, lateral ethmoid or orbitosphenoid. Diogo *et al* (2004) examined *Franciscodoras marmoratus*, *Anadoras weddellii*, *Acanthodoras cataphractus*, and *Ossancora punctata* and they found the *dilatator operculi* originating from the pterosphenoid, frontal, and hyomandibulo-metapterygoid. I found no evidence of fibers of the *dilatator* rising from the pterosphenoide in any of the species analyzed. The DO3 portion originates from the hyomandibula, which is a bone separated from the metapterygoid.

5. Hyohyoideus abductor

In Doradidae, the *hyohyoidei abductores* are connected in a medial aponeurosis but never connected to the hypohyals. Diogo et al (2004) described this muscle as running from the first branchiostegal ray to a median aponeurosis and with two strong tendons attached to the ventral hypohyals. The description of Diogo *et al* (2004) is more aligning with the condition observed in Auchenipteridae (e.g. *Ageneiosus*). In *Ageneiosus*, the tendons that arise from the *hyohyoidei abductores* cross over the *hyohyoidei inferioris* to reach the hypohyals.

6. *Abductor profundus*

The muscle identified in Diogo et al (2004) as the *abductor profundus* corresponds to the *adductor profundus.* The *abductor profundus* is a short muscle that lies dorsally to the *abductor superficialis* connecting the coracoid with the branched fin rays. Diogo *et al* (2004) described the *abductor profundus* as a "…highly-developed muscle that originates on the porterior surface of the scapulo-coracoid and inserts on the medial surface of the dorsal condyle of the pectoral spine". Their description is better suited for the *adductor profundus* and does not correspond with the description of Winterbottom (1974). They cited the nomenclature of Winterbottom, which states that the *abductor profundus* is connected to the branched rays and not to the pectoral spine.

Comparison with other catfishes

The overall musculature of the Doradidae recalls that of other catfishes, however, there are some variations in the *adductor mandibulae*, *extensor tentaculi*, *levator arcus palatini*, *dilatator operculi*, and *protractor hyoidei*.

The *adductor mandibulae* in Doradidae is constituted by the A2 and A3 portions, which is sometimes fused towards the insertion and developed as a single muscle mass. There is no evidence of more than two portions of the *adductor mandibulae* or any evidence of the presence of A1 or Aw. Several authors (Takahasi, 1925; Winterbottom, 1974; and Howes, 1983) described the muscle as commonly divided in four sections, A1, A2, A3 and Aw, but Fink & Fink (1981) stated that Siluriformes have the plesiomorphic condition of an undifferentiated adductor that inserts on the mandible. Gosline (1989) mentioned an external and internal portion of the *adductor mandibulae* in catfishes that corresponds to the A2 and A3 of the Doradidae, respectively. In Auchenipteridae, Aspredinidae, and *Diplomystes,* the adductor appears as a single mass.

In Doradidae the *extensor tentaculi* is not highly specialized. Most of the genera developed two portions inserted dorsally on the autopalatine and the others develop a single portion, also inserted dorsally on the autopalatine. Cases of highly specialized musculature related to the abduction of the maxillary barbel are found in some species of Pimelodidae (Ghiot, 1978). *Pimelodus clarias*, *Pseudoplatystoma fasciatum*, *and Sorubim lima* have an *extensor tentaculi* divided in five portions.

The origin of the *levator arcus palatini* is dislocated posteriorly and there is an apparent reduction of the muscle size. In other catfish such as Pimelodidae (Nass, 1991), Claridae (Adriaens & Verraes, 1996; Devaere et al, 2006), Bagridae, Siluridae, and Ictaluridae (Lundberg pers. comm.) the origin of the muscle is more anterior than in Doradidae, including even the lateral ethmoid. Also the same authors describe a bigger muscle mass than the one present in Doradidae.

Portions of the *dilatator operculi* in Doradidae are comparable to portions of the *dilatator* in Trichomycteridae. Doradidae present a well-developed *dilatator operculi* divided into three portions (DO1, DO2, and DO3) with different area of origin and with a common area of insertion. Datovo & Bockman (2010) found a highly specialized condition for this muscle in trychomicterids, where there are two main recognizable sections. They described the sections as primary and secondary, the primary corresponding to the single section on other Siluriformes and the secondary section only found on Trichomycteridae. They claimed that the sections are somewhat continuous with each other in the area of insertion but separate at their origins. The comparison of the position of the portions of the *dilatator operculi* in Doradidae and in Trichomycteridae leads to the establishment of two positional homologies. DO1 is homologous to the primary section of Datovo & Bockman and DO2 is homologous to the secondary portion of Trichomycteridae. In Doradidae, DO2 is highly reduced and is present as a thin layer of fibers running from the sphenotic to the opercle.

The *protractor hyoidei* is one of the cranial muscles with variation reported in the literature for the Siluriformes. In Doradidae, the muscle is divided in two or three portions, dependent on the genera. Up to seven portions of the muscle have been identified for some families (e.g. Bagridae and Pimelodidae).

Takahasi (1925) examined specimens of Bagridae, Siluridae, Plotosidae, and Amblycipitidae and he observed a simple division of the *protractor* in superior and inferior portions. Datta Munshi (1960) refers to this muscle as the *intermandibularis posterior.* He reviewed *Mystus sp.* and stated that the siluroids present three different portions: pars superficialis, pars medialis, and pars lateralis according to their position on the specimen. Winterbottom (1974) examined *Diplomystes* and *Ictalurus* finding only a single myocomma and he stated that previous authors had overlooked this muscle. Diogo and Chardon (2000) recognized three portions of the muscle: pars dorsalis, pars ventralis and pars lateralis. They based the names of their portions on the position but they do not establish homologies with the previous work of Datta Munshi (1960). They also named several muscles related with movement of the mental barbels besides the *protractor*. Ghiot (1978) and Ghiot *et al* (1984) identified up to seven portions of the *protractor* after the analysis of some specimens of Bagridae and Pimelodidae. P1 connecting the hyoid bar with the basal process of the external mandibular barbel, P2 between the cartilaginous plate and the external mandibular barbel base, P3 between the bases of the internal and the external barbels, P4 between the internal barbel base and the median aponeurosis, P5 between the caudal tip of the external mandibular barbel base and the median aponeurosis, P6 between the base of the internal mandibular barbel and the hyoid bar, and P7 running from the hyoid bar up to the median aponeurosis. Adriaens (1998) distinguishes four of Ghiot portions as present on *Clarias*, the P1, P3, P4 and P7.

Present study	**Ghiot (1978) and Ghiot *et al* (1984)**	**Diogo & Chardon (2000)**	**Datta Munshi (1960)**	**Takahasi (1925)**
PH1		Pars dorsalis	Pars medialis	Geniohyodeus superior externo
PH2a	P1	Protractor externi mandibularis tentaculi	Pars superficialis posterior (outer portion)	
PH2b	P2		Retractor tentaculi (outer barbel)	
PH2b	P3	Retractor externi mandibularis tentaculi	Protractor tentaculi (outer barbel, outer portion)	
PH2b			Protractor tentaculi (outer barbel, inner portion)	
PH1+ PH2 +PH3		Pars lateralis	Pars lateralis	
PH2c		Retractor interni mandibularis tentaculi	Protractor tentaculi (inner barbel)	
PH3	P4	Depresor interni mandibularis tentaculi	Pars superficialis middle + Retractor tentaculi (inner barbel)	
PH3	P7	Pars ventralis	Pars superficialis posterior (inner portion)	Geniohyodeus superior interno
PH3			Pars superficialis anterior	Geniohyodeus inferior
PH3	P6			
PH3	P5			

Conflict to establish the true composition of the *protractor hyoidei* is due to the variety of families studied and the use of different names for the portions recognized. The table 1 illustrates possible positional homologies of the different portions of the *protractor hyoidei* and muscles related with the movement of the mental barbels, based on the descriptions of the divisions published previously.

In Doradidae, there was an apparent simplification of the *protractor hyoidei* that seems to be the product of the fusion of different groups of fibers. Some of the portions found in Doradidae are equivalent to several portions found by other authors. For instance portion PH3 appears to be a mixture of portions P4, P5, P6 and P7 of Ghiot and its correspondent portions in other studies.

In simple barbel doradids, there are always three portions PH1, PH2, and PH3. All the fibers related with the movement of mental barbels are supported by section PH2 semi-divided to reach the cartilage correspondent to the inner and outer barbel. The structure of the *protractor* is even simpler in some of the Doraidae with fimbriate barbel where just two portions of the *protractor hyoidei* are visible. PH2 and PH3 are fused toward the insertion and slightly separated at the origin.

The variation of the muscles in the pectoral fin in Siluriformes is related to the amount of muscles that attach to the pectoral spine. In *Diplomystes,* there are three muscles associated to the pectoral spine, one working as adductor and two abductors. Auchenipteridae present two different conditions; in the first one, three muscles are attached to the pectoral spine (one adductor and three abductors). In the second condition, there are one adductor and four abductors, resembling that of Doradidae. Aspredinidae (e.g. *Aspredo*) have one adductor and three abductors. Ictaluridae have four muscles inserting on the spine, three abductors and one adductor (Friel comm pers.)

Functional morphology.

Inferences in this chapter are the result of the direct observation and analysis of the interaction between the different muscular entities.

The width of the mouth dictates the size, robustness, and strength of the *adductor mandibulae.* The *adductor mandibulae* is the muscle that adducts the lower jaw and closes the mouth. The evidence shows that in Doradidae, species with a narrow mouth have smaller *adductor* *mandibulae.* In Doradidae with fimbriate barbel, the mouth is usually narrow and the *adductor is* smaller, more laminar, and weaker. Conversely, in Doradidae with simple barbel the mouth is wide and the *adductor* is bigger, more robust, and stronger.

The size of some muscle of the cheek, the eye, and the mouth is correlated. Doradidae with simple barbel usually have smaller eyes and wider mouths. In those genera, the *adductor mandibulae* and the *levator arcus palatini* are at least twice as big as species with fimbriate barbels. In genera with simple barbel, the origin of the *dilatator operculi* fills the frontals and sometimes reaches the lateral ethmoid. In genera with fimbriate barbel, the origin of the *dilatator* is restricted to the sphenotic and posterior portion of the frontals. The correlation of these features can be explained as a result of spatial competition during ontogenetic development.

The variation in size of the *hyohyoidei abductores* is inversely related to the variation in size of the origin of *dilatator operculi.* The *hyohyoidei abductores* is responsible for the expansion of the branquiostegal membrane. It works together with the *dilatator operculi* on the suction pump system as part of the aquatic respiration (Adriaens, 1998). The observations show that the genera with thin and weakly developed *hyohyoidei abductores* are the same genera in which the *dilatator operculi* fills the frontals and sometimes reaches the lateral ethmoid. When the area of origin of the *dilatator operculi* is restricted to the sphenotic, the *hyohyoidei abductores* is developed as a strong muscle mass.

The *retractor tentaculi* was identified based on its position and function independently on the area of insertion. In Siluriformes, the *retractor* is medial to the *adductor* (Adriaens, 1998). I found the retractor in Doradidae as a muscle mass medial to the *adductor mandibulae.* The *retractor tentaculi* is commonly known as the muscle that attaches to the maxilla and retracts the maxillary barbel (Winterbottom, 1974). I found that the *retractor* in Doradidae might be inserted on the dentary, the dentary and the maxilla, only in the maxilla, or in the buccopalatal membrane (see appendix for detailed information).

The presence of the coronomeckelian ligament is related to the movement of the maxillary barbels. The coronomaxilar ligament is a dense irregular connective tissue that attaches posterior to the anterior rim of the coronoid process and anteriorly to the base of the maxillary barbel and often to the maxilla (Datovo & Bockman, 2010). The coronomaxilar ligament is present in *Acanthodoras*, *Agamyxis*, *Amblydoras*, *Anadoras*, *Astrodoras*, *Hypodoras*, *Merodoras*, *Physopyxis*, and *Scorpiodoras*. In those genera the *retractor tentaculi* is never attached to the maxilla. This evidence suggests that in species were the ligament is present the movement of the maxillary barbel will be directly related with movement of coronoid process. Then when the *retractor* is attached to the lower jaw or the bucopalatal membrane, it works synchronously with the coronomaxilar ligament to produce movement of the maxillary barbel. Functional studies are needed to test this hypothesis.

Modifications of the *extensor tentaculi* yield to further specializations of the extension mechanism of the barbels, allowing movements such as depression and elevation. The division of the *retractor tentaculi* and its dorsal insertion on the autopalatine suggests that the contraction of the fibers result in the simple elevation of the barbels. In *Orinocodoras*, *Rhinodoras*, and *Rhynchodoras,* some fibers of the *extensor tentaculi* insert ventrally to the autopalatine. The ventral insertion suggests that during contraction, apart from a forward sliding, the muscle also performs a rotation of the palatine. This rotation results in a depression of the barbel.

Within the family, the variation in size of the *levator arcus palatini* is related to the variation in size of the suspensorium. In genera where the hyomandibula and other suspensorial elements are not expanded, they tend to have a reduced *levator arcus palatini.* The muscle is flat, does not protrude from the hyomandibula, and is not robust. This tendency is observed in Doradidae with more compressed bodies, for example *Hemidoras*, *Hassar*, *Leptodoras*, *Nemadoras*, and *Trachydoras.* In Doradidae with more depressed bodies like *Anadoras*, *Kalyptodoras*, *Merodoras*, and *Megalodoras,* the hyomandibular elements are expanded and the *levator arcus palatini* is not reduced. This reduction could be the result of the functional morphology of the muscle. Contraction of this muscle results on the abduction of the suspensorium. Then a smaller suspensorium will yield to a smaller *levator arcus palatini.*

Doradidae, as well as other Siluriformes, have the first ray of the pectoral fin modified in a strong spine that is used as a defense weapon. The spine can be locked making the specimens look bigger and making it difficult to swallow for predators.

The locking mechanism allows the spine to be abducted and lock after abduction. A special rotation must be applied on the spine to produce its adduction. According to Fine *et al* (1999), two steps are involved on the locking mechanism: the binding that requires active muscular force and the locking that occurs only in the fully abducted position and do not involve muscular force.

In order to produce the full abduction of the spine, the mechanism requires the synchronization of different muscles. In Doradidae, four muscles are related with the abduction of the spine: *arrector ventralis, arrector dorsalis* (dorsal and ventral portion) and the *abductor rotator.* It is known that the locking is achieved by the slight rotation of the spine in fully abduction (Fine et al, 1999). Looking at the position of the muscles and the way they insert on the spine, it is inferred that the *arrector dorsalis* produce the abduction of the spine and that the *arrector ventralis* and the *abductor rotator* work together to rotate the spine allowing the full locking.

Only one muscle, the *adductor profundus,* is needed to adduct the pectoral spine. The position of this muscle and the angle of attachment to the posterior most margin of the dorsal process of the spine suggest that the contraction of the muscle, creates a slight rotation that will allow the releasing of the locking mechanism as well as the adduction of the spine.

The musculature of Doradidae recalls that of other catfish families previously studied by other authors. The structure of muscles of the basal taxa in Doradidae and Auchenipteridae resemble one another. It is evident how in genera like *Ageneiosus* or *Auchenipterus*, the general body modification yielded into muscle modification, but still, homologies between the two families are traceable. The anatomy of muscles on the pectoral spine in Aspredinidae is similar to that of Doradidae and Auchenipteridae. Other muscular complexes, although similar, exhibit a greater variation due to the depression of the Aspredinidae body.

Future research

This study represents an important contribution to knowledge of anatomy of catfishes with an emphasis in Doradidae. Data produced by this work can be used for posterior comparisons and applied to different fields such as systematics. Information referent to functional morphology was extrapolated from studies in other groups of fishes. It shows the need for studies on functional morphology as well as the need for ontogenetic studies. This will allow a better understanding of the development of anatomical structures and the way they work together in the body.

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Appendix 1. Origin and insertion of the some of the cranial and pectoral muscles of Doradidae

SPECIES	*Adductor mandibulae*							*Retractor tentaculi*				*Extensor tentaculi*				*Levator Arcus Palatini*			
	Origin					Insertion		Origin	Insertion			Origin			Insertion	Origin		Insertion	
	POP	HYO	QUA	MET	SPH	AA	DEN	HYO	DEN	MAX	BUC M	LE	FRO	OBSP	PAL	SPH	FRO	HYO	QUA
Acanthodoras cataphractus	●	●	●	●		●		●	●			●			●	●		●	
Acanthodoras spinosissimus	●	●	●	●		●		●	●			●			●	●	●	●	
Agamyxis albomaculatus	●	●	●			●	●	●	●	●		●			●	●	●	●	
Agamyxis pectinifrons	●	●	●			●	●	●	●	●		●			●	●	●	●	
Amblydoras affinis	●	●	●			●		●			●	●			●	●		●	
Amblydoras nauticus	●	●	●			●		●			●	●			●	●		●	
Anadoras grypus	●	●	●			●		●	●		●	●			●	●		●	
Anadoras weddellii	●	●	●			●		●	●		●	●			●	●	●	●	
Anduzedoras oxyrhynchus	●	●				●	●	●		●		●			●	●		●	
Astrodoras asterinifrons	●	●				●		●			●	●			●	●		●	
Centrochir crocodili	●	●				●		●		●		●			●	●		●	
Centrodoras brachiatus	●	●				●	●	●	●	●		●			●	●	●	●	
Doraops zuloagai	●	●				●	●	●	●	●		●			●	●	●	●	
Doras carinatus	●	●	●			●		●		●		●			●	●		●	
Doras higuchi	●	●	●			●	●	●		●		●			●	●		●	
Doras phyzakion	●	●	●			●		●		●		●			●	●		●	
Franciscodoras marmoratus	●	●	●			●		●	●	●		●			●	●	●	●	
Hassar affinis	●	●				●		●		●		●			●	●		●	
Hassar orestis	●	●				●	●	●		●		●			●	●		●	
Hassar wilderi	●	●				●		●		●		●			●	●		●	
Hemidoras morrisi	●	●				●		●		●		●			●	●		●	
Hemidoras stenopeltis	●	●	●			●		●		●		●			●	●		●	
Hypodoras forficulatus	●	●				●		●	●			●			●	●		●	
Kalyptodoras bahiensis	●	●	●		●	●		●	●	●		●			●	●	●	●	
Leptodoras cataniai	●	●	●			●		●		●		●			●	●		●	
Leptodoras hasemani	●	●	●			●		●		●		●			●	●		●	
Leptodoras juruensis	●	●	●			●		●		●		●			●	●		●	
Leptodoras linelli	●	●	●			●		●		●		●			●	●		●	
Leptodoras oyakawai	●	●	●			●		●		●		●			●	●		●	
Leptodoras praelongus	●	●				●		●		●		●			●	●		●	
Lithodoras dorsalis	●	●	●			●	●	●	●	●		●			●	●		●	
Megalodoras guayoensis	●	●	●			●		●	●	●		●			●	●		●	
Megalodoras uranoscopus	●	●				●		●	●	●		●			●	●		●	
Merodoras nheco	●	●	●			●		●	●			●			●	●		●	
Nemadoras elongatus	●	●	●			●		●		●		●			●	●		●	

SPECIES	*Adductor mandibulae*							*Retractor tentaculi*				*Extensor tentaculi*				*Levator Arcus Palatini*			
	Origin					Insertion		Origin	Insertion			Origin			Insertion	Origin		Insertion	
	POP	HYO	QUA	MET	SPH	AA	DEN	HYO	DEN	MAX	BUC M	LE	FRO	OBSP	PAL	SPH	FRO	HYO	QUA
Nemadoras humeralis	●	●	●			●	●	●		●		●			●	●		●	
Nemadoras leporhinus	●	●	●			●		●		●		●			●	●		●	
Nemadoras trimaculatus	●	●	●			●		●		●		●			●	●		●	
Opsodoras ternetzi	●	●	●			●		●		●		●			●	●		●	
Opsodoras morei	●	●	●			●		●		●		●			●	●		●	
Orinocodoras eigenmanni	●	●	●		●	●		●		●		●			●	●	●	●	
Ossancora eigenmanni	●	●	●			●		●		●		●			●	●		●	
Ossancora punctata	●	●	●			●		●		●		●			●	●		●	
Ossancora fimbriata	●	●	●			●		●		●		●			●	●		●	
Ossancora asterophysa	●	●	●			●		●		●		●			●	●		●	
Oxydoras niger	●	●	●			●		●		●		●			●	●		●	
Oxydoras sifontesi	●	●	●			●		●		●		●			●	●		●	
Physopyxis ananas	●	●	●			●		●	●			●			●	●		●	
Physopyxis lira	●	●	●			●		●	●			●			●	●		●	
Platydoras armatulus	●	●	●	●		●		●		●		●			●	●		●	
Platydoras hancocki	●	●	●	●		●		●		●		●			●	●		●	
Pterodoras granulosus	●	●				●		●		●		●			●	●	●	●	
Rhinodoras boehlkei	●	●	●			●	●	●	●	●		●			●	●	●	●	
Rhinodoras dorbignyi	●	●	●			●	●	●	●	●		●			●	●	●	●	
Rhynchodoras woodsi	●	●			●	●		●		●		●			●	●	●	●	
Scorpiodoras heckelii	●	●	●			●		●	●		●	●			●	●		●	
Trachydoras brevis	●	●	●			●		●		●		●			●	●		●	
Trachydoras microstomus	●	●	●			●		●		●		●			●	●		●	
Trachydoras nattereri	●	●	●			●		●		●		●			●	●		●	
Trachydoras paraguayensis	●	●	●			●		●		●		●			●	●		●	
Trachydoras steindachneri	●	●	●			●		●		●		●			●	●		●	
Wertheimeria maculata	●	●	●		●	●		●	●	●		●			●	●	●	●	
Ageneiosus brevifilis	●	●	●			●		●	●				●		●	●		●	
Ageneiosus ucayalensis	●	●	●			●		●	●				●		●	●		●	
Auchenipterus nigripinnis	●	●	●			●		●	●			●		●	●	●		●	
Aspredo aspredo	●	●				●	●	●		●		●	●		●	●	●		●
Bunocephalus verrucosus	●	●				●	●	●		●			●	●	●	●	●	●	●
Centromochlus heckelii	●	●	●			●	●	●		●				●	●	●		●	
Glanidium leopardum	●	●	●		●	●		●	●					●	●	●	●	●	
Liosomadoras oncinus	●	●	●			●		●	●			●			●	●		●	
Trachelyopterus galeatus	●	●	●		●	●		●	●			●	●		●	●		●	

SPECIES	*Adductor arcus palatini*									*Dilatator operculi*							
	Origin					Insertion				Origin DO1				Origin DO2		Origin DO3	Insertion of DO1, DO2, DO3
	LE	OBSP	PTSP	PASP	VOM	HYO	MET	MES	QUA	FRO	SPH	OBSP	LE	SPH	PTO	HYO	OPE
Acanthodoras cataphractus	●	●	●	●		●	●	●		●				●		●	●
Acanthodoras spinosissimus	●	●	●	●		●	●	●		●				●		●	●
Agamyxis albomaculatus	●	●	●	●		●	●			●	●		●	●		●	●
Agamyxis pectinifrons	●	●	●	●		●	●			●	●		●	●		●	●
Amblydoras affinis	●	●	●	●		●	●			●	●			●		●	●
Amblydoras nauticus	●	●	●	●		●	●			●	●			●		●	●
Anadoras grypus	●	●	●	●		●	●			●	●		●	●		●	●
Anadoras weddellii	●	●	●	●		●	●			●	●			●		●	●
Anduzedoras oxyrhynchus			●	●		●		●		●	●			●	●	●	●
Astrodoras asterinifrons	●	●	●	●		●	●			●	●			●		●	●
Centrochir crocodili	●	●	●	●		●	●	●		●	●			●		●	●
Centrodoras brachiatus	●	●	●	●		●	●	●		●	●			●		●	●
Doraops zuloagai	●	●	●	●		●	●	●		●	●		●	●		●	●
Doras carinatus	●	●	●	●		●	●	●		●	●			●		●	●
Doras higuchi	●	●	●	●		●	●	●		●	●			●		●	●
Doras phyzakion	●	●	●	●		●	●	●		●	●			●		●	●
Franciscodoras marmoratus	●	●	●	●		●	●	●		●	●		●	●		●	●
Hassar affinis	●	●	●	●		●	●	●		●	●			●		●	●
Hassar orestis	●	●	●	●		●	●	●		●	●			●		●	●
Hassar wilderi	●	●	●	●		●	●	●		●	●			●		●	●
Hemidoras morrisi	●	●	●	●		●	●	●		●	●			●		●	●
Hemidoras stenopeltis	●	●	●	●		●	●	●		●	●			●		●	●
Hypodoras forficulatus	●	●	●	●		●	●	●		●	●		●	●		●	●
Kalyptodoras bahiensis	●	●	●	●		●	●	●		●		●		●		●	●
Leptodoras cataniai	●	●	●	●		●	●	●		●	●			●		●	●
Leptodoras hasemani	●	●	●	●		●	●	●		●	●			●		●	●
Leptodoras juruensis	●	●	●	●		●	●	●		●	●			●		●	●
Leptodoras linelli	●	●	●	●		●	●	●		●	●			●		●	●
Leptodoras oyakawai	●	●	●	●		●	●	●		●	●			●		●	●
Leptodoras praelongus	●	●	●	●		●	●	●		●	●			●		●	●
Lithodoras dorsalis	●	●	●	●		●	●	●		●		●	●	●		●	●
Megalodoras guayoensis	●	●	●	●		●	●	●		●		●	●	●		●	●
Megalodoras uranoscopus	●	●	●	●		●	●	●		●		●	●	●		●	●
Merodoras nheco	●	●	●	●		●	●	●		●		●		●		●	●
Nemadoras elongatus	●	●	●	●		●		●		●	●			●		●	●

	Adductor arcus palatini									*Dilatator operculi*							
SPECIES	Origin					Insertion				Origin DO1				Origin DO2		Origin DO3	Insertion of DO1, DO2, DO3
	LE	OBSP	PTSP	PASP	VOM	HYO	MET	MES	QUA	FRO	SPH	OBSP	LE	SPH	PTO	HYO	OPE
Nemadoras humeralis	●	●	●	●		●	●	●		●	●			●		●	●
Nemadoras leporhinus	●	●	●	●		●	●	●		●	●			●		●	●
Nemadoras trimaculatus	●	●	●	●		●	●	●		●	●			●		●	●
Opsodoras ternetzi	●	●	●	●		●	●	●		●	●			●		●	●
Opsodoras morei	●	●	●	●		●	●	●		●		●		●		●	●
Orinocodoras eigenmanni	●	●	●	●		●	●	●		●		●	●	●		●	●
Ossancora eigenmanni	●	●	●	●		●	●	●		●	●			●		●	●
Ossancora punctata	●	●	●	●		●	●	●		●	●			●		●	●
Ossancora fimbriata	●	●	●	●		●	●	●		●	●			●		●	●
Ossancora asterophysa	●	●	●	●		●	●	●		●	●			●		●	●
Oxydoras niger	●	●	●	●		●	●	●		●		●		●		●	●
Oxydoras sifontesi	●	●	●	●		●	●	●		●		●		●		●	●
Physopyxis ananas	●	●	●	●		●	●	●		●				●		●	●
Physopyxis lira	●	●	●	●		●	●	●		●				●		●	●
Platydoras armatulus	●	●	●	●		●	●	●		●		●		●		●	●
Platydoras hancocki	●	●	●	●		●	●	●		●				●		●	●
Pterodoras granulosus	●	●	●	●		●	●	●		●	●		●	●		●	●
Rhinodoras boehlkei	●	●	●	●		●	●	●		●		●	●	●		●	●
Rhinodoras dorbignyi	●	●	●	●		●	●	●		●		●	●	●		●	●
Rhynchodoras woodsi	●	●	●	●		●	●	●		●		●		●		●	●
Scorpiodoras heckelii	●	●	●	●		●	●	●		●	●			●		●	●
Trachydoras brevis	●	●	●	●		●	●	●		●	●			●		●	●
Trachydoras microstomus	●	●	●	●		●	●	●		●	●			●		●	●
Trachydoras nattereri	●	●	●	●		●	●	●		●	●			●		●	●
Trachydoras paraguayensis	●	●	●	●		●	●	●		●	●			●		●	●
Trachydoras steindachneri	●	●	●	●		●	●	●		●	●			●		●	●
Wertheimeria maculata	●	●	●	●		●	●	●		●		●		●		●	●
Ageneiosus brevifilis	●	●	●	●		●	●		●	●					●	●	●
Ageneiosus ucayalensis	●	●	●	●		●	●		●	●				●		●	●
Auchenipterus nigripinnis				●	●	●	●	●		●	●		●	●		●	●
Aspredo aspredo				●	●	●			●		●			-		●	●
Bunocephalus verrucosus				●	●	●			●		●			●		●	●
Centromochlus heckelii				●	●	●	●	●		●	●			-		●	●
Glanidium leopardum				●	●	●	●	●		●		●		●		●	●
Liosomadoras oncinus				●	●	●	●			●		●	●	●		●	●
Trachelyopterus galeatus				●	●	●	●				●			-		●	●

SPECIES	*Levator opeculi*			*Adductor operculi*				*Protractor hyoideus*		
	Origin		Insertion	Origin			Inserion	Origin	Insertion	
	PTO	SCL	OPE	PTO	SCL	EXOCC	OPE	DEN	A.CER	P.CER
Acanthodoras cataphractus	●	●	●	●			●	●	●	
Acanthodoras spinosissimus	●	●	●	●			●	●	●	
Agamyxis albomaculatus	●		●			●	●	●	●	
Agamyxis pectinifrons	●	●	●	●			●	●	●	
Amblydoras affinis	●	●	●	●			●	●	●	
Amblydoras nauticus	●		●	●			●	●	●	
Anadoras grypus	●	●	●	●			●	●	●	
Anadoras weddellii	●		●	●			●	●	●	
Anduzedoras oxyrhynchus		●	●			●	●	●	●	●
Astrodoras asterinifrons	●	●	●	●			●	●	●	
Centrochir crocodili	●		●	●			●	●	●	
Centrodoras brachiatus	●		●	●			●	●	●	
Doraops zuloagai	●		●	●			●	●	●	●
Doras carinatus	●	●	●			●	●	●	●	
Doras higuchi	●	●	●			●	●	●	●	●
Doras phyzakion	●	●	●			●	●	●	●	●
Franciscodoras marmoratus	●	●	●	●			●	●	●	
Hassar affinis	●	●	●	●			●	●	●	●
Hassar orestis	●	●	●	●			●	●	●	●
Hassar wilderi	●	●	●	●			●	●	●	●
Hemidoras morrisi	●		●	●			●	●	●	●
Hemidoras stenopeltis	●		●	●			●	●	●	●
Hypodoras forficulatus	●		●	●			●	●	●	
Kalyptodoras bahiensis	●	●	●	●			●	●	●	
Leptodoras cataniai	●		●	●			●	●	●	●
Leptodoras hasemani	●		●	●			●	●	●	●
Leptodoras juruensis	●		●	●			●	●	●	●
Leptodoras linelli	●		●	●			●	●	●	●
Leptodoras oyakawai	●		●	●			●	●	●	●
Leptodoras praelongus	●		●	●			●	●	●	●
Lithodoras dorsalis	●	●	●	●			●	●	●	
Megalodoras guayoensis	●	●	●	●			●	●	●	
Megalodoras uranoscopus	●		●	●			●	●	●	
Merodoras nheco	●	●	●	●			●	●	●	
Nemadoras elongatus	●	●	●	●			●	●	●	

Species	*Levator operculi*			*Addcutor operculi*				*Protractor hyoidei*		
	Origin		Insertion	Origin			Insertion	Origin	Insertion	
	PTO	SCL	OPE	PTO	SCL	EXOCC	OPE	DEN	A.CE	P.CE
Nemadoras humeralis	●	●	●	●			●	●	●	●
Nemadoras leporhinus	●	●	●	●			●	●	●	●
Nemadoras trimaculatus	●	●	●	●			●	●	●	
Opsodoras ternetzi	●	●	●	●			●	●	●	●
Opsodoras morei	●	●	●	●			●	●	●	●
Orinocodoras eigenmanni	●	●	●	●			●	●	●	●
Ossancora eigenmanni	●	●	●	●			●	●	●	●
Ossancora punctata	●	●	●	●			●	●	●	●
Ossancora fimbriata	●	●	●	●			●	●	●	●
Ossancora asterophysa	●	●	●	●			●	●	●	●
Oxydoras niger	●		●	●			●	●	●	
Oxydoras sifontesi	●		●	●			●	●	●	
Physopyxis ananas	●	●	●	●			●	●	●	
Physopyxis lira	●	●	●	●			●	●	●	
Platydoras armatulus	●		●	●			●	●	●	
Platydoras hancocki	●		●	●			●	●	●	
Pterodoras granulosus	●		●	●			●	●	●	
Rhinodoras boehlkei	●	●	●	●			●	●	●	
Rhinodoras dorbignyi	●	●	●	●			●	●	●	
Rhynchodoras woodsi	●	●	●	●			●	●	●	●
Scorpiodoras heckelii	●	●	●	●			●	●	●	
Trachydoras brevis	●	●	●	●			●	●	●	●
Trachydoras microstomus	●	●	●	●			●	●	●	●
Trachydoras nattereri	●	●	●	●			●	●	●	●
Trachydoras paraguayensis	●	●	●	●			●	●	●	●
Trachydoras steindachneri	●	●	●	●			●	●	●	●
Wertheimeria maculata	●		●	●			●	●	●	
Ageneiosus brevifilis		●	●		●		●	●	●	
Ageneiosus ucayalensis			●				●	●	●	●
Auchenipterus nigripinnis	●		●	●			●	●	●	
Aspredo aspredo	●		●				●	●	●	●
Bunocephalus verrucosus	●		●				●	●	●	
Centromochlus heckelii		●	●	●	●		●	●	●	
Glanidium leopardum		●	●	●			●	●	●	●
Liosomadoras oncinus	●		●	●			●	●	●	
Trachelyopterus galeatus	●	●	●	●			●	●	●	

MOLECULAR PHYLOGENY OF THORNY CATFISHES (TELEOSTEI: SILURIFORMES: DORADIDAE)

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ABSTRACT

Existing phylogenetic hypotheses of interrelationships of the catfish family Doradidae are based almost entirely on morphological data. A complete phylogenetic analysis is provided for representatives of all Doradidae genera, including 77 described and six undescribed species. This analysis is based on fragments of the mitochondrial *16s* and *cytochrome c oxidase subunit 1* (*co1*) and the *recombination activating subunit 1 gene* (*rag1*). We obtained an aligment of 3011 base pairs for 146 specimens of Doradidae and the outgroup Auchenipteridae and Aspredinidae. Data were analysed using Maximum Parsimony, Maximum Likelihood, and Bayesian analyses. The analysis of the molecular data uncovered newly hypothesized relationships. Astrodoradinae is recovered as the most basal clade of the family. The monotypic *Wertheimeria*, *Franciscodoras*, and *Kalyptodoras*, endemic to the east-coast drainages of Brazil, are recovered as a clade. The monotypic *Doraops* and *Centrochir*, endemic to TransAndean drainages, are recovered as sister to widely distributed *Pterodoras* and *Platydoras* respectively. The Doradidae with fimbriate barbels are recovered as a monophyletic group and not as sister to *Oxydoras*. The recently described *Ossancora* is not recovered as a monophyletic group.

KEY WORDS

Systematics, Catfish, *rag1*, *16s*, *co1*.

INTRODUCTION

Doradidae is a monophyletic catfish family endemic to South America that is often recognized by having a conspicuous row of midlateral scutes, each usually bearing a medial retrorse thorn. Doradidae is promptly diagnosed by a true synapomorphy, the presence of a infranuchal scute, that is unique among catfishes,. The infranuchal scute is a superficial plate-like bone co-formed by fusion of an expanded ossicle of the lateral line canal and an ossified ligament extending from beneath the posterior nuchal plate to the tip of the first rib.

Recent years have witnessed a surge in the descriptions of doradid taxa with the addition of 18 newly described species including one fossil and the validation of four nominal species, two new genera, and a subfamily raising the total diversity of the family to 92 species in 32 genera.

Phylogenetic studies of doradids have traditionally been based on morphological characters and only one work has been based on molecular characters which conflicts with previous morphological results. Higuchi (1992), Sabaj (2002) Birindelli (2006), Birindelli (2010), and Sousa (2010) used morphological data to establish the phylogenetic relations of the family. To date, only Moyer *et al.* (2004) used molecular data (*12s* and *16s* rRNA mitochondrial genes and *elongation factor 1 alpha* nuclear gene). Moyer *et al* included 23 genera in their study but they did not include the basal-most taxa (*Wertheimeria*, *Kalyptodoras*, and *Franciscodoras*) recovered from Higuchi's analysis. Moyer *et al.*'s phylogenetic analysis yielded strong support for the monophyly of Doradidae and subfamily Astrodoradinae, but otherwise showed significant conflict with Higuchi's morphological results including a lack of support for the monophyly of subfamily Platydoradinae, and tribes Centrochirini and Doradini.

In this paper we report the results of a phylogenetic analysis using Maximum Parsimony, Maximum Likelihood, and Bayesian analysis of a large dataset of nuclear and mitochondrial gene sequences.

This study represents the most comprehensive molecular data set assembled for Doradidae in which all genera and nearly all species are represented. Our dataset includes 3011 aligned bases of the *recombination activating subunit 1 gene* (*rag1*), *cytochrome c oxidase subunit 1* (*co1*) and

16s for 77 described and six undescribed species of Doradidae. We seek to establish a phylogenetic foundation for future total evidence analyses in preparation by the authors.

MATERIAL AND METHODS

Taxon Sampling

The main goal of this study is to produce a phylogenetic hypothesis for the catfish family Doradidae. Sequence data were gathered for one nuclear gene (*recombination activating subunit 1 gene*) and two mitochondrial genes (*cytochrome c oxidase subunit 1* and ribosomal *16s*) in a total of 133 specimens, of Doradidae, representing all 32 genera, 77 of 92 formally described species, and six undescribed species. Of the described species included, 80% are represented by more than one specimen. To date, this study represents the most comprehensive sampling of Doradidae for molecular phylogenetic analysis.

Following previous molecular (e.g., Moyer *et al.* 2004) and morphological authors, we included 10 species of Auchenipteridae and five species of Aspredinidae as outgroups. Using nuclear markers (*rag1* and *rag2*) Sullivan *et al.* (2006) recovered Auchenipteridae as the sister group to Doradidae, and also recovered the clade (((Doradidae) Auchenipteridae) Aspredinidae). Birindelli (2010), in a complete phylogenetic analysis based on morphology, found Auchenipteridae as the sister group to Doradidae, forming the superfamily Doradoidea. Friel (1994), in his unpublished thesis, described shared derived features suggesting that aspredinids are most closely related to doradoids and African mochokids. Molecular studies, however, do not support a close relationship between the African family Mochokidae and Neotropical catfishes. In fact, molecular evidence (Sullivan et al. 2006) places Mochokidae sister to Malapteruruidae + Amphiliidae in a clade composed exclusively of African catfish families (“Big Africa”). For this reason, the family Mochokidae is not included in the present analysis. Appendix 1 details the specimens.

Marker Selection

The *recombination activation subunit 1 gene* (*rag1*) is commonly used for the reconstruction of molecular phylogenies of vertebrates, and was used in the largest study to date of catfishes (Sullivan *et al.* 2006). *Cytochrome c oxidase subunit 1* (*co1*) exhibits a greater range of phylogenetic signal than any other mitochondrial gene (Hebert *et al,* 2003). In common with other protein- coding genes, its third-position nucleotides show a high incidence of base substitutions, leading to a rate of molecular evolution that is about three times greater than that of *12s* or *16s* rDNA (Knowlton & Weigt 1998). *16s* is a mitochondrial gene that codes for an rRNA that constituted the small subunit of the ribosoma and due to its fast evolution rate it has been widely used in species phylogenies. Moyer *et al.* (2004) used the *16s* gene in their molecular study of Doradidae, and several of their sequences are available on Genbank.

DNA Amplification and Sequencing

DNA was extracted using the Quiagen DNeasy blood and tissue kit. PCR reactions were carried out in 20 µl reactions. For *co1* and *16s*, the PCR reaction mixture consisted of 10 µl of Apex Taq DNA Polymerase Master Mix, 1.5 mM $MgCl_2$ (Genesee Scientific), 0,5µM of forward and reverse primer, 5 to 8 µl of distilled water and 4 to 1 µl of DNA template respectively. The PCR reaction for *co1* and *16s* consisted on an initial denaturation step of 4min at 95°C followed by 10 cycles of 95°C for 1min, annealing at 50-55°C for 30s, and extension at 72°C for 2min (the anneling temperature decreased after the first cycle by 1°C in each cycle). The process is followed by 30 cycles of 95°C for 1min, annealing at 40-44°C for 30s, and extension at 72°C for 2min. This was followed by a final 10 min at 72°C extension step. For *rag1* we followed the protocol of Sullivan *et. al* (2006). The PCR reaction for *rag1* consisted on an initial denaturation step of 4min at 95°C followed by 35 cycles of 95°C for 30s, annealing at 55–59°C for 30s, and extension at 72°C for 2min. This was followed by a final 4min at 72°C extension step. Primers for amplification and sequencing are listed on table 1

Sequences were edited and combined into cotings for each fragment using Sequencher 4.7 (GeneCodes Corporation, Ann Arbor, MI).

Gene	Primer Name	Primer	Reference
Rag1(5’)	F74	TTT CGG AAT GGA AGT TTA AGC TsT TTC G	Sullivan *et al.*(2006)
Rag1(5’)	R1333	GTC AAA CAC ACA GAC TTC ACA TC	Sullivan *et al.*(2006)
Rag1(5’)	F354	CAG AGC ATG AGG TvC AGG GAG ATC T	Sullivan *et al.*(2006)
Rag1(5’)	R798	TGA GTT ATA TTC TTT ACC CA	Sullivan *et al.*(2006)
Rag1(5’)	F89I*	TTT AAG CTG TTT CGA GTT CGT TCA TTG G	Sullivan *et al.*(2006)
Co1	LCO1490	GGT CAA CAA ATC ATA AAG ATA TTG G	Folmer *et al.*(1994)
Co1	HCO2198	TAA ACT TCA GGG TGA CCA AAA AAT CA	Folmer *et al.*(1994)
16s	16s BR	CCG GTC TGA ACT CAG ATC ACG T	Palumbi *et al.* (1991)
16s	16s AR	CGC CTG TTT ATC AAA AAC AT	Palumbi *et al.* (1991)

Table 1. Primers for amplification and sequencing of the DNA fragments. *Alternative amplification primer for the first forward fragment of *rag1*.

Sequence Alignment

Sequences for each gene were aligned using MUSCLE 3.7 (Edgar, 2004) with default parameters. The alignments were refined manually in MacClade 4.0 (Maddison and Maddison, 2000). We combined sequences from all three fragments into a single dataset. In addition to those gathered in this study, sequence data were incorporated from Genbank and from the personal archive of J.P. Sullivan (i.e., *Ageneiosus ucayalensis*, *Centromochlus heckeli*, *Trachelyopterus galeatus*, *Bunocephalus verrucosus*, and *Micromyzon akamai* for *rag1*, *co1*, and *16s*).

Phylogenetic Analysis

We analyzed nuclear and mitochondrial data combined and separate using Maximum Parsimony (MP), Maximum Likelihood (ML), and Bayesian. The concatenated data matrix was divided into eight partitions: one for 16s, one for each nucleotide position per codon of *co1*, one for each nucleotide position per codon of *rag1*, and one for the *rag1* intron. The data were concatenated using Mesquite 2.74 (Maddison & Maddison, 1997).

For each method (MP, ML, Bayesian) a total of five topologies were produced based on the following sequence data: 1) *rag1* only for all specimens, 2) *16s* only for all specimens, 3) *co1* only for all specimens, 4) combined *rag1*, *16s* and *co1* for all specimens, and 5) combined *rag1*, *16s* and *co1* restricted to specimens represented by sequence data for at least two loci (i.e., taxa represented by only one locus excluded). Trees based on sequence data for all specimens are represented by 196 terminals, whereas those based on specimens represented by at least two loci comprise 146 terminals. All the resultan topologies for this analysis are presented in appendix 2.

For Maximum Parsimony the trees were generated using the new technologies search implemented in TNT (Goloboff *et al.*, 2008). The search was performed in two steps: the first step used a combination of sectorial searches (RSS and CSS), 100 iterations of ratchet, 100 cycles of tree fusing, and 100 rounds of Drift. The driven was set to reach the minimum length 50 times. The second step used the trees produced in the first step to perform a traditional TBR search. We treated gaps as missing data, and we considered all the characters to have the same weight. For nodal support, we calculated absolute Bremer (Bremer, 1998), relative Bremer, and 1000 resamples for Jacknife. All the support values were plotted on the strict consensus tree.

Maximum Likelihood (ML) analyses were conducted using RAxML7.2.8 (Stamatakis, 2006) based on 1000 replicates under the GTR + GAMMA model. Nodal support was evaluated with 1000 non-parametric bootstrap pseudoreplicates.

Bayesian analyses were conducted using MrBayes 3.1.2 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003), with data partitioned as in the ML analyses. In order to make the trees comparable, we set the model for all partitions to GTR + Gamma. We ran three heated chains and one cold chain from 60 million generations sampling every 10000th generation. To ensure sampling of the posterior distribution, a burn-in period for all analyses was diagnosed in two ways. First, by the average standard deviation of split frequencies between two MCMCMC analyses run independently, with levels below 0.01 being considered indicative of convergence. Second, via direct visualization of split frequencies throughout the course of each analysis using the cumulative plotting feature of the on-line application AWTY (Wilgenbusch *et al,* 2004) with burn-in being diagnosed as the point after which split frequencies for the 20 most variable nodes have achieved stable values. Both analyses converged around 10-20 million generations, so we set the burn-in to be 30 million.

RESULTS

Dataset characteristics

The *rag1* dataset included 132 terminals (i.e., specimens) and 1807 bp, of which 566 were parsimony-informative. The 16s dataset included 187 terminals and 578 bp, of which 175 were parsimony-informative. The *co1* dataset included 145 terminals and 626 bp, of which 254 were parsimony-informative. The combined dataset (*rag1*, *16s* and *co1*) for all 196 terminals included 3011 bp, of which 995 characters are parsimony informative. The combined dataset for 146 terminals (i.e., those represented by at least 2 loci) included 3011 bp of which 995 characters are parsimony-informative.

Phylogenetic results

Trees generated from the two combined datasets (i.e., all terminals and restricted terminals) using the three different methodologies (MP, ML, Bayesian) recovered similar relationships. Results presented and discussed below are based on the MP analysis of the combined dataset for restricted terminals which recovered 36 most parsimonious trees, each with 6509 steps (fig. 1). By comparison, the MP analysis of the combined dataset for all terminals recovered more than 50,000 trees of 6764 steps. In the analysis of all terminals, the inclusion of multiple conspecific specimens with incomplete sequence data leads to the recovery of several short branches (i.e., the number of short branches with little support increased tremendously the total number of trees recovered). As a result, the consensus tree for all terminals includes many polytomies; its topology is less resolved but remains consistent with that of the analysis of restricted terminals.

Topologies resulting from the ML (fig. 2) and Bayesian (fig. 3) analyses of the restricted-terminals dataset were used for comparison. The Maximum Likelihood analysis of the restricted-terminal dataset produced a best tree with a likelihood of –35155.341412 (compared to –36442.4528 for the all terminal dataset). The majority of clades supported by the MP analysis were also recovered in the ML and Bayesian analyses. For each clade supported by all three analyses, we provide the Bremer support (BS), Maximum Parsimony Jacknife (MPJ), Bayesian posterior probability (BPP), and Maximum Likelihoood Bootstrap (MLBS).

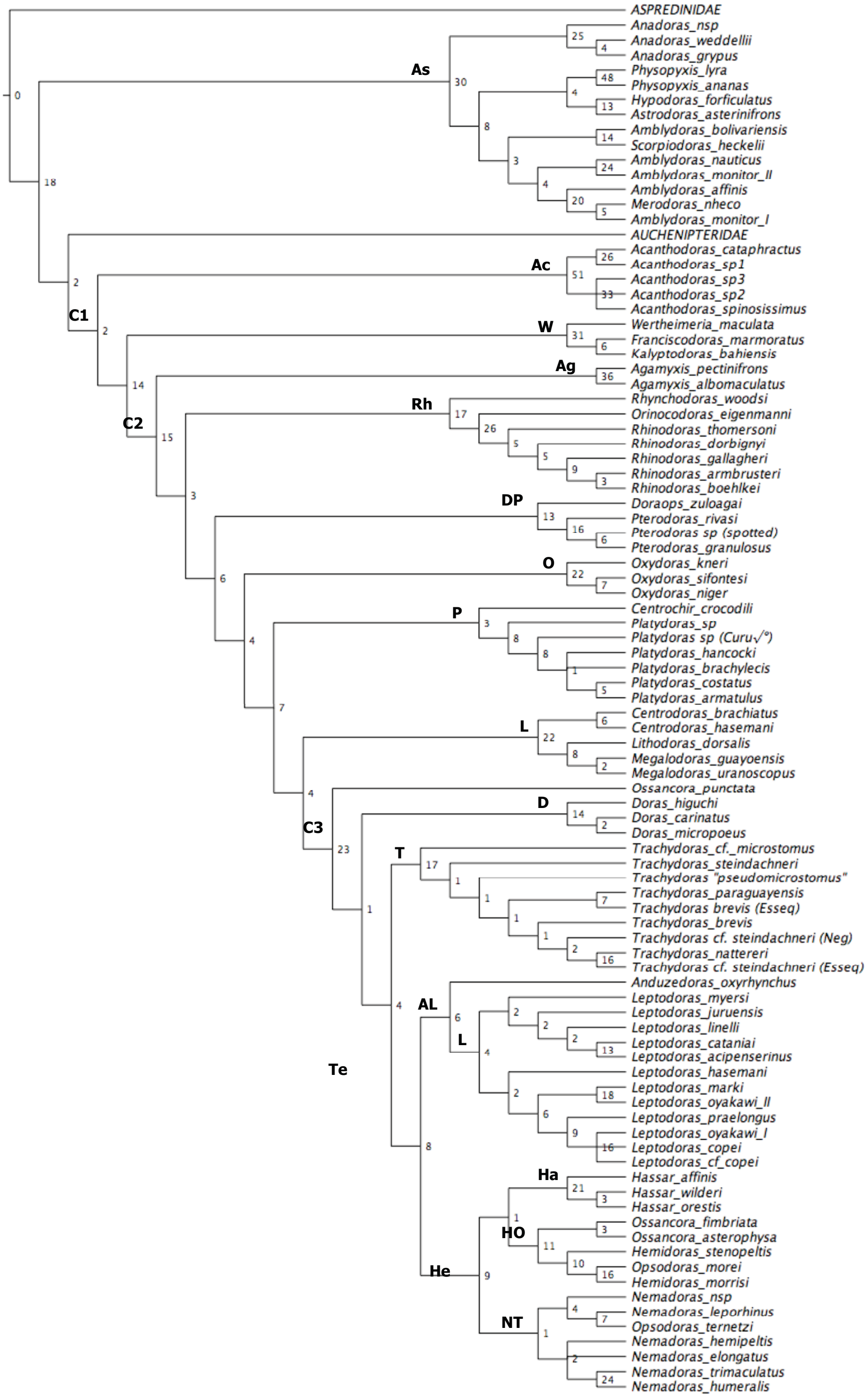

Figure 1. Strict consensus phylogram of the 36 shortest tress from Maximum Parsimony analysis of the combined nuclear and mitochondrial sequences (restricted terminals). Node values correspond to Bremer support.

Node labels: As = subfamily astrodoradinae, C1 = clade 1, Ac = *Acanthodoras*, W = *Wertheimeria* clade, C2 = clade 2, Ag = *Agamyxis*, Rh = rhinodoradini tribe, DP = *Doraops* + *Pterodoras* clade, O = *Oxydoras*, P = subfamily platydoradinae, L = *Lithodoras* clade, C3 = clade 3, D = *Doras*, T = *Trachydoras*, AL = *Anduzedoras* + *Leptodoras* clade, L = *Leptodoras* clade, He = *Hemidoras* clade, HO = *Hemidoras* + *Ossancora* clade, NT = *Nemadoras* + *"Tenellus"* cladeTe = "*Tenellus*"

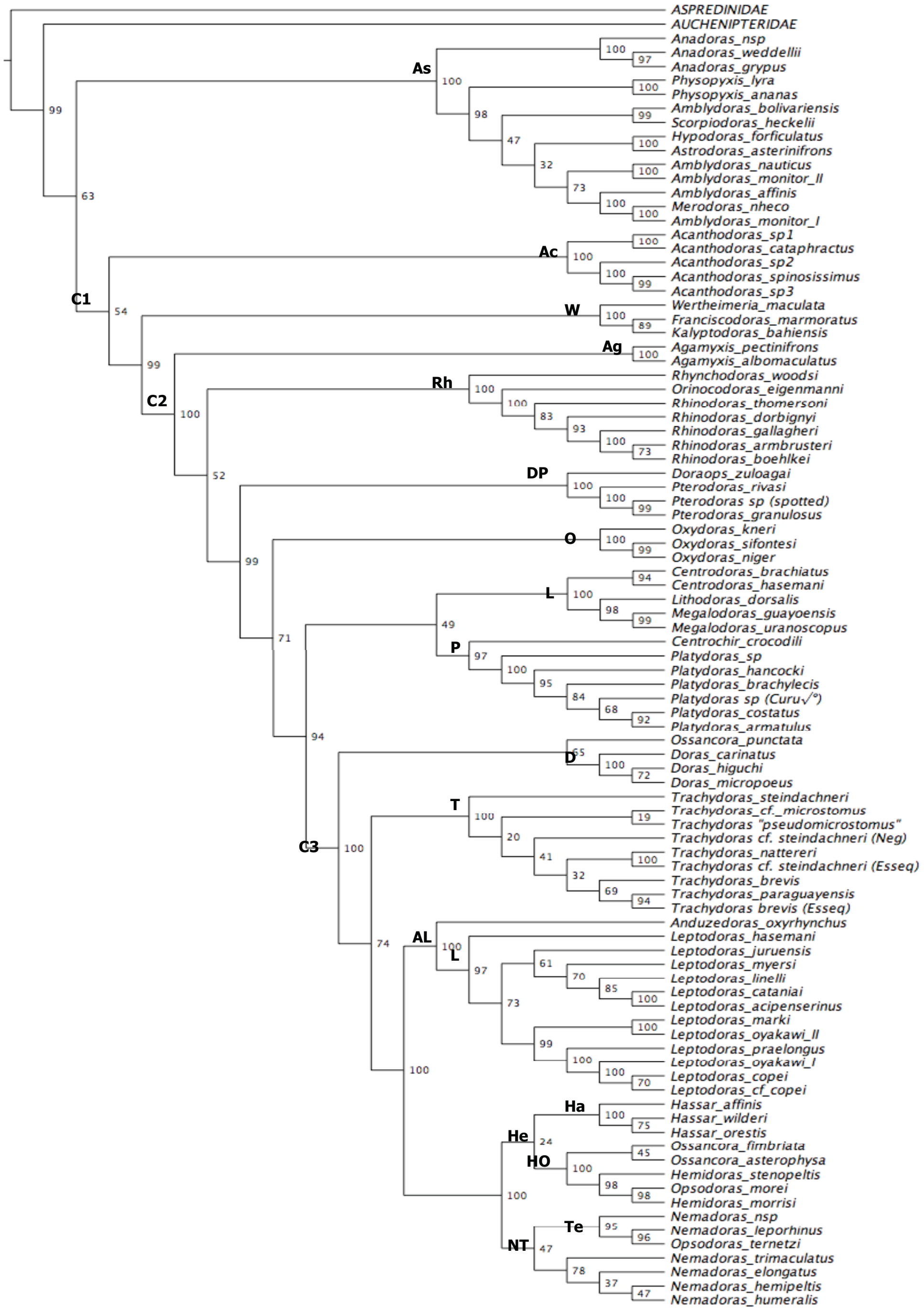

Figure 2. Phylogram obtained by the Maximum Likelihood analysis of the combined nuclear and mitochondrial dataset (restricted terminals). Node values correspond to Bootstrap support values.

Node labels: As = subfamily astrodoradinae, C1 = clade 1, Ac = *Acanthodoras*, W = *Wertheimeria* clade, C2 = clade 2, Ag = *Agamyxis*, Rh = rhinodoradini tribe, DP = *Doraops + Pterodoras* clade, O = *Oxydoras*, P = subfamily platydoradinae, L = *Lithodoras* clade, C3 = clade 3, D = *Doras*, T = *Trachydoras*, AL = *Anduzedoras + Leptodoras* clade, L = *Leptodoras* clade, He = *Hemidoras* clade, HO = *Hemidoras + Ossancora* clade, NT = *Nemadoras + "Tenellus"* cladeTe = "*Tenellus*"

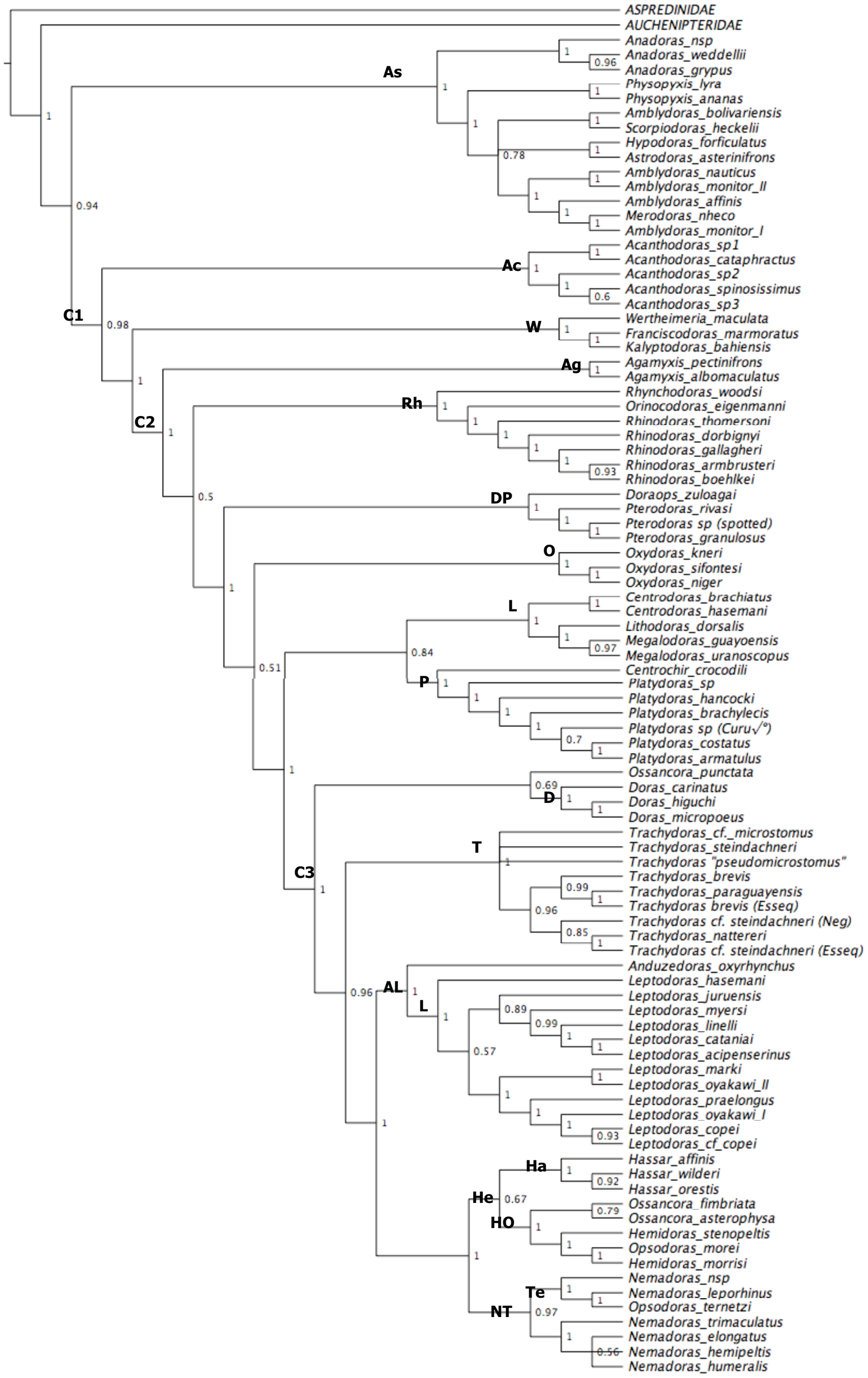

Figure 3. Phylogram obtained by the Bayesian analysis of the combined nuclear and mitochondrial dataset (restricted terminals). Node values correspond to posterior probability values.

Node labels: As = subfamily astrodoradinae, C1 = clade 1, Ac = *Acanthodoras*, W = *Wertheimeria* clade, C2 = clade 2, Ag = *Agamyxis*, Rh = rhinodoradini tribe, DP = *Doraops* + *Pterodoras* clade, O = *Oxydoras*, P = subfamily platydoradinae, L = *Lithodoras* clade, C3 = clade 3, D = *Doras*, T = *Trachydoras*, AL = *Anduzedoras* + *Leptodoras* clade, L = *Leptodoras* clade, He = *Hemidoras* clade, HO = *Hemidoras* + *Ossancora* clade, NT = *Nemadoras* + *"Tenellus"* cladeTe = "*Tenellus*"

Doradid clades strongly supported by all three analyses (MP, ML, Bayesian)

Subfamily *Astrodoradinae* sensu Higuchi et al. 2007

A clade composed of *Amblydoras, Anadoras, Astrodoras, Hypodoras, Merodoras, Physopyxis,* and *Scorpiodoras* is strongly supported with BS = 30, BPP = 1, and MLBS = 100. *Anadoras* is recovered at the base of this clade with strong support (MLBS = 98) for grouping the remaining taxa.

Acanthodoras

Members of the genus *Acanthodoras* (represented by one of three valid nominal species and two undescribed species) are recovered as monophyletic with strong support: BS = 51, MPJ = 100, BPP = 1, and MLBS = 100.

Clade 1

A clade composed by all doradids except subfamily Astrodoradinae and *Acanthodoras* is recovered with strong support: BS = 14, MPJ = 99, BPP = 1, and MLBS = 89.

Wertheimeria clade

The clade (*Wertheimera* (*Franciscodoras, Kalyptodoras*)) is recovered in all the topologies as the base of clade 1. The clade is strongly supported with BS = 31, MPJ = 100, BPP = 1, and MLBS = 100.

Clade 2

A clade composed by *Agamyxis*, tribe Rhinodoradini, Platydoradinae, members of the Pterodoradini, *Oxydoras*, and fimbriated-barbel doradids is recovered. *Agamyxis* is recovered at the base of this clade, and although the members of the Pterodoradini are recovered in this clade, they are not grouped together. The clade is strongly supported with BS = 15, MPJ = 97, BPP = 1, and MLBS = 100.

Agamyxis

A reciprocally monophyletic clade formed by the two nominal valid species of *Agamyxis, A. pectinifrons* and *A. albomaculatus,* is recovered in all topologies. The clade is supported with BS = 36, MPJ = 100, BPP = 1, and MLBS = 100.

Tribe Rhinodoradini sensu Birindelli (in press)

The clade (*Rhynchodoras* (*Orinocodoras*, *Rhinodoras*) is supported with BS = 17, MPJ = 100, BPP = 1, and MLBS = 100.

Doraops + Pterodoras

Monotypic *Doraops zuolagai* is recovered as sister to a clade composed of *Pterodoras granulosus* and *Pterodoras rivasi.* The clade is supported with BS = 13, MPJ = 99, BPP = 1, and MLBS = 100.

Oxydoras

The three nominal valid species of *Oxydoras* group together as (*O. kneri* (*O. niger*, *O. sifontesi*)). The clade is supported with BS = 22, MPJ = 100, BPP = 1, and MLBS = 100.

Subfamily Platydoradinae sensu Birindelli (in press.)

Monotypic *Centrochir crocodili* is recovered as sister to a clade composed of the four nominal valid species of *Platydoras* plus two additional undescribed species. The clade is supported with BS = 3, MPJ = 44, BPP = 1, and MLBS = 96.

Lithodoras clade

Clade composed of *Centrodoras* (two nominal valid species) sister to *Lithodoras* (monotypic) + *Megalodoras* (two nominal valid species). The clade is supported with BS = 22, MPJ = 100, BPP = 1, and MLBS = 100.

Clade 3

All doradid species sharing fimbriate barbels (uniquely derived in Doradidae) form a monophyletic clade supported with BS = 23, MPJ = 100, BPP = 1, and MLBS = 98.

Doras

The genus *Doras* is recovered as monophyletic although two (*D. phlyzakion* and *D. zuanoni*) of the five nominal valid extant species were not included in the analyses. The clade is supported with BS = 14, MPJ = 100, BPP = 1, and MLBS = 100.

Trachydoras

The genus *Trachydoras* is recovered as monophyletic and is represented by all five nominal valid species plus several undescribed. The clade is supported with BS = 17, MPJ = 100, BPP = 1, and MLBS = 100.

Anduzedoras + Leptodoras clade

Monotypic *Anduzedoras* is recovered sister to *Leptodoras* represented by 10 of 12 nominal valid species. The clade is supported with BS = 6, MPJ = 93, BPP = 1, and MLBS = 100.

Leptodoras

The genus Leptodoras is recovered as monophyletic although two (*L. nelsoni* and *L. rogersae*) of the 12 nominal valid species were not included in the analyses. The clade is supported with BS = 4, MPJ = 68, BPP = 1, and MLBS = 97.

Hemidoras clade

The *Hemidoras* clade is composed of *Hassar* (represented by three of four nominal valid species), *Hemidoras* (three of four or five nominal valid species), *Nemadoras* (three of three nomial valid species), *Ossancora* (two of four valid nominal species), and "*Tenellus*" (three of three valid nominal species plus one undescribed). Although one species of *Ossancora* (*O. eigenmanni*) was not analyzed, a second species (*O. punctata*) was included, but recovered near the base of the tribe Doradini (minus *Oxydoras*), either in a clade as sister to *Doras* or as the sister to a clade of all other doradids with fimbriate barbels. The clade is supported with BS = 10, MPJ = 57 , BPP = 98, and MLBS = 1.

Hemidoras + Ossancora (minus *O. punctata*) clade

Two of the three species of *Ossancora* analyzed (*O. fimbriatus* and *O. asterophysa*) group together in a clade sister to one composed of three species of *Hemidoras*. The clade is supported with BS = 11, MPJ = 99, BPP = 1, and MLBS = 100.

"Tenellus"

Of the three nominal species assigned to the genus *Tenellus* recently described by Birindelli (in press.), two (*T. leporhinus*, *T. ternetzi*) plus one undescribed form a well-supported monophyletic group. The clade is supported with BS = 4, BPP = 1, and MLBS = 95.

DISCUSSION

Monophyly of Doradidae

The Bayesian analysis recovered Doradidae as monophyletic with high support (posterior probability 0.94). ML also recovered Doradidae as monophyletic, but with moderate support (bootstrap value 63). MP recovered Doradidae as paraphyletic with the Astrodoradinae sister to Auchenipteridae + clade of remaining doradids. However, support for the sister group relationship between Auchenipteridae and non-astrodoradins is extremely low (Bremer support value 2), and in the separate MP analysis of complete dataset with unrestricted taxa this relationship collapses into a polytomy with Astrodoradinae.

The monophyly of Doradidae is strongly supported by phylogenetic analyses of morphological data. Higuchi (1992) proposed three synapomorphies for the family: tympanic area connected to Müllerian ramus of parapophysis of fourth vertebra by a strong ligament and delimited by supracleithrum, postoccipital process, infranuchal plate and humeral process of cleithrum; presence of at least two ossified lateral plates in the postcranial region, one articulating with posterior nuchal plate and first pleural rib; and reduction or absence of middle posterodorsal process of cleithrum, between the articular and humeral processes. Birindelli (2010, in press.) reevaluated Higuchi's synapomorphies within a broader analysis of the superfamily Doradoidea, and rediagnosed Doradidae on the basis of three synapomorphies: presence of the infranuchal scute, the laminar expansion of the lateral line ossicles, and by the presence of the Müllerian ligament between Müllerian ramus and lateral line. Given the strong morphological evidence, we do not dispute the monophyly of Doradidae based on the MP analysis.

Doradid clades

The Astrodoradinae is recovered as the monophyletic sister group to all the other doradids (bootstrap value 61, posterior probability of 0.94). Based on morphology, Higuchi (1992) and Birindelli (2006) recovered the monotypic *Wertheimeria* as basal-most taxon sister to a clade of all other doradids. Their analysis used *Wertheimeria* as the root, which does not allow for testing the real position of the taxon. In an expanded phylogenetic study of the Doradoidea, Birindelli (2010) recovered *Wertheimeria* + *Kalyptodoras* as the most basal clade of Doradidae.

Subfamily *Astrodoradinae*

The monophyly of Astrodoradinae (sensu Higuchi et al. 2007) is strongly supported by all analyses (Bremer support value 30, relative Bremer support 47, bootstrap value 100, posterior probability of 1). Higuchi (1992) and Higuchi et al. (2007) proposed Astrodoradinae for seven genera: *Amblydoras*, *Anadoras*, *Astrodoras*, *Hypodoras*, *Merodoras*, *Physopyxis*, and *Scorpiodoras*. Sousa (2010) and Birindelli (2010) subsequently presented morphological evidence for including *Acanthodoras* and *Agamyxis* as sister taxa within Astrodoradinae. Sousa, the more complete of the two studies, listed seven non-exclusive synapomorphies for Astrodoradinae inclusive of *Acanthodoras* + *Agamyxis*. Moyer et al. (2004) found no molecular evidence for a close relationship between Astrodoradinae (represented by four genera in his analysis) and *Agamyxis*. They did recover *Acanthodoras* within a clade composed astrodoradins based on a phylogenetic analysis of nuclear gene EF1 alpha, but with low support (ML boostrap value 50, MP bootstrap value <50). Their analysis of the combined dataset (EF1, 12s and 16s) placed *Acanthodoras* and Astrodoradinae as successive sister-groups to all other doradids.

Within Astrodoradinae (excluding *Acanthodoras* and *Agamyxis*), several relationships proposed by Sousa (2010) are consistent with the present study (e.g., *Anadoras* is the basal most taxon, and *Hypodoras* and *Astrodoras* are sister groups). Unlike Sousa (2010), *Amblydoras bolivarensis* was recovered as sister to *Scorpiodoras heckelii*, and *Physopyxis* is not closely related to *Amblydoras*, but is sister to all other astrodoradins except *Anadoras*. Both the current study and that of Sousa agree on the synonymization of *Merodoras* with *Amblydoras*.

Clade 1

The present study found weak support for a sister group relationship between *Acanthodoras* and a clade of all remaining non-astrodoradin taxa (BS = 2, MPJ = 5, BPP = 0.98, and MLBS = 54).More convincing is the support for the clade composed of all doradids except Astrodoradinae and *Acanthodoras* (BS = 14, MPJ = 99, BPP = 1, and MLBS = 89).

Wertheimeria clade

Wertheimeria is the sister group to *Franciscodoras* + *Kalyptodoras.* Birindelli (2010) found evidence of the sister group relationship between *Wertheimeria* and *Kalyptodoras,* and recovered this clade at the base of Doradidae, sister to *Franciscodoras* + all other doradids. However, in the diagnosis of the *Wertheimeria,* Birindelli (2010) included some characteristics that are shared with *Kalyptodoras* and *Franciscodoras.* He mentioned that the seventh vertebra is not fused to the complex vertebrae, the posterodorsal process of the cleithrum is well developed, and the pelvic fin has six branched rays.

Wertheimeria, Franciscodoras, and *Kalyptodoras* are monotypic genera endemic to the coastal drainages of eastern Brazilian. Based on phylogenetic relationships available at the time, Stiassny and de Pinna (1994) and Ribeiro (2006) considered monotypic *Wertheimeria* exemplary of a depauperate basal lineage with a restricted geographical range and a highly diverse sister group. Ribeiro designated Pattern A for cases where the depauperate basal lineage inhabits coastal drainages of eastern Brazil. Based on the results of our analysis, the *Wertheimeria* clade more closely matches Riberio's Pattern B wherein the basal (or in this case, subbasal) lineage underwent some subsequent radiation (in this case, into three monotypic, yet closely related genera).

Tribe Rhinodoradini

Tribe "Rhinodoradini" is a clade consisting of *Rhynchodoras* as sister to *Orinocodoras* + *Rhinodoras*. Birindelli (2006) first recognized this clade as a tribe. Higuchi (1992) and Moyer et al.(2004) did not include material of *Rhynchodoras* in their studies. Although both recovered *Orinocodoras* as a sister group to *Rhinodoras,* and Higuchi suggested a possible relationship of that clade with *Rhynchodoras.* Birindelli (2010) found five synapomorphies for the clade. The study of the cranial musculature of Doradidae (Arce, in prep) shows similarities of the muscle configuration for the three genera and the existence of an additional synapomorphy for the tribe. In *Rhinodoras, Orinocodoras,* and *Rhynchodoras,* the *extensor tentaculi* is inserted ventrally on the autopalatine versus dorsally inserted in all the other doradids.

Doraops + Pterodoras

Doraops and *Pterodoras* form a clade. Moyer *et al.*(2004) and Birindelli (2006) previously recovered the relationship between *Doraops* and *Pterodoras.* These two genera share a unique morphological characteristic; both genera have a paired elongated diverticulum curving anteromedially from the shoulder of the anterior chamber on their swimbladder (Birindelli *et al,* 2009).

Doraops is endemic to the Maracaibo basin, while *Pterodoras* is widely distributed in the Orinoco, Amazon, and Parana-Paraguay basins. Fossils of *Doraops* are present on the Urumaco formation establishing the minimum age of divergence of these two genera at about 8 Ma. This relationship between *Pterodoras* and *Doraops* supports the persistence of related lineages in the Trans-Andean (Maracaibo) and Cis-Andean (Orinoco, Amazon, Parana-Paraguay) basins (Sabaj-Perez *et al,* 2007).

Doraops + *Pterodoras* clade is not recovered as a sister to the clade formed by *Centrodoras, Lithodoras* and *Megalodoras.* Both Higuchi (1992) and Birindelli (2006 and 2010) coincide on a clade formed by these five species. The relationships between the species vary depending on the study. Higuchi (1992) found ((*Pterodoras* (*Centrodoras*, *Megalodoras*))(*Lithodoras*, *Doraops*)) and Birindelli (2010) found ((*Centrodoras*, *Megalodoras*)(*Doraops* (*Lithodoras*, *Pterodoras*)). Our study recovers these five species as two not consecutive clades; in the first clade, *Doraops* and *Pterodoras* are sister; in the second clade, *Centrodoras* is sister to *Lithodoras* + *Megalodoras.* Moyer *et al.*(2004) found the same arrangement for the five species.

Oxydoras

The three valid species of *Oxydoras* formed a monophyletic group. Previous morphological studies (Higuchi, 1992 and Birindelli, 2010) suggested that *O. sifontesis* and *O. niger* should be synonyms. Molecular data recovered the two species in a well-supported clade corroborating the morphological statement.

The genus *Oxydoras* is not recovered as sister to fimbriate-barbel doradids. The morphological evidence provided by Higuchi (1992) and Birindelli (2006 and 2010) pointed to *Oxydoras* as the sister group to fimbriate barbels. Birindelli (2010) stated that *Oxydoras* plus the doradids with fimbiate barbels is one of the clades supported by more sinapomorphies. The molecular evidence on our study, as well as on Moyer *et al.*(2004), does not support this claim. Some of the synapomorphies listed by Birindelli (2010) to group *Oxydoras* and fimbriate barbel doradids, can be the result of body shape convergences. *Oxydoras* is the only long-snouted doradid with simple barbels. The common shape of the snout can result in a similar shape of mesethmoid and premaxila. Also the same type of snout will lead to related feeding strategies and in consequence to similar teeth and branquial structures.

Subfamily *Platydoradinae* sensu Birindelli (in press.)

Centrochir and *Platydoras* are sister groups. Sousa (2010) also recovered these two genera in a clade. He found that *Centrochir* and *Platydoras* present a posterodorsal crest on the infraorbital one. He stated that this characteristic constituted a non-exclusive synapomorphy that is also present in Astrodoradinae, except in *Anadoras.* Birindelli (2010) did not find resolution for this clade, but he included the two genera in a subfamily named “Platydoradinae”.

Centrochir is endemic to the Magdalena River, while *Platydoras* is widely distributed in the Orinoco, Amazon, and Parana-Paraguay basins. This clade constitutes another example of the persistence of related lineages on the trans-Andean and cis-Andean basins.

Lithodoras clade

Molecular data revealed the relationship of *Lithodoras* sister to *Megalodoras*. Morphological data recognized *Centrodoras* and *Megalodoras* forming a clade that is sister to *Lithodoras Pterodoras* and *Doraops* (Higuchi, 1992 and Birindelli, 2006 and 2010).

The position of the clade formed by *Centrodoras*, *Lithodoras*, and *Megalodoras* is variable. Under MP ((*Centrodoras* (*Lithodoras*, *Megalodoras*)) constitutes the sister group to all doradids with fimbriate barbels. Under Bayes and ML, the clade ((*Centrodoras* (*Lithodoras*, *Megalodoras*))(*Platydoras*, *Centrochir*)) is the sister to the doradids with fimbriate barbels.

Clade 3

The doradids with fimbriate barbels constitute a monophyletic clade. Morphological characters strongly supported a clade formed by the doradids with fimbriate barbels (Higuchi, 1992 and Birindelli, 2006 and 2010). This result is also consistent with the molecular data of Moyer *et al.*(2004). They found the clade to be supported by a 100% of the posterior probability of Bayes and 100% of the bootstrap replicas under ML and MP.

Ossancora

The genus *Ossancora* was recovered as a paraphyletic group. *Ossancora* is a genus recently described by Birindelli & Sabaj Perez (2011) to group the species that were placed by Higuchi (1992) in his "*Petalodoras*" genus. The entire genus is diagnosed by the combination of the following: barbels with smooth elongated fimbriae, teeth present on the dentary and premaxilla, posterior cranial fontanel occluded, and posterior coracoid process approximately as long as posterior cleithral process.

Ossancora is divided in our topology in two non-consecutive clades. The first clade, formed by two specimens of *O. punctata,* recovered at the base of the fimbriate barbel doradids. The second clade, formed by *O. asterophysa* and *O. fimbriata,* recovered together with *Hassar, Hemidoras,* and *Opsodoras.* On their recent description of the genus, Birindelli & Sabaj Perez (2011) recognized within the genus a clade, named *fimbriata* clade, formed by *Ossancora* *asterophysa*, *O. eigenmanni*, and *O. fimbriata.* The *fimbriata* clade is defined by a unique synapomorphy, the fimbriae inserted in two distinct rows, one dorsally and one ventrally.

Our study included three of the four valid species of *Ossancora.* The species belonging to the *fimbriata* clade are grouped together. The clades formed in the molecular topology could be explained by the lack of molecular information for the genus. Sequences for *O. eigenmanni* as well as *rag1* sequences for *O. punctata* were not included. The resolution of this genus will remain uncertain until more data can be generated.

Doras

Doras is found as a monophyletic group. We included three of the five valid species of the genus and we recovered *Doras higuchi* as the sister group to *D. carinatus* plus *D. micropoeus.* Sabaj Perez & Birindelli (2008) stated that the genus is separated in two groups. The monophyletic *phlyzakion* group composed of *D. phlyzakion* and *D. zuanoni*, and the *carinatus* group composed of *D. carinatus, D. micropoeus*, and *D. higuchii.* This hypothesis could not be tested due to the lack of material of *D. phlyzakion* and *D. zuanoni.*

The position of *Doras* is variable. Under MP, the genus is sister to all the other fimbriate-barbel doradids except *Ossancora punctata.* Under ML and Bayesian, *Doras* is sister to *Ossancora punctata.* The clade formed by *Doras* and *Ossancora* is the sister group to all the other fimbriate-barbel doradids. Morphological studies placed *Doras* as a more derived genus (fig). Moyer *et al.*(2004) recovered *Doras* as the most basal taxon of the doradids with fimbriate barbels.

Anduzedoras + Leptodoras

Anduzedoras and *Leptodoras* are sister groups. Higuchi (1992) was the first to establish this relationship. He mentioned that these two genera have a frontal concave and much narrower at interorbital, and an extremely developed bulging first vertebra. Following Higuchi's discovery, Sabaj (2002) included *Anduzedoras* in his revision and phylogeny of *Leptodoras*. He also found *Anduzedoras* as a sister group to *Leptodoras.* This clade is diagnosed by two synapomorphies, the development of a pair of conjoined bony capsules on the ventral surface of the anteriormost vertebrae (Birindelli *et al.*(2008), and the mental barbels basally connected to lower lip membrane (Birindelli, 2006; Biridelli & Sousa, 2010).

Leptodoras

The relationships between species of *Leptodoras* are not completely consistent with those recovered by Sabaj (2002). He established the phylogeny of *Leptodoras,* based on an analysis of thirty-five morphological characters for ten species of *Leptodoras*. Most of the characters analyzed by Sabaj corresponded to external morphology. Also two new species of *Leptodoras* were described after his study.

We found the *Leptodoras* clade to be subdivided into two clades. The first clade is comprised of *L. myersi*, *L. juruensis*, *L. linelli*, *L. cataniai*, and *L. acipenserinus.* The second clade groups together *L. marki*, *L. oyakawai*, *L. praelongus*, and *L. copei.* The position of *L. hasemani* is variable. Under MP, the species is recovered as the most basal taxon on the second clade. Using ML and Bayes, *L. hasemani* is the most basal taxon of the genus *Leptodoras.*

In the first clade, we recovered similar looking species that Sabaj (2002) recovered as the most derived *Leptodoras.* In these species the configuration of the neurocranium is similar, where the suture between the anterior nuchal plate and epioccipital is completely or partially replaced by an elongate formamen (Birindelli *et al,* 2008). Also the labial structures are similar in all the species of the clade except *L. linelli.*

In the second clade, we recovered species with variable swimbladder. In most *Leptodoras*, the gas bladder is greatly reduced with two distinct hornlike diverticula projecting form posterior walls of posterior chambers and a pair of bulbous diverticula projecting form each lateral wall of anterior chamber (Birindelli *et al*, 2008). *Leptodora oyakawai* and *L. marki* are known as the only *Leptodoras* in which the swimblader is not reduced. It is known that *L. praelongus* has a less modified gassbladder. The posterior chambers are relatively large, the posterior horns are relatively long, and the pair of anterolateral diverticula appear as large tuberous swellings with highly irregular surfaces (Sabaj 2005).

The species *Leptodoras oyakawai* was recovered as paraphyletic. Birindelli *et al*, (2008) mentioned that the dorsal fin pigmentation of *L. oyakawai* is variable and depends on the specimen's locality. Specimens from the Jamanxin (middle Tapajós) have a distinct dusky black triangular blotch on the base of the dorsal fin. In specimens from the Teles Pires (upper Tapajós) and upper Xingu, the dark pigment is limited to the proximal third of anterior margin of dorsal spine and the basal blotch is narrower, more faint, and sometimes absent (Birindelli *et al,* 2008). Our study had samples from the two localities and we found that the specimens from the Jamaxin (*L. oyakawai II*, *L. oyakawai III*) do not group together with specimens from the Teles Pires (*L. oyakawai I*). It is necessary the review and include more specimens from those localities as well as more specimens from related *Leptodoras* in order to establish the true identity of these morphospecies.

Hassar

The three valid species of *Hassar* formed a clade. *Hassar affinis* is sister to *H. wilderi* + *H. orestis.* The position of the clade is not consistent with findings of morphological phylogenies. Birindelli *et al.*(2011) established the relationship of *Hassar* with *Anduzedoras* plus *Leptodoras* based on four synapomorphies that are found as homoplastic characters also in *Doras.* Moyer *et al.*(2004) recovered *Hassar* as a sister group to *Nemadoras*, which is a sister group to *Hemidoras* plus *Opsodoras.*

Hemidoras

Our study recovers a clade of *Opsodoras morei* plus *Hemidoras morrisi* as sister to *Hemidoras stenopeltis.* This corroborates the results of Birindelli (2006 & 2010) and agrees with the sinonimyzation of *Opsodoras* and *Hemidoras*. Moyer *et al.*(2004) also found *Opsodoras* in a monophyletic clade with *Hemidoras,*

Nemadoras + *"Tenellus"* clade

All the described species of *Nemadoras,* one new species of the genus and *Opsodoras ternetzi* formed a clade. Morphological observations and comparison with other members of *Nemadoras,* plus the result of the molecular analysis allow us to infer that *Opsodoras ternetzi* is a synonym of *Nemadoras.*

Nemadoras is recovered as a monophyletic group where two clades can be differentiated. Birindelli (in press.) suggest that the genus *Nemadoras* should be restricted to *N. elongatus, N. hemipeltis*, and *N. humeralis.* He proposed that *N. trimaculatus*, *N. leporhinus*, and *N. ternetzi* should belong to a different "*Tenellus*". Our results do not agree with those of Birindelli. Molecular data differ from Birindelli on the placement of *Nemadoras trimaculatus.* Analysis of *rag1* partition under ML recovers the clades mentioned by Birindelli (2010).

The molecular data contributed substantially to the resolution of the Doradidae phylogeny and uncovered new relationships within the family. The astrodoradinae is recovered as the basal-most clade of the family. Newly hypothesized relationships are uncovered for the family with interesting biogeographic implications. For example, *Wertheimeria*, *Franciscodoras* and *Kalyptodoras*, three monotypic genera inhabiting separate Atlantic drainages along the easternmost coast of Brazil, are recovered in a monophyletic group near the base of the doradid tree. *Centrochir*, a monotypic genus endemic to the Magdalena, is sister to *Platydoras*, a widespread cis-Andean genus occurring throughout the Amazon, Orinoco, Paraná-Paraguay, and Atlantic coastal drainages. *Doraops*, a monotypic genus endemic to the Maracaibo basin, is sister to *Pterodoras*, another widespread cis-Andean genus.

Some of the results contradict morphological relationships. For example, *Acanthodoras* and *Agamyxis* do not form a clade and do not group with Astrodoradinae; morphological studies of Birindelli (2010) and Sousa (2010) recovered these two genera as part of Astrodoradinae. The clade *Centrodoras* + (*Lithodoras* + *Megalodoras*) is recovered as a sister group to the monophyletic fimbrate barbells doradids instead of *Oxydoras*, normally placed as sister group using morphological data (Higuchi, 1992 and Birindelli, 2006 and 2010). Species of the genus *Ossancora* do not form a monophyletic clade.

Additional effort employing molecular and morphological characters are needed to resolve uncertainities and to complete the taxon sample. For certain genera, such us *Trachydoras*, further study is need to evaluate cases of interbasin and cryptic differentation. Nomenclatural changes and new classification will be proposed after the addition of morphological evidence.

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Appendix 1. Material examined

Terminal taxon	Voucher	Tissue number	Field tag	Locality Country, basin	*RAG 1* bp	*CO1* bp	*16s* bp
Acanthodoras cataphractus I	ANSP 182251	637	P6060	Peru, Amazon			588
Acanthodoras sp1	ANSP 191096	2088	7602	Venezuela, Orinoco	1471	725	620
Acanthodoras sp2	ANSP 182240	788	V177	Venezuela, Orinoco	1453	611	601
Acanthodoras sp2	AUM 44128	2151	V5306	Venezuela, Orinoco	1481	690	613
Acanthodoras sp3	AUM 43737	2150	V5211	Venezuela, Orinoco	1325	678	602
Acanthodoras spinossissimus	LBP 4441	1786	24313	Brazil, Negro	1471	725	620
Agamyxis albomaculatus A	INHS 54563		288	Venezuela, Orinoco	1410	720	598
Agamyxis albomaculatus I	LBP 3036	1780	19176	Venezuela, Orinoco	1459	689	602
Agamyxis pectinifrons I	INHS 43281	2145	PERU 97-7	Peru, Amazon	1411	681	603
Agamyxis pectinifrons II	INHS 52017	2147	PERU 99-18	Peru, Amazon	1448	689	601
Agamyxis pectinifrons III	INHS 52017	2146		Peru, Amazon	1456	681	605
Amblydoras affinis	ANSP 179797	727	2157	Guyana, Essequibo	1376	682	592
Amblydoras bolivariensis	ANSP 182267	791	V183	Venzuela, Amazon	1428	721	590
Amblydoras monitor I	ANSP 191474	2092	078	Peru, Amazon	1362	721	620
Amblydoras monitor II	ANSP 191474	2093	155	Peru, Amazon	1367	719	622
Amblydoras nauticus I	ANSP 182525	671	6021	Peru, Amazon	1333	687	594
Anadoras grypus I	ANSP 179473	t2465		Peru, Amazon	1415	682	591
Anadoras nsp	MZUSP 89108			Brazil, Goiás	1460		617
Anadoras weddelli	MZUSP 103567		103567-49	Brazil, Pará	1294	720	619
Anduzedoras oxyrhynchus I	ANSP 180293			Venezuela, Orinoco	1405	641	
Anduzedoras oxyrhynchus III	ANSP 191093		VEN10-17	Venezuela, Amazon	1385	689	598
Astrodoras asterinifrons	INPA 24660	1532	ARI 68	Brazil, Madeira	1480	701	591
Astrodoras asterinifrons I	INPA 34100	1907		Brazil, Negro	1372	704	602
Centrochir crocodili I	ANSP 189332	1595	C001	Colombia, Magdalena	1460	718	619
Centrochir crocodili II	ANSP 189332	1596	C005	Colombia, Magdalena	1470	723	621
Centrodoras brachiatus A	ANSP 178542		92	Brazil, Amazonas		689	615
Centrodoras brachiatus B	ANSP 178542	1499		Brazil, Amazonas	849	692	591
Centrodoras hasemani I	ANSP 182227	797	4844	Venzuela, Amazon	1427	688	596
Centrodoras hasemani II	ANSP 182227	1500		Venzuela, Amazon	1449	657	592
Doraops zuloagai I	N020		OC-09-006-20	Venezuela, Maracaibo	1418		600
Doras carinatus A	INHS 49321	211	788	Guyana, Essequibo	1371	723	597
Doras higuchi	MZUSP 96333		7279	Brazil, Amazonas	1406	682	582
Doras micropoeus I	ANSP 187110		6932	Suriname, Maroni	1408	673	594
Doras micropoeus III	ANSP 187110	1768	6941 sk	Suriname, Maroni	1415	683	596

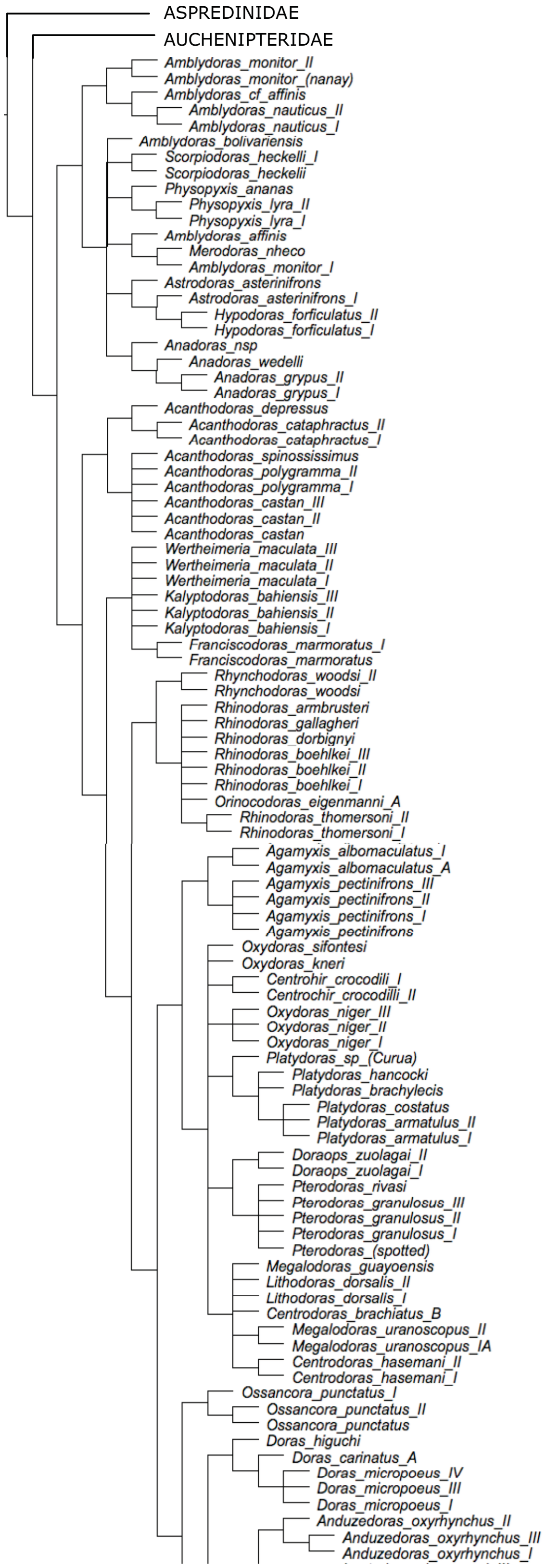
Terminal taxon	Voucher	Tissue number	Field tag	Locality Country, basin	***RAG 1*** **bp**	***CO1*** **bp**	***16s*** **bp**
Doras micropoeus IV	ANSP 187110	1858	6945	Suriname, Maroni	1402	681	599
Franciscodoras marmoratus	LBP 272	4193		Brazil, São Francisco	1447	761	590
Franciscodoras marmoratus I	MNRJ 23012			Brazil, São Francisco			602
Hassar affinis	UFMA	1487		Rio Mearim	1427	713	584
Hassar orestis	ANSP 181090	662	6154	Peru, Amazon	1402	639	585
Hassar wilderi	MZUSP 86216			Brazil, Tapajós	1444	683	585
Hemidoras morrisi I	ANSP 182512	687	6081	Peru, Amazon	1424	692	588
Hemidoras stenopeltis I	ANSP 182756	695	6241	Peru, Amazon	1387	675	649
Hypodoras forficulatus I	ANSP 179009	757	1540	Peru, Amazon	1451	624	592
Hypodoras forficulatus III	ANSP 182517	668	6017	Peru, Amazon		682	
Kalyptodoras bahiensis I	MZUSP 87839			Brazil, Paraguassú	889	725	595
Kalyptodoras bahiensis II	MZUSP 87841	87841		Brazil, Paraguassú		793	555
Kalyptodoras bahiensis III		MDP2007		Brazil, Paraguassú	1479		618
Leptodoras acipenserinus I	ANSP 182202	663	p6346	Peru, Amazon	1425	699	587
Leptodoras cataniai I	ANSP 181043	676	6092	Peru, Amazon	1421	700	587
Leptodoras cf copei A	ANSP 178540	1501	CALH 149	Brazil, Amazonas	1384	716	579
Leptodoras copei	ANSP 182225	777	V073	Venezuela, Orinoco	1407	680	580
Leptodoras hasemani I	ANSP 180897	793	4033	Venezuela, Orinoco	1416	706	594
Leptodoras hasemani III	MZUSP 97363	2194	7262	Brazil, Jamanxin	1269	683	596
Leptodoras juruensis I	ANSP 181046	683	6090	Peru, Amazon	1412	703	584
Leptodoras linelli I	ANSP 179631	1585	2093	Guyana, Essequibo			
Leptodoras linelli III	ANSP 179177	733	2433	Guyana, Rupununni	1393	686	589
Leptodoras marki	MNRJ 33067	M2439		Brazil, Xingú	1351		613
Leptodoras myersi	ANSP 181045	692	6205	Peru, Amazon	1427	679	596
Leptodoras oyakawai I	MZUSP 96597		7079	Brazil, Amazon	1364	724	594
Leptodoras oyakawai II	MZUSP 97395		7208	Brazil, Tapajós	1409	687	600
Leptodoras oyakawai III	MZUSP 97395		2191	Brazil, Tapajós	1463	690	934
Leptodoras praelongus I	ANSP 180913	1502	CALH 195	Brazil, Negro	1435	687	537
Leptodoras praelongus IIIA	ANSP 178534	1503	CALH 54	Brazi, Branco		670	592
Lithodoras dorsalis I	ANSP 187376	1207	7332	Brazil, Amazon	1445	684	592
Megalodoras uranoscopus IA	ANSP 178249	753	1685	Peru, Amazon	1335	682	595

Terminal taxon	Voucher	Tissue number	Field tag	Locality Country, basin	*RAG 1* bp	*CO1* bp	*16s* bp
Megalodoras guayoensis	MHG	CV001	CV001	Venezuela, Maracaibo	1432	763	600
Merodoras nheco	MZUSP 96174	664	7328	Brazil, Paraguay	1394	696	561
Nemadoras elongatus I	ANSP 182295	664	p6282	Peru, Amazon	1409	720	583
Nemadoras elongatus II	ANSP 182613	665	6299	Peru, Amazon	1461	716	586
Nemadoras elongatus III	ANSP 182850	1524		Brazil, Amazon	1386	717	581
Nemadoras hemipeltis I	ANSP 181095	709	6111	Peru, Amazon	1456	689	596
Nemadoras hemipeltis II	ANSP 182283	699	6272	Peru, Amazon	1409	691	456
Nemadoras humeralis I	ANSP 178550	1523		Brazil, Amazon	1377	715	584
Nemadoras humeralis II	ANSP 182596	703	6301	Peru, Amazon	1363	706	586
Nemadoras humeralis III	ANSP 182721	696	6228	Peru, Amazon	1346	719	583
Nemadoras leporhinus II	ANSP 180297	780	V104	Venezuela, Orinoco	1459	733	594
Nemadoras leporhinus III	ANSP 182825	795	4319	Venezuela, Orinoco	1425	709	583
Nemadoras leporhinus IV	MZUSP 96596		7082	Brazil, Tapajós	1469	671	584
Nemadoras nsp I	ANSP 180551	773	4076	Peru, Madeira	1449	717	578
Nemadoras nsp II	ANSP 182744	689	6096	Peru, Amazon	1395	719	595
Nemadoras trimaculatus I	ANSP 178252	752	1679	Peru, Amazon	1462	694	581
Nemadoras trimaculatus II	ANSP 182633	704	6306	Peru, Madeira	1469	726	601
Nemadoras trimaculatus III	ANSP 182824	801	4589	Venezuela, Orinoco	1432	688	594
Opsodoras morei	ANSP 183028	864	4570	Brazil, Negro	1418	695	596
Opsodoras ternetzi I	ANSP 179203	1527		Guyana, Takutu	1396	695	596
Opsodoras ternetzi II	ANSP 182852	1525		Brazil, Negro	1379	684	584
Opsodoras ternetzi III	ANSP 180177	766	2292	Peru, Amazon	1415	687	595
Opsodoras ternetzi IV	ANSP 180905	798		Venezuela, Orinoco	1432	699	583
Orinocodoras eigenmanni A	INHS 54564	290	290	Venzuela, Amazon	1333	722	594
Ossancora asterophysa	ANSP 178546	1505	CALH 200	Brazil, Negro	877	715	590
Ossancora asterophysa II	ANSP 182516	669	6003	Peru, Amazon	1391	717	589
Ossancora fimbriata I	ANSP 192477		M353	Brazil, Jutai		693	568
Ossancora fimbriata I	ANSP 192477		M354	Brazil Jutai		704	606
Ossancora punctata	ANSP 187005	1803	P6333	Peru, Amazon	1456	727	613
Ossancora punctata I	ANSP 181015	716	5118	Argentina, Paraná	1330	635	586
Oxydoras kneri	ANSP 182203		5196	Argentina, Paraná	1445	684	592
Oxydoras niger I	ANSP 181080		p6056	Peru, Amazon	1423	662	588

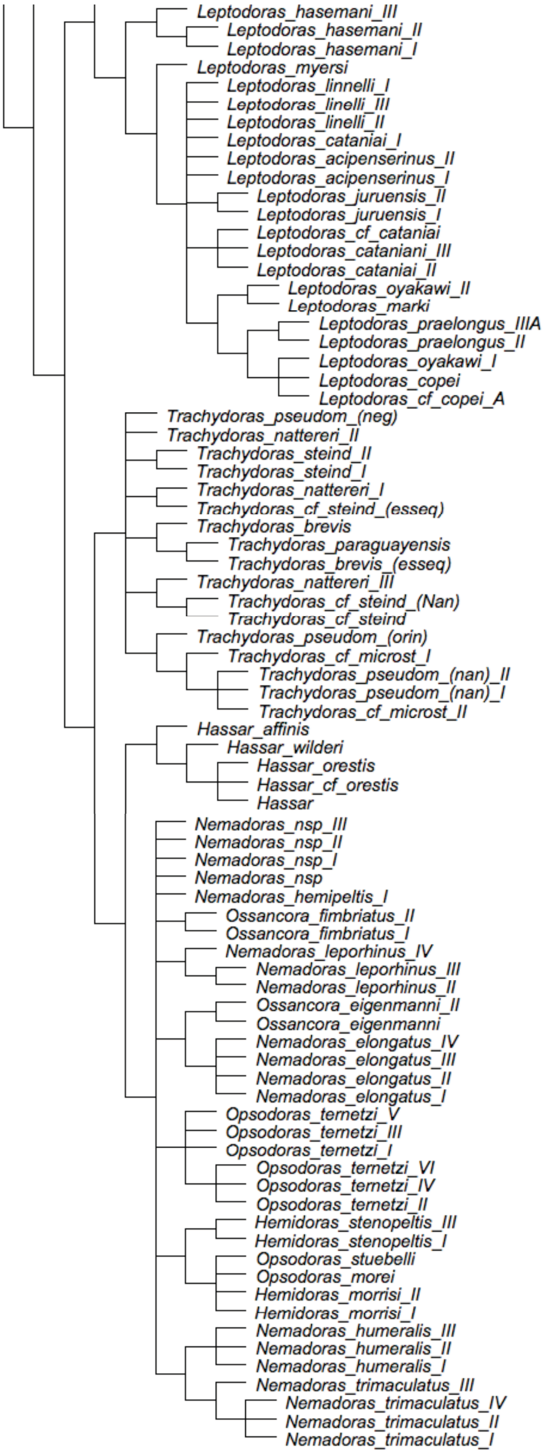
Terminal taxon	Voucher	Tissue number	Field tag	Locality Country, basin	*RAG 1* bp	*CO1* bp	*16s* bp
Oxydoras sifontesi	ANSP 189324	866	4340	Venezuela, Orinoco	1434	649	603
Physopyxis ananas	ANSP 190508	2118	7576	Venezuela, Orinoco	1471	722	621
Physopyxis lyra I	ANSP 180176	762	2300	Peru, Amazon	1441	701	667
Platydoras armatulus I	ANSP 181008	714	5200	Argentina, Paraná	1447	715	597
Platydoras brachylecis	UFMA	1482		Brazil, Maranhão	1428	721	606
Platydoras costatus	ANSP 187111		7064	Suriname, Surinam	1462	715	604
Platydoras hancocki	ANSP 179144		2032	Guyana, Rupununni	1423	782	601
Platydoras sp	ANSP 187377	1285	7050	Guyana, Maroni	1288	682	596
Platydoras sp (Curua)	MZUSP 96336		7290	Brazil, Amazon	1396	718	566
Pterodoras (spotted)	ANSP 181197		6203	Peru, Amazon	1388	691	596
Pterodoras granulosus I	ANSP 178350	758	1560	Peru, Amazon	1425	648	595
Pterodoras granulosus II	ANSP 180883	710	5100	Argentina, Paraná	1428	688	594
Pterodoras rivasi	MHG	CV002	CV002	Venezuela, Apure	1411	681	583
Rhinodoras armbrusteri	ANSP 179096			Guyana, Rupununni	1398	630	595
Rhinodoras boehlkei I	ANSP 181044	675	6059	Peru, Amazon	1399	680	605
Rhinodoras dorbignyi	LBP 3218	1785	19423	Brazil, Paraguay	1451	728	623
Rhinodoras gallagheri	ANSP 191086	1777	T09020 alc	Venezuela, Guanare	1448	725	603
Rhinodoras thomersoni I	MHG		OC-09-006-21	Venezuela, Maracaibo	1389	696	557
Rhynchodoras woodsi	ANSP 181042	677	6052	Peru, Amazon	1813	708	608
Rhynchodoras woodsi I	ANSP 191480	2096		Brazil, Amazon			
Rhynchodoras woodsi II	ANSP 181042	679	6061	Peru, Amazon	1757	658	611
Scorpiodoras heckelii	ANSP 182790	792	5404	Venezuela, Orinoco	1449	693	590
Scorpiodoras heckelii I	AUM42953	1512	V5406	Venezuela, Orinoco	2269	678	607
Trachydoras brevis	MHNG 2650.062		GY04091	Guyana, Rupununni	1462	713	587
Trachydoras brevis (esseq)	ANSP 179855	729	2211	Guyana, Rupununni	1398	685	563
Trachydoras cf microstomus	ANSP 185014	1504	CALH 257	Brazil, Negro		714	565
Trachydoras cf microstomus I	MZUSP 92813			Brazil, Tapajós	1426	716	589
Trachydoras cf pseudomicrostomus I	ANSP 182619	705	6310	Peru, Amazon	1428	716	591
Trachydoras cf steindachneri	ANSP 185040	865	4576	Brazil, Negro	1408	669	605
Trachydoras cf steindachneri (esseq)	ANSP 179853	2099		Peru, Amazon	1422	686	589
Trachydoras nattereri I	ANSP 182593	706	6313	Peru, Amazon	1423	547	587
Trachydoras paraguayensis	ANSP 181011	713	5134	Argentina, Paraná	1402	664	589
Trachydoras pseudomicrostomus (nan) I	ANSP 179866	767	2475	Peru, Amazon	1351	689	619

Terminal taxon	**Voucher**	**Tissue number**	**Field tag**	**Locality Country, basin**	***RAG 1* bp**	***CO1* bp**	***16s* bp**
Trachydoras pseudomicrostomus (nan) II	ANSP 187373	2293		Peru, Amazon		675	586
Trachydoras pseudomicrostomus (orin)	ANSP 185076		v20	Venezuela, Orinoco	1070	704	586
Trachydoras steindachneri I	ANSP 178256	751	1673	Peru, Amazon	1380	703	593
Wertheimeria maculata I	MCP 43855		WM1	Brazil, Jequitinhonha	1492	686	602
Wertheimeria maculata II	MZUSP 88614			Brazil, Jequitinhonha		725	605
Wertheimeria maculata III	MCP 43855		WM2	Brazil, Jequitinhonha	1295		607
Auchenipteridae							
Ageneiosus inermis	ANSP 189090		6996		1442		593
Ageneiosus ucayalensis	INHS 52920			Peru, Amazon			
Auchenipterus nigripinnis	ANSP 182418			Argentina, Paraná	1451	724	625
Centromochlus heckeli	ANSP 182773			Brazil, Amazon			
Gelanoglanis	ANSP 180806			Peru, Madeira	1422	695	583
Glanidium leopardum	ANSP 189104			Suriname, Maroni	1478	726	619
Liosomadoras oncinus	ANSP 191102	2087		Venezuela, Orinoco	1467	726	604
Pseudoepapterus hasemani	ANSP 178311			Peru, Amazon	1421	699	557
Trachelyopterus galeatus	INHS 49034			Guyana, Maroni			
Trachycorystes	ANSP 180820			Venezuela, Orinoco	1435	586	597
Aspredinidae							
Aspredo aspredo	ANSP 191475	2094		Brazil, Amazon		722	621
Bunocephalus verrucosus	CU 91989						
Micromyzon akamai	ANSP 182777			Brazil, Amazon		647	
Pterobunocephalus rugosus	ANSP 185102	2091		Argentina, Paraná	865	721	619
Xyliphius	ANSP 182322			Peru, Amazon	1339	726	592

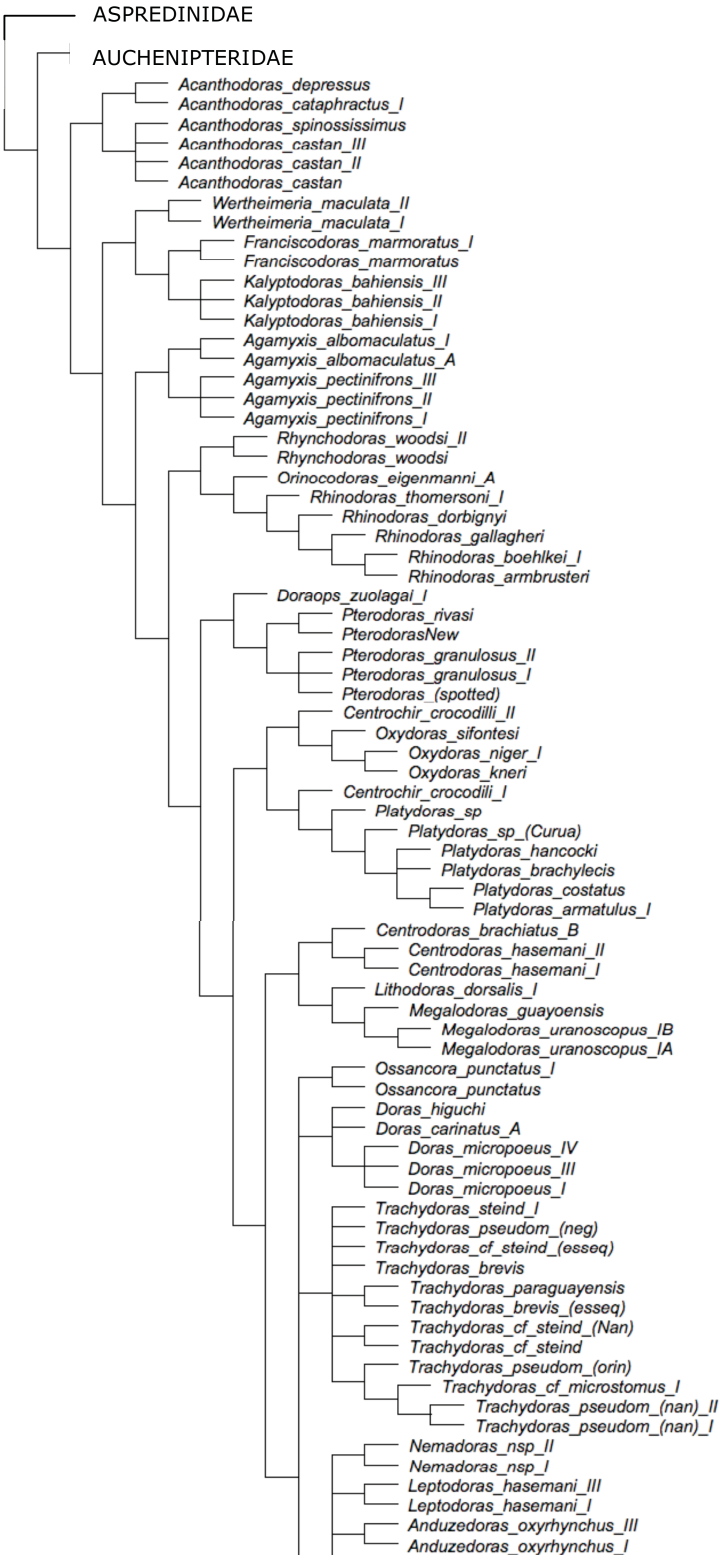
Appendix 2. Topologies obtained by the diverse analysis of the nuclear, mitochondrial and combined datasets



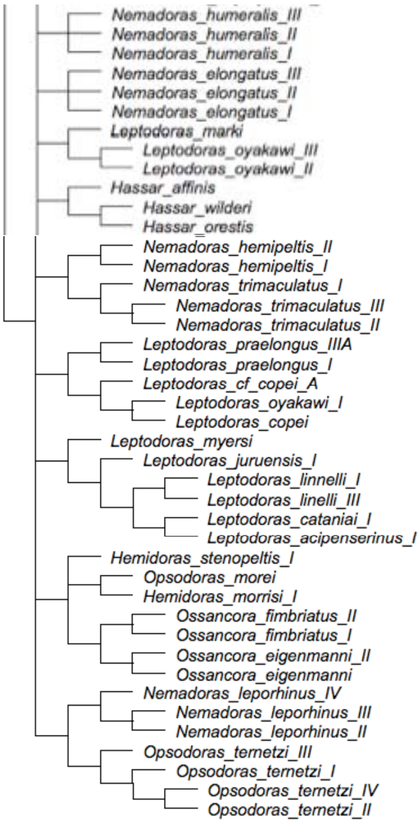
MP1a. Strict consensus of the Maximum Parsimony analysis of the *16s* dataset.



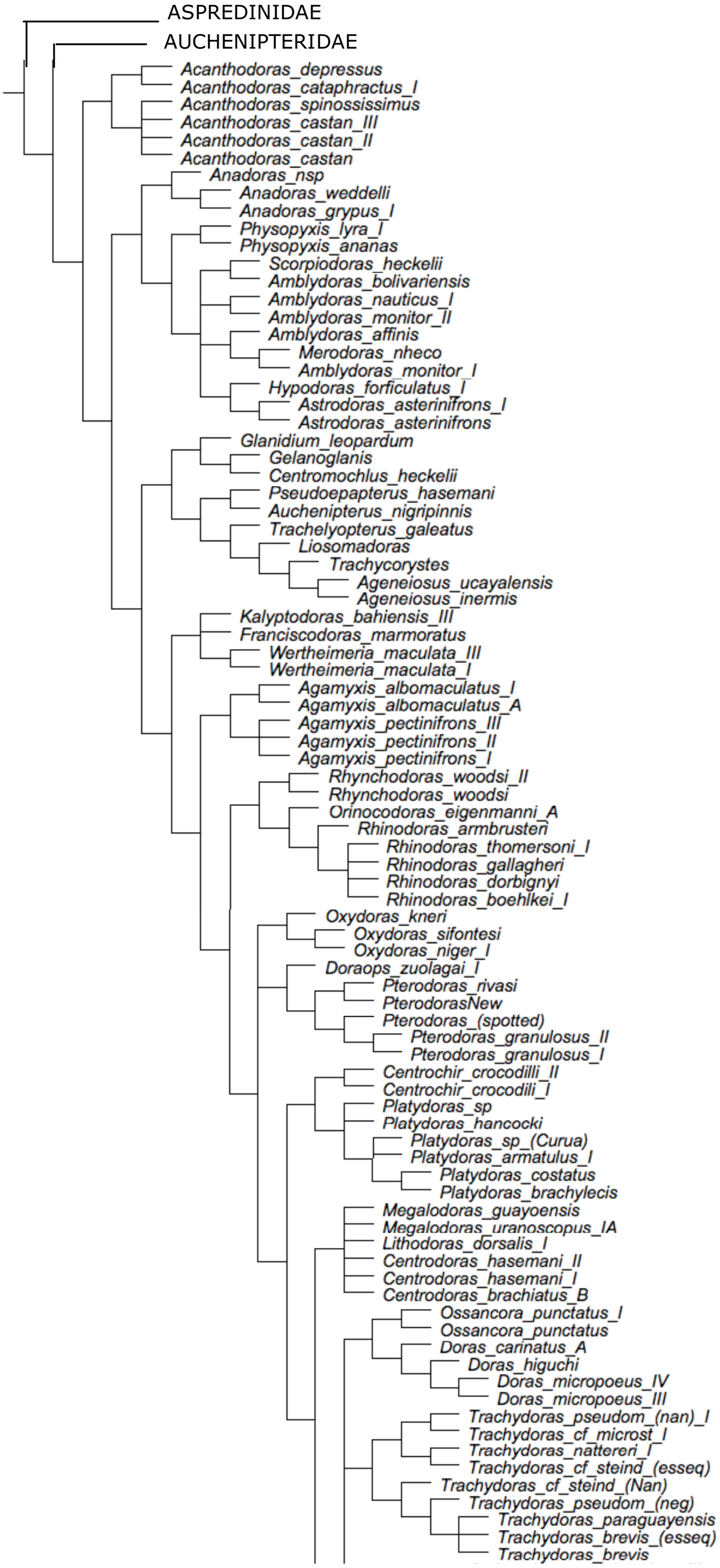
MP1b. Strict consensus of the Maximum Parsimony analysis of the *16s* dataset.



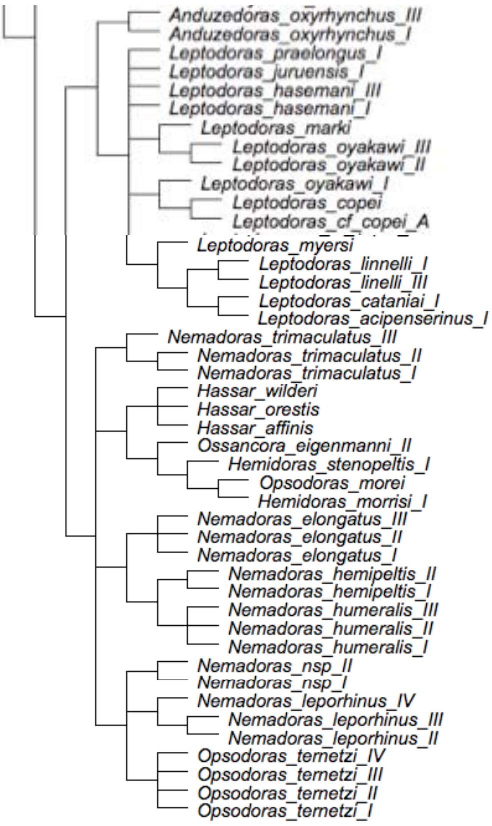
MP2a. Strict consensus of the Maximum Parsimony analysis of the *co1* dataset.



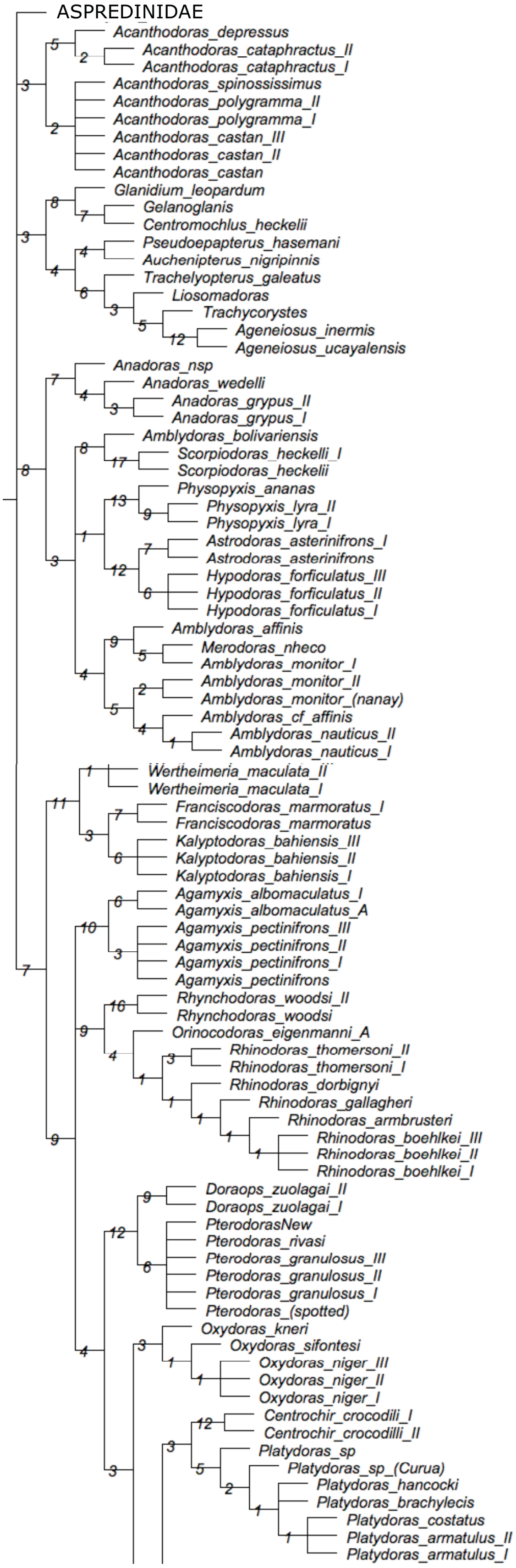
MP2b. Strict consensus of the Maximum Parsimony analysis of the *co1* dataset.



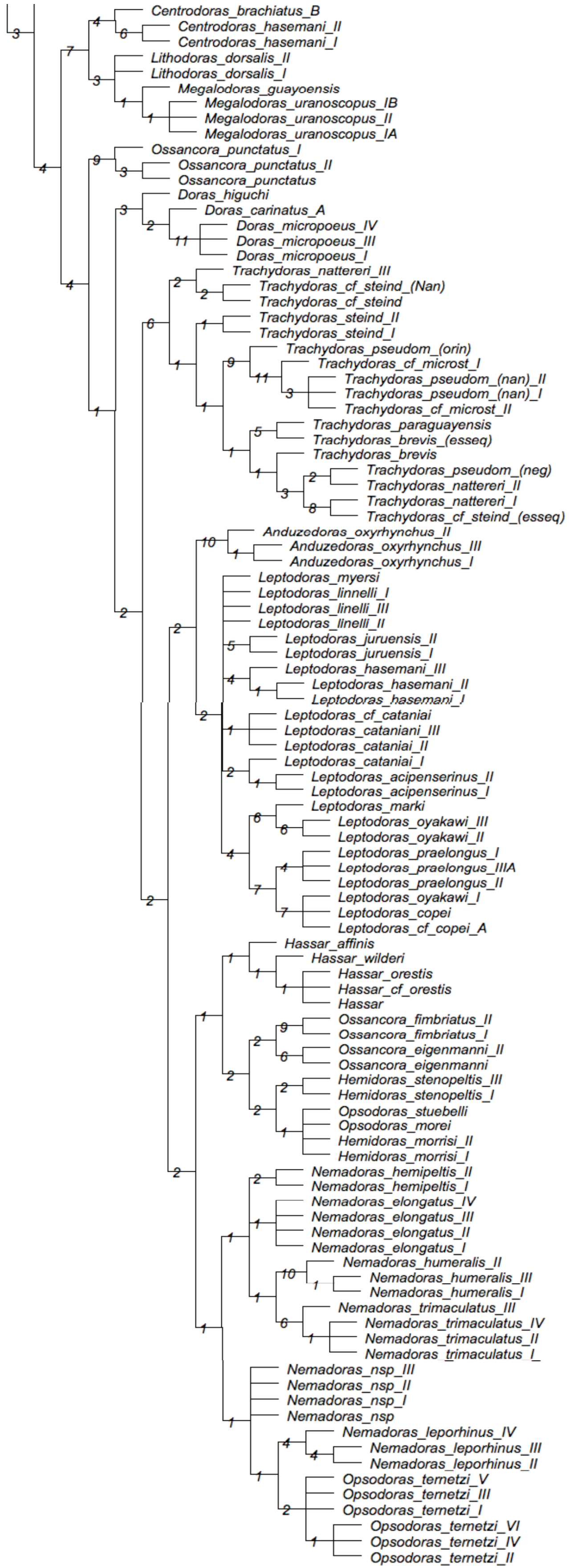
MP3a. Strict consensus of the Maximum Parsimony analysis of the *rag1* dataset



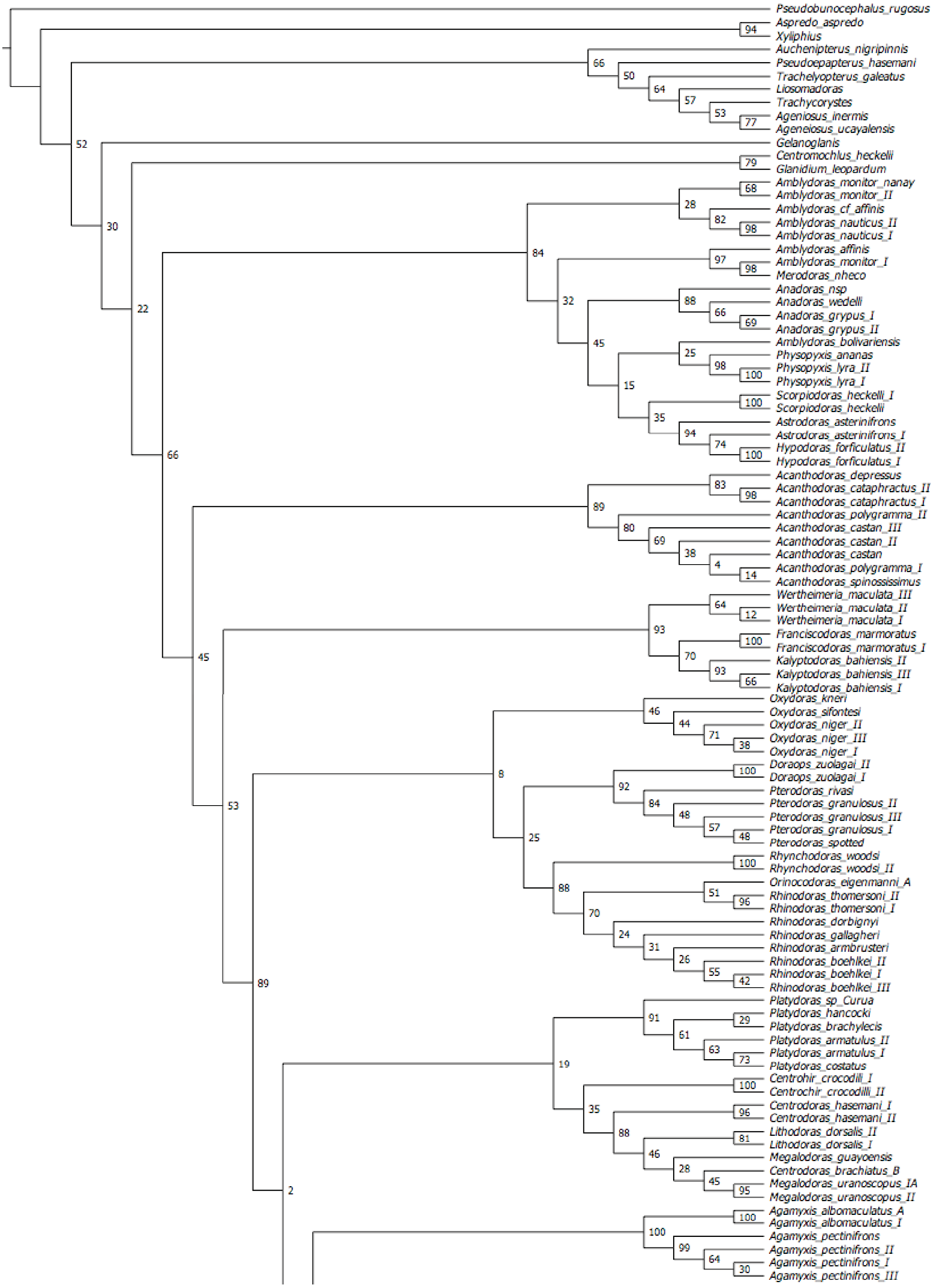
MP3b. Strict consensus of the Maximum Parsimony analysis of the *rag1* dataset.



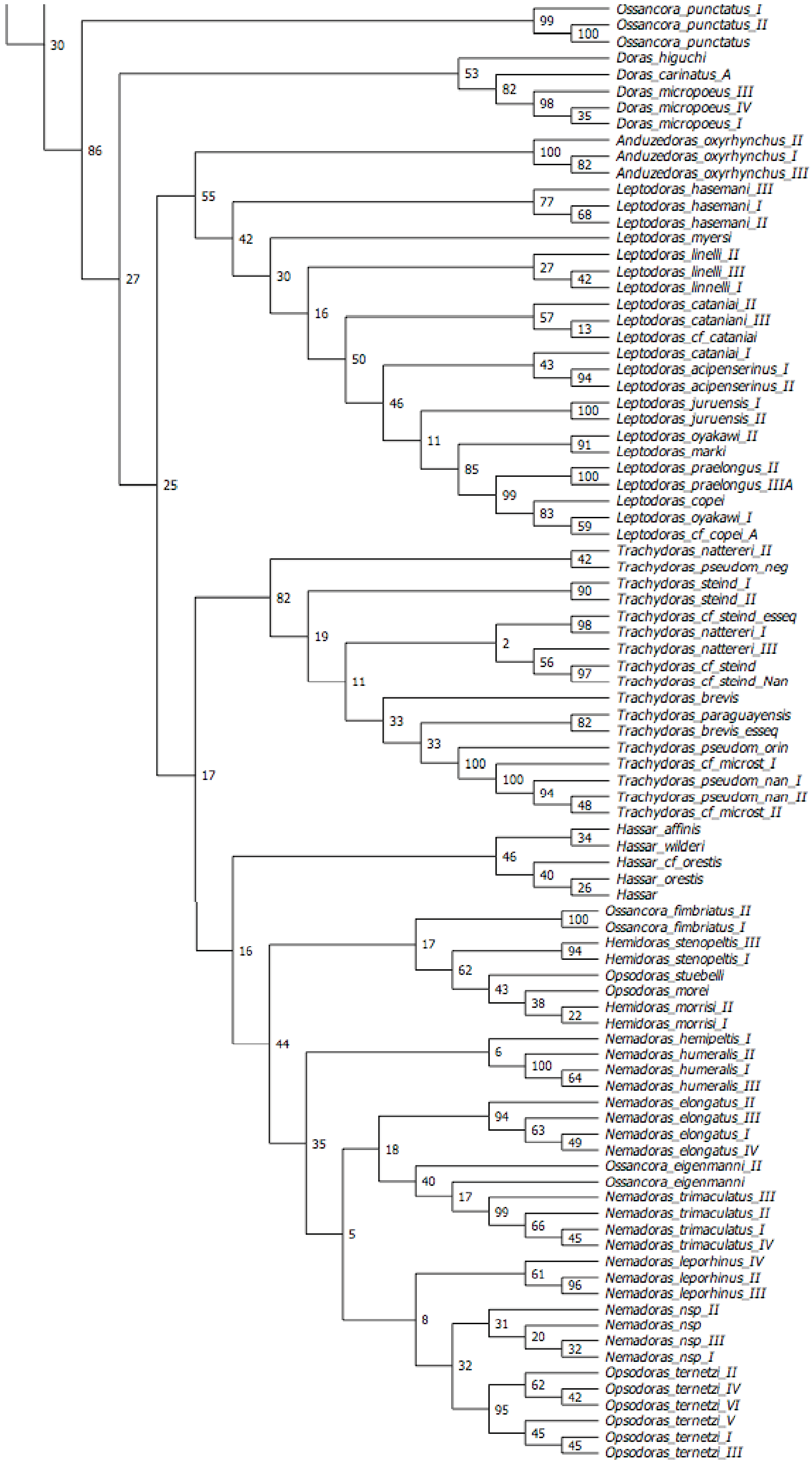
MP4a. Strict consensus of the Maximum Parsimony analysis of the combined dataset.



MP4b. Strict consensus of the Maximum Parsimony analysis of the combined dataset.



ML1a. Topology obtained from the Maximum Likelihood analysis of the *16s* dataset.



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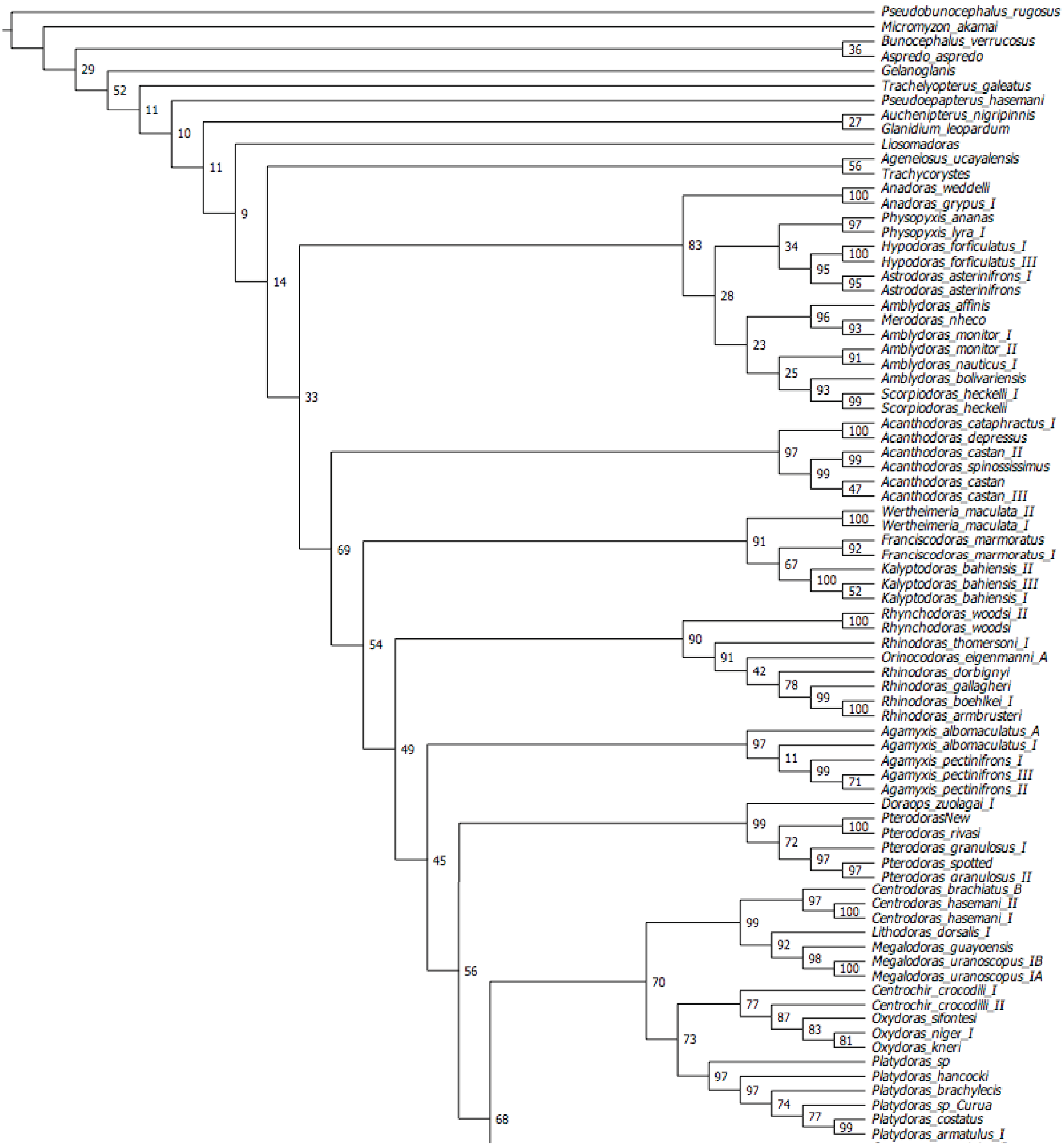

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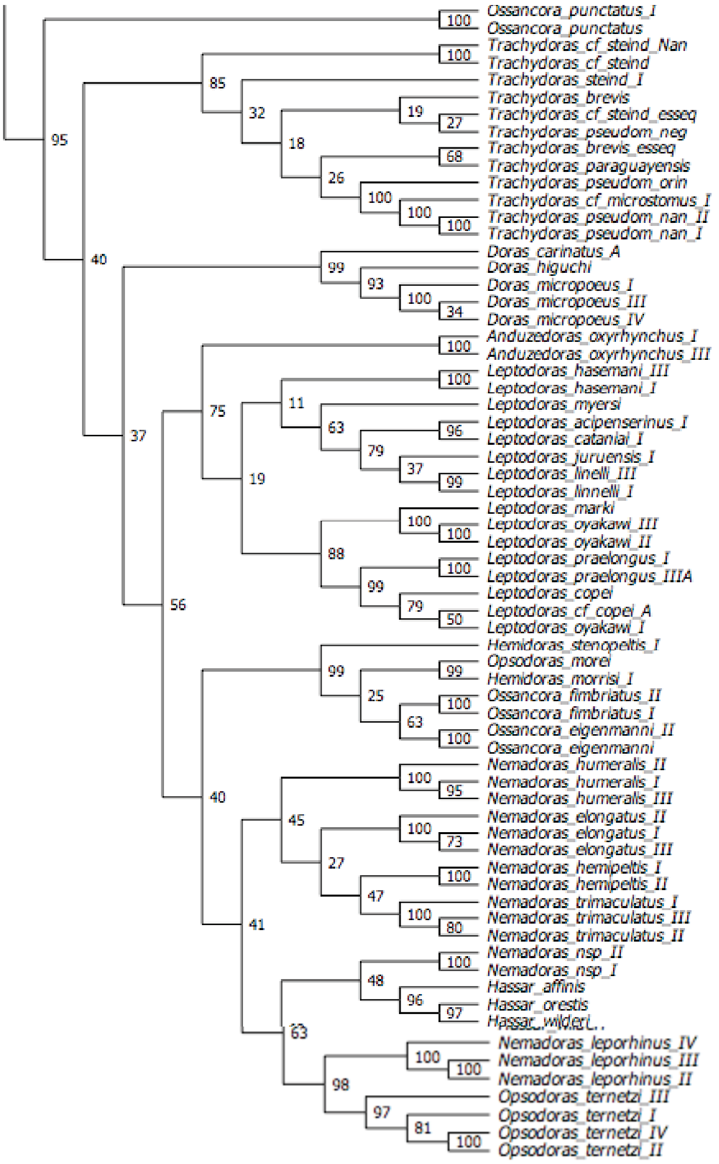
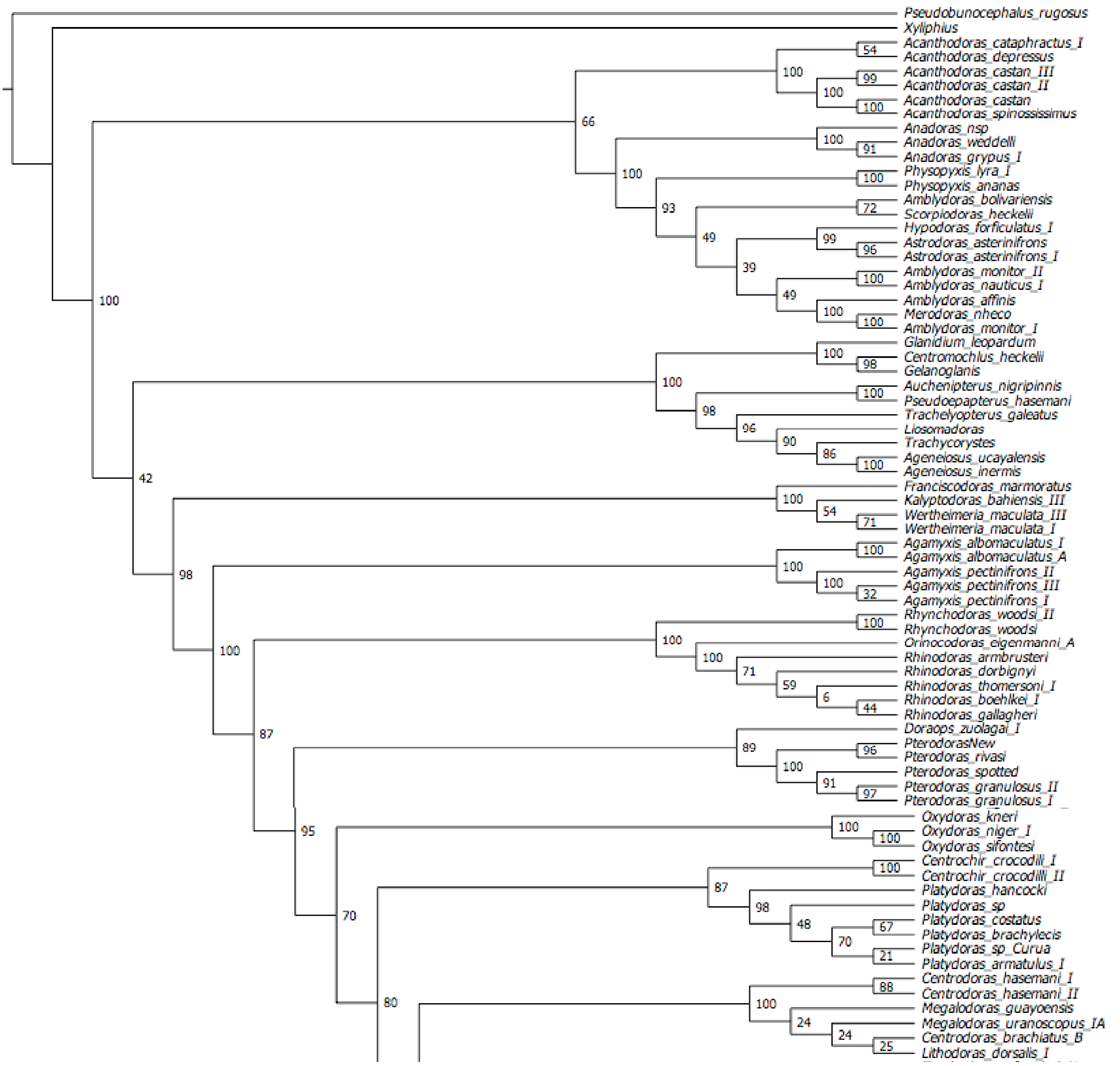
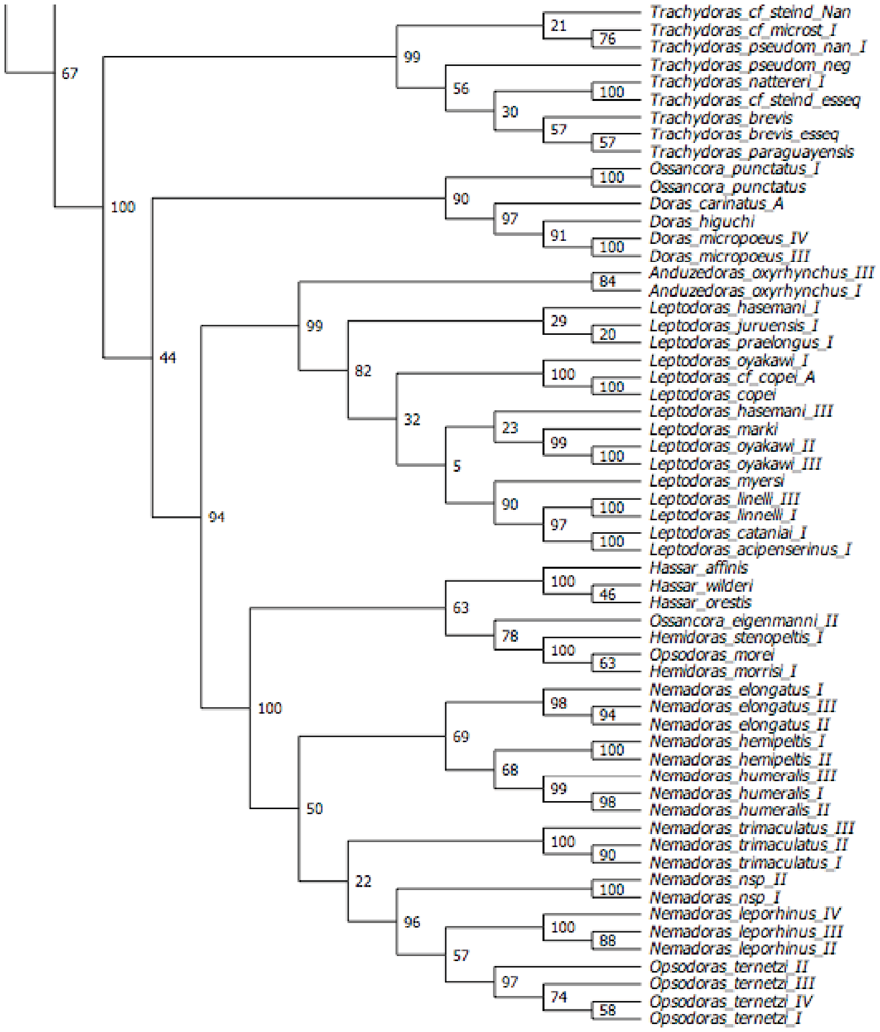


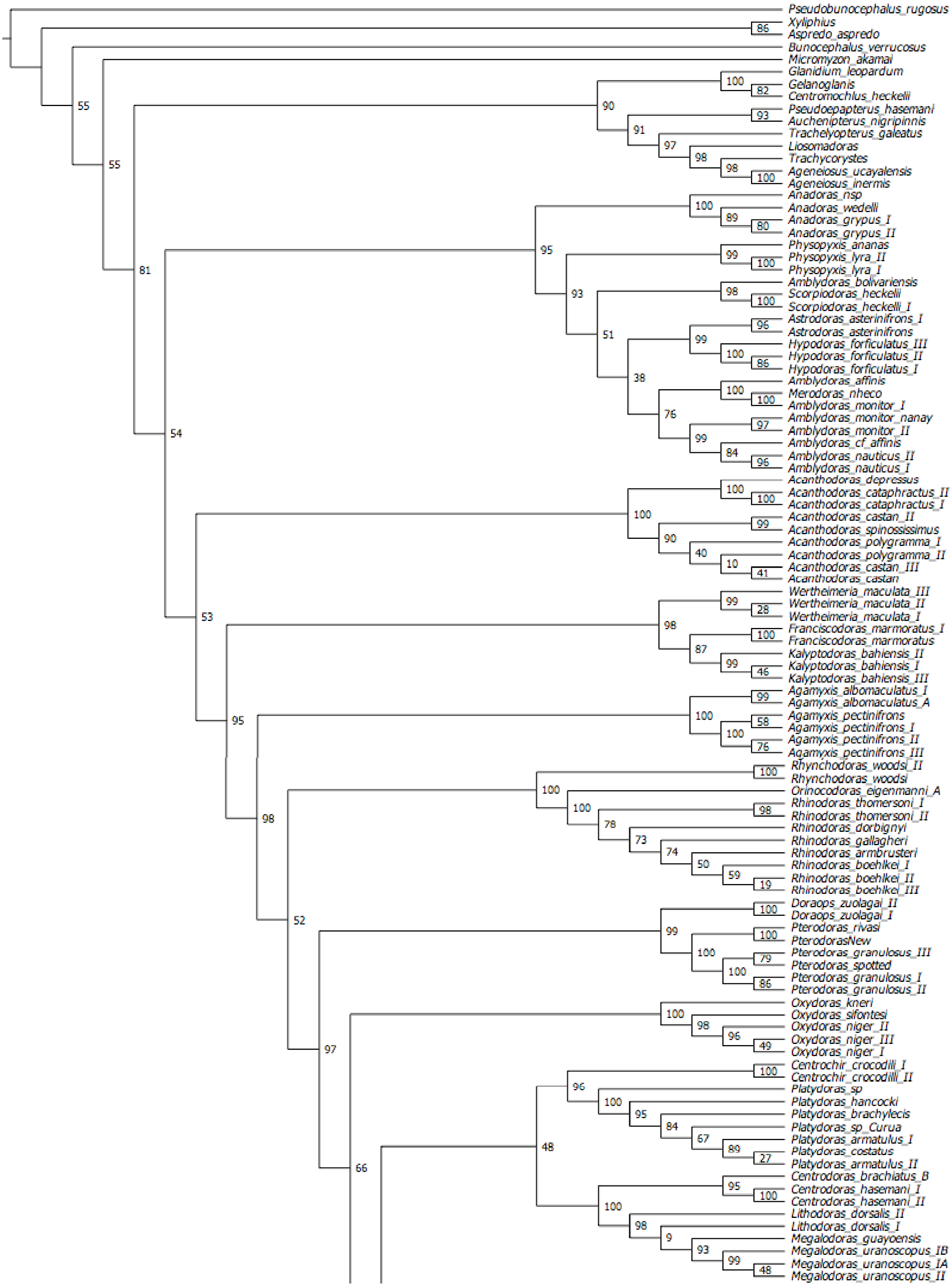
ML2b. Topology obtained from the Maximum Likelihood analysis of the *co1* dataset.



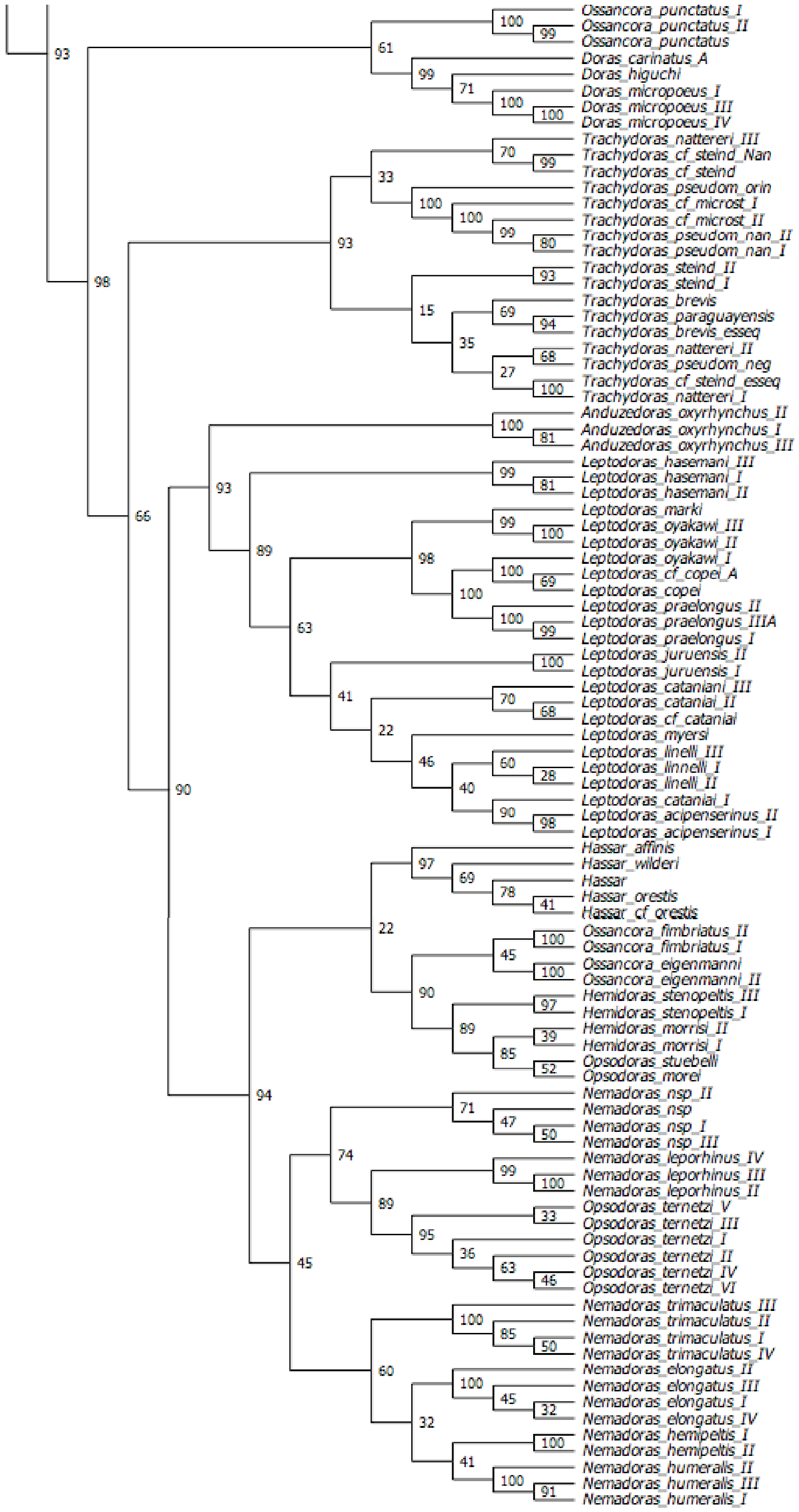
ML3a. Topology obtained from the Maximum Likelihood analysis of the *rag1* dataset.



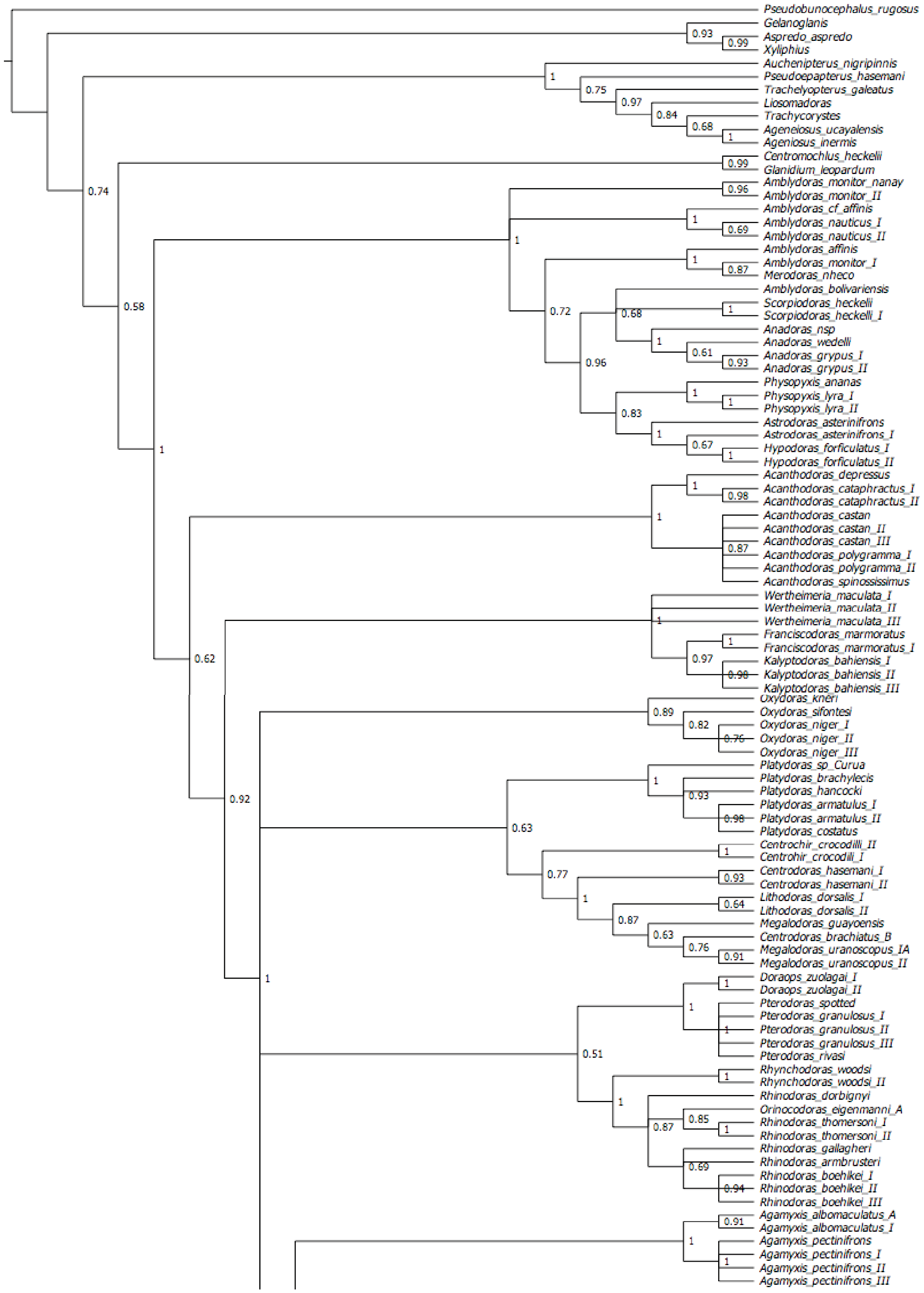
ML3b. Topology obtained from the Maximum Likelihood analysis of the *rag1* dataset.



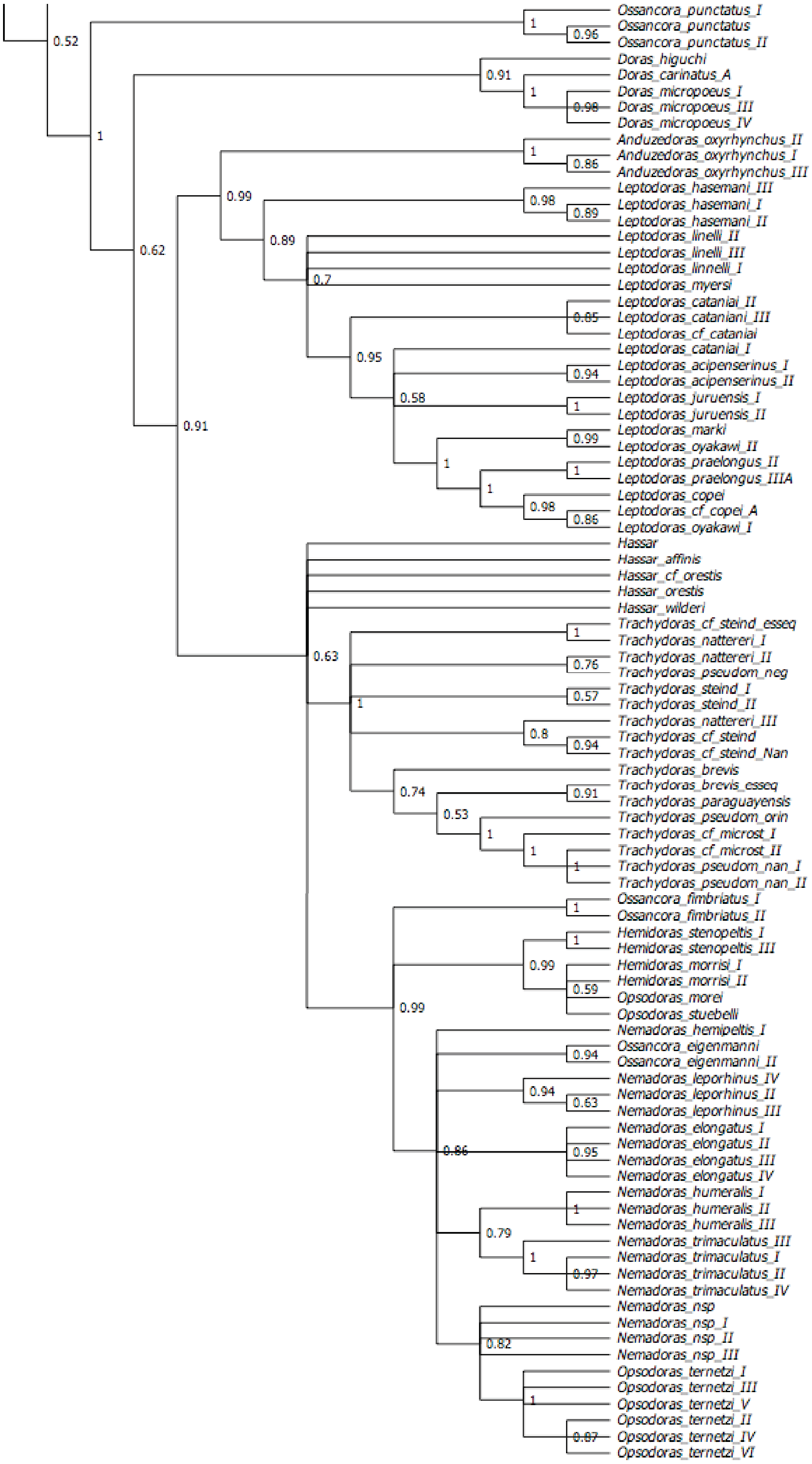
ML4a. Topology obtained from the Maximum Likelihood analysis of the combined dataset.



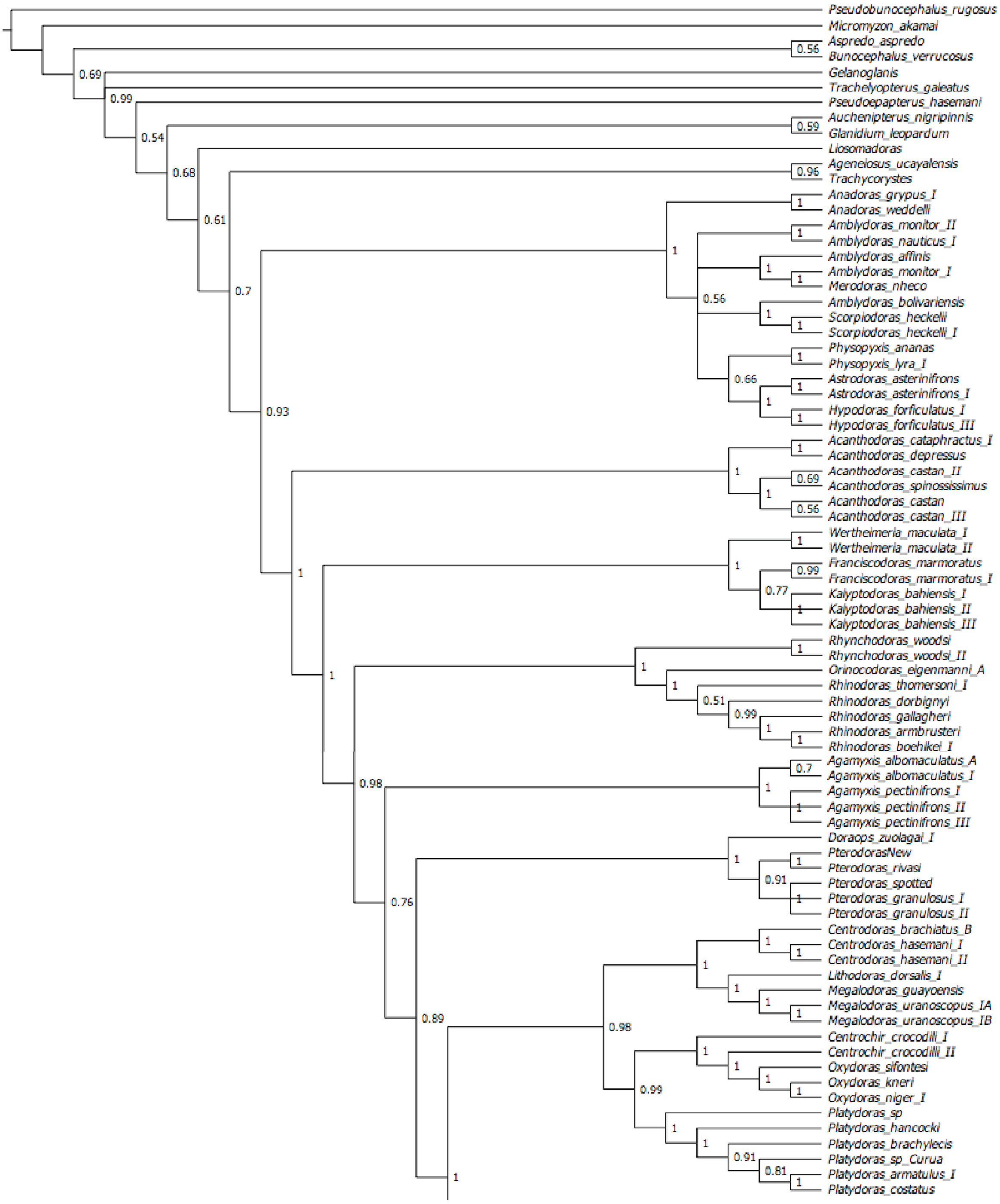
ML4b. Topology obtained from the Maximum Likelihood analysis of the combined dataset.



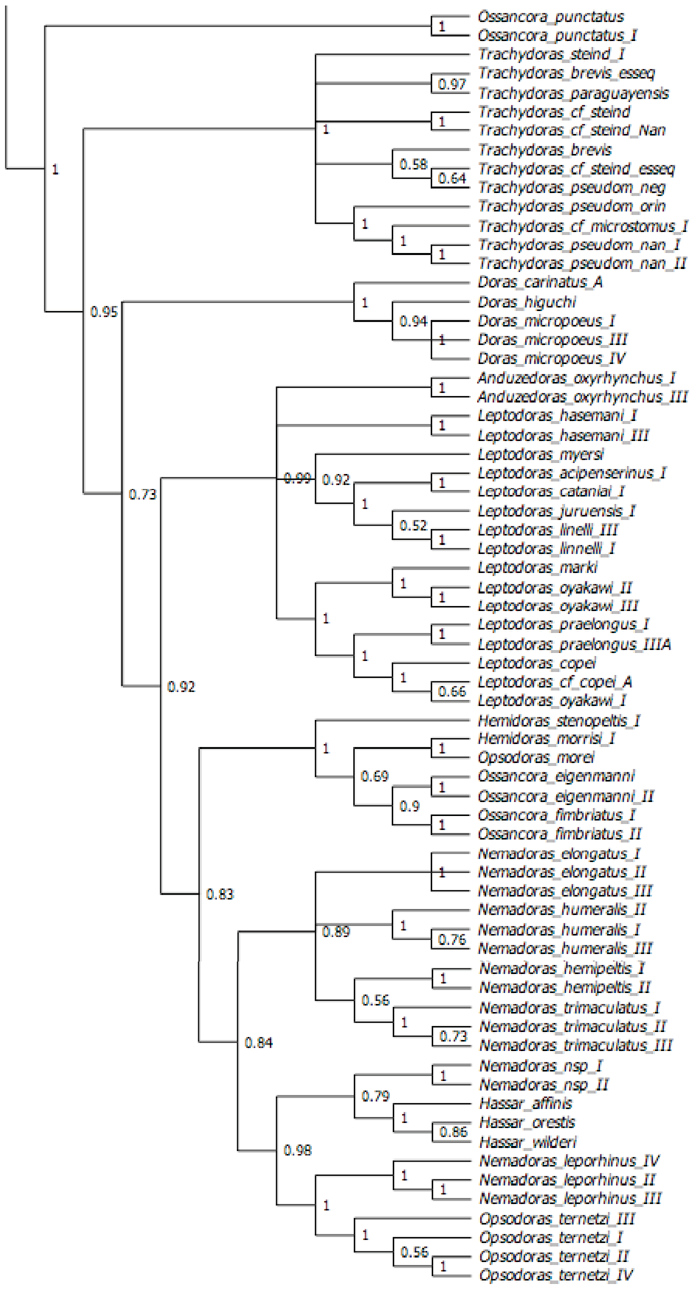
BA1a. Topology obtained from the Bayesian analysis of the *16s* dataset.



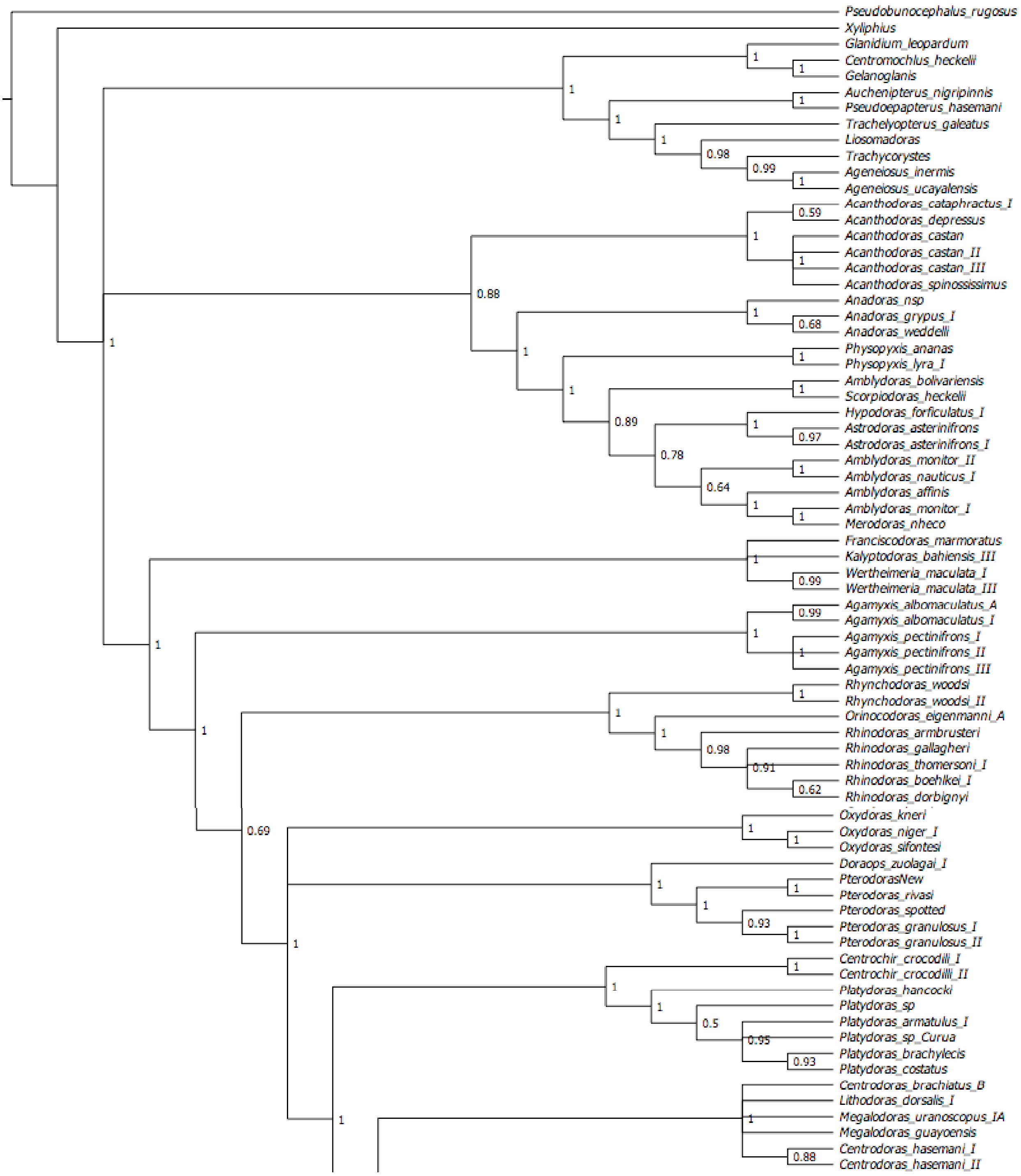
BA1b. Topology obtained from the Bayesian analysis of the *16s* dataset.



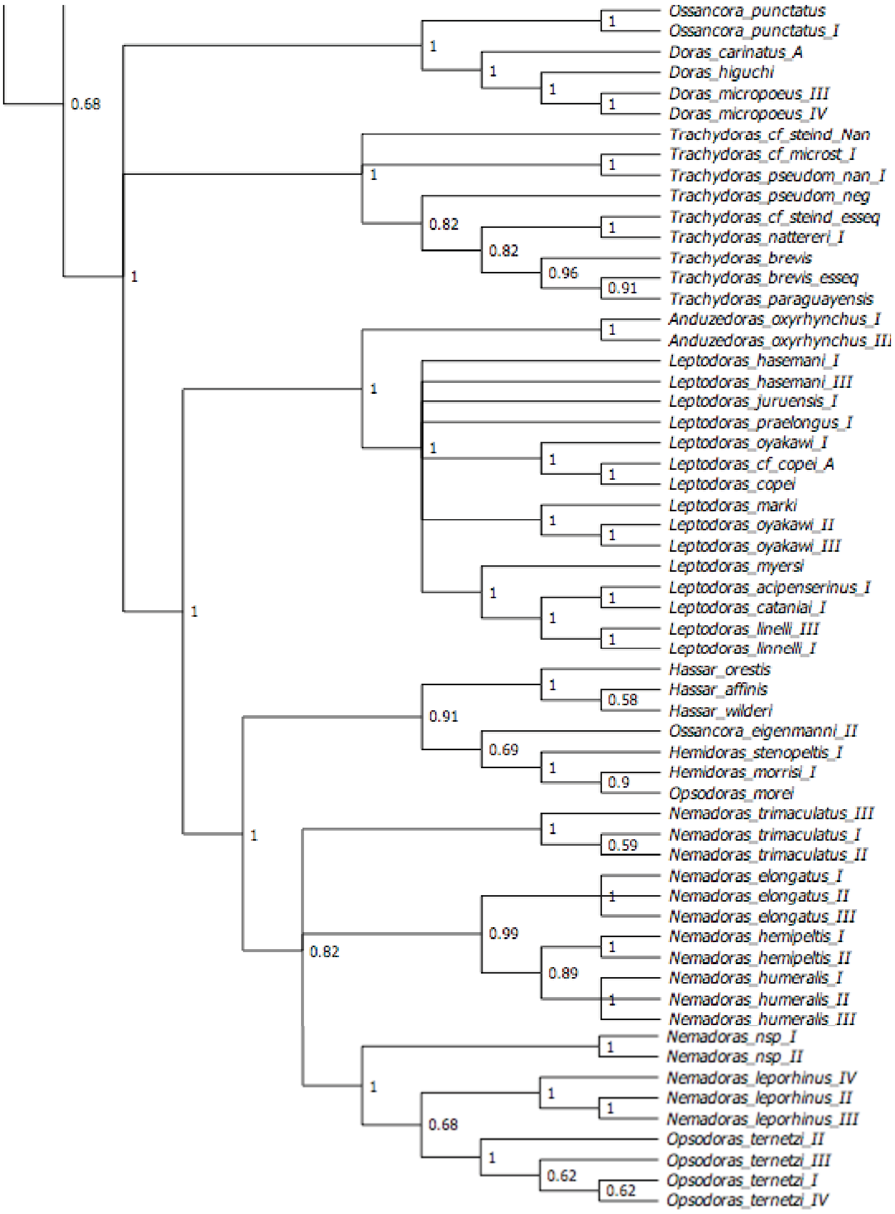
BA2a. Topology obtained from the Bayesian analysis of the *co1* dataset.



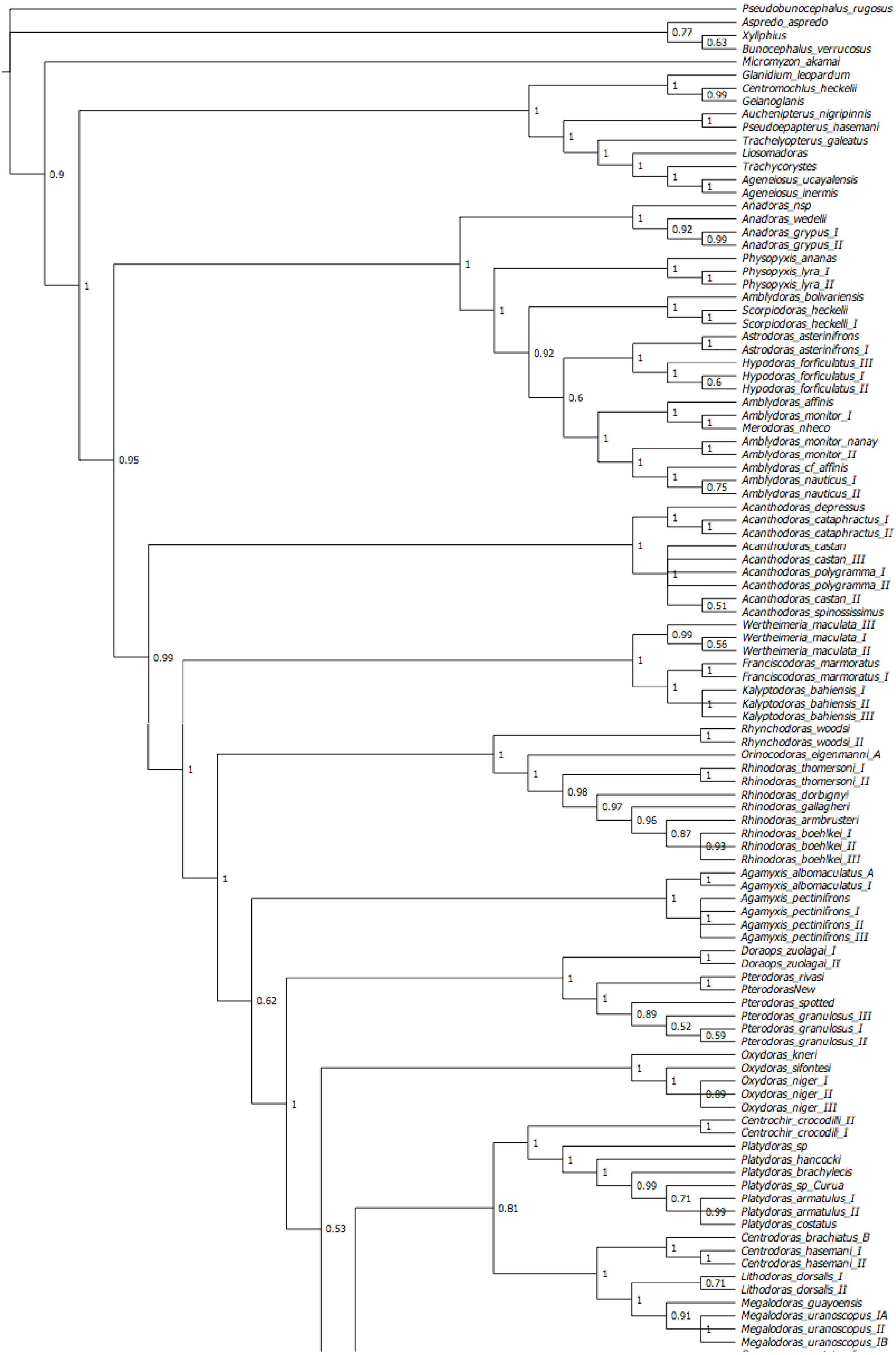
BA2b. Topology obtained from the Bayesian analysis of the *co1* dataset.



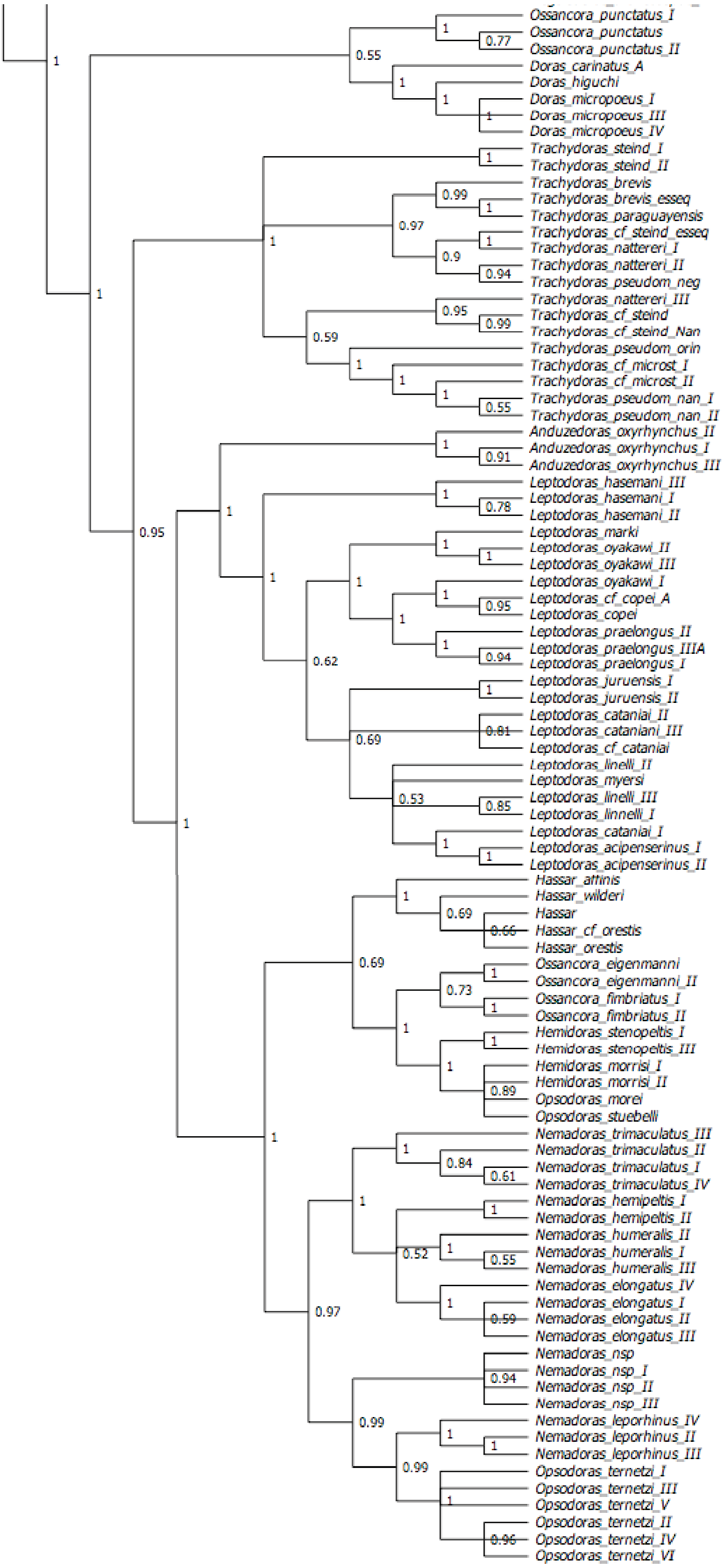
BA3a. Topology obtained from the Bayesian analysis of the *rag1* dataset.



BA3b. Topology obtained from the Bayesian analysis of the *rag1* dataset.



BA4a. Topology obtained from the Bayesian analysis of the combined dataset.



BA4b. Topology obtained from the Bayesian analysis of the combined dataset.

TOTAL EVIDENCE ANALYSIS OF DORADIDAE (PISCES, SILURIFORMES)

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ABSTRACT

This paper presents the phylogenetic hypothesis produced by the analysis of all the previously available data for Doradidae and newly gathered morphological and molecular data. 200 characters referring to external morphology, osteology, gonads, and swimbladder were reviewed from previous authors. 91 myological characters were analyzed and proposed here for the first time in a phylogenetic context. 3011 molecular characters were gathered correspondent to two mitochondrial genes (*16s* and *co1*) and one nuclear gene (*rag1*). Compiling 3302 characters for 94 species. Data were analyzed using Maximum Parsimony. The topology obtained through the total evidence analysis was compared and discussed against previous morphological and molecular hypotheses.

KEY WORDS

Morphology, Myology, *rag1*, *16s*, *co1*, Catfish

INTRODUCTION

In this paper we report the results of a study on the phylogeny of Doradidae using morphological and molecular characters.

Studies of Doradidae phylogeny have focused on morphological characters. Higuchi (1992) proposed a phylogeny of the family and recovered the monotypic *Weithermeria* as the most basal genus. Birindelli (2010) studied the relationships of Doradoidea with emphasis in Doradidae. He included 55 species of the family and confirmed the monophyly based on three synapomorphies. He also presented evidence of (Mochockidae (Doradidae, Auchenipteridae). Other authors aimed to established relationships of clades inside Doradidae. Sabaj (2002) reviewed the taxonomy of Doradidae and established the phylogenetic relationships of *Leptodoras* using *Doras*, *Anduzedoras*, *Hassar*, and *Hemidoras* as outgroup. Birindelli (2006) completed a taxonomic revision of the three genera in the tribe Rhinodoradini and a phylogenetic analysis that included 46 doradid species, most belonging to the subfamily Doradinae. Sousa (2010) studied the taxonomy and systematics of the subfamily Astrodoradinae including *Acanthodoras* and *Agamyxis.*

To date only two studies used molecular characters to establish the relationships of the members of Doradidae. Moyer et al (2004) used 12S and 16S rRNA mitochondrial genes and elongation factor-1 alpha nuclear gene to propose a phylogeny for 23 Doradidae genera, but their study did not include the two basal-most taxa (*Wertheimeria* and *Franciscodoras*) recovered from Higuchi's analysis. Moyer et al (2004) study showed significant conflict with Higuchi's morphological results including a lack of support for the monophyly of subfamily Platydoradinae, and tribes Centrochirini and Doradini. Arce *et al* (in prep) used *16s* and *co1* mithocondrial genes and *rag1* nuclear gene and included all the 77 described and six undescribed species of Doradidae pertaining to the 32 genera of the family.

Data from Arce *et al* (in prep) are used in the present study and are analyzed together with morphological characters. Morphological information correspond to osteological characters used by previous authors (de Pinna, 1993; Ferraris, 1998; Britto, 2002; Birindelli, 2006 and 2010; Sousa, 2010) and myological characters, proposed here for the first time, in the phylogenetic context.

MATERIAL AND METHODS

Taxon Sampling

The main goal of this study was to produce the most comprehensive phylogeny, including all the available evidence, for the catfish family Doradidae. DNA sequences data and morphological characters were collected for 76 described and four undescribed species in 32 genera of Doradidae. Following previous molecular studies (Moyer et al, 2004; Sullivan et al., 2006; Arce, in prep) ten species of Auchenipteridae and four species of Aspredinidae were included as outgroups.

A list of the material examined is presented in Appendix 1.

Molecular methodology

Dataset

DNA data consisted of a combined matrix of one nuclear gene (*recombination activation subunit 1 gene*, *rag1*) and two mitochondrial genes (*cytochrome oxydase c subunit 1 – co1* and ribosomal *16s*). The dataset included 91 terminals (i.e., specimens) and 3011 base pairs of which 884 characters are parsimony-informative. We selected genes that are commonly used in molecular phylogenetic studies of vertebrates and that were previously used to recover phylogenetic relationships of Doradidae. DNA information was previously obtained trough standard protocols as described in Arce *et al.* (in prep.). Data were used to establish the molecular phylogeny of Doradidae.

A complete list of the material examined is presented in Appendix 1.

Morphological methodology

Dataset

Two hundred and ninety one morphological characters were analyzed separately and in combination with the molecular data. Morphological characters used in this study are divided in two main groups. The first group (200 characters) corresponds to external morphology, osteology, swimbladder, and gonads. These characters were based on previous morphological studies of Higuchi (1992), de Pinna (1993), Ferraris (1998), Royero (1999), Britto (2002), Akama (2004), Birindelli (2006 and 2010), and Sousa (2010). The information gathered on those studies was used and completed for most of the species.

The second group (91 characters) corresponds to myology. This source of information was never studied in the phylogenetic context for Doradidae. Some myological characters (indicated in the character description) are adaptations of Diogo (2005) and Datovo & Bockman (2010). References to the original paper where characters were first proposed are given when appropriate. Characters without bibliographic reference are proposed here for the first time in the phylogenetic context. All phenotypic characters were considered unordered.

Anatomical nomenclature and anatomical preparations

Description and scoring of characters derived from external morphology, swimbladder, and gonads were based on literature (Higuchi, 1992; Sabaj, 2002; Birindelli, 2006 and 2010; and

Sousa, 2010) and direct observation of specimens preserved in alcohol. Osteological characters were recorded from cleared and stained specimens (Taylor & Van Dyke, 1985) and from dry skeletons. Myologycal characters were recorded from stained specimens (Datovo & Bockman, 2010) carefully dissected (Arce, in prep). Whenever possible observations were made on more than one specimen for each species. A complete list of the material examined is presented in Appendix 2.

Osteological nomenclature follows Weitzman (1962) with modifications made by Birindelli (2010). Myological nomenclature follows Winterbottom (1974) with the modifications proposed by Arce (in prep).

Phylogenetic Analysis

Maximum Parsimony trees were generated using the new technologies search implemented in TNT (Goloboff *et al.*, 2008). We analyzed the morphological dataset separated and in combination with the molecular data. Molecular data alone were analyzed in a previous work (Arce *et al.*, in prep). For the morphological data alone the search was performed in two steps: the first step used a combination of sectorial searches (RSS and CSS), 50 iterations of ratchet, 50 round of tree fusing, and 50 cycles of tree drifting. The driven was set to reach the minimum length 20 times. The second step used the trees produced in the first step to perform a traditional TBR search. For the combined molecular and morphological data a similar search strategy was performed. The iterations, rounds and cycles were increased to 100 and the driven was set to reach the minimum length 50 times.

Gaps were treated as missing data, all characters were considered unordered and equally weighted. Absolute and relative Bremer values (decay index) were calculated for nodal support and plotted on the most parsimonious tree.

RESULTS

Phylogenetic relationships

Morphology

The analysis of the dataset composed of 291 morphological characters for 69 species produced eight most parsimonious trees of 1540 steps. The eight topologies differ on the position of the species within the genus *Ossancora*, *Trachydoras*, and *Nemadoras.* The strict consensus of the morphological analysis is presented in Fig. 1. The description of the morphological characters is presented in Appendix 3 and the matrix of morphological characters are presented in Appendix 4.

Combined analysis

The combined analysis of the morphological and molecular datasets included 94 taxa and 3302 characters, 1169 of which were parsimony-informative. The analysis produced one most parsimonious tree of 7388 steps. The topology recovered is shown in Fig. 2.

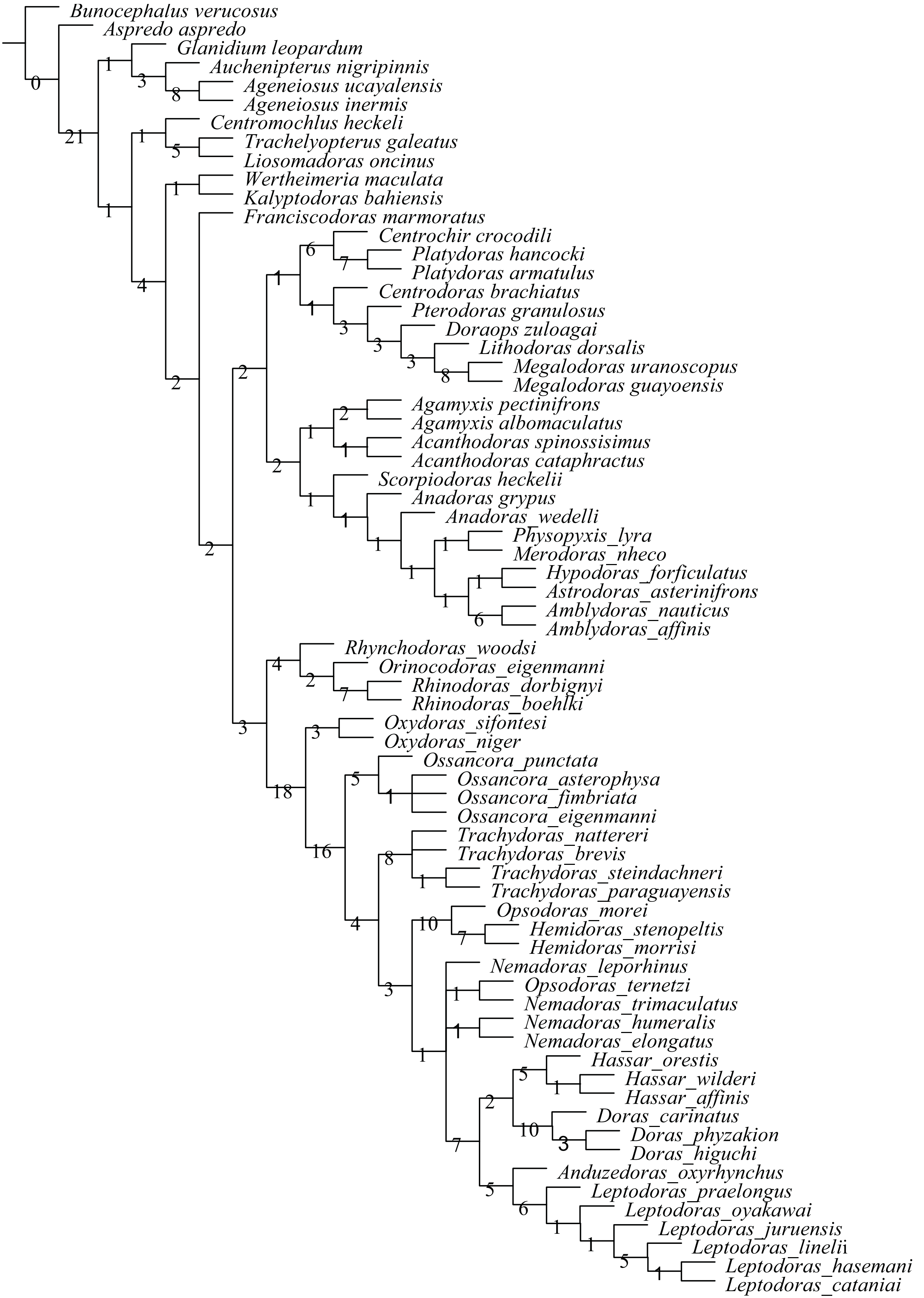

Figure 1. Topology recovered by the analysis of the osteological and myological characters. Node values correspond to the absolute Bremer support.

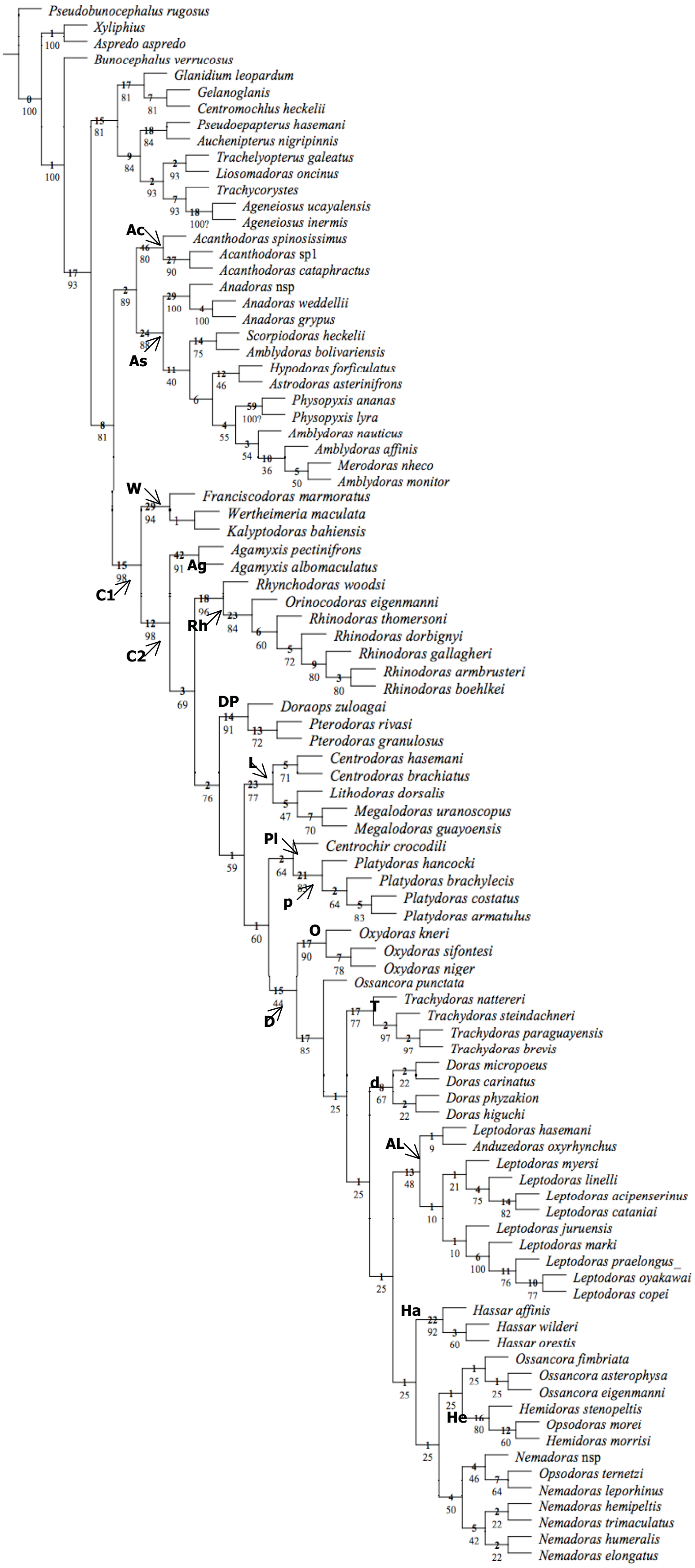

Figure 2. Topology recovered from the Maximum Parsimony analysis of all the data available for Doradidae. Node values correspond to absolute Bremer support (bold) and relative Bremer support.

Node labels: Ac = *Acanthodoras*, As = subfamily astrodoradinae, W = *Wertheimeria* clade, Ag = *Agamyxis*, C1 = clade 1, C2 = clade 2, Rh = rhinodoradini tribe, DP = *Doraops* + *Pterodoras* clade, L = *Lithodoras* clade, Pl = subfamily platydoradinae, p = Platydoras, O = *Oxydoras*, D = doradini*,* T = *Trachydoras*, d = *Doras*, AL = *Anduzedoras* + *Leptodoras* clade, Ha = *Hassar*, He = *Hemidoras*.

Clades recovered with strong support by the total evidence analysis

Acanthodoras

Members of the genus *Acanthodoras* are recovered as monophyletic with a strong Bremer support of 46. The clade is supported by 12 morphological and 65 molecular synapomorphies. Species of *Acanthodoras* present deep lateral scutes, the articulation between the hyomandibula and neurocranium on the sphenotic, thorns on the lateral margins of the dorsal spine, thorns on all the dorsal surface of the pectoral spine, a straight crest on the coracoid ventral surface, a rounded caudal fin, the A2A3 originating on the preopercle, hyomandibula, quadrate, and metapterygoid, the *hyohyoides inferioris* with a muscular insertion and lying ventral to the *protractor hyodes*, and the *arrector dorsalis* fibers directed from the origin to the insertion confluent into one or two tendons.

Subfamily Astrodoradinae sensu Higuchi et al. 2007

A clade composed of *Amblydoras*, *Anadoras*, *Astrodoras*, *Hypodoras*, *Merodoras*, *Physopyxis*, and *Scorpiodoras* is recovered with Bremer support of 24. The clade is supported by two morphological and 42 molecular synapomorphies. Members of the Astrodoradinae are diagnosed by the pigmentation on the lateral margin of the cranium characterized by a dark stripe that runs along the ventro-lateral margin of the cranium, also by the insertion of the *addcutor arcus palatini* not attached to the mesopterygoid

Higuchi et al. (2007) proposed Astrodoradinae for the seven genera mentioned above and diagnosed the subfamily by the combination of four non-exclusive characters. The subfamily can be distinguished by the following characters: spinous postcleithral process (except in *Anadoras*); lacrimal serrated (except in *Anadoras*), forming anterior corner of orbit (except in *Physopyxis*; also present in *Pterodoras* and *Lithodoras*); and reduced number of pleural ribs (four to seven, also shared with *Acanthodoras*, *Agamyxis*, *Trachydoras*, *Ossancora fimbriata*, *O. punctata*, and *O. eigenmanni*).

Clade 1

A clade composed by all Doradidae except the subfamily Astrodoradinae and *Acanthodoras* is recovered with a strong support of 15. The clade is supported by four morphological and 22 molecular synapomorphies. The clade can by diagnosed by the muscular and tendinous insertion of the A2A3 portion of the *adductor mandibulae*, the *retractor tentaculi* inserted mainly in the maxilla and also in the lower jaw through a tendon as long as half of the total length of the muscle, and the absence of the coronomaxillar ligament.

Wertheimeria clade

The clade (*Franciscodoras* (*Wertheimeria*, *Kalyptodoras*)) is recovered with Bremer support of 29. The clade is supported by four morphological and 32 molecular synapomorphies. The clade is diagnosed by having the trigeminal-facial foramen delimited posteriorly by the prootic, the dorsal and ventral hypohyal dorsolaterally sutured, the posterodorsal process of the chleitrum well developed, and the *retractor tentaculi* with two separate points of insertion.

Clade 2

A clade composed by *Agamyxis*, Rhinodoradini, Platydoradinae, members of the Pterodoradini, *Oxydoras*, and the Doradidae with fimbriated barbel is recovered with a Bremer support of 12. The clade is supported by 23 molecular synapomorphies. *Agamyxis* is recovered at the base of this clade, and although the members of the Pterodoradini are recovered in this clade, they are not grouped together.

Agamyxis

A monophyletic group formed by the two nominal valid species of *Agamyxis*, *A. pectinifrons* and *A. albomaculatus*, is recovered with a Bremer support of 42. *Agamyxis* is supported by 11 morphological and 36 molecular synapomorphies. The clade is diagnosed by having the margin of the lateral ethmoid serrated, a transversal crest on the infraorbital 1, deep lateral scutes (as in *Acanthodoras*), the articulation between the hyomandibula and the neurocranium on the sphenotic (as in *Acanthodoras*), thorns on the lateral margins of the dorsal spine (as in *Acanthodoras*), thorns on all the dorsal surface of the pectoral spine (as in *Acanthodoras*), the insertion of the A2A3 portion of the *adductor mandibulae* on the retroanguloarticular and dentary, the insertion of the *adductor arcus palatini* on the metapterygoid, the fibers of the *extensor tentaculi* directed transversally from the origin to the insertion, the insertion of the *hyohyoides inferioris* through tendinous fibers that cross over the muscular fibers, and the *sternohyoideus* covered ventrally by the *hyohyoidei abductores*.

Tribe Rhinodoradini sensu Birindelli (in press.)

The clade (*Rhynchodoras* (*Orinocodoras*, *Rhinodoras*) is recovered with Bremer support of 10. The tribe is supported by eight morphological and 18 molecular synapomorphies. "Rhinodoradini" is diagnosed by having the anterior rami of the mesethmoid coalescent, a long autopalatine that reach posteriorly at least half of the orbit diameter, the posterior process of the cleithrum triangular, deep, and short, the *adductor mandibilae* originating from all the preoperle length, the *levator arcus palatini* wider than the *dilatator operculi*, the insertion of the *extensor tentaculi* ventral on the autopalatine, and an elongated cartilage surrounding the mental barbels. Birindelli (2006) first recognized this clade as a tribe and Birindelli (2010) found five synapomorphies for the clade.

Doraops + *Pterodoras* clade

Monotypic *Doraops zuolagai* is recovered as sister to a clade composed of *Pterodoras granulosus* and *P. rivasi* with a Bremer support of 14. The clade is supported by six morphological and 16 molecular synapomorphies. The clade is diagnosed by the presence of internal trabecules on the swimbladder, the mesethmoid quadrangular, the eighth vertebra partially fused to the complex vertebra, the *adductor mandibulae* divided at the origin and inserted through muscular fiber, the *extensor tentaculi* divided into two slips with the inner portion wider than the outer.

These two genera share a unique morphological characteristic: a paired elongated diverticulum curving anteromedially from the shoulder of the anterior chamber on their swimbladder (Birindelli *et al*, 2009).

Lithodoras clade

Clade composed of *Centrodoras* (two nominal valid species) sister to *Lithodoras* (monotypic) + *Megalodoras* (two nominal valid species) is recovered with a Bremer support of 23. The clade is supported by two morphological and 29 molecular synapomorphies. The *Lithodoras* clade present a secondary chamber on the swimbladder with an internal septum and the *retractor tentaculi* inserted in two separate points (as in the *Wertheimeria* clade).

Platydoras

The four nominal valid species of *Platydoras* were recovered as monophyletic with a Bremer support of 21. The genus is supported by five morphological and 26 molecular synapomorphies. *Platydoras* is diagnosed by having a secondary chamber on the swimblader without an internal septum, the nasal dorsally expanded and apparently exposed, the last three infraorbitals expanded, deep lateral scutes (as in *Anadoras* and *Agamyxis*), the procurrent rays modified as plates that cover the caudal peduncle dorsally and ventrally, and the *arrector ventralis* margin slightly concave and divided.

Doradini sensu Birindelli (in press.)

All doradid species sharing fimbriate barbels (uniquely derived in Doradidae) and *Oxydoras* (only doradid with deep body and simple barbels) form a monophyletic clade with Bremer support of 15. The clade is supported by 21 morphological and four molecular synapomorphies. Doradini is diagnosed by having an anteroventral keel on the mesethmoid not differentiated as a ventral process, the transcapular process ventrally tapered as a lamina, the opening of the infraorbital canal on the posterior portion of the sphenotic, the third timpanic plate conspicuously smaller than the remaining lateral scutes, the premaxilla as a cone-like bone with a dorsal apex, the contact between the coronomeckelian bone and the dentary through a bony suture, the autopalatine long, the accessory lamella on the ceratobranchial restricted to the gill arches, the fourth basibranchial with a long ventral process, the fifth ceratobranchial pedunculated with teeth located distally form the anterior end, the pharyngobranchial toothplate elongated, the posterior margin of the coracoid extremely expanded dorsally forming a bony diaphragm, the *adductor mandibulae* not covering all the other muscles of the cheek, the *retractor tentaculi* undivided, the posterior portion of the *retractor tentaculi* located mesially to the *adductor mandibulae* and the anterior portion of the muscle located dorsally, the cartilage of the mental barbel elongated (as in Rhinodoradini), the *protractor hyoides* divided into two portions with different area of origin, the *hyohyoidei abductores* connected on the most anterior portion only covering partially the *sternohyoideus*, and the origin of the *adductor superficialis* on the Baudelot ligament.

Oxydoras

The three valid species of *Oxydoras* group together as (*O. kneri* (*O. niger*, *O. sifontesi*)) with a Bremmer support of 17. The clade is supported by 24 molecular synapomorphies.*Oxydoras* do not have any exclusive synapomorphies and the genus is diagnosed by the big body size, reaching up to 1 m of SL (similar condition in "Pterodoradini), the presence of a secondary chamber on the swimbladder without an internal septum (also in *Platydoras* and some species of *Doras*), the posterior fontanel small and almost completely closed (as in *Nemadoras elongatus* and *N. humeralis*), the lateral ethmoid not participating on the orbital margin, the absence of teeth on the premaxilar (also in *Trachydoras*, *Doras*, *Hemidoras*, *Nemadoras*, *Anduzedoras*, and *Leptodoras*) and the dentary (also in *Trachydoras*, *Hemidoras morei*, *H. morrisi*, *Leptodoras marki*, and *L. oyakawai*).

Two species of *Oxydoras*, *O. sifontesi* and *O. niger* present a unique characteristic, the enlargement of a thin bony nodule from the anterior face of the parapophysis of the sixth vertebra in specimens greater than 200 ml SL (Birindelli *et al.*, 2009).

Doradidae with fimbriate barbel

All the Doradidae with fimbriate barbels are recovered as a monophyletic group with a Bremer support of 17. The clade is supported by 16 morphological and 25 molecular synapomorphies. The clade is diagnosed by the presence of sub-barbels on the ventral face of the maxillary barbel, by having the external and internal mental barbels of about the same length, the epoccipital participating on the lateral margin of the cephalic shield, the supracleithrum connected to the pterotic and epoccipital, the lateral scutes oblicuosly placed, lack of a medial expansion on the hyomandibular which does not contact the metapterygoid, the second basibranchial ossified, the anteromesial process of the pelvic girdle incorporated into the basipterygium, the *levator operculi* originating from the pterotic and supracleithrum, the *extensor tentaculi* divided into two slips with the inner portion wider than the outer (as in *Doraops* and *Pterodoras*), the *intermandibularis* located dorsally to the mental barbels not visible in ventral view, the *protractor hyoides* inserting on the dentary ventrally to the *intermandibularis* and originating on the posterior and anterior ceratohyal, and the *hyohyoidei inferioris* inserting trough two tendinous fibers developed at the anterior-most portion of the muscle.

Trachydoras

The genus *Trachydoras*, represent by four nominal valid species, is recovered as monophyletic with a Bremer support of 17. The genus is supported by six morphological and 13 molecular synapomorphies. *Trachydoras* is diagnosed by the presence of an anteroventral keel on the mesethmoid differentiated as a ventral process, the basioccipital with an extension forming a laminar process, the absence of a bony suture between the infraorbital and the mesethmoid, the absence of accessory lamella on the ceratobranchial, the basibranchial with a ventral process on a tripartite shape, and the fibers of the *hyohyides abductores* not organized in bundles.

Doras

Doras is recovered as monophyletic with a Bremer support of eight. The genus is supported by eight morphological and 21 molecular synapomorphies. *Doras* is diagnosed by the presence of multiple pores on the ventral surface of the body, the absence of lateral diverticula on the swimbladder, the lateral scutes with an smooth margin, the *adductor* operculi originating on the exoccipital, the *protractor hyoides* divided in three portions and inserting laterally to the *intermandibularis*, the mental barbels originating from the PH2 section of the *protractor hyoides*, and the *hyohyoidei abductores* interdigitated with its antimere.

Anduzedoras + Leptodoras

Monotypic *Anduzedoras* is recovered within the genus *Leptodoras*, represented by 10 of 12 nominal valid species, with a Bremer support of 13. The clade is supported by seven morphological and 11 molecular synapomorphies. The clade is diagnosed by the presence of oral hood, the possession of 16 to 25 gill rakers on the first branchial arch, the hypobranchial tubular, a bony capsule on the first vertebra, the *hyohyoidei abductores* originating from a portion of the first branchiostegal ray, and the *hyohyoidei abductores* posterior to the *sternohyoideus* not covering it.

Hassar

The three nominal valid species of *Hassar* are recovered as a monophylectic group with Bremer support of 22. The genus is supported by nine morphological and 24 molecular synapomorphies. *Hassar* is diagnosed by the presence of a ventral extension on the basioccipital, the lateral scutes heterogeneously developed along the body, the *adductor mandibulae* originating on the preopercle and hyomandibula, the fibers of the *levator operculi* directed posteriorly, the *adductor arcus palatini* inserted through muscular fibers, the coronomaxilar ligament present, the mental barbels originating from the PH2 section of the *protractor hyoides* (as in *Doras*), the *hyohyoidei abductores* interdigitated with its antimere (as in *Doras*), the *hyohyoidei adductores* not grouped on bundles, and the *protractor pectoralis* weakly developed and covered by the supracleithrum.

<u>*Hemidoras*</u>

Our study recovered a clade of *Opsodoras morei* plus *Hemidoras morrisi* as sister to *Hemidoras stenopeltis* with a Bremer support of 16. The clade is supported by eight molecular and 12 morphological synapomorphies. This corroborates the results of Birindelli (2006 & 2010) and agrees with the synonymization of *Opsodoras* and *Hemidoras*. *Hemidoras* is diagnosed by the presence of terminal diverticula joined on the swimbladder, the posterior process of the cleithrum elongated, shallow, and pointed posteriorly, the fibers of the *retractor tentaculi* located mesially to the *adductor mandibulae*, the tendon for insertion of the *retractor tentaculi* developed as more than half of the total length of the muscle, the mental barbels originating form the PH2 portion of the *protractor hyoides*, the fibers of the *hyohyoidei abductores* originating from a portion of the first branchiostegal ray, and the *sternohyoideus* partially exposed on ventral view.

DISCUSSION

<u>Relationships of Astrodoradinae, *Acanthodoras* and *Agamyxis*.</u>

The relationship between *Acanthodoras* and Astrodoradinae has a lower Bremer support of two. The clade is supported by only two morphological and eight molecular synapomorphies. There is no evidence, in the combined analysis, of the relationship between Astrodoradinae and *Agamyxis*.

The morphological analyses recovered Astrodoradinae inclusive of *Acanthodoras* + *Agamyxis* with a Bremer support of 2. The clade is supported by six non-exclusive synapomorphies. Sousa

(2010), in a complete phylogenetic analysis of Astrodoradinae, found the clade supported by seven non-exclusive synapomorphies.

Arce *et al*. (in prep) found no molecular evidence for a close relationship between Astrodoradinae and *Acanthodoras* or *Agamyxis.* Moyer *et al*. in their analysis of the combined dataset (EF1, 12s and 16s) found *Acanthodoras* and Astrodoradinae as successive sister-groups to all other Doradidae.

Astrodoradinae

Within Astrodoradinae (excluding *Acanthodoras* and *Agamyxis*), several relationships proposed by Sousa (2010) are consistent with the present study. The same relationships were recovered by Arce *et al*. (in prep) (e.g., *Anadoras* is the basal most taxon, and *Hypodoras* and *Astrodoras* are sister groups). Unlike Sousa (2010), *Amblydoras bolivarensis* was recovered as sister to *Scorpiodoras heckelii*. Both the current study and that of Sousa agree on the synonymization of *Merodoras* with *Amblydoras*. Although *Physopixys* is recovered as sister to the *Merodoras* + *Amblydoras*, the support of the clade is low and we do not consider the synonymization of *Physopyxis*.

Wertheimeria clade

The *Wertheimeria* clade is the multigeneric clade with the highest support of Doradidae (i.e. 29) and grouped mainly by a big amount of molecular synapomorphies (i.e. 32 vs four morphological). The combined analysis recovered (*Franciscodoras* (*Wertheimeria*, *Kalyptodoras*)) while the molecular analysis of Arce *et al.* recovered (*Wertheimeria* (*Franciscodoras*, *Kalyptodoras*)). The differences within the clade are due to the morphological evidence that group together *Wertheimeria* and *Kalyptodoras.* The support for the clade *Wertheimeria* + *Kalyptodoras* is as low as 1. The two genera shared one exclusive synapomorphy and seven non-exclusive synapomorphies, three of which are also shared by some genera of Auchenipteridae.

The morphological analyses do not recovered the *Wertheimeria* clade, the morphological evidence is just enough to group *Kalyptodoras* and *Wertheimeria* on the basis of one exclusive synapomorphy and three non-exclusive synapomorphies. Also this clade is the most basal of the family, followed by *Franciscodoras* as sister to all the other Doradidae.

Subfamily Platydoradinae sensu Birindelli (in press.)

Monotypic *Centrochir crocodili* is recovered as sister to a clade composed of the four nominal valid species of *Platydoras* with a Bremer support of 2. Although the support is not high the clade is diagnosed by five morphological and nine molecular synapomorphies. Previous molecular (Arce *et al.*, in prep) and morphological evidence (Sousa, 2010) recovered the Platydoradinae. Birindelli (in press.) did not find resolution for this clade, but he included the two genera in a subfamily named "Platydoradinae". The morphological analysis found Platydoradinae with a high Bremer support of 6.

Pterodoradini sensu Birindelli (in press.)

Combined analysis did not find evidence to group together members of the Pterodoradini sensu Birindelli (in press.). The genera are found as consecutive clades formed as (*Doraops*, *Pterodoras*) and (*Centrodoras* (*Lithodoras*, *Megalodoras*)). The same results were found by Moyer *et al.* (2004) and Arce *et al.* (in prep).

The morphological analysis groups them as a clade with a Bremer support of 1, supported by six non-exclusive synapomorphies.

Anduzedoras + Leptodoras

Anduzedoras was recovered as sister to *Leptodoras hasemani*, and them as sister to all the other *Leptodoras* included in this study. This arrangement will suggest the synonymization of *Anduzedoras*. The sister relationship of *Anduzedoras* to *Leptodoras hasemani* is only supported by two non-exclusive morphological and nine molecular synapomorphies.

Ossancora

The genus *Ossancora* was recovered as a paraphyletic group in the combined analysis. This arrangement will suggest the need to create a new genus to place *Ossancora punctata.* Although the morphological study recovered the genus as monophyletic the molecular evidence drove the combined analysis into paraphyletism. Also in their recent description of the genus Birindelli &

Sabaj Perez (2011), recognized within *Ossancora* a clade named *fimbriata*. The *fimbriata* clade is formed by *Ossancora asterophysa*, *O. eigenmanni*, and *O. fimbriata* and is defined by a unique synapomorphy: the fimbriae inserted in two distinct rows, one dorsally and one ventrally.

Nemadoras and "*Tenellus"*

Nemadoras is recovered as a monophyletic group where two clades can be differentiated. Birindelli (in press.) suggest that the genus *Nemadoras* should be restricted to *N. elongatus*, *N. hemipeltis*, and *N. humeralis*. He proposed that *N. trimaculatus*, *N. leporhinus*, and *N. ternetzi* should belong to a different "*Tenellus*". Our results do not agree with those of Birindelli. The combined analysis differs from Birindelli's on the placement of *Nemadoras trimaculatus*.

The morphological analysis shows the species of *Nemadoras* on a polytomy. The lack of resolution under the morphological analysis and the low Bremer support for the clades within Nemadoras suggest the need for more data in order to establish the relationship within the genus and the validity of "*Tenellus*".

Remaining work

This study compiles all the phylogenetic relevant information available for Doradidae, even though nomenclatural and classification changes are not proposed. The combined analysis of morphological and molecular data yields to one most-parsimonious tree where more than 50% of the clades are strongly supported. There are still some clades with low Bremer support that can lead to erroneous interpretations. As we deliver this paper we are working on gathering more molecular sequences for terminals not included in the present study. The new data will be gathered and included in the analysis to finally propose nomenclature and classification changes.

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Appendix 1. Material examined for molecular analyses..

Terminal taxon	Voucher	Tissue number	Field tag	Locality Country, basin	*RAG 1* bp	*CO1* bp	*16s* bp
Acanthodoras cataphractus I	ANSP 182251	637	P6060	Peru, Amazon			588
Acanthodoras sp1	ANSP 191096	2088	7602	Venezuela, Orinoco	1471	725	620
Acanthodoras spinossissimus	LBP 4441	1786	24313	Brazil, Negro	1471	725	620
Agamyxis albomaculatus I	LBP 3036	1780	19176	Venezuela, Orinoco	1459	689	602
Agamyxis pectinifrons I	INHS 43281	2145	PERU 97-7	Peru, Amazon	1411	681	603
Amblydoras affinis	ANSP 179797	727	2157	Guyana, Essequibo	1376	682	592
Amblydoras bolivariensis	ANSP 182267	791	V183	Venzuela, Amazon	1428	721	590
Amblydoras monitor I	ANSP 191474	2092	078	Peru, Amazon	1362	721	620
Amblydoras nauticus I	ANSP 182525	671	6021	Peru, Amazon	1333	687	594
Anadoras grypus I	ANSP 179473	t2465		Peru, Amazon	1415	682	591
Anadoras weddelli	MZUSP 103567		103567-49	Brazil, Pará	1294	720	619
Anduzedoras oxyrhynchus I	ANSP 180293			Venezuela, Orinoco	1405	641	
Astrodoras asterinifrons	INPA 24660	1532	ARI 68	Brazil, Madeira	1480	701	591
Centrochir crocodili I	ANSP 189332	1595	C001	Colombia, Magdalena	1460	718	619
Centrodoras brachiatus A	ANSP 178542		92	Brazil, Amazonas		689	615
Centrodoras hasemani I	ANSP 182227	797	4844	Venzuela, Amazon	1427	688	596
Doraops zuloagai I	N020		OC-09-006-20	Venezuela, Maracaibo	1418		600
Doras carinatus A	INHS 49321	211	788	Guyana, Essequibo	1371	723	597
Doras higuchi	MZUSP 96333		7279	Brazil, Amazonas	1406	682	582
Doras micropoeus I	ANSP 187110		6932	Suriname, Maroni	1408	673	594
Franciscodoras marmoratus	LBP 272	4193		Brazil, São Francisco	1447	761	590
Hassar affinis	UFMA	1487		Rio Mearim	1427	713	584
Hassar orestis	ANSP 181090	662	6154	Peru, Amazon	1402	639	585
Hassar wilderi	MZUSP 86216			Brazil, Tapajós	1444	683	585
Hemidoras morrisi I	ANSP 182512	687	6081	Peru, Amazon	1424	692	588
Hemidoras stenopeltis I	ANSP 182756	695	6241	Peru, Amazon	1387	675	649
Hypodoras forficulatus I	ANSP 179009	757	1540	Peru, Amazon	1451	624	592
Kalyptodoras bahiensis I	MZUSP 87839			Brazil, Paraguassú	889	725	595
Leptodoras acipenserinus I	ANSP 182202	663	p6346	Peru, Amazon	1425	699	587
Leptodoras cataniai I	ANSP 181043	676	6092	Peru, Amazon	1421	700	587
Leptodoras copei	ANSP 182225	777	V073	Venezuela, Orinoco	1407	680	580
Leptodoras hasemani I	ANSP 180897	793	4033	Venezuela, Orinoco	1416	706	594
Leptodoras juruensis I	ANSP 181046	683	6090	Peru, Amazon	1412	703	584
Leptodoras linelli I	ANSP 179631	1585	2093	Guyana, Essequibo			

Terminal taxon	Voucher	Tissue number	Field tag	Locality Country, basin	*RAG 1* bp	*CO1* bp	*16s* bp
Leptodoras marki	MNRJ 33067	M2439		Brazil, Xingú	1351		613
Leptodoras myersi	ANSP 181045	692	6205	Peru, Amazon	1427	679	596
Leptodoras oyakawai I	MZUSP 96597		7079	Brazil, Amazon	1364	724	594
Leptodoras praelongus I	ANSP 180913	1502	CALH 195	Brazil, Negro	1435	687	537
Lithodoras dorsalis I	ANSP 187376	1207	7332	Brazil, Amazon	1445	684	592
Megalodoras uranoscopus IA	ANSP 178249	753	1685	Peru, Amazon	1335	682	595
Megalodoras guayoensis	MHG	CV001	CV001	Venezuela, Maracaibo	1432	763	600
Merodoras nheco	MZUSP 96174	664	7328	Brazil, Paraguay	1394	696	561
Nemadoras elongatus I	ANSP 182295	664	p6282	Peru, Amazon	1409	720	583
Nemadoras hemipeltis I	ANSP 181095	709	6111	Peru, Amazon	1456	689	596
Nemadoras humeralis I	ANSP 178550	1523		Brazil, Amazon	1377	715	584
Nemadoras leporhinus II	ANSP 180297	780	V104	Venezuela, Orinoco	1459	733	594
Nemadoras nsp I	ANSP 180551	773	4076	Peru, Madeira	1449	717	578
Nemadoras trimaculatus I	ANSP 178252	752	1679	Peru, Amazon	1462	694	581
Opsodoras morei	ANSP 183028	864	4570	Brazil, Negro	1418	695	596
Opsodoras ternetzi I	ANSP 179203	1527		Guyana, Takutu	1396	695	596
Orinocodoras eigenmanni A	INHS 54564	290	290	Venzuela, Amazon	1333	722	594
Ossancora asterophysa	ANSP 178546	1505	CALH 200	Brazil, Negro	877	715	590
Ossancora fimbriata I	ANSP 192477		M353	Brazil, Jutai		693	568
Ossancora punctata	ANSP 187005	1803	P6333	Peru, Amazon	1456	727	613
Oxydoras kneri	ANSP 182203		5196	Argentina, Paraná	1445	684	592
Oxydoras niger I	ANSP 181080		p6056	Peru, Amazon	1423	662	588
Oxydoras sifontesi	ANSP 189324	866	4340	Venezuela, Orinoco	1434	649	603
Physopyxis ananas	ANSP 190508	2118	7576	Venezuela, Orinoco	1471	722	621
Physopyxis lyra I	ANSP 180176	762	2300	Peru, Amazon	1441	701	667
Platydoras armatulus I	ANSP 181008	714	5200	Argentina, Paraná	1447	715	597
Platydoras brachylecis	UFMA	1482		Brazil, Maranhão	1428	721	606
Platydoras costatus	ANSP 187111		7064	Suriname, Surinam	1462	715	604
Platydoras hancocki	ANSP 179144		2032	Guyana, Rupununni	1423	782	601

Terminal taxon	Voucher	Tissue number	Field tag	Locality Country, basin	*RAG 1* bp	*CO1* bp	*16s* bp
Pterodoras granulosus I	ANSP 178350	758	1560	Peru, Amazon	1425	648	595
Pterodoras rivasi	MHG	CV002	CV002	Venezuela, Apure	1411	681	583
Rhinodoras armbrusteri	ANSP 179096			Guyana, Rupununni	1398	630	595
Rhinodoras boehlkei I	ANSP 181044	675	6059	Peru, Amazon	1399	680	605
Rhinodoras dorbignyi	LBP 3218	1785	19423	Brazil, Paraguay	1451	728	623
Rhinodoras gallagheri	ANSP 191086	1777	T09020 alc	Venezuela, Guanare	1448	725	603
Rhinodoras thomersoni I	MHG		OC-09-006-21	Venezuela, Maracaibo	1389	696	557
Rhynchodoras woodsi	ANSP 181042	677	6052	Peru, Amazon	1813	708	608
Rhynchodoras woodsi I	ANSP 191480	2096		Brazil, Amazon			
Scorpiodoras heckelii	ANSP 182790	792	5404	Venezuela, Orinoco	1449	693	590
Trachydoras brevis	MHNG 2650.062		GY04091	Guyana, Rupununni	1462	713	587
Trachydoras nattereri I	ANSP 182593	706	6313	Peru, Amazon	1423	547	587
Trachydoras paraguayensis	ANSP 181011	713	5134	Argentina, Paraná	1402	664	589
Trachydoras steindachneri I	ANSP 178256	751	1673	Peru, Amazon	1380	703	593
Wertheimeria maculata I	MCP 43855		WM1	Brazil, Jequitinhonha	1492	686	602
Auchenipteridae							
Ageneiosus inermis	ANSP 189090		6996		1442		593
Ageneiosus ucayalensis	INHS 52920			Peru, Amazon			
Auchenipterus nigripinnis	ANSP 182418			Argentina, Paraná	1451	724	625
Centromochlus heckeli	ANSP 182773			Brazil, Amazon			
Gelanoglanis	ANSP 180806			Peru, Madeira	1422	695	583
Glanidium leopardum	ANSP 189104			Suriname, Maroni	1478	726	619
Liosomadoras oncinus	ANSP 191102	2087		Venezuela, Orinoco	1467	726	604
Pseudoepapterus hasemani	ANSP 178311			Peru, Amazon	1421	699	557
Trachelyopterus galeatus	INHS 49034			Guyana, Maroni			
Trachycorystes	ANSP 180820			Venezuela, Orinoco	1435	586	597
Aspredinidae							
Aspredo aspredo	ANSP 191475	2094		Brazil, Amazon		722	621
Bunocephalus verrucosus	CU 91989						
Pterobunocephalus rugosus	ANSP 185102	2091		Argentina, Paraná	865	721	619
Xyliphius	ANSP 182322			Peru, Amazon	1339	726	592

Appendix 2. Material examined for morphological analyses.

Museum abbreviations follow Sabaj Pérez (2010). The standard length (mm) is presented in parenthesis whenever available..

Doradidae: *Acanthodoras cataphractus*; ANSP 179854 (69.0), MCP 33158 (52.21). *Acanthodoras spinosissimus*; MCP 37476. *Agamyxis albomaculatus*; ANSP 153646 (97.8). *Agamyxis pectinifrons*; MCP 33150 (51.2). *Amblydoras affinis*; ANSP 179797 (67.4). *Amblydoras nauticus*; ANSP 178207 (60.9). *Anadoras grypus*; MCP 26187 (51.6), MCP 29527 (78.5). *Anadoras weddellii*; AUM 45441 (2) (60.3). *Anduzedoras oxyrhynchus*; MZUSP 45553, ANSP 178781. *Astrodoras asterinifrons*; MCP 33218 (61.2). *Centrochir crocodili*; CU 47930 (157.2), ANSP 189332. *Centrodoras brachiatus*; ANSP 181021 (108.4), MCP 26443 (146.7). *Doraops* zuloagai; ANSP 179558. *Doras carinatus*; ANSP 177276 (137.4), ANSP 180986. *Doras higuchi*; ANSP 10359 (139.9), ANSP 189363. *Doras phlyzakion*; MZUSP 82294 (145.58). *Franciscodoras marmoratus*; MCP 14115 (174.8). *Hassar affinis*; MCP 45010 (106.9), MCP 22526 (41.00). *Hassar orestis*; ANSP 180295, MCP 29721 (176.0). *Hassar wilderi*; INPA 5299 (170.7). *Hemidoras morrisi*; ANSP 180191, MCP 24078 (82.5), MCP 44320 (120.7). *Hemidoras stenopeltis*; ANSP 179162, MCP 24295 (67.8), MCP 29887 (88.3). *Hypodoras forficulatus*; ANSP 182517 (100.6). *Kalyptodoras bahiensis*; MCP 45009 (141,5 & aprox. 180.0). *Leptodoras cataniai*; ANSP 191822, MCP 29659 (65.8 & 146.1). *Leptodoras hasemani*; ANSP 179209, INPA 17705 (103.6). *Leptodoras juruensis*; ANSP 179173, MCP 24603 (2) (109.3 & 94.5). *Leptodoras linelli*; ANSP 180817, MCP 39806 (88.8 & 149.8). *Leptodoras oyakawai*; ANSP 187336, MZUSP 94141 (70.1). *Leptodoras praelongus*; ANSP 179156, INPA 21428 (169.6). *Lithodoras dorsalis*, ANSP 181024 (163.4), ANSP 187376, MZUSP 52585. *Megalodoras guayoensis*; MHNLS 20354 (135.8). *Megalodoras uranoscopus*; ANSP 181184 (131.0). *Merodoras nheco*; MCP 45548 (2) (41.9 & 56.1). *Nemadoras elongatus*; MCP 24579 (74.9). *Nemadoras humeralis*; MCP 24426 (64.9), MCP 44318 (84.7). *Nemadoras leporhinus*; ANSP 179585 (148.12), MZUSP 95617 (127.9). *Nemadoras trimaculatus*; INPA 18063, MZUSP 55774 (63.0 & 68.5). *Opsodoras morei*; ANSP 183028, MZUSP 32526 (134.4). *Opsodoras ternetzi*; ANSP 181077, ANSP 182874 (2) (87,9 & 72.3). MCP 24607 (76.0). *Orinocodoras eigenmanni*; ANSP 180891 (121.1). *Oxydoras niger*; MCP 20951 (158.7). *Oxydoras sifontesi*; ANSP 179246, ANSP 181069 (137.9); MCP 19921 (136.2). *Ossancora eigenmanni*; ANSP 182612, MCP 24575, MCP 29658 (55,6 & 55,4 & 71,4). *Ossancora asterophysa*; MZUSP 7838, ANSP 182612, MCP 25590 (71.9 & 71.6). *Ossancora fimbriata*; MCP 32951, MCP 32952 (50.8 & 74.1 & 66.9). *Ossancora punctata*; ANSP 166265, MCP 26181, MCP 29663 (62.4 & 63.7 & 38,5), MCP 45552. *Physopyxis ananas*; MCP 36418 (3) (18.7 & 16.7 & 18.6). *Physopyxis lyra*; MCP 36430 (23.4). *Platydoras armatulus*; MCP 15359 MCP 44317 (64.7). *Platydoras hancocki*; ANSP 162763 (177.0). *Platydoras* sp; MCP 22532. *Pterodoras granulosus*; MCP 24599, MCP 26275 (88.05 & 62.25). *Rhinodoras boehlkei*; SIUC 39703 (110.0). *Rhinodoras dorbignyi*; MCP 13067 (134.6). *Rhynchodoras woodsi*; ANSP 181042 (67.5). *Scorpiodoras heckelii*; MCP 15271 (71.5). *Trachydoras brevis*; ANSP 155869, MCP 36417 (59.45). *Trachydoras microstomus*; MCP 36423 (35.1). *Trachydoras nattereri*; ANSP 182454 (76.7), ANSP 182593, ANSP 191841, MCP 29390 (90.4). *Trachydoras paraguayensis*; INPA 634 (112.9), MZUSP 21109 (78.7). *Trachydoras* *steindachneri*; ANSP 179171, ANSP 183076 (58.8 & 59.5), MCP 24370 (71,2), MCP 24627, MCP 44319 (66.8). Wertheimeria *maculata*; MCP 34689 (157.7), MCP 43855 (98.2).

Auchenipteridae: *Ageniosus inermis*, ANSP 162406 (270.0), ANSP 181020. *Ageneiosus ucayalensis*; MCP 32832 (224.0), ANSP 182423. *Auchenipterus nigripinnis*; MCP 17601 (153.5). *Centromochlus heckelii*; ANSP 178331 (77.4). *Glanidium leopardum*; MZUSP 64256 (103.1). *Liosomadoras oncinus*; MCP 45029 (51.68). *Trachelyopterus galeatus*; ANSP 178388, ANSP 182244 (126.2).

Aspredinidae: *Aspredo aspredo*; ANSP 191477 (289.0). *Bunocephalus verrucosus*; ANSP 177200 (57.3).

Diplomystidae: *Diplomystes sp* MCP 18595 (127.8).

Appendix 3

Description of morphological characters.

Coloration pattern

1. Head pigmentation of Doradidae is mainly uniform and similar to the remaining parts of the body, some species of Astrodoradinae can exhibit a difference on the epithelium adjacent to the latero-ventral border of the cranium: (0) epithelium with the same color of the remaining portions of the head and body; (1) epithelium exhibit a dark stripe running along the latero-ventral margin of the neurocranium. Sousa, 2010: #1

2. Some Doradidae exhibit a conspicuous clear band along the longitudinal axis of the body, located below the lateral scutes. The origin of the stripe is variable: (0) originating on the first lateral scute, the first post-infranuchal; (1) originating on the anterior border of the postemporo-supracleithrum; (2) originating on the upper margin of the orbit, on the frontal. Sousa, 2010: #5

3. Pigmentation of the area ventral to the lateral scutes is also variable: (0) same color of the adjacent areas, sometimes exhibit conspicuous spots that are not continuous; (1) with a continuous dark band originated on the posterior process of the cleithrum and running to the caudal fin. Sousa, 2010: #6

4. Coloration of the caudal fin: (0) dark spots on the rays sometimes forming vertical lines; (1) two dark longitudinal stripes one on each lobe of the fin. Sousa, 2010: #7

External morphology

5. There is an adipose tissue, referred here as adipose eyelid, that covers the eye in some species of the family such us *Nemadoras*, *Leptodoras*, and *Opsodoras*. Well-developed adipose eyelid: (0) absent; (1) present. Birindelli, 2006: #6

6. Shape of the lips: (0) thin, without any postero-lateral projections (1) thick, with marked postero-lateral projections. Birindelli, 2006: #3;

7. Adipose fin: (0) present; (1) absent. Birindelli, 2010: #3

8. Shape of the adipose fin: (0) long and bulky; (1) elongated anteriorly as a low keel; (2) short, drop-shape. Birindelli, 2010: #4

Barbels

9. Species of *Anduzedoras* and *Leptodoras* have the mental barbels connected to lower lip by membrane, this structure is known as the oral hood. Oral hood: (0) absent; (1) present. Birindelli, 2010: #7

10. The dorsolabial membrane is a laminar expansion along the dorsomedial surface of the lower labial extension that originates on the ventrolateral corner of the snout just posterior to the base of the maxilla (Sabaj, 2002). Dorsolabial membrane: (0) absent; (1) present. Birindelli, 2010: #8

11. Length of the maxillary barbel: (0) long, it extends posteriorly beyond the anterior margin of the orbit; (1) short, it does not reach the anterior margin of the orbit. Birindelli, 2010: #10.

12. Secondary barbels on the ventral face of the maxillary barbel (0) absent (1) present. Birindeli, 2010: #11

13. Secondary barbels on the dorsal face of the maxillary barbel (0) absent; (1) present. Birindelli, 2010: #12

14. On species of Auchenipteridae there is a groove on skin of the cheek for the barbel to rest when fully abducted. Suborbital groove: (0) absent (1) present. Ferraris, 1998: #J16.

15. Transversal striae developed on the barbels: (0) absent; (1) present. Birindelli, 2006: #16.

16. Amount of pairs of mental barbels: (0) two pairs; (1) none, mental barbels absent. (Birindeli, 2010: #16

17. Rows of secondary barbels on the mental barbels: (0) none, secondary barbels absent; (1) one row; (2) two rows. Birindelli, 2010: #17

18. Length of the mental barbels when compared one to another: (0) external distinctly longer than internal; (1) external and internal with similar lengths. Birindelli, 2010: #18

19. The proximal portions of mental barbels can be conjoined to point slightly beyond terminus of dentary. Join of the mental barbels at the base: (0) absent; (1) present. Birindelli, 2010: #21

Skin and dermal accessories.

20. Dermal unculiferous tubercles are present in Doradidae and their development can be different dependent on the species: (0) small sometimes inconspicuous; (1) big and conspicuous. Birindelli, 2010: #23

21. Multiple pores in skin beneath postcleithral process: (0) absent; (1) present. Birindelli, 2006: #7.

22. Multiple conspicuous pores in skin on breast and abdomen: (0) absent; (1) present. Birindelli, 2006: #8.

23. A medial row of bony scutes between dorsal and adipose fin and between anal fin and anus: (0) absent; (1) present. Birindelli, 2006: #9.

Swimbladder

24. Size of the swimbladder: (0) not reduced as an overall; (1) reduced as an overall. Birindelli, 2010: #35

25. External tunica covering the swimbladder: (0) not ossified; (1) ossified. Birindelli, 2010: #36

26. Terminal diverticula on the swimbladder: (0) absent; (1) present and joined (2) present and distally separated. Birindelli, 2010: #39

27. Secondary chamber of the swimbladder (unordered): (0) absent; (1) present and with and internal septum; (2) present and without and internal septum. Birindelli, 2010: #40

28. Accessory posterior diverticula of the swimbladder: (0) absent; (1) finger-like shape with a basal constriction; (2) horn-like shape without basal constriction; (3) extremely well developed and branched. Birindelli, 2010: #41

29. Internal trabeculae on the swimbladder: (0) absent; (1) present. Birindelli, 2006: #26

30. Ventral surface of the swimbladder: (0) smooth; (1) with wrinkles. Birindelli, 2006: #24.

31. Accessory lateral diverticula on the swimbladder: (0) absent; (1) present. Birindelli, 2010: #44

32. Accessory lateral diverticula on the secondary chamber of the swimbladder: (0) absent; (1) present. Birindelli, 2010: #45

33. Some accessory lateral diverticula of the swimbladder, are characterized by its anterior position and because they are comparatively bigger than the remaining (Birindelli *et al.*, 2009). Those are known as anterior diverticula on the swimbladder: (0) absent; (1) present. Birindelli, 2006: #27.

34. An accessory diverticula recognizable among the remaining diverticula by its antero-lateral position: (0) absent; (1) present. Birindelli, 2006: #28.

35. Diverticula on the ventral and dorsal surfaces of the swimbladder: (0) absent; (1) present. Birindelli, 2010: #48.

Gonads and related structures

36. Posterior lobes of the testicle: (0) similar to the anterior lobes without modifications; (1) modified as hypertrophied bags; (2) rudimentary or absent. Birindelli, 2010: #49.

37. Main duct of the testicle: (0) tubular, unmodified; (1) modified as a storer vesicle. Birindelli, 2010: #50.

38. Position of the urogenital opening in males: (0) near to the anus; (1) on the base of the anal fin; (2) on the tips of the anterior rays of the anal fin. Birindelli, 2010: #51.

39. Width of the urogenital pore on females: (0) narrow; (1) wide and modified for insemination. Birindelli, 2010: #56.

40. Position of the urogenital pore on females: (0) approximately at the middle point between pelvic and anal fin; (1) immediately anterior to the anal fin. Birindelli, 2010: #57

Neurocranium

41. Dorsal profile of the mesethmoid: (0) concave; (1) convex. Birindelli, 2006: #34.

42. Shape of the mesethmoid: (0) bone broad more or less quadrangular; (1) with the distal tips slightly separated giving the bone an X shape; (2) bone distally acute with a medial expansion. Birindelli, 2010: #60.

43. Length of the mesethmoid: (0) shorter than the eye diameter; (1) longer than the eye diameter. Birindelli, 2010: #61.

44. Anterior portion of the mesethmoid: (0) similar to the posterior portion and cover by thin skin; (1) different from the posterior portion (e. g different texture and level) and cover by thick skin. Birindelli, 2010: #62.

45. The anterior rami of the mesethmoid coalesced: (0) absent; (1) present. Birindelli, 2010: #63.

46. Dorso-medial bulge on the mesethmoid: (0) absent: (1) present. Birindelli, 2010: #64.

47. Antero-ventral keel on the mesethmoid: (0) absent; (1) present but not differentiated as a ventral process; (2) present and differentiated as a ventral process. Birindelli, 2010: #65.

48. Notch posterior to the transversal mesethmoid crest: (0) absent; (1) present. Sousa, 2010: #11.

49. Longitudinal crest running along the lateral margin of the mesethmoid: (0) absent; (1) present. Sousa, 2010: #13.

50. Division of the anterior fontanel: (0) absent; (1) anterior fontanel divided in two portions by a narrow bar between the frontals; (2) anterior fontanel divided in two portions by a wide bar between the frontals. Birindelli, 2010: #67.

51. Posterior fontanel: (0) big; (1) small and almost completely closed; (2) absent, closed. Birindelli, 2010: #68.

52. Posterior cranial fontanel: (0) reaching the supraoccipital; (1) not reaching the supraoccipital. Birindelli, 2006: #60.

53. Lateral margin of the lateral ethmoid: (0) smooth or granulated; (1) serrated. Birindelli, 2006: #40;

54. Lateral process of the sphenotic: (0) absent; (1) present. Birindelli, 2010: #73.

55. Postero-lateral margin of the sphenotic: (0) slightly concave; (1) extremely concave. Birindelli, 2010: #74.

56. Frontal bone participating on the orbital margin: (0) present; (1) absent. Birindelli, 2010: #75.

57. Lateral ethmoid participating on the orbital margin: (0) present; (1) absent. Birindelli, 2006: #42.

58. Posterior process of the parieto-supra-occipital: (0) present; (1) absent. Birindelli, 2010: #80

59. Shape of the vomer: (0) anterior portion differentiated producing a T shape; (1) anterior process rudimentary producing an I shape. Birindelli, 2010: #84

60. Ventral keel on the roof of the neurocranium: (0) ventrally rounded and short; (1) ventrally acute and long. Birindelli, 2010: #89.

61. Trigeminal-facial foramen: (0) delimited posteriorly by the prootic; (1) not delimited posteriorly by the prootic. Sousa, 2010: #18.

62. Ventral extension on the basioccipital: (0) absent; (1) present forming an arch under the aorta; (2) present forming a laminar process. Birindelli, 2010: #92.

63. Suture between the exoccipital and the neural arch of the complex vertebrae: (0) absent; (1) present. Birindelli, 2010: #93.

64. The epoccipital bone participating on the lateral margin of the cephalic shield: (0) absent; (1) present. Birindelli, 2010: #95.

65. Posterior process of the epoccipital: (0) absent; (1) mainly constituted by ligament; (2) mainly constituted by bone. Birindelli, 2010: #96.

66. Suture between the posterior process of the epoccipital and the posterior nuchal plate: (0) absent; (1) present. Birindelli, 2010: #97

67. Suture between the posterior process of the epoccipital and the parapophyses of the 5th and 6th vertebrae: (0) absent; (1) present. Birindelli, 2010: #98.

68. Dorsal contact of the supracleithrum with surrounding bones of the neurocranium: (0) connected to the pterotic, epoccipital, and middle nuchal plate; (1) connected only to the pterotic and epoccipital. Birindelli, 2006: #58.

69. Orientation of the trans-scapular process: (0) approximately perpendicular to the body axis; (1) forming an acute angle (approximately 45°) with the body axis. Akama, 2004: #44.

70. Shape of the trans-scapular process: (0) ventrally rounded; (1) ventrally tapered, as a lamina. Birindelli, 2010: #105

Latero sensorial system

71. Shape of the nasal: (0) tubular; (1) dorsally expanded, apparently exposed. Birindelli, 2010: #106.

72. Contact between the infraorbital one and the lateral ethmoid: (0) weak; (1) strong, through strong ligaments and bony suture. Birindelli, 2010: #107

73. Infraorbital one participating on the orbital margin: (0) absent; (1) present. Birindelli, 2010: #109

74. Ventral process of the infraorbital one: (0) absent and short; (1) long. Birindelli, 2010: #110.

75. Transversal crest serrated on the infraorbital one: (0) absent, (1) present. Birindelli, 2006: #49.

76. Size of the anterior portion of the infraorbital one: (0) anterior portion smaller than the posterior portion, acuted; (1) anterior and posterior portion of similar size, expanded anteriorly. Birindelli, 2010: #112

77. Bony suture between the infraorbital one and the mesethmoid: (0) absent; (1) present. Birindelli, 2010: #113.

78. Expansion of the infraorbitals: (0) all infraorbitals tubular, not expanded; (1) last three infraorbitals expanded; (2) last and next to last infraorbital expanded; (3) only the next to last infraorbital expanded; (4) only last infraorbital expanded. Birindelli, 2006: #55.

79. Thorns on the infraorbitals: (0) absent; (1) present. Birindelli, 2006: #54.

80. Opening of the infraorbital canal through the sphenotic: (0) on the anterior portion of the sphenotic; (1) on the posterior portion of the sphenotic. Birindelli, 2010: #117.

81. Mandibular sensory canal: (0) present; (1) absent. Britto, 2002: #67

82. Shape of the lateral line: (0) straight, (1) sinuous. Birindelli, 2010: #124

83. Length of the lateral line: (0) lateral line incomplete; (1) lateral line complete. Sousa, 2010: #27

84. Shape of the posterior portion of the lateral line: (0) straight, not forked at the caudal fin; (1) forked with two divergent rami. Birindelli, 2010: #125

85. Neuromasts dorsal to the lateral line displayed as vertical lines: (0) absent; (1) present. Birindelli, 2010: #126

86. Lateral scutes formed from the lateral line tubules: (0) absent; (1) heterogeneously developed along the body; (2) homogeneously developed along the body. Birindelli, 2010: #127.

87. Margin of the lateral scutes: (0) smooth; (1) serrated. Sousa, 2010: #30.

88. Retrorse spines on the lateral scutes: (0) absent; (1) present. Birindelli, 2010: #128.

89. Arrange of the secondary thorns on the lateral scutes: (0) disposed in one row; (1) disposed in several rows.

90. Shape of the lateral scutes: (0) vertically elongated (1) rounded. Birindelli, 2006: #117.

91. Position of the lateral scutes: (0) vertical to the body axis; (1) inclined to the body axis. Birindelli, 2010: #129.

92. Lateral scutes depth: (0) shallow scutes, about 1/2 to 1/5 of the body depth measured at the anal fin; (1) deep scutes, about more than half of the body depth measured at the anal fin. Birindelli, 2010: #130

93. Size of the third tympanic scute: (0) conspicuously smaller than the lateral scutes; (1) about the same size of the lateral scutes. Birindelli, 2010: #131.

Mandibular arch

94. Shape of the premaxilla: (0) rectangular; (1) cone-like with a dorsal apex; (2) quadrangular; (3) extremely long reaching posteriorly beyond the lateral margin of the mesethmoid. Birindelli, 2010: #134

95. Premaxillary teeth: (0) numerous, arranged in several rows; (1) few; (2) absent. Birindelli, 2010: #137

96. Size of the maxilla: (0) short; (1) long and thin; (2) long and thick. Birindelli, 2010: #139

97. Condyles at the proximal end of the maxillar: (0) absent; (1) present. Birindelli, 2010: #140.

98. Contact between the coromeckelian bone and the dentary: (0) weak; (1) strong trough a bony suture. Birindelli, 2010: #144.

99. Teeth on the dentary: (0) numerous; (1) few; (2) absent. Birindelli, 2006: #74).

100. Length of the autopalatine: (0) short; (1) long. Birindelli, 2006: #72.

101. Posterior limit of the autopalatine: (0) reaching the anterior margin of the orbit; (1) reaching at least half of the orbit diameter. Birindelli, 2006: #73.

102. Medial expansion on the hyomandibular: (0) present; (1) absent. Birindelli, 2010: #160.

103. Crest on the hyomandibular bone for the insertion of the *levator arcus palatini* muscle: (0) absent or rudimentary; (1) slightly developed; (2) well developed. Birindelli, 2010: #161.

104. Orientation of the crest on the hyomandibular for insertion of the *levator arcus palatini* muscle: (0) horizontal; (1) vertical. Birindelli, 2010: #162.

105. Postero-dorsal process on the hyomandibular: (0) absent; (1) present. Royero, 1999: #61.

106. Opercular condyle on the hyomandibular: (0) located on a rudimentary process; (1) located on a distinct process. Birindelli, 2010: #167.

107. Hyomandibular canal for the passage of a branch of trigeminofacial nerve: (0) simple; (1) double. Royero, 1999: #60.

108. Cranial surface of hyomandibular articulation: (0) contacting the sphenotic, pterotic, and prootic; (1) contacting the sphenotic and pteroric; (2) contacting only the sphenotic. Britto, 2002: #181.

109. Dorsomedially directed lamina on the quadrate between articular surfaces of the hyomandibula and metapterygoid: (0) absent; (1) present. Birindelli, 2010: #170.

110. Contact between the hyomandibular and the metapterigoid: (0) present; (1) absent. Britto, 2002: #189.

111. Size of the mesopterygoid: (0) smaller than the metapterygoid; (1) bigger than metapterygoid but never embracing it; (2) bigger than metapterygoid and embracing it. Birindelli, 2010: #172

Opercular series

112. Supraopercle: (0) absent; (1) present. Britto, 2002: #196.

113. Subopercle: (0) absent; (1) present. Britto, 2002: #197.

114. Interopercle: (0) covered by thick skin; (1) covered by thin skin. Birindelli, 2010: #176.

115. Thorns on the preopercle: (0) absent, (1) present. Sousa, 2010: #45.

Hyoid arch

116. Ventral laminar expansions on the parurohyal: (0) present; (1) absent. Britto, 2002: #81.

117. Shape of the ventral hypohyal: (0) rectangular, wider than larger; (1) quadrangular, larger than wider. Birindelli, 2010: #180.

118. Articulation between the ventral and dorsal hypohyal: (0) totally synchondral, (1) dorsolaterally sutured. Sousa, 2010: #38.

119. Anterior margin of the ventral hypohyal: (0) smooth without thorns; (1) with thorns. Birindelli, 2010: #181.

120. Anterior process developed on the anterior ceratohyal: (0) absent; (1) small; (2) big. Birindelli, 2010: #182.

121. Articulation between the ventral hypohyal and the anterior ceratohyal: (0) without any suture or with a suture just at the anterior face of the articulation; (1) with a suture at the anterior and posterior portions of the articulation between the ventral hypohyal and the anterior ceratohyal. Birindelli, 2010: #183.

Branchial arch

122. Accessory gill lamellae on the ceratobranchial: (0) absent; (1) restricted to gill arches; (2) expanded onto the medial/lateral faces of the gill filaments. Birindelli, 2010: #187.

123. Accessory gill lamellae on the epibranchial: (0) absent; (1) present and similar to those on the ceratobranchial; (2) present as three big lamellae; (3) present as a fleshy lobule. Birindelli, 2010: #188

124. Gill rakers are located on the gill arches and distributed on rows: (0) first and fourth gill arch with two rows of gill rakers; (1) first and second gill arch supporting one row of gill rakers, while the third and fourth gill arch supported two rows; (2) first gill arch supporting one row of gill rakers, all the other gill arches without any rows of gill rakers; (3) none of the gill arches support any rows of gill rakers. Birindelli, 2010: #189.

125. Shape of the gill rakers: (0) rudimentary; (1) short; (2) long; (3) with serrated margin. Birindelli, 2010: #190.

126. Base of the gill rakers: (0) narrow, the distal and proximal portion about the same width; (1) wide, the distal portion narrower than the base. Birindelli, 2010: #191.

127. Amount of gill rakers on the first gill arch: 0) up to 15; (1) between 16 and 25; (2) more than 30. Birindelli, 2010: #192

128. Second basibranchial: (0) partially ossified; (1) totally ossified. Birindelli, 2006: #86.

129. Third basibranchial: (0) partially ossified; (1) totally ossified. Birindelli, 2006: #87.

130. The basibranchial four have a ventral process located close to the branching of the posterior gill arteries, this process have a posterior prolongation of variable length. Length of the posterior prolongation of the ventral process of the basibranchial four: (0) short; (1) long. Birindelli, 2010: #194.

131. Shape of the tip of the ventral process of the basibranchial four: (0) simple; (1) tripartite. Birindelli, 2010: #195

132. Accessory basibranchial cartilage located between the third and fourth basibranchial: (0) absent; (1) present. Ferraris, 1988: #G2.

133. Shape of the basibranchial one: (0) rounded; (1) tubular. Birindelli, 2010: #197.

134. Shape of the fifth ceratobranchial: (0) with medial portion gradually expanded; (1) pedunculated with teeth located distally from the anterior end. Birindelli, 2010: #199.

135. Arrangement and amount of teeth on the ceratobranchial five: (0) numerous teeth disposed on a large portion of the bone surface; (1) few, restricted to one row disposed on the medial rim of the bone. Birindelli, 2010: #200.

136. Shape of the first epibranchial: (0) with medial portion not expanded; (1) with medial portion expanded. Birindelli, 2010: #201.

137. First pharyngobranchial: (0) present; (1) absent. de Pinna, 1993: #140.

139. Shape of the pharyngobranchial toothplate: (0) rounded; (1) elongated; (2) extremely long. Birindelli, 2010: #207.

Axial skeleton

140. Lateral expansion of the first vertebra: (0) absent; (1) present. Birindelli, 2010: #208.

141. Bony capsule on the first vertebrae: (0) absent; (1) present. Birindelli, 2010: #209.

142. Shape of the bony capsule of the first vertebrae: (0) short with posterior opening big; (1) short with posterior opening small; (2) wide and globular with posterior opening small. Birindelli, 2010: #210.

143. Degree of development of the *tripus*: (0) well developed with a bony extension curved weakly connected to the swimbladder wall; (1) not well developed with a flat structure strongly connected to the swimbladder wall. Birindelli, 2010: # 211.

144. Degree of development of the *os suspensorium*: (0) normally developed fused to the parapophysis of the complex vertebra; (1) reduced into a bony nodule connected to the parapophysis of the complex vertebra only by a ligament. Birindelli, 2010: #212.

145. Shape of the disc on the Müllerian ramus: (0) long and thin; (1) compact and conic; (2) reduced and tapered. Birindelli, 2010: #219.

146. Size of the parapophysis of the fifth vertebra: (0) big, similar size to those on the other vertebrae; (1) reduced, sometimes absent or conspicuously smaller than those on the other vertebrae; (2) extremely big, bigger than those on the other vertebrae. Birindelli, 2010: #221.

147. Ligament between the Müllerian ramus (anterior limb of parapophysis 4) and the lateral line: (0) absent; (1) present. Birindelli, 2010: #222.

148. Ligament between the first rib and the posterior nuchal plate: (0) absent; (1) present and not ossified; (2) present and ossified. Birindelli, 2010: #223.

149. Humero vertebral ligament: (0) absent; (1) present. Birindelli, 2010: #225.

150. Aortic canal: (0) ventrally open; (1) ventrally cover by a superficial ossification. Birindelli, 2010: #226.

151. Sixth vertebra: (0) free from the complex vertebra; (1) partially fused to the complex vertebra. Birindelli, 2006: #95.

152. Seventh vertebra: (0) free from the complex vertebra; (1) partially fused to the complex vertebra. Higuchi, 1992: #69.

153. Eighth vertebra: (0) free from the complex vertebra; (1) partially fused to the complex vertebra. Higuchi, 1992: #70.

154. Bony nodule on the parapophysis of the sixth vertebra: (0) absent; (1) present. Higuchi, 1992: #A53.

155. Articulation of the first ribs to parapophysis of the vertebra: (0) ventral; (1) dorsal. Birindelli, 2010: #233.

Dorsal fin

156. Bones on the cephalic shield: (0) compact; (1) trabeculated. Birindelli, 2010: #237.

157. Dorsal profile of the cephalic shield on a transversal view: (0) slightly convex forming an angle of about 180°; (1) arched forming and angle of about 90°. Birindelli, 2010: #238.

158. Nuchal foramina: (0) absent; (1) present and well developed; (2) present and not well developed. Birindelli, 2006: #106.

159. Anterior nuchal plate: (0) present; (1) absent. Birindelli, 2010: #242.

160. Contact between the middle nuchal plate and the supraoccipital: (0) absent; (1) present. Royero, 1999: #23.

161. Locking mechanism of the dorsal fin: (0) present; (1) absent. Birindelli, 2010: #249.

162. Mobility of the dorsal-fin spine in an angle bigger than 90° in mature males: (0) absent; (1) present. Royero, 1999: #127.

163. Serrae on the anterior margin of the dorsal fin: (0) absent or rudimentary; (1) present. Royero, 1999: #80.

164. Serrae on the posterior margin of the dorsal spine: (0) absent; (1) present. Royero, 1999: #79.

165. Thorns on the lateral margins of the dorsal spine: (0) absent; (1) present. Birindelli, 2006: #114.

Pectoral girdle

166. Anterior margin of the pectoral girdle: (0) arched, slightly convex; (1) anteriorly elongated with the margins convergent and the end truncated; (2) anteriorly elongated with the margins convergent and the end pointed. Birindelli, 2006: #126.

167. Fenestrae on the locking mechanism of the pectoral spine: (0) present; (1) absent. Birindelli, 2010: #266.

168. Size of the second radial proximal of the pectoral fin: (0) normal; (1) big, supporting several rays. Birindelli, 2010: #268.

169. Dorsal process at the base of the pectoral fin spine: (0) big, helicoidal, strongly embedded on the cleithrum; (1) small, not helicoidal, weakly embedded on the cleithrum. Birindelli, 2010: #269.

170. Thorns on the anterior margin of the pectoral fin spine: (0) absent; (1) present. Ferraris, 1988: #P7.

171. Thorns on the dorsal face of the pectoral fin spine: (0) absent; (1) present only on the anterodorsal margin of the spine; (2) present on all the dorsal face of the spine. Birindelli, 2010: #273.

172. Length of the pectoral spine: (0) less than 1/3 of the standard length; (1) more than 1/3 of the standard length. Birindelli, 2010: #274.

173. Anteromedial notch on the dorsal process of the cleithrum: (0) absent; (1) present. Sousa, 2010: #62.

174. Postero-dorsal process of the cleithrum: (0) well developed; (1) absent or weakly developed. Birindelli, 2010: #277.

175. Posterior process of the cleithrum: (0) absent; (1) small; (2) big. Birindelli, 2010: #278.

176. Shape of the posterior process of the cleithrum: (0) elongated, shallow and pointed posteriorly; (1) triangular, deep, and short; (2) trapezoidal; (3) narrow in all its length. Birindelli, 2010: #279.

177. Thorns on the exposed portion of the posterior process of the cleithrum: (0) absent; (1) present and unevenly distributed; (2) present and aligned over longitudinal crests. Birindelli, 2006: #129.

178. Posterior process of the coracoid: (0) small; (1) big, ventrally flat and covered by thin skin; (2) big and laminar. Birindelli, 2010: #282.

179. Posterior margin of the coracoid: (0) slightly expanded dorsally; (1) extremely expanded dorsally, forming a bony diaphragm. Birindelli, 2010: #283.

180. Postero-ventral margin of the coracoid: (0) laminar forming a small ventral rim; (1) ventrally flat and apparently exposed. Birindelli, 2010: #284.

181. Crest on the coracoid that separates the muscles *abductor superficialis* and *arrector ventralis*: (0) absent; (1) present. Birindelli, 2006: #133.

182. Direction of the crest on the coracoid that separates the muscles *abductor superficialis* and *arrector ventralis*: (0) oblique, curved towards the front; (1) straight, approximately transversal to the body axis. Birindelli, 2010: #286.

183. Bony lamina posterior to the transversal bony diaphragm of the coracoid: (0) absent; (1) present. Sousa, 2010: #72.

Pelvic girdle

184. Position of the pelvic girdle: (0) in the posterior half of the body; (1) on the anterior half of the body. Higuchi, 1992: #108.

185. Amount of branched rays on the pelvic fin: (0) 5; (1) 6; (2) between 9 and 16. Birindelli, 2010: #288.

186. Cartilaginous radial of the pelvic fin: (0) present; (1) absent. Britto, 2002: #277.

187. Anterior process of the basipterygium: (0) present; (1) absent. Birindelli, 2010: #297.

188. Medial process of the basypterygium: (0) absent; (1) present. Sousa, 2010: #78.

189. Relation between the antero-medial rami of the basipterygium and the basipterygium: (0) antero-medial rami free of the basipterygium; (1) antero medial rami partially incorporated to basipterygium; (2) antero-medial rami completely incorporated to basipterygium. Birindelli, 2010: #298.

190. Cartilaginous lateral process of the basipterygium; (0) absent; (1) present. Birindelli, 2010: #300.

191. Posterior process of the basipterygium: (0) present; (1) absent. Birindelli, 2010: #301.

Anal fin

192. Shape of the first unbranched ray of the anal fin: (0) normal, nor modified as a plate; (1) modified as a plate. Birindelli, 2010: #313.

193. Size of the anterior rays of the anal fin on mature males: (0) small, similar to the other ones; (1) big, more expanded than the other ones. Birindelli, 2010: #316.

Caudal skeleton

194. Shape of the caudal fin: (0) forked; (1) truncated; (2) rounded. Birindelli, 2010: #317.

195. Shape of the procurrent rays: (0) cylindrical, similar to all the other rays of the caudal fin; (1) modified as plates that cover the caudal peduncle dorsally and ventrally. Birindelli, 2010: #318.

196. Distribution of the procurrent rays of the caudal fin: (0) not reaching the base of the adipose and anal fin; (1) reaching the bases of the adipose and anal fin. Sousa, 2010: #84.

197. Lateral thorns on caudal fin rays: (0) absent; (1) present. Birindelli, 2010 #319.

198. Amount of branched rays on the dorsal lobe of the caudal fin: (0) 8; (1) 7; (2) 6.

199. Fusion of the dorsal elements of the caudal skeleton: (0) third, fourth, and fifth hypural not fused; (1) third and fourth hypural fused and fifth hypural free; (2) third, fourth, and fifth hypural fused. Birindelli, 2010: #326.

200. Fusion of the ventral element of the caudal skeleton: (0) parypural and hypurals one and two not fused; (1) hypurals one and two fused and parahypural free; (2) parypural and hypurals fused. Birindelli, 2010: #327.

Miology

Adductor mandibulae

201. The *adductor mandibulae* is the most conspicuous muscle in the cheek with a variable shape that can cover other muscles also located on the cheek. The A2A3 potion of the *adductor mandibulae*: (0) covering all the other muscles of the cheek; (1) covering partially other muscles of the cheek; (2) not covering other muscles of the cheek.

202. The A2A3 shows different degree of developments: (0) muscle developed as a robust mass of fiber with a dorsal surface flat; (1) muscle developed as a thin mass with a dorsal surface laminar.

203. Bones of the suspensorium related to the origin of the A2A3 portion: (0) preopercle and hyomandibula; (1) preopercle, hyomandibula, and quadrate; (2) preopercle, hyomandibula, quadrate, and metapterygoid.

204. Origin of the A2A3 portion on the neurocranium, fibers attached to the sphenotic: (0) absent;(1) present.

205. Portion of the preopercle to which the *adductor mandibulae* is attached: (0) origin of the muscle covering the preopercle in all its length; (1) origin of the muscle not covering the total length of the bone.

206. Origin of the A2A3: (0) divided; (1) not divided.

207. Bones on which the A2A3 portion inserts: (0) retroanguloarticular; (1) retroanguloarticular and dentary; (2) dentary. Modified from Diogo, 2005: #210 and Datovo, 2010: #1

208. The *adductor mandibulae* runs along the preopercle. Ventrally the A2A3 portion: (0) is completely attached to the preopercle; (1) not totally attached to the preopercle, leaving a ventral portion free from the bone.

209. Type of insertion of the A2A3 portion: (0) trough muscular fibers; (1) trough a mixture of muscular and tendinous fibers.

210. The A2A3 receive this name as it represents two different sections of the *adductor mandibulae* (Arce in prep). In some specimens there are remnant tendinous fibers that can constitute evidence of the separation of the portions. These fibers are located on the mesial surface of the muscle. Tendinous fiber on the A2A3: (0) absent; (1) present.

Retractor tentaculi

211. The *retractor tentaculi*: (0) undivided along all its length; (1) divided partially or totally along its length. Modified from Datovo & Bockman, 2010: #6.

212. Width of the *retractor tentaculi* along its length: (0) uniform, the muscle appears to have the same width along all the length; (1) not uniform, area of origin conspicuously wider than area of insertion.

213. Area of origin of the *retractor tentaculi*: (0) on suspensorium; (1) on neurocranium; (2) fibers originating from the *adductor arcus palatini*. Modified from Diogo, 2005: #219 and Datovo & Bockman, 2010: #8.

214. Portion of the suspensorial elements related to the origin of the *retractor tentaculi*: (0) muscular fibers arising from the dorsal margin of the suspensorial elements; (1) muscular fibers rising from the dorsal surface of the suspensorial elements.

215. Type of origin of the *retractor tentaculi*: (0) only through muscular fibers; (1) through muscular and tendinous fibers. Modified from Datovo & Bockman, 2010: #10.

216. The *retractor tentaculi* and the *adductor mandibulae* originate from the same area of the suspensorium. Relation between the fibers of the *retractor tentaculi* and the fibers of the *adductor mandibulae* at the origin: (0) fibers of the *retractor tentaculi* and *adductor mandibulae* totally mixed at the origin; (1) fibers of the *retractor tentaculi* and *adductor mandibulae* partially mixed but origins are recognizable (0) fibers of the *retractor tentaculi* and *adductor mandibulae* not mixed, origin of each muscle completely separated.

217. Position of the *retractor tentaculi* compared to the *adductor mandibulae*: (0) the *retractor tentaculi* located dorsally to the *adductor mandibulae*; (1) fibers of the *retractor* tentaculi mesial to those of the *adductor tentaculi*; (2) *retractor tentaculi* located anteriorly to the *adductor mandibulae*; (3) posterior half of the *retactor tentaculi* located behind fibers of the *adductor mandibulae*, anterior half located dorsally to the *adductor mandibulae*.

218. Sites of insertion of the *retractor tentaculi*: (0) solely onto the lower jaw; (1) onto the lower jaw and mainly in the maxilla; (2) onto the bucopalatal membrane; (3) onto the maxilla, in some specimens even reaching the premaxilla and anteriormost portion of the autopalatine; (4) onto the dentary and bucopalatal membrane. Modified from Datovo & Bockman, 2010: #7.

219. Type of insertion of the *retractor tentaculi*: (0) through tendinous fibers; (1) through muscular fibers; (2) through muscular and tendinous fibers.

220. The fibers of the *retractor tentaculi* can be divided towards the insertion allowing multiple areas of contact between the muscle and the bone. Points of insertion of the *retractor*: (0) one point; (1) two different points; (2) three different points.

221. In some species the *retractor tentaculi* developed tendinous fibers to insert on the bone. Length of the tendon toward the insertion: (0) the tendon of the *retractor tentaculi* is developed on the anterior half or even more than half of the total length of the muscle; (1) the tendon of the *retractor tentaculi* is developed on less than half of the total length of the muscle.

222. The *retractor tentaculi* originates from the hyomandibula and inserts on structures related to the lower jaw. The anterior area of the muscle occupies the same area where the autopalatine is located. Relation between the *retractor tentaculi* and the autopalatine: (0) the *retractor tentaculi* does not contact the autopalatine, usually the muscle is located posterior to the bone and diagonal to it; (1) the *retractor tentaculi* contact the autopalatine, usually runs along with the bone.

Levator arcus palatini

223. Appearance of the *levator arcus palatini* in lateral view: (0) muscle flat, located posteriorly to the eye and attached to the surface of the hyomandibula (fig); (1) muscle outstanding from the hyomandibula (fig).

224. Relation between the fibers of the *levator arcus palatini* at the insertion and the fibers of the *adductor mandibulae* at the origin: (0) insertion of the *levator arcus platini* splits the origin of the *adductor mandibulae*; (1) insertion of the *levator arcus palatini* slightly contacting without splitting the origin of the *adductor mandibulae*; (2) insertion of the *levator arcus palatini* not contacting the origin of the *adductor mandibulae*.

225. Size of the *levator arcus palatini* compared to the size of the *dilatator operculi* in lateral view: (0) *levator arcus palatini* wider than the *dilatator operculi*; (1) *levator arcus palatini* narrower than *dilatator operculi*; (2) *levator arcus palatini* and *dilatator operculi* of approximately the same size.

226. Bones related to the origin of the *levator arcus palatini*: (0) sphenotic; (1) sphenotic and frontal; (2) sphenotic and lateral ethmoid; (3) pterotic.

227. In most species the sphenotic participates on the origin of the *levator arcus palatini*. Portion of the sphenotic from where the fibers originate: (0) anterior half of the bone; (1) posterior half of the bone. In *Liosomadoras* and *Leptodoras cataniai*, the fibers originate from the middle of the bone. The character was coded as inapplicable for those two species.

228. Direction of the fibers of the *levator arcus palatini* at the origin: (0) longitudinal to the bone; (1) transversal to the bone; (2) fibers are disposed longitudinally and transversally.

229. Direction of the fibers of the *levator arcus palatini* at the insertion: (0) longitidinal to the bone; (1) transversal to the bone; (2) fibers are disposed longitudinally and transversally.

230. Area of insertion of the *levator arcus palatini*: (0) on hyomandibula; (1) on hyomandibula and quadrate or just quadrate. Modified from Diogo, 2005: #240.

Dilatator operculi

In Doradidae, the *dilatator operculi* is divided in portions named DO1, DO2 and DO3 (Arce, in prep).

231. Differentiation of the *dilatator operculi*: (0) in one portion; (1) in two portions; (2) in three portions.

232. Origin of the DO1 portion of the *dilatator operculi*: (0) frontal bone; (1) frontal and sphenotic; (2) frontal and orbitosphenoid; (3) frontal, lateral ethmoid and orbitosphenoid; (4) frontal, sphenotic and lateral ethmoid. Modified from Diogo, 2005: #243 and Datovo & Bockman, 2010: #27.

233. Insertion of the DO1 portion compared to the position of the DO2 portion of the *dilatator operculi*: (0) insertion of the DO1 lateral to the DO2 portion; (1) insertion of the DO1 ventral to the DO2; (2) insertion of the DO1 ventrolateral to the DO2 portion.

234. DO2 portion of the *dilatator operculi*: (0) absent; (1) present. Modified from Datovo & Bockman, 2010: #29.

235. DO3 portion of the *dilatator operculi*: (0) absent; (1) present. Modified from Datovo & Bockman, 2010: #32.

236. Insertion of the DO3 portion of the *dilatator operculi*: (0) covering the same area as the insertion of the DO1; (1) wider than the insertion of the DO1 portion appearing in lateral view; (2) narrower than the insertion of DO1 and restricted to the posterodorsal portion of the opercle.

Levator operculi

237. Origin of *levator operculi*: (0) restricted to the pterotic; (1) pterotic and supracliethrum; (2) restricted to the supracleithrum.

238. Insertion of *levator operculi* on opercle: (0) *levator operculi* not attaching on significant part of lateral surface of opercle; (1) *levator operculi* attaching on significant part of lateral surface of opercle. Diogo, 2005: #250.

239. Orientation of the fibers of the *levator operculi* running from the origin to the insertion: (0) anteriorly; (1) posteriorly; (2) transversally.

Adductor operculi

240. Origin of the *adductor operculi*: (0) prootic; (1) pterotic; (2) supracleithrum; (3) pterotic and supracleithrum; (4) exoccipital. Modified from Diogo, 2005: #246.

241. Insertion of *adductor operculi*: (0) the area of insertion of the *adductor operculi* is the same as the area of insertion of the *levator operculi*; (1) the area of insertion of the *adductor operculi* is wider than the area of insertion of the *levator operculi*; (2) the *adductor operculi* is inserted anteriorly to the insertion of the *levator operculi.* Modified from Diogo, 2005: #248.

242. Orientation of the fibers of the *adductor operculi* running from the origin to the insertion: (0) anteriorly; (1) posteriorly; (2) transversally

Adductor arcus palatini

243. Origin of *adductor arcus palatini*: (0) vomer and parasphenoid; (1) lateral ethmoid, orbitosphenoid, pterophenoid and parasphenoid; (2) parasphenoid and pterosphenoid.

244. The insertion of the *adductor arcus palatini* always involves the hyomandibula. Some other bones work as the area of attachment of the *addcutor arcus palatini*: (0) metapterygoid and mesopterygoid; (1) metapterygoid; (2) mesopterygoid; (3) quadrate; (4) quadrate and metapterygoid.

245. Type of insertion of the *adductor arcus palatini*: (0) muscular; (1) muscular and membranous.

246. Relation between *adductor arcus palatini* and the mesopterygoid: (0) *adductor arcus palatini* not associated with the mesopterygoid; (1) significant part of fibers of the *adductor arcus palatini* attached to the mesopterygoid. Modified from Diogo, 2005: #246.

Extensor tentaculi

247. Bones involved on the origin of *extensor tentaculi*: (0) lateral ethmoid and orbitosphenoid; (1) frontal; (2) lateral ethmoid and frontal; (3) lateral ethmoid; (4) orbitosphenoid.

248. Subdivisions of the *extensor tentaculi*: (0) muscle not divided; (1) muscle divided in two slips that are partially mixed towards the insertion; (2) muscle divided in two slips with a slit in between the two portions.

249. Orientation of the fibers of the *extensor tentaculi*: (0) all fibers of the muscle directed transversally from the origin to insertion; (1) fibers of the muscle obliquely disposed, some directed anteriorly and some directed posteriorly.

250. On species with *extensor tentaculi* divided: (0) inner and outer portions of about the same width; (1) inner portion of the muscle wider than the outermost portion appearing in lateral view.

251. Insertion of the *extensor tentaculi*: (0) dorsal to the autopalatine; (1) ventral to the autopalatine.

252. Portion of the autopalatine related with insertion of the *extensor tentaculi*: (0) *extensor tentaculi* inserted in the anterior portion of the palatine, reaching less than half of the length of the bone; (1) *extensor tentaculi* inserted in the anterior portion of the palatine, reaching half of the length of the bone.

Coronomaxilar ligament.

The coronomaxillar ligament is defined as a ligament that connects the maxilla to the lower jaw (Arce in prep.)

253. Coronomaxilar ligament: (0) present; (1) absent.

Ventral muscles

Barbels

254. Mandibular barbels are associated with a basal “elastic/cell-rich cartilage” which usually consists on an anterior and a posterior part (Diogo *et al*., 2003). Shape of the cartilage in which the barbel is embedded: (0) oval to rounded; (1) quadrangular; (2) elongated; (3) irregular.

Intermandibularis* and *protractor hyoidei

255. Shape and position of the *intermandibularis*: (0) rounded muscle that join left and right side of the dentary, appearing in ventral view; (1) transversal fibers running form one side to another of the dentary, the muscle is located dorsal to the mental barbels, not appearing in ventral view.

256. The *protractor hyoides* is located posterioly to the *intermandibularis* and the fibers of one another are related in different ways: (0) fibers of the *protractor hyoidei* embracing the *intermandibularis* to reach the dentary; (1) fibers of the *protractor hyoidei* pass ventrally to the *intermandibularis* to insert on the dentary; (2) fibers of the *protractor hyoidei* run laterally to the *intermandibularis.*

257. Divisions of the *protractor hyoide*: (0) undivided; (1) divided in two portions; (2) divided in three portions; (3) divided in more than three portions. Modified from Diogo, 2005: #30.

258. The mental barbels originate in different portions of the *protractor hyoidei*: (0) barbels originating from the external ventral portion of the *protractor* PH2; (1) barbels originating from the internal ventral portion of the *protractor* PH3; (2) barbels originating from the external and internal portions PH2 and PH3.

259. Origin of the *protractor hyoidei*: (0) on the anterior ceratohyal; (1) on the anterior and posterior ceratohyal.

260. Origin of all the portions of the *protractor hyoidei*: (0) all the portions originating on the same area, sometimes the portions can not be differentiated at the origin; (1) the portions have different areas of origin, usually the dorsal-most fibers originate more posteriorly than the ventral-most fibers.

261. The *protractor hyoidei* inserts always on the dentary, but the type of insertion is variable: (0) tendinous; (1) muscular; (2) muscular and tendinous.

262. Portions of the *protractor hyoidei* meets its antimere on a mesial aponeurosis: (0) only the ventral PH3 portion meeting on a mesial aponeurosis; (1) ventral PH3 and dorsal PH1 portions meeting on a mesial aponeurosis. Modified from Diogo, 2005: #34.

Hyohyoides inferioris

263. Origin of the *hyohyoides inferioris*: (0) on the anterior ceratohyal; (1) on the anterior and posterior ceratohyal.

264. Fibers at the origin of the *hyohyoides inferioris* related to fibers at the origin of the *protractor hyoides*: (0) fibers of the *hyohyoides inferioris* slightly contacting fibers of the *protractor hyoides*; (1) fibers of the *hyohyoides inferioris* lay ventrally to the *protractor hyoides*; (2) fibers of the *hyohyoides inferioris* lay dorsally to the *protractor hyoides*.

265. The *hyohyoides inferioris* meets its antimere in a mesial aponeurosis and in some species a tendon is also developed for the insertion to the hypohyal: (0) tendon absent, the muscle only meets its antimere on the medial aponeurosis; (1) two tendinous fibers developing from the mesial aponeurososis and crossing ventrally to the muscular fibers, conspicuously meeting in a medial point before reaching the bone; (2) two tendinous fibers developing from the anteriormost portion of the muscle.

266. Type of insertion of the hyohyiodes inferioris: (0) muscular; (1) muscular and tendinous.

267. Disposition of the fibers of the *hyohyoides inferioris*: (0) muscle disposed transversally; (1) muscle disposed obliquely

268. Fibers of the *hyohyiodes inferioris* related to the urohyal: (0) urohyal covered by the *hyohyoides inferioris*; (1) urohyal exposed.

Hyohyoidei abductores and adductores.

269. Origin of the *hyohyoiodes abductores*: (0) muscular fibers originating from the entire length of the first branquiostegal ray; (1) muscular fibers originating from a portion of the first branchiostegal ray.

270. Contact between *hyohyoiodes abdcutores* and pectoral girdle: (0) *hyohyoiodes abdcutor* does not come into contact with the pectoral girdle; (1) *hyohyoiodes abdcutor* hypertrophied, with median aponeurosis firmly attached to pectoral girdle; (2) *hyohyoideus abductor* even more hypertrophied, with some of its fibers inclusively inserted directly on ventral surface of pectoral girdle. Diogo, 2005: #37.

271. Contact between left and right *hyohyiodes abductores*: (0) left and right muscles connected by a membrane; (1) left and right muscles connected on the most anterior portion; (2) left and right muscles connected along all the length of the *hyohyoidei abductores*; (3) left and right muscles interdigitated.

272. Orientation of the fibers of the *hyoioides abductores* originated on the anterior half of the branchiostegal ray: (0) transversally; (1) anteriorly.

273. Orientation of the fibers of the *hyoioides abductores* originated on the posterior half of the branchiostegal ray: (0) transversally; (1) anteriorly; (2) posteriorly.

274. Position of the *hyoioides abductores* muscle in relation to the *sternohyoideus*: (0) *hyoioides abductores* ventral to the origin of the *sternohyoideus* covering it partially; (1) *hyoioides abductores* posterior to the *sternohyoideus.*

275. Distribution of the fibers of *hyohyiodes abductores*: (0) muscle constituted of independent fibers; (1) muscle constituted of bundles.

276. Distribution of the fibers of *hyohyiodes adductores*: (0) muscle constituted of independent fibers; (1) muscle constituted of bundles.

Sternohyoideus

277. *Sternohyoideus*: (0) partially exposed in ventral view; (1) not exposed in ventral view.

278. Division of the *sternohyoideus*: (0) undivided; (1) divided.

279. Posteroventral attachment of *sternohyoideus*: (0) fibers of *sternohyoideus* attach on anterodorsomedial surface of pectoral girdle; (1) fibers of *sternohyoideus* attach not only on anterodorsomedial but also on dorsolateral surface of pectoral girdle. Diogo, 2005: #39.

Protractor Müllerian

280. Presence of *protractor Müllerian*: (0) absent; (1) present. Diogo, 2005: #254.

281. Differentiation of *protractor Müllerian*: (0) undivided; (1) divided. Modified from Diogo, 2005: #255.

Protractor pectoralis

282. Development of the *protractor pectoralis*: (0) well-developed muscle inserting on the anterodorsal portion of the pectoral girdle. Not cover by the supracleithrum, appearing in lateral view, and even sometimes appear slightly anterior to the supracleithrum leaving a space between the bone and the muscle; (1) muscle inserting on the anterodorsal portion of the pectoral girdle, usually short. Covered by the supracleithrum, not appearing in lateral view. Modified from Diogo, 2005: #50.

Muscles of the pectoral fin

283. *Abductor superficialis*: (0) exposed; (1) partially to totally covered by bone.

284. *Arrector ventralis*: (0) exposed; (1) partially to totally covered by bone.

285. *Arrector dorsalis*: (0) exposed; (1) partially to totally covered by bone.

286. Origin of the *abductor superficialis*: (0) fibers originating mainly from the keel on the coracoid ventral surface, some fibers could reach farther than the keel on the ventral surfaces of the bone; (1) fibers originating from the keel and the posterior the surface of the coracoid meeting its antimere on the suture of the left and right coracoids. Fibers never reach farther than the posterior half of the pectoral girdle; (2) fibers originating from the keel and the posterior surface of the coracoid meeting its antimere on the suture of the left and right coracoids. Fibers reach farther than the posterior half of the pectoral girdle; (3) fibers originating on the anterior portion of the posterior process of the coracoid; (4) along the internal margin of the pectoral girdle on the cleithrum and coracoid.

287. Relation between origin of *abdcutor superficialis* and origin of *arrector dorsalis*: (0) fibers of the two muscles meeting; (1) fibers of the *abductor superficialis* covered by the most posterior fibers of the *arrector dorsalis*.

288. Origin of the *adductor superficialis*: (0) on the dorsal process of the cleithrum; (1) on the Baudelot's ligament.

289. Origin of the *arrector ventralis*: (0) on the ventral surface and margins of cleithrum and coracoid; (1) on the ventral surface and margins of cleithrum and coracoid and on the coracoid keel; (2) anteriormost area of the cleithrum.

290. Shape of the *arrector ventralis* internal margin: (0) muscle margin straight to slightly convex; (1) muscle margin divided with some shorter fibers appearing more internally, in some species could appear as a concave margin.

291. Orientation and division of the fibers of ventral portion of the *arrector dorsalis*: (0) all the fibers of the muscle directed diagonally from origin to insertion; (1) fibers along the pectoral girdle transversally disposed; (2) fibers of the muscle directed to the middle portion of the muscle confluent into one or two tendons that go to the area of insertion; (3) fibers of the muscle directed to the middle portion and divided.

Appendix 4. Matrix of morphological characters

Doradidae

Acanthodoras cataphractus
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Acanthodoras spinossisimus
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Agamyxis albomaculatus
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Agamyxis pectinifrons
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Amblydoras affinis
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Amblydoras nauticus
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Anadoras grypus
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Anadoras wedelli
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Anduzedoras oxyrhynchus
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Astrodoras asterinifrons
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Centrochir crocodili
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Centrodoras brachiatus
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Doraops zuolagai
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Doras carinatus
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Doras higuchi
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Doras phyzakion
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Franciscodoras marmoratus
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Hassar affinis
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Hassar orestis
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Hemidoras stenopeltis
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Hypodoras forficulatus
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Leptodoras juruensis
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Leptodoras linelii
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Leptodoras oyakawai
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Leptodoras praelongus
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Lithodoras dorsalis
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Megalodoras guayoensis
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Megalodoras uranoscopus
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Merodoras nheco
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Nemadoras elongatus
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Nemadoras humeralis
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Nemadoras leporhinus
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Nemadoras trimaculatus
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Opsodoras ternetzi
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Opsodoras morei
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Orinocodoras eigenmanni
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Ossancora eigenmanni
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Ossancora punctata
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Ossancora fimbriata
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Ossancora asterophysa
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Oxydoras niger
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Scorpiodoras heckelii
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Auchenipteridae
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Centromochlus heckelii
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Glanidium leopardum
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Liosomadoras oncinus
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0 0 0 0 0 0 2 0 0 0 1 1 0 0 0 1 0 1 0 0 0 0 0 1 1 0 1 0 0 1 0 1 0 0 0 1 0 0 1 1 3

Trachelyopterus galeatus
? ? ? ? 0 0 0 2 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 2 0 0 0 0 0 ? ? ? 0 1 0 2 1 1 0 0 0 1 0 0 0 0 0 1 2 1 0 0 0 1 0 1 0 0 1 0 1
1 2 0 0 1 0 0 1 1 1 0 0 0 0 0 0 0 0 1 1 1 1 0 - ? - - ? ? ? 0 0 0 1 0 0 0 0 0 1 1 1 0 1 2 0 0 0 1 1 0 0 1 0 ? 0 0 0 0 0 1 0 0
0 ? ? 0 0 1 1 0 0 0 1 1 0 0 0 ? 1 1 0 1 0 1 0 1 1 1 1 0 1 0 0 0 0 0 0 0 0 1 0 0 0 0 1 1 0 0 0 0 1 0 0 0 0 0 1 0 0 0 0 0 1 0 0
0 1 0 0 1 1 0 0 0 1 1 2 0 0 1 1 0 1 0 ? 0 1 0 1 0 1 0 1 3 0 0 0 - 0 1 0 0 0 0 0 0 0 2 5 2 0 0 - 1 0 1 1 1 1 0 1 1 - 2 0 0 - 0
0 0 1 0 0 2 1 0 0 1 0 0 0 1 1 0 0 0 0 0 0 0 1 1 0 1 0 1 1 0 1 0 0 0 1 0 1 1 0 3

Aspredinidae

Aspredo aspredo
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0 0 - - 1 1 0 1 0 0 0 0 - 0 0 0 0 0 0 ? 0 ? 0 - - - ? - - - 2 1 2 1 1 0 0 0 1 0 - 0 - 0 1 0 1 0 0 0 0 0 1 1 - 0 0 0 0 0 0 0 1 0 ?
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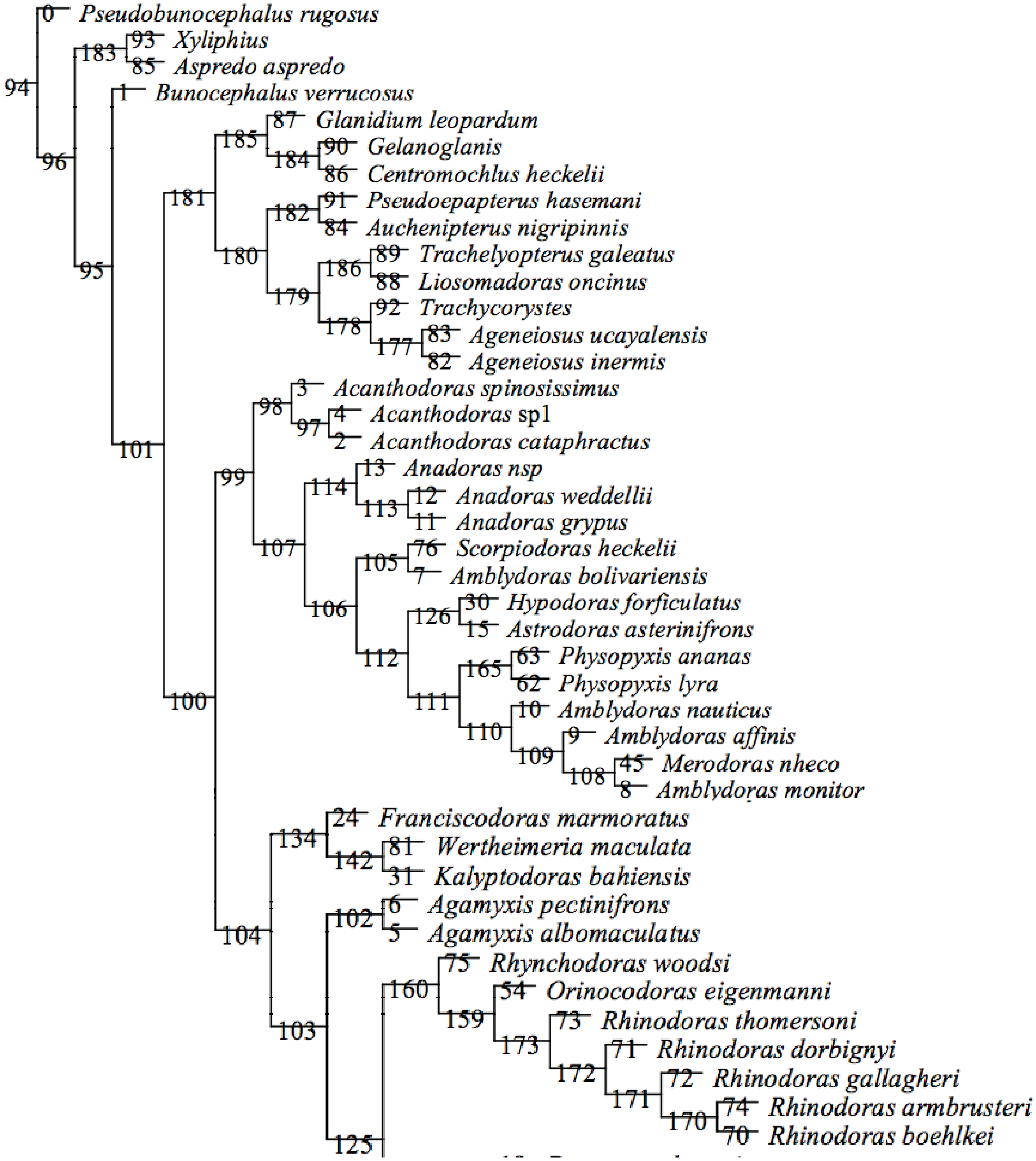
0 ? ? 0 ? ? ? ? - - 0 0 0 1 2 0 0 1 0 0 0 1 0 2 0 3 2 0 1 - - - 0 1 0 0 0 1 0 5 - - - - 0 0 0 - - - 0 3 0 - 2 2 1 0 0 0 0 0 1 0 0 -
1 0 2 - 0 0 2 1 0 0 0 1 1 0 0 1 0 0 1 0 1 0 - 0 0 0 1 3 0 0 0 0 0 0

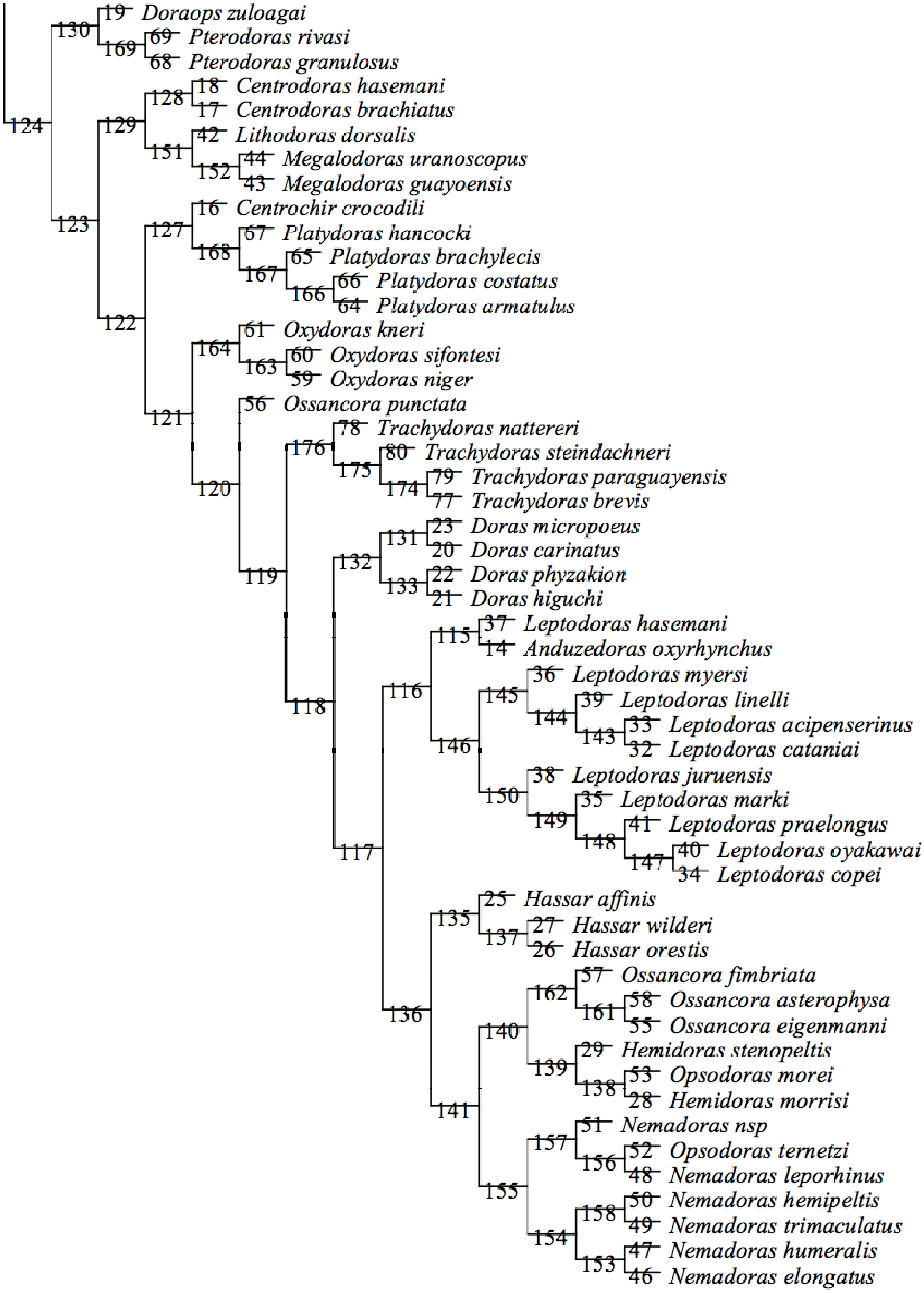
Bunocephalus verrucosus
? ? ? ? ? ? 0 - 0 0 ? ? ? ? ? 0 ? ? ? 1 ? ? 0 0 0 0 0 0 1 0 0 - 0 - 0 0 0 0 ? ? 2 0 0 0 0 0 ? 0 0 0 0 0 0 0 0 0 0 0 1 0 ? ? ? - 0
- ? ? 0 0 0 0 0 0 0 0 ? ? ? 0 ? 0 0 0 ? 0 - - - ? - - - 0 0 0 0 1 0 0 1 0 0 - 0 - 0 1 0 0 0 ? ? 0 0 1 ? ? ? ? ? 0 0 3 - - - ? ? ? ?
? ? ? ? ? ? ? ? 0 0 - 1 1 0 2 ? 0 ? 0 0 0 0 0 0 0 0 0 1 - 1 ? 0 0 0 2 0 ? 0 1 0 0 ? 1 2 0 0 2 ? 0 0 - ? 1 0 0 1 ? ? ? ? 0 ? 2 0
0 0 ? ? ? - - 0 0 0 1 1 1 0 0 0 - 0 1 0 2 0 3 0 0 1 1 - - 0 1 0 0 0 1 0 5 - 1 0 - 0 0 0 ? 2 1 0 3 0 - 0 1 1 0 0 0 0 ? 1 2 0 ? 0
0 1 - 0 0 0 0 0 0 0 0 0 0 0 1 0 0 1 0 1 0 - 0 0 1 1 3 0 0 0 0 0 0

Appendix 5

Synapomorphyes for the total evidence analysis

Synapomorphies common to one tree. Node numbers refer to nodes in consensus tree. Character numbers larger than 291 refer to molecular synapomorphies.




19 Doraops zuloagai
130
69 Pterodoras rivasi
169
68 Pterodoras granulosus
18 Centrodoras hasemani
128
17 Centrodoras brachiatus
124
129
42 Lithodoras dorsalis
151
44 Megalodoras uranoscopus
152
43 Megalodoras guayoensis
16 Centrochir crocodili
123
127
67 Platydoras hancocki
168
65 Platydoras brachylecis
167
66 Platydoras costatus
166
64 Platydoras armatulus
122
61 Oxydoras kneri
164
60 Oxydoras sifontesi
163
59 Oxydoras niger
56 Ossancora punctata
121
78 Trachydoras nattereri
176
80 Trachydoras steindachneri
175
79 Trachydoras paraguayensis
174
77 Trachydoras brevis
120
23 Doras micropoeus
131
20 Doras carinatus
132
22 Doras phyzakion
133
21 Doras higuchi
119
37 Leptodoras hasemani
115
14 Anduzedoras oxyrhynchus
36 Leptodoras myersi
116
145
39 Leptodoras linelli
144
33 Leptodoras acipenserinus
143
32 Leptodoras cataniai
118
146
38 Leptodoras juruensis
150
35 Leptodoras marki
149
41 Leptodoras praelongus
148
40 Leptodoras oyakawai
147
34 Leptodoras copei
117
25 Hassar affinis
135
27 Hassar wilderi
137
26 Hassar orestis
57 Ossancora fimbriata
162
58 Ossancora asterophysa
161
55 Ossancora eigenmanni
136
140
29 Hemidoras stenopeltis
139
53 Opsodoras morei
138
28 Hemidoras morrisi
141
51 Nemadoras nsp
157
52 Opsodoras ternetzi
156
48 Nemadoras leporhinus
155
50 Nemadoras hemipeltis
158
49 Nemadoras trimaculatus
154
47 Nemadoras humeralis
153
46 Nemadoras elongatus

***Pseudobunocephalus_rugosus**:* no autoapomorphies.

Bunocephalus_verrucosus:19: 0 > 1,96: 1 > 0 100: 0 > 1 165: 0 > 2 207: 0 > 1 209: 1 > 0 264: 2 > 0 265: 1 > 0 283: 0 > 1

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***Acanthodoras_spinosissimus**:* 28: 0 > 1 45: 0 > 1 47: 0 > 1 92: 1 > 0 112: 1 > 0 115: 1 > 0 142: 1 > 0 143: 1 > 0 144: 0 > 1 149: 1 > 0 168: 1 > 0 197: 1 > 0 464: 1 > 3 528: 1 > 3 702: 1 > 3 909: 1 > 3 945: 3 > 1 987: 0 > 2 1005: 0 > 2 1032: 0 > 1 1035: 0 > 2 1068: 0 > 2 1071: 3 > 1 1077: 0 > 2 1104: 1 > 2 1128: 2 > 1 1137: 0 > 2 1146: 0 > 2 1167: 1 > 2 1215: 1 > 3 1233: 0 > 2 1236: 0 > 2 1278: 0 > 3 1281: 3 > 1 1282: 0 > 2 1284: 3 > 1 1335: 0 > 2 1353: 1 > 3 1371: 0 > 2 1383: 0 > 2 1401: 0 > 2 1446: 0 > 2 1449: 0 > 2 1455: 0 > 2 1473: 0 > 2 1636: 2 > 0 1688: 0 > 1 2198: 2 > 3 2199: 0 > 3 2447: 0 > 3 2562: 1 > 3 2568: 1 > 3 3198: 1 > 3

Acanthodoras_depressus: 556: 1 > 3 630: 0 > 2 951: 3 > 1 1087: 1 > 3 1248: 1 > 0 1576: 1 > 2 1749: 3 > 2 2210: 3 > 0 2224: 0 > 3 2229: 3 > 0 2675: 3 > 1 3106: 0 > 2

Agamyxis_albomaculatus: 25: 0 > 1 49: 0 > 1 97: 1 > 0 114: 0 > 1 172: 0 > 1 191: 0 > 1 196: 0 > 1 197: 1 > 2 236: 1 > 0 239: 1 > 4 277: 0 > 1 295: 1 > 3 557: 0 > 2 704: 1 > 3 1032: 0 > 2 1281: 3 > 1 1380: 0 > 2 1443: 2 > 0 1499: 1 > 3 1848: 3 > 0

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Amblydoras_nauticus: 184: 1 > 0 236: 1 > 0 524: 0 > 2 530: 0 > 1 534: 3 > 0 535: 1 > 3 567: 1 > 3 654: 0 > 2 883: 3 > 1 900: 3 > 1 919: 3 > 1 1002: 3 > 1 1029: 1 > 3 1044: 1 > 2 1077: 0 > 2 1104: 1 > 3 1107: 0 > 3 1176: 3 > 1 1206: 0 > 3 1209: 1 > 3 1210: 1 > 3 1231: 1 > 3 1239: 3 > 2 1266: 1 > 3 1311: 0 > 2 1350: 3 > 0 1395: 3 > 1 1431: 0 > 1 1464: 1 > 3 1470: 3 > 1 1525: 2 > 0 1615: 3 > 1 1703: 1 > 3 1704: 3 > 12 1710: 3 > 0 1719: 2 > 0 1721: 1 > 3 2206: 0 > 1 2362: 1 > 2 2372: 0 > 2 2451: 1 > 0 2639: 3 > 1 2709: 0 > 2 2744: 1 > 3 2817: 3 > 1 2832: 2 > 0 2961: 1 > 3 3151: 1 > 3 3152: 1 > 3 3208: 3 > 1 3295: 2 > 0

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1212: 0 > 2 1248: 3 > 1 1275: 0 > 3 1323: 1 > 2 1332: 0 > 2 1413: 1 > 3 1449: 0 > 2 1458: 1 > 3 1481: 3 > 1 2259: 1 > 3 2946: 1 > 3 3106: 0 > 3

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Anduzedoras_oxyrhynchus: 202: 1 > 0 206: 0 > 1 214: 0 > 1 219: 0 > 1 228: 2 > 1 232: 1 > 3 239: 1 > 4 242: 1 > 2 243: 0 > 2 244: 1 > 0 257: 2 > 1 262: 1 > 0 270: 1 > 3 278: 1 > 0 286: 1 > 0 288: 1 > 0 312: 1 > 3 395: 2 > 0 506: 0 > 3 524: 2 > 0 543: 1 > 3 555: 2 > 0 603: 0 > 2 616: 2 > 0 667: 3 > 1 873: 1 > 3 915: 1 > 3 987: 0 > 2 999: 2 > 0 1071: 1 > 3 1114: 3 > 1 1116: 0 > 2 1128: 0 > 2 1137: 1 > 3 1164: 1 > 3 1167: 3 > 1 1179: 1 > 3 1221: 1 > 3 1257: 0 > 2 1266: 3 > 1 1275: 0 > 2 1311: 0 > 2 1320: 0 > 1 1323: 0 > 2 1332: 0 > 1 1392: 3 > 2 1449: 0 > 2 1452: 0 > 1 1455: 0 > 1 1470: 3 > 1 1722: 0 > 1 2309: 0 > 3 2987: 2 > 0

Astrodoras_asterinifrons: 183: 0 > 1 191: 0 > 1 213: 1 > 0 223: 0 > 1 227: 0 > 2 243: 0 > 1 273: 1 > 0 274: 1 > 0 463: 0 > 2 464: 1 > 3 502: 1 > 3 528: 1 > 3 556: 1 > 3 626: 1 > 0 909: 0 > 1 927: 3 > 1 1038: 1 > 3 1044: 1 > 0 1083: 3 > 1 1086: 0 > 2 1107: 0 > 2 1119: 1 > 3 1125: 3 > 1 1167: 1 > 3 1218: 3 > 1 1231: 1 > 3 1252: 1 > 3 1269: 1 > 3 1281: 3 > 1 1284: 3 > 1 1302: 1 > 3 1305: 1 > 3 1311: 0 > 2 1335: 0 > 2 1353: 1 > 3 1362: 0 > 2 1372: 1 > 3 1381: 1 > 3 1535: 1 > 2 1745: 0 > 2 1850: 2 > 0 2196: 3 > 0 2268: 3 > 0 2628: 2 > 3 2634: 3 > 0 2639: 3 > 1 2640: 0 > 3 2681: 2 > 0 2758: 2 > 0 2773: 2 > 3 2949: 2 > 0 2987: 2 > 0 3197: 1 > 2 3205: 2 > 0

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Hassar_orestis: 206: 0 > 1 214: 0 > 1 227: 2 > 1 602: 3 > 1 882: 1 > 3 885: 1 > 3 1134: 2 > 0 1149: 0 > 1 1265: 0 > 3 1299: 0 > 1 1322: 1 > 0 1359: 3 > 1 1481: 3 > 1 1492: 2 > 3 2225: 3 > 1 2478: 2 > 0 3261: 3 > 1 3265: 0 > 3

Hassar_wilderi: 28: 0 > 1 44: 0 > 1 46: 1 > 0 50: 0 > 2 54: 0 > 1 58: 1 > 0 59: 1 > 0 95: 1 > 0 96: 1 > 0 101: 1 > 0 107: 1 > 0 112: 1 > 0 142: 1 > 0 143: 1 > 0 159: 1 > 0 162: 1 > 0 163: 1 > 0 173: 1 > 0 184: 1 > 0 567: 0 > 2 1071: 1 > 3 1074: 3 > 1 1125: 3 > 1 1167: 3 > 1 1197: 0 > 2 1215: 1 > 3 1530: 2 > 01 1539: 2 > 3 1566: 3 > 2 1587: 2 > 3 1588: 1 > 3 1590: 0 > 3 1591: 0 > 1 1592: 0 > 3 1601: 0 > 1 1602: 0 > 23 1604: 2 > 0 1605: 3 >2 1751: 2 > 0 2327: 1 > 2 2393: 2 > 3

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Hemidoras_stenopeltis: 686: 3 > 0 704: 1 > 3 919: 3 > 1 924: 3 > 1 1104: 0 > 1 1134: 2 > 0 1140: 0 > 2 1143: 0 > 2 1158: 1 > 3 1210: 1 > 3 1275: 0 > 2 1281: 3 > 1 1392: 0 > 3 1410: 0 > 2 1456: 2 > 0 1458: 1 > 0 1461: 0 > 2 1462: 0 > 3 2764: 2 > 0 2865: 1 > 3

Hypodoras_forficulatus: 158: 0 > 1 197: 0 > 2 207: 0 > 1 231: 1 > 4 236: 1 > 0 241: 0 > 2 259: 0 > 1 275: 0 > 1 289: 0 > 1 290: 0 > 2 419: 1 > 3 459: 0 > 2 466: 1 > 3 511: 0 > 3 560: 1 > 3 569: 1 > 2 646: 0 > 2 659: 1 > 3 686: 1 > 3 891: 0 > 2 990: 2 > 0 1059: 3 > 1 1077: 0 > 2 1089: 0 > 3 1104: 1 > 3 1116: 0 > 2 1134: 0 > 2 1158: 1 > 0 1170: 1 > 2 1182: 1 > 3 1209: 1 > 3 1233: 0 > 2 1242: 1 > 0 1296: 1 > 2 1314: 1 > 3 1371: 1 > 3 1374: 2 > 0 1395: 3 > 1 1402: 1 > 03 1410: 0 > 3 1420: 1 > 3 1435: 3 > 1 1454: 2 > 3 1455: 0 > 23 1456: 2 > 0 1537: 2 > 0 2210: 3 > 0 2712: 3 > 1 2739: 2 > 0

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Conclusões Gerais

Este trabalho representa uma importante contribuição para o entendimento da anatomia, taxonomia e filogenia da família Doradidae.

Foram examinados e descritos um total de 22 músculos das regiões craniana, ventral e peitoral da família Doradidae e foram realizadas algumas comparações com material da família Auchenipteridae, Aspredinidae e Diplomystidae. De maneira geral pode-se afirmar que a musculatura de Doradidae é similar a de outros Siluriformes estudados por outros autores (*i.e.* Siluridae, Ictaluridae). Porém, algumas variações na forma, proporções, origem e inserções são descritas no texto.

Da musculatura craniana foram registrados nove músculos. Na região mais anterior se encontram o *adductor mandibulae*, *retractor* e *extensor tentaculi*. O *adductor mandibulae* é o mais conspícuo e é responsável pelo fechamento da mandíbula, o músculo pode ou não estar dividido em duas porções. O *retractor* e o *extensor tentaculi* são responsáveis pelos movimentos dos barbilhões. Em algumas espécies a função de recolhimento do barbilhão parece estar também relacionada à presença do ligamento coronomaxilar. Posterior a este conjunto de músculos se encontram o *levator arcus palatini* e o *dilatator operculi*, que conectam o neurocrânio aos elementos do suspensório. Músculos pertencentes à região craniana também são o *levator operculi*, *adductor operculi*, e *adductor arcus palatini*, os quais apresentam pouca variação entre os gêneros.

Na região ventral foram analisados seis músculos: intermandibularis, *protractor hyoidei*, *hyohyoides inferioris*, *hyohyoidei abductores*, *hyohyoidei adductores* e *sternohyoideus.* A maioria relacionados com os movimentos de ventilação das branquias. Entre os músculos desta região destaca-se o *protractor hyoides* por sua ampla variação. O estudo apresenta uma compilação de informações prévias sobre este músculo e tenta estabelecer homologias e padronizar a nomenclatura. É destacada a necessidade de estudos posteriores referentes à morfologia funcional e desenvolvimento ontogenético deste músculo para ter certeza sobre a identificação das porções e das homologias.

A nadadeira peitoral de Doradidae é movimentada por sete músculos: *adductor superficialis* e *profundus*, *abductor superficialis* e *profundus*, *arrector ventralis* e *dorsalis* e *abductor rotator*. Cinco desses músculos participam na abdução do acúleo peitoral, pois o desenvolvimento do mecanismo de trava exige a rotação do acúleo ao ser aberto e para isso é necessária a ação de vários músculos. No entanto, para o fechamento do acúleo é empregado somente um músculo, o *adductor profundus*, que pelo tamanho e posição permitem esse movimento.

Foi observado e descrito um músculo não encontrado em descrições prévias da musculatura, aqui nomeado como *abductor rotator*. Analisando a posição e estrutura do músculo, infere se que produz uma pequena rotação do acúleo para ajudar na completa abdução do mesmo.

Os resultados das observações anatômicas mostram a necessidade de estudos referentes à morfologia funcional assim como estudos sobre desenvolvimento da musculatura em Siluriformes.

As observações da musculatura foram usadas para o levantamento de caracteres morfológicos. Foram levantados 91 caracteres da miologia que foram concatenados com mais 200 caracteres de osteologia, morfologia externa, gônadas e bexiga natatória, usados por autores prévios. Quando analisado por máxima parcimônia, o conjunto dos 291 caracteres da morfologia revelam uma topologia similar a aquela achada sem incluir os dados miológicos.

Os 291 caracteres de morfologia foram concatenados com os 3011 caracteres moleculares e analisados sob o princípio de evidência total para construir a mais completa hipótese sobre as relações de Doradidae.

A inclusão de toda a informação disponível para a família apresenta uma nova hipótese sobre o relacionamento dos gêneros de Doradidae. A monofilia da família é corroborada assim como a relação com o seu grupo irmão, a família Auchenipteridae.

A subfamília Astrodoradinae é recuperada como o grupo irmão de todos os outros doradideos, e a evidência sugere a inclusão do gênero *Acanthodoras* como parte da subfamília. *Wertheimeria*, *Kalyptodoras* e *Franciscodoras* são gêneros monotípicos, endêmicos da costa leste brasileira, recuperados formando um clado monofilético.

A tribo Rhinodoradini é monofilética e esta formada pelos gêneros *Rhynchodoras*, *Orinocodoras* e *Rhinodoras*. A análise encontrou os clados (*Doraops*, *Pterodoras*) (*Centrodoras* (*Lithodoras* e *Megalodoras*)) como grupos irmãos consecutivos e não como parte da tribo Pterodoradini. Clados como *Doraops* + *Pterodoras* e *Centrochir* + *Platydoras* constituem exemplos de gêneros endêmicos de bacias transandinas como grupo irmão de gêneros amplamente distribuídos em bacias cisandinas.

Os Doradidae com barbilhões fimbriados formam um grupo monofilético altamente suportado e são o grupo irmão de *Oxydoras*, o único doradidae de corpo alto com barbilhões simples.

Foram achados alguns clados que contradizem filogenias propostas anteriormente, mas com baixo suporte de Bremer absoluto e relativo. O gênero *Ossancora*, recentemente descrito, não foi recuperado como monofilético. *Anduzedoras* agrupa se com *Leptodoras* formando um clado. Espécies do gênero "*Tenellus*" (ainda não descrito) agrupam-se dentro do clado formado por espécies de *Nemadoras*. Mudanças taxonômicas e de classificação não são propostas neste estudo. Devido ao baixo suporte de alguns clados, mais informação será adicionada e as mudanças taxonômicos serão propostos após isso.