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Towards a complete classification of the Neotropical thorny catfishes (Siluriformes: Doradidae)

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We propose a revised classification of Doradidae based on phylogenetic analyses of sequence data for one nuclear (rag1) and two mitochondrial (co1, 16s) genes, and corroborated by caudal-fin morphology. The molecular dataset comprises 174 doradid specimens representing all 31 valid genera, 83 of the 96 valid extant species and 17 species-level taxa that remain undescribed or nominally unassigned. Parsimony and Bayesian analyses of molecular data support six major lineages of doradids assigned here to three nominal subfamilies (Astrodoradinae, Doradinae, Wertheimerinae) and three new ones (Acanthodoradinae, Agamyxinae, Rhinodoradinae). The maximum parsimony topology of Doradidae was sensitive to ingroup density and outgroup age. With the exceptions of Astrodoradinae and Doradinae, each subfamily is diagnosed by caudal-fin characteristics. The highest degree of fusion among skeletal elements supporting the caudal fin is observed in Acanthodoradinae and Aspredinidae, lineages that are sister to the remaining doradids and aspredinoids (*i.e.*, Auchenipteridae + Doradidae), respectively. Fusion among caudal-fin elements tends to be higher in taxa with rounded, truncate or emarginate tails and such taxa typically occupy shallow, lentic habitats with ample structure. Caudal-fin elements are more separated in taxa with moderately to deeply forked tails that occupy lotic habitats in medium to large river channels.

Keywords: Biogeography, Caudal fin, Osteology, Systematics, Taxonomy.

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Propomos uma classificação revisada de Doradidae baseada na análise filogenética de dados moleculares dos genes rag1, co1 e 16s, e suportada pela morfologia da nadadeira caudal. A matriz molecular inclui 174 espécimes de doradídeos representando os 31 gêneros válidos, 83 das 96 espécies viventes e 17 táxons não descritos ou nominalmente não designados. As análises de parcimônia e bayesiana suportam seis linhagens principais de doradídeos atribuídas a três subfamílias nominais (Astrodoradinae, Doradinae, Wertheimerinae) e três novas subfamílias (Acanthodoradinae, Agamyxinae, Rhinodoradinae). A árvore de máxima parcimônia de Doradidae é sensível à densidade de grupo interno e a idade do grupo externo. Com exceção de Astrodoradinae e Doradinae, cada subfamília é diagnosticada por características da nadadeira caudal. Dentro da família Doradidae e da superfamília Aspredinioidea (Aspredinidae, Auchenipteridae e Doradidae), o maior grau de fusão entre os elementos da nadadeira caudal é observado nas linhagens mais antigas, Acanthodoradinae e Aspredinidae, respectivamente. A fusão entre os elementos da nadadeira caudal é maior em táxons com a caudal arredondada, truncada ou emarginada e esses táxons normalmente ocupam habitats lênticos rasos. Os elementos da nadadeira caudal são mais separados em táxons com a cauda bifurcada ocupando habitats lóticos em canais de rios médios a grandes.

Palavras-chave: Biogeografia, Nadadeira caudal, Osteologia, Sistemática, Taxonomia.

INTRODUCTION

Thorny catfishes (Siluriformes: Doradidae) form a monophyletic group of about 96 valid extant and one fossil species endemic to freshwaters of South America on both sides of the Andes Mountains. Most doradids are easily distinguished from other catfishes by having a conspicuous midlateral row of bony scutes, each one with a central, caudally directed thorn (Fig. 1). Each midlateral scute is formed by dorsal and ventral aliform expansions of a lateral-line tubule. A single enlarged pore perforates the skin in the axil of each thorn. The infranuchal scute is exceptionally composed of both an expanded tubule and an ossified ligament that runs between the nuchal region of the cranium and the rib supported by the sixth vertebra, which is the first long-formed rib. As such, the infranuchal scute represents an unambiguous synapomorphy for Doradidae (Birindelli, 2014). Another synapomorphy for doradids is the presence of Sörensen's ligament (Fig. 2), an unossified ligament between the anterolateral rim of the Müllerian disk and an ossified tubule or scute in the tympanic region (Birindelli, 2014).

Adult thorny catfishes vary in standard length from about 22 mm (*Physopyxis ananas* Sousa & Rapp Py-Daniel, 2005) to over one meter (*Oxydoras* spp.). Doradids generally occupy benthic habitats in lowland lakes and rivers, although a few taxa frequent pelagic habitats, such as *Nemadoras hemipeltis* (Eigenmann, 1925) and *Pterodoras* Bleeker, 1862. Many of the smaller species are peculiar to floodplains and occupy sluggish streams and river margins during the low-water season. The larger species are restricted to the main channels of medium to large rivers. A few doradids (*e.g.*, *Rhinodoras* Bleeker, 1862) often associate with large rocky rapids in rivers draining the Brazilian and Guiana shields. The propensity of thorny catfishes for large river channels and lowland floodplains, coupled with an absence from upland headwaters, makes Doradidae a prime candidate for investigating large scale shifts in Neotropical drainage patterns.

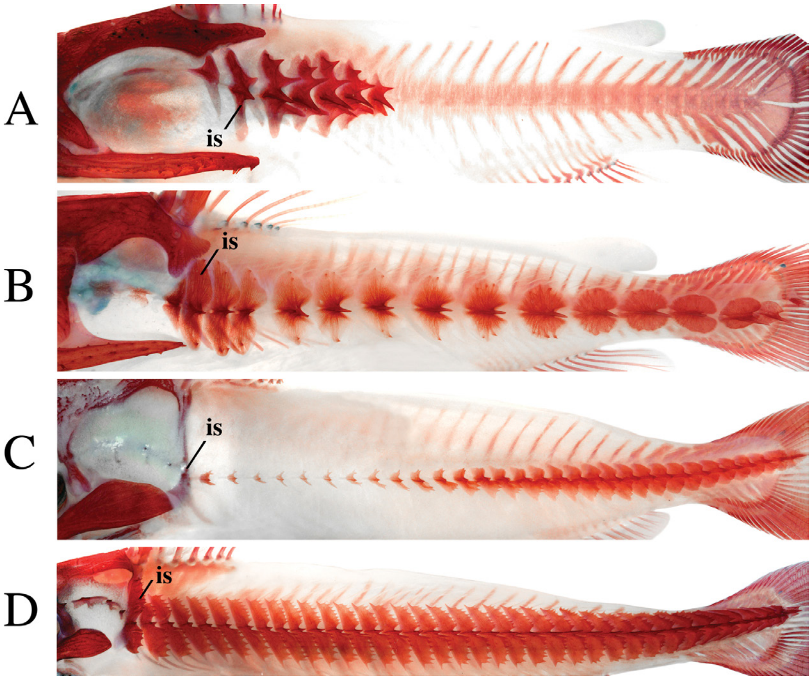

FIGURE 1 | Variation in scute morphology in cleared and stained specimens of Doradidae. **A.** *Amblydoras nheco* (ANSP 187416); **B.** *Megalodoras uranoscopus* (ANSP 178302); **C.** *Hassar orestis* (ANSP 181094); **D.** *Leptodoras linnelli* (ANSP 182791). Infranuchal scute (is), exceptionally composed of expanded lateral-line tubule and ossified ligament between nuchal region of skull and rib supported by 6th vertebra.

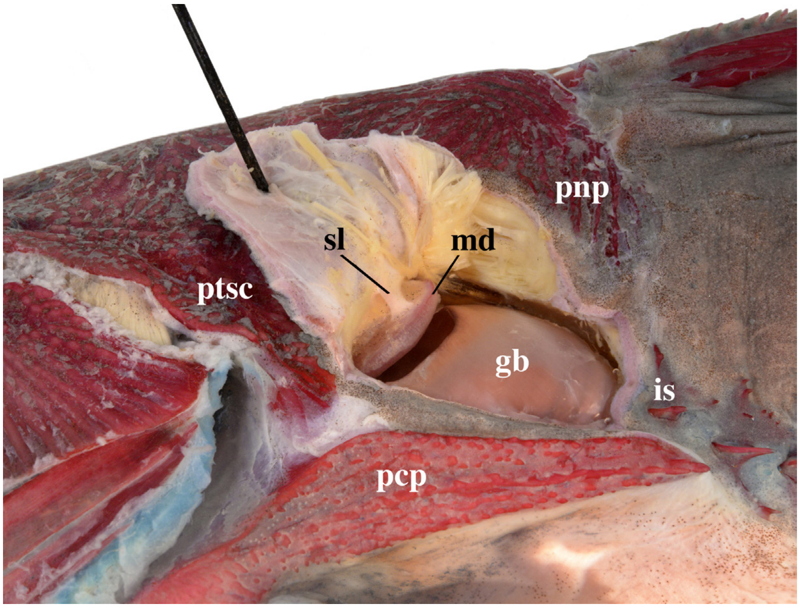

FIGURE 2 | Sörensen's ligament (sl), unossified ligament between anterolateral rim of Müllerian disk (md) and first ossified tubule or scute (not visible) in tympanic region; stained specimen of *Oxydoras sifontesi* (ANSP 181069, 149.5 mm SL). gb = gas bladder, is = infranuchal scute, pcp = posterior cleithral process, pnp = posterior nuchal plate, ptsc = posttemporal-supracleithrum.

The taxonomic history of thorny catfishes includes 43 nominal genera and 146 nominal species (Fig. 3) dating back to the Linnaean (Linnaeus,1758) descriptions of *Acanthodoras cataphractus* and *Platydoras costatus* (Sabaj Pérez, 2014). Lacepède (1803) proposed the first genus (*Doras*), Bleeker (1858) established the family-group name Doradidae (van der Laan *et al*., 2014), and Higuchi *et al*. (2007) described the first valid subfamily, Astrodoradinae. Kner (1853, 1855) published the first detailed descriptions of doradids in his treatment of 18 species including 13 proposed as new. Although Kner recognized only one genus (*Doras*), his species spanned 14 of the 31 genera considered valid in the family. Eigenmann (1925) compiled a comprehensive monograph on Doradidae that is rich with figures and acute observations that continue to inform modern studies. Sabaj, Ferraris (2003) assembled an annotated checklist of doradids that clarified or highlighted a number of nomenclatural and taxonomic issues. The next fifteen years witnessed the descriptions of two new genera and 23 new species, nearly a quarter of the total species considered valid here. Although the classification of Doradidae is more or less complete to the genus level, taxonomic work remains at the species level for a number of genera, especially *Acanthodoras* Bleeker, 1862, *Amblydoras* Bleeker, 1862, *Anadoras* Eigenmann, 1925, *Hemidoras* Bleeker, 1858, *Platydoras* Bleeker, 1862, and *Pterodoras* Bleeker, 1862.

Cladistic studies of doradids began with Higuchi (1992) who used morphology to hypothesize relationships within the family inclusive of a previously contentious member, *Wertheimeria maculata* Steindachner, 1877. Arce H. *et al.* (2013) provided robust support for alternative relationships based on phylogenetic analyses of molecular data. Birindelli

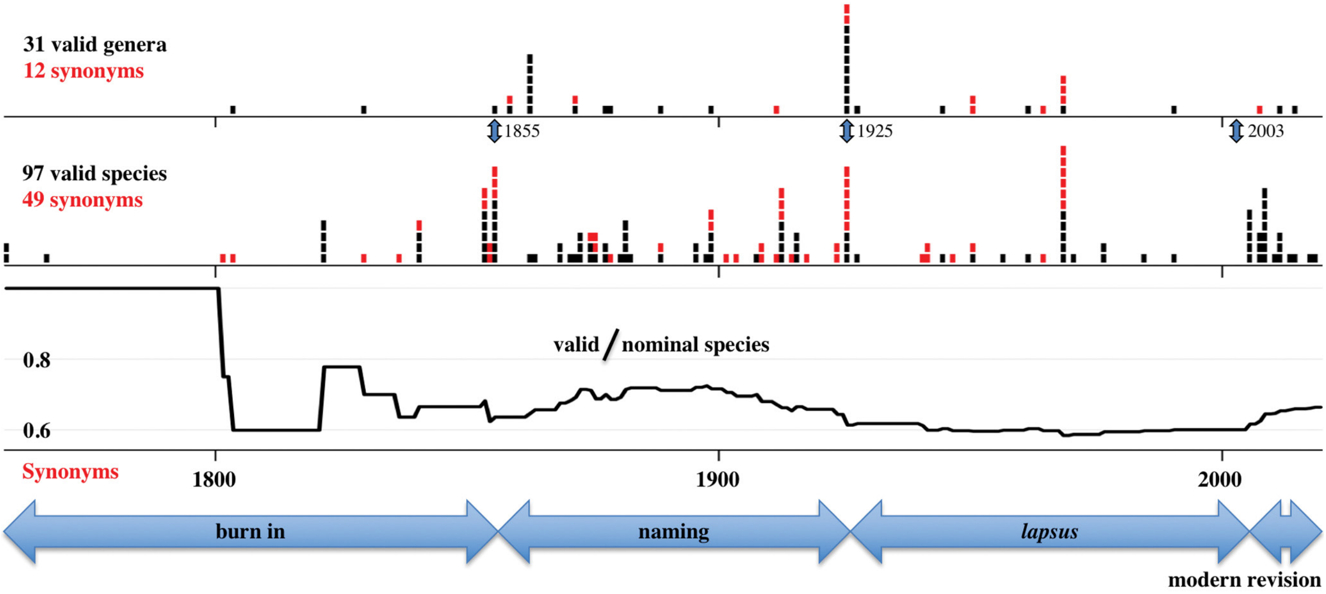

FIGURE 3 | Summary of taxonomic history of Doradidae. Each square represents a nominal valid taxon (black) or putative synonym (red) plotted against the year of its description (two *nomina oblita* and four replacement names not included). Continuous black line traces ratio of valid to nominal species through four time periods: burn in, naming, *lapsus* and modern revision. Monographs by Kner (1855) and Eigenmann (1925) mark ends of burn in and naming periods, respectively. Monograph by Sabaj, Ferraris (2003) marks beginning of modern revision.

(2014) assembled the most comprehensive morphological data set to date to investigate phylogenetic relationships among Doradidae and its sister family Auchenipteridae. Based on those results, Birindelli (2014) firmly diagnosed Doradidae and proposed a new subfamily, Wertheimerinae. Other recent studies have described variation in gas bladder morphology (Birindelli *et al*., 2009), sperm morphology (Quagio-Grassiotto *et al*., 2011), bioacoustics (Kaatz, Stewart, 2012; Zebedin, Ladich, 2013; Knight, Ladich, 2014), digestive tube morphology (de Melo Germano *et al*., 2014) musculature (Arce H., 2015) and cytogenetics (Baumgärtner *et al*., 2018; Takagui *et al*., 2019). Drawing heavily from variation in caudal-fin morphology, Birindelli, Sousa (2018) assembled a key to the 26 doradid genera inhabiting the Amazon, Orinoco and Guianas.

The primary goals of this study are to advance the classification and summarize the geographic distributions of thorny catfishes. We expanded the taxon sampling of the molecular data set analyzed by Arce H. *et al.* (2013) and compiled comprehensive data on the caudal skeleton for all doradid taxa. Based on our analyses of those data, we propose a revised classification of Doradidae and comment on morphological trends observed in caudal-fin evolution among doradids and other catfishes.

MATERIAL AND METHODS

Molecular Data: markers and taxon sampling. Sequence data were assembled for one nuclear gene, recombination activating gene 1 (rag1), and two mitochondrial genes, cytochrome c oxidase subunit 1 (co1) and 16s ribosomal RNA (16s), from 218 specimens representing 37 outgroup taxa (44 specimens) and 100 ingroup taxa (174 specimens) (Tab. 1). The current analysis employed the same three markers used by Arce H. *et al.* (2013), but added 74 specimens (43 doradids and 31 outgroups) and 38 species-level taxa (14 doradids and 24 outgroups).

Outgroup taxa were selected on the basis of molecular studies (Sullivan *et al*., 2006; Lundberg *et al*., 2007; Nakatani *et al*., 2011; Arcila *et al*., 2017; Betancur-R. *et al*., 2017; Calegari *et al*., 2019) that support Diplomystidae as the sister group to Siluroidei, Cetopsidae as the sister group to all other siluroids, and Aspredinidae as sister to Auchenipteridae + Doradidae, with those three families comprising the superfamily Aspredinoidea Adams, 1854 (van der Laan, 2019:121; see also Results). The ingroup taxa represented all 31 valid genera of Doradidae, 83 of the 96 extant valid species, and 17 taxa that are undescribed species or currently unassigned to nominal ones.

Molecular Data: DNA extraction, amplification and sequencing. Generally, tissues (*e.g*., fin, muscle or gill) were taken in the field and preserved in 95–100% ethanol; voucher specimens were fixed in 10% buffered formalin, then transferred to 70–75% ethanol for long-term museum storage. Ideally, the tissue sample is associated with a field tag number that is tied to the voucher specimen. Additional tissue samples were provided by generous colleagues (see Acknowledgments).

Total DNA was extracted using the Qiagen DNeasy blood and tissue kit. PCR was carried out in 20 µl reactions; primers for amplification and sequencing are listed in Arce H. *et al.* (2013:561, tab. 1). For co1 and 16s, the PCR reaction mixture consisted of

TABLE 1 | List of taxa, voucher specimens and DNA sequences analyzed. *Denotes individuals sequenced in Arce H. *et al.* (2013). Museum codes follow Sabaj (2020). [a] Sequence data published by Sullivan *et al.* (2006) for voucher ANSP 180476. [b] Sequence data submitted to GenBank by Heok Hee Ng (2006) for voucher ANSP 180476 (tag 4515) from an unpublished study. [c] Sequence data published by Nakatani *et al.* (2011); no voucher data. [d] Genus assignment based on Calegari *et al.* (2019). [e] Questionably a junior synonym of *Hemidoras boulengeri* (Steindachner, 1915).

Higher-level classification	**Voucher data**					**GenBank Accession No.**		
SUBORDER: Superfamily								
Family **Terminal taxon**	**Voucher museum and catalog no. when available**	**Voucher tag or other identifier**	**ANSP tissue reference number**	**Country**	**Basin: Sub-basins**	***rag 1***	***CO1***	***16S***
DIPLOMYSTOIDEI								
Diplomystidae Eigenmann, 1890								
Diplomystes nahuelbutaensis Arratia, 1987	ANSP 180476	4515	t499	Chile	Bio Bio: Laja	DQ492574.1[a]	EF014945.1[b]	AP012011[c]
SILUROIDEI								
Cetopsidae Bleeker, 1858								
Cetopsis coecutiens (Lichtenstein, 1819)	ANSP 182760	P6118	t1883	Peru	Amazon	MF489619	MF489362	MF489296
Helogenes marmoratus Günther, 1863	INHS 49125	T426	t13700	Guyana	Demerara	DQ492586	–	MT355999
SILUROIDEI: Aspredinoidea								
Aspredinidae Adams, 1854								
Amaralia hypsiura (Kner, 1855)	ANSP 197607	t4103	t11334	Brazil	Amazon: Xingu: Jarauaçu	MF489532	KT820068	MF489323
Aspredinichthys tibicen (Valenciennes, 1840)	ROM 87369	T08362	–	Guyana	Moruka: Barima-Waini	MF489538	MF489354	MF489281
**Aspredo aspredo* (Linnaeus, 1758)	ANSP 191475	CALH 205	t2094	Brazil	Amazon: Trombetas	–	KC555595	KC555853
Bunocephalus coracoideus (Cope, 1874)	LBP 6974	34015	–	Brazil	Amazon: Negro	MF489337	MF489425	MF489337
Ernstichthys megistus (Orcés V., 1961)	AUM 57485	t10371	–	Peru	Amazon: Madeira: Madre de Dios	MF489590	MF489380	MF489325
Pseudobunocephalus iheringii (Boulenger, 1891)	MCP 23009	JAC007	–	Brazil	Laguna dos Patos	MF489596	MF489373	MF489342
**Pseudobunocephalus rugosus* (Eigenmann & Kennedy, 1903)	ANSP 185102	A5067	t2091	Argentina	Paraná: Guayquiraro	KC555830	KC555682	KC555935
Pterobunocephalus depressus (Haseman, 1911)	ANSP 180019	T2330	t11064	Guyana	Amazon: Negro: Branco	MF489604	MF489436	MF489286
**Xyliphius sofiae* Sabaj, Carvalho & Reis, 2017	ANSP 182322	P6291	t1513	Peru	Amazon	KC555831	KU736764	KC555965
Auchenipteridae Bleeker, 1862								
Ageneiosus inermis (Linnaeus, 1766)	ANSP 181020	A5026	t4815	Argentina	Paraná: Guayquiraro	MT431627	MT712791	MT356000
**Ageneiosus inermis* (Linnaeus, 1766)	ANSP 189090	6996	t1519	Suriname	Maroni: Litanie	KC555823	–	KC555843
Ageneiosus magoi Castillo & Brull G., 1989	ANSP 198873	t4781	t12994	Venezuela	Orinoco: Apure	MT431626	MT712792	MT356001
Ageneiosus militaris Valenciennes, 1835	ANSP 182423	A5031	t4812	Argentina	Paraná: Guayquiraro	MT671303	MT712793	MT356002
Ageneiosus pardalis Lütken, 1874	CZUT 11755	59	t13295	Colombia	Atrato	MT671304	MT712794	MT356003
Ageneiosus pardalis Lütken, 1874	CZUT 11856	35	t13294	Colombia	Atrato	MT671305	MT708514	MT356004
Ageneiosus ucayalensis Castelnau, 1855	ROM 83897	T04098	t13902	Guyana	Essequibo: Mazaruni	MT671306	MT712795	MT356005
**Ageneiosus ucayalensis* Castelnau, 1855	INHS 52920	26669	t4932	Peru	Amazon: Napo	DQ492540	EU490849	unpublished
Ageneiosus uranophthalmus Ribeiro & Rapp Py-Daniel, 2010	ANSP 188784	P4904	t9901	Venezuela	Amazon: Negro: Casiquiare	MT671307	MT712796	MT356007
Auchenipterichthys coracoideus (Eigenmann & Allen, 1942)	ANSP 182589	P6302	t1787	Peru	Amazon: Nanay	–	MT712797	MT356008
Auchenipterus dentatus Valenciennes, 1840	ANSP 189102	7032	t2298	Suriname	Maroni: Litanie	MT671308	MT712798	MT356009
**Auchenipterus nigripinnis* (Boulenger, 1895)	ANSP 182418	A5053	t2090	Argentina	Paraná: Guayquiraro	KC555824	KC555598	KC555856

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TABLE 1 | (Continued)

Higher-level classification	Voucher data					GenBank Accession No.		
SUBORDER: Superfamily								
Family **Terminal taxon**	**Voucher museum and catalog no. when available**	**Voucher tag or other identifier**	**ANSP tissue reference number**	**Country**	**Basin: Sub-basins**	***rag 1***	***CO1***	***16S***
Balroglanis schultzi (Rössel, 1962)	ANSP 193030	B2120	t5906	Brazil	Amazon: Xingu	MT671309	MT712799	MT356010
**Centromochlus heckelii* (De Filippi, 1853)	ANSP 182773	CALH –	–	Brazil	Amazon	DQ492465	–	MT356011
Centromochlus heckelii (De Filippi, 1853)	ANSP 182253	P6114	t1881	Peru	Amazon	–	MT712800	MT356012
Duringlanis perugiae (Steindachner, 1882)[d]	ANSP 180565	t4812	t1165	Peru	Amazon: Madeira: Madre de Dios	MT711301	MT712801	MT356013
Epapterus dispilurus Cope, 1878	INHS 54692	26896	t4938	Peru	Amazon	MT671310	MT712802	MT356014
**Gelanoglanis* sp. "Madre de Dios"	ANSP 180806	P4074	t1174	Peru	Amazon: Madeira: Madre de Dios	KC555825	KC555612	KC555870
**Gephyromochlus leopardus* (Hoedeman, 1961)	ANSP 189104	7034	t2089	Suriname	Maroni: Litanie	KC555826	KC555613	KC555871
**Liosomadoras oncinus* (Jardine, 1841)	ANSP 191102	BO6148	t2087	Venezuela	Orinoco	KC555827	KC555638	KC555894
Pseudepapterus hasemani (Steindachner, 1915)	ANSP 178311	1577	t1701	Peru	Amazon	–	MT712803	MT356015
Tetranematichthys wallacei Vari & Ferraris, 2006	ANSP 197097	T09068	t10358	Venezuela	Orinoco: Parhueña	MT671311	MT712804	MT356016
Tocantinsia piresi (Miranda Ribeiro, 1920)	INPA 38058	B2110	t5896	Brazil	Amazon: Xingu	MT711295	MT712805	MT356017
**Trachelyopterus galeatus* (Linnaeus, 1766)	INHS 49034	T401	t13698	Guyana	Mahaica	DQ492634	EU490848	JX899742
Trachelyopterus galeatus (Linnaeus, 1766)	ANSP 191120	7599	t4454	Venezuela	Orinoco: Ventuari	MT671312	–	MT356018
Trachycorystes trachycorystes (Valenciennes, 1840)	ANSP 179152	–	t206	Guyana	Essequibo: Rupununi	MT671313	–	MT356019
**Trachycorystes trachycorystes* (Valenciennes, 1840)	ANSP 180820	V121	t1514	Venezuela	Orinoco: Ventuari	KC555829	KC555697	KC555950
Tympanopleura atronasus (Eigenmann & Eigenmann, 1888)	ANSP 178307	1565	t1689	Peru	Amazon	MT671314	MT712806	MT356020
Tympanopleura longipinna Walsh, Ribeiro & Rapp Py-Daniel, 2015	ANSP 178310	1563	t632	Peru	Amazon	MT671315	MT712807	MT356021
Tympanopleura longipinna Walsh, Ribeiro & Rapp Py-Daniel, 2015	ANSP 178310	1564	t1691	Peru	Amazon	MT671316	MT712808	MT356022
Tympanopleura piperatus Eigenmann, 1912	ROM 86042	T06991	t13904	Guyana	Essequibo: Rupununi	MT671317	MT712809	MT356023
Tympanopleura rondoni (Miranda Ribeiro, 1914)	ANSP 194014	–	t9689	Brazil	Amazon: Purus	MT671318	MT712810	MT356024
Doradidae Bleeker, 1858								
Acanthodoras cataphractus (Linnaeus, 1758)	ANSP 179854	2023	t1587	Guyana	Essequibo: Rupununi	MT671319	MT712811	MT356025
**Acanthodoras* sp. "deep scute" (*sensu* Arce H. *et al.*, 2013)	LBP 4441	24313	t1786	Brazil	Amazon: Negro	KC555714	KC555580	KC555837
**Acanthodoras* sp. "deep scute" (*sensu* Arce H. *et al.*, 2013)	AUM 43737	V5211	t2150	Venezuela	Amazon: Negro: Casiquiare	KC555712	KC555577	KC555834
**Acanthodoras* sp. "deep scute" (*sensu* Arce H. *et al.*, 2013)	AUM 44128	V5306	t2151	Venezuela	Orinoco: Atabapo	KC555713	KC555578	KC555835
**Acanthodoras* sp. "deep scute" (*sensu* Arce H. *et al.*, 2013)	ANSP 182240	V177	t788	Venezuela	Orinoco: Ventuari	KC555711	KC555576	KC555833
**Acanthodoras* sp. "shallow scute" (sensu Arce H. *et al.* 2013)	ANSP 191096	7602	t2088	Venezuela	Orinoco: Ventuari	KC555832	KC555579	KC555836
**Agamyxis albomaculatus* (Peters, 1877)	LBP 3036	19176	t1780	Venezuela	Orinoco	KC555715	KC555582	KC555839
**Agamyxis albomaculatus* (Peters, 1877)	INHS 54563	MH288/GM794	t11293	Venezuela	Orinoco: Apure	KC555716	KC555581	KC555838
**Agamyxis pectinifrons* (Cope, 1870)	INHS 43281	–	t2145	Peru	Amazon: Itaya	KC555717	KC555583	KC555840
**Agamyxis pectinifrons* (Cope, 1870)	INHS 52017	26733	t2147	Peru	Amazon: Itaya	KC555718	KC555584	KC555841
**Agamyxis pectinifrons* (Cope, 1870)	INHS 52017	26732	t2146	Peru	Amazon: Itaya	KC555719	KC555585	KC555842
**Amblydoras affinis* (Kner, 1855)	ANSP 179797	2157	t727	Guyana	Essequibo: Rupununi	KC555720	KC555586	KC555844
**Amblydoras nauticus* (Cope, 1874)	ANSP 182525	P6021	t671	Peru	Amazon: Nanay	KC555722	KC555590	KC555848
**Amblydoras nheco* Higuchi, Birindelli, Sousa & Britski, 2007	ANSP 187416	7328	t14841	Brazil	Paraná: Paraguai	KC555724	KC555642	KC555897

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TABLE 1 | (Continued)

Higher-level classification	Voucher data					GenBank Accession No.		
SUBORDER: Superfamily								
Family **Terminal taxon**	**Voucher museum and catalog no. when available**	**Voucher tag or other identifier**	**ANSP tissue reference number**	**Country**	**Basin: Sub-basins**	***rag 1***	***CO1***	***16S***
**Amblydoras* sp. “bold pattern”	ANSP 191474	078	t2092	Peru	Amazon: Nanay	KC555723	KC555588	KC555846
**Amblydoras* sp. “small eye”	ANSP 191473	155	t2093	Peru	Amazon: Nanay	KC555721	KC555589	KC555847
**Anadoras grypus* (Cope, 1872)	ANSP 179473	T2465	t639	Peru	Amazon: Itaya	KC555725	KC555591	KC555849
**Anadoras* sp. “Araguaia” (*sensu* Sousa, 2010)	MZUSP 89108	CBE08	t9499	Brazil	Amazon: Tocantins: Araguaia	KC555726	–	KC555850
**Anadoras weddellii* (Castelnau, 1855)	MZUSP 103567	49	t14849	Brazil		KC555727	KC555592	KC555851
**Anduzedoras oxyrhynchus* (Valenciennes, 1821)	ANSP 191093	–	t4459	Venezuela	Orinoco: Atabapo	KC555728	KC555594	KC555852
**Anduzedoras oxyrhynchus* (Valenciennes, 1821)	ANSP 180293	V111	t784	Venezuela	Orinoco: Ventuari	DQ492547	KC555593	MT356026
**Astrodoras asterifrons* (Kner, 1853)	INPA 34100	–	t1907	Brazil	Amazon: Negro	KC555729	KC555597	KC555855
**Astrodoras* sp. (*sensu* Roa-Fuentes *et al*., 2010)	INPA 24660	ARI 68	t1532	Brazil	Amazon: Madeira: Atininga	KC555730	KC555596	KC555854
Centrochir birindellii (Sousa, Santana, Akama, Zuanon & Sabaj, 2018)	ANSP 193073	B2160	t5952	Brazil	Amazon: Xingu	–	MT712812	MT356027
Centrochir birindellii (Sousa, Santana, Akama, Zuanon & Sabaj, 2018)	ANSP 199617	B1986	t5779	Brazil	Amazon: Xingu	MT671320	MT712813	MT356028
**Centrochir crocodili* (Humboldt, 1821)	ANSP 189332	C001	t1595	Colombia	Magdalena	KC555731	KC555599	KC555861
**Centrochir crocodili* (Humboldt, 1821)	ANSP 189332	C005	t1596	Colombia	Magdalena	KC555732	KC555600	KC555857
**Centrodoras brachiatus* (Cope, 1872)	ANSP 178542	CALH 50	t1499	Brazil	Amazon	KC555733	KC555601	KC555858
Centrodoras brachiatus (Cope, 1872)	ANSP 197594	t4244	t11870	Brazil	Amazon: Xingu	MT671321	MT712814	MT356029
**Centrodoras hasemani* (Steindachner, 1915)	ANSP 185027	CALH 188	t1500	Brazil	Amazon: Negro	KC555735	KC555603	KC555860
**Centrodoras hasemani* (Steindachner, 1915)	ANSP 182227	P4844	t797	Venezuela	Amazon: Negro: Casiquiare	KC555734	KC555602	KC555859
Doraops zuloagai Schultz, 1944	ANSP 205981	t8277	t14621	Colombia	Maracaibo: Catatumbo	MT671322	MT712815	MT356030
**Doraops zuloagai* Schultz, 1944	MCNG (field no. OC-09-006)	N020	t9497	Venezuela	Maracaibo: Santa Ana	KC555736	KC555604	KC555862
**Doras carinatus* (Linnaeus, 1766)	INHS 49321	MH211/GM788	t211	Guyana	Essequibo	KC555737	KC555605	KC555863
**Doras higuchii* Sabaj & Birindelli, 2008	MZUSP 96333	7279	t14836	Brazil	Amazon: Xingu: Iriri	KC555738	KC555606	KC555864
**Doras micropoeus* (Eigenmann, 1912)	ANSP 187110	6932	t1518	Suriname	Maroni: Lawa	–	KC555607	KC555865
**Doras micropoeus* (Eigenmann, 1912)	ANSP 187110	6945	t1858	Suriname	Maroni: Lawa	KC555739	KC555609	KC555867
**Doras micropoeus* (Eigenmann, 1912)	ANSP 187110	6941	t1768	Suriname	Maroni: Lawa	KC555740	KC555608	KC555866
Doras phlyzakion Sabaj & Birindelli, 2008	INPA 41907	P26860/102701	t13405	Brazil	Amazon: Purus	MT711291	MT712816	MT356031
Doras phlyzakion Sabaj & Birindelli, 2008	INPA 41907	P26861/102702	t13406	Brazil	Amazon: Purus	MT671323	MT712817	MT356032
**Doras punctatus* Kner, 185	ANSP 181015	A5118	t716	Argentina	Paraná	KC555788	KC555670	KC555924
**Doras punctatus* Kner, 185	ANSP 187005	P6333	t1803	Peru	Amazon: Nanay	KC555789	KC555669	KC555923
**Franciscodoras marmoratus* (Lütken, 1874)	MNRJ 23012	MNTI 39018	t11280	Brazil	São Francisco	–	KC555611	KC555869
**Franciscodoras marmoratus* (Lütken, 1874)	LBP 272	4193	t11294	Brazil	São Francisco	KC555741	KC555610	KC555868
**Hassar affinis* (Steindachner, 1881)	MCP 45010	P1	t1487	Brazil	Mearim	KC555742	KC555614	KC555872
Hassar gabiru Birindelli, Fayal & Wosiacki, 2011	INPA 47404	t3276	t12245	Brazil	Amazon: Xingu	MT671324	MT712818	MT356033
**Hassar orestis* (Steindachner, 1875)	ANSP 181090	P6154	t662	Peru	Amazon	KC555743	KC555615	KC555873
**Hassar wilderi* Kindle, 1895	MZUSP 86216	–	–	Brazil	Amazon: Tocantins: Araguaia	KC555744	KC555616	KC555874

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TABLE 1 | (Continued)

Higher-level classification	Voucher data					GenBank Accession No.		
SUBORDER: Superfamily								
Family Terminal taxon	**Voucher museum and catalog no. when available**	**Voucher tag or other identifier**	**ANSP tissue reference number**	**Country**	**Basin: Sub-basins**	***rag 1***	***CO1***	***16S***
*_Hemidoras morei_ (Steindachner, 1881)	ANSP 183028	4570	t864	Venezuela	Amazon: Negro	KC555781	KC555659	KC555913
*_Hemidoras morrisi_ Eigenmann, 1925[e]	ANSP 182512	P6081	t687	Peru	Amazon: Nanay	KC555745	KC555617	KC555875
*_Hemidoras stenopeltis_ (Kner, 1855)	ANSP 182756	P6241	t695	Peru	Amazon	KC555746	KC555618	KC555876
Hemidoras stuebelii (Steindachner, 1882)	ANSP 200805	–	t14157	Peru	Amazon	MT671325	–	MT356034
*_Hypodoras forficulatus_ Eigenmann, 1925	ANSP 179009	1540	t757	Peru	Amazon: Itaya	KC555747	KC555619	KC555877
*_Kalyptodoras bahiensis_ Higuchi, Britski & Garavello, 1990	MZUSP 87839	–	–	Brazil	Paraguaçu	–	KC555620	KC555878
*_Kalyptodoras bahiensis_ Higuchi, Britski & Garavello, 1990	MZUSP 87841	–	–	Brazil	Paraguaçu	–	KC555621	KC555879
*_Kalyptodoras bahiensis_ Higuchi, Britski & Garavello, 1990	MZUSP 100737	–	–	Brazil	Paraguaçu	KC555748	KC555622	KC555880
*_Leptodoras acipenserinus_ (Günther, 1868)	ANSP 182202	P6346	t663	Peru	Amazon: Nanay	KC555749	KC555623	KC555881
Leptodoras cataniai Sabaj, 2005	ANSP 181043	P6092	t676	Peru	Amazon	MT671326	MT712819	MT356035
*_Leptodoras_ cf. _copei_ “Teles pires”	MZUSP 96597	7079	t14829	Brazil	Amazon: Tapajós: Teles Pires	KC555762	KC555633	KC555891
*_Leptodoras_ cf. _copei_ “Amazon” (_sensu_ Arce H. _et al._, 2013)	ANSP 178540	CALH 149	t1501	Brazil	Amazon	KC555751	KC555625	KC555883
Leptodoras copei (Fernández-Yépez, 1968)	AUM 43243	P4303	t1508	Venezuela	Orinoco	MT671327	MT712820	MT356036
*_Leptodoras copei_ (Fernández-Yépez, 1968)	ANSP 182225	V073	777	Venezuela	Orinoco: Ventuari	KC555752	KC555626	KC555884
*_Leptodoras hasemani_ (Steindachner, 1915)	MZUSP 97363	7258	t2194	Brazil	Amazon: Tapajós: Jamanxim	KC555754	KC555628	KC555886
Leptodoras hasemani (Steindachner, 1915)	ANSP 199566	B1959	t5783	Brazil	Amazon: Xingu	–	MT712821	MT356037
Leptodoras hasemani (Steindachner, 1915)	INPA 40808	t1586	t9229	Brazil	Amazon: Xingu	–	MT712822	MT356038
Leptodoras hasemani (Steindachner, 1915)	ANSP 179209	2055	t726	Guyana	Essequibo: Rupununi	MT671328	MT712823	MT356039
*_Leptodoras hasemani_ (Steindachner, 1915)	ANSP 180897	4033	t793	Venezuela	Orinoco	KC555753	KC555627	KC555885
Leptodoras hasemani (Steindachner, 1915)	AUM 43046	P4021	t794	Venezuela	Orinoco	MT671329	MT712824	MT356040
*_Leptodoras juruensis_ Boulenger, 1898	ANSP 181046	P6090	t683	Peru	Amazon	KC555755	KC555629	KC555887
*_Leptodoras linnelli_ Eigenmann, 1912	ANSP 179631	2093	t1585	Guyana	Essequibo	DQ492604	MT712825	MT356041
*_Leptodoras linnelli_ Eigenmann, 1912	ANSP 179177	2433	t733	Guyana	Amazon: Negro: Branco	KC555756	KC555630	KC555888
Leptodoras linnelli Eigenmann, 1912	ANSP 180903	4602	t800	Venezuela	Amazon: Negro: Casiquiare	MT671330	MT712826	MT356042
Leptodoras linnelli Eigenmann, 1912	ANSP 180296	V103	t782	Venezuela	Orinoco: Ventuari	MT671331	MT712827	MT356043
*_Leptodoras marki_ Birindelli & Sousa, 2010	MNRJ 33067	MNTI 2439	t11285	Brazil	Amazon: Xingu: Fresco	KC555757	KC555631	KC555889
*_Leptodoras myersi_ Böhlke, 1970	ANSP 181045	P6205	t692	Peru	Amazon	KC555758	KC555632	KC555890
Leptodoras nelsoni Sabaj, 2005	IAvH-P (GUA-YA18-P-16)	t8875	t15055	Colombia	Orinoco: Guaviare: Guayabero	MT671332	MT712828	MT356044
*_Leptodoras oyakawai_ Birindelli, Sousa & Sabaj, 2008	ANSP 187336	7209	t2191	Brazil	Amazon: Tapajós: Jamanxim	KC555759	KC555635	–
*_Leptodoras oyakawai_ Birindelli, Sousa & Sabaj, 2008	MZUSP 97395	7208	t14834	Brazil	Amazon: Tapajós: Jamanxim	KC555760	KC555634	KC555892
*_Leptodoras praelongus_ (Myers & Weitzman, 1956)	ANSP 178534	CALH 54	t1503	Brazil	Amazon: Negro: Branco	–	KC555637	KC555893
*_Leptodoras praelongus_ (Myers & Weitzman, 1956)	ANSP 180913	CALH 195	t1502	Brazil	Amazon: Negro	KC555761	KC555636	–
Leptodoras sp. “Volta Grande”	ANSP 194483	t0484	t8129	Brazil	Amazon: Xingu	MT671333	MT712829	MT356045
Leptodoras sp. “Volta Grande”	ANSP 195038	t1582	t9225	Brazil	Amazon: Xingu	MT671334	MT708513	MT356046

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TABLE 1 | (Continued)

Higher-level classification	Voucher data					GenBank Accession No.		
SUBORDER: Superfamily								
Family **Terminal taxon**	**Voucher museum and catalog no. when available**	**Voucher tag or other identifier**	**ANSP tissue reference number**	**Country**	**Basin: Sub-basins**	***rag 1***	***CO1***	***16S***
Leptodoras sp. "Volta Grande"	ANSP 199567	B1956	t5750	Brazil	Amazon: Xingu	MT671335	MT712830	MT356047
Leptodoras sp. "Volta Grande"	ANSP 199567	B1957	t5751	Brazil	Amazon: Xingu	MT671336	MT712831	MT356048
**Lithodoras dorsalis* (Valenciennes, 1840)	ANSP 187376	7332	1207	Brazil	Amazon	KC555763	KC555639	KC555895
**Megalodoras guayoensis* (Fernández-Yépez, 1968)	MHNLS 20354	24222/CV001	t11299	Venezuela	Orinoco	KC555764	KC555640	KC555896
Megalodoras sp. "Xingu"	ANSP 195481	t2558	t10706	Brazil	Amazon: Xingu	MT671337	MT712832	MT356049
**Megalodoras uranoscopus* (Eigenmann & Eigenmann, 1888)	ANSP 178249	1685	t753	Peru	Amazon	MT906155	KC555641	MT878223
**Nemadoras elongatus* (Boulenger, 1898)	ANSP 182850	CALH 198	t1524	Brazil	Amazon: Purus	KC555767	KC555645	KC555900
**Nemadoras elongatus* (Boulenger, 1898)	ANSP 182295	P6282	t664	Peru	Amazon	KC555765	KC555643	KC555898
**Nemadoras elongatus* (Boulenger, 1898)	ANSP 182613	P6299	t665	Peru	Amazon: Nanay	KC555766	KC555644	KC555899
**Nemadoras hemipeltis* (Eigenmann, 1925)	ANSP 181095	P6111	t709	Peru	Amazon	KC555768	KC555646	KC555901
**Nemadoras hemipeltis* (Eigenmann, 1925)	ANSP 182283	P6272	t699	Peru	Amazon	KC555769	KC555647	–
**Nemadoras humeralis* (Kner, 1855)	ANSP 178550	CALH 197	t1523	Brazil	Amazon: Purus	KC555770	KC555648	KC555902
**Nemadoras humeralis* (Kner, 1855)	ANSP 182721	P6228	t696	Peru	Amazon: Itaya	KC555772	KC555650	KC555904
**Nemadoras humeralis* (Kner, 1855)	ANSP 182596	P6301	t703	Peru	Amazon: Nanay	KC555771	KC555649	KC555903
**Nemadoras trimaculatus* (Boulenger, 1898)	ANSP 178252	1679	t752	Peru	Amazon	KC555778	KC555656	KC555910
**Nemadoras trimaculatus* (Boulenger, 1898)	ANSP 182633	P6306	t704	Peru	Amazon: Nanay	KC555779	KC555657	KC555911
**Nemadoras trimaculatus* (Boulenger, 1898)	ANSP 182824	P4589	t801	Venezuela	Amazon: Negro: Casiquiare	KC555780	KC555658	KC555912
**Orinocodoras eigenmanni* Myers, 1927	INHS 54564	MH290/GM801	t9500	Venezuela	Orinoco: Apure	KC555786	KC555664	KC555918
**Ossancora asterophysa* Birindelli & Sabaj, 2011	ANSP 178546	CALH 200	t1505	Brazil	Amazon	–	KC555665	KC555919
**Ossancora asterophysa* Birindelli & Sabaj, 2011	ANSP 182516	P6003	t669	Peru	Amazon: Nanay	KC555787	KC555666	KC555920
**Ossancora fimbriata* (Kner, 1855)	ANSP 192457	M353	–	Brazil	Amazon: Jutai	–	KC555667	KC555921
**Ossancora fimbriata* (Kner, 1855)	ANSP 192457	M354	–	Brazil	Amazon: Jutai	–	KC555668	KC555922
**Oxydoras kneri* Bleeker, 1862	ANSP 182203	A5196	t1520	Argentina	Paraná	KC555790	KC555671	KC555925
**Oxydoras niger* (Valenciennes, 1821)	MCNG ex. ANSP 181080	P6056	t635	Peru	Amazon	KC555791	KC555672	KC555926
Oxydoras sifontesi Fernández-Yépez, 1968	IAvH-P (GUA-YA18-P-2)	t8866	t15046	Colombia	Orinoco: Guaviare: Guayabero	–	MT712833	MT356050
**Oxydoras sifontesi* Fernández-Yépez, 1968	ANSP 189324	P4340	t866	Venezuela	Orinoco	KC555792	KC555673	KC555927
**Physopyxis ananas* Sousa & Rapp Py-Daniel, 2005	ANSP 190508	7576	t2118	Venezuela	Orinoco: Atabapo	KC555793	KC555674	KC555928
**Physopyxis lyra* Cope, 1872	ANSP 180176	2300	t762	Peru	Amazon: Nanay	KC555794	KC555675	KC555929
Platydoras armatulus (Valenciennes, 1840)	MLP uncat.	A5105	t4856	Argentina	Paraná: Guayquiraro	MT711296	MT712834	MT356051
**Platydoras armatulus* (Valenciennes, 1840)	ANSP 181008	A5200	t714	Argentina	Paraná	KC555795	KC555676	KC555930
**Platydoras brachylecis* Piorski, Garavello, Arce H. & Sabaj, 2008	MCP 45249	PB1	t1482	Brazil		KC555796	KC555677	KC555931
Platydoras costatus (Linnaeus, 1758)	ROM 87181	T07942	t11247	Guyana	Courantyne	MT671338	–	MT356052
**Platydoras costatus* (Linnaeus, 1758)	ANSP 187111	7064	t1516	Suriname	Suriname	KC555797	KC555678	KC555932
Platydoras hancockii (Valenciennes, 1840)	ANSP 179145	2319	t730	Guyana	Amazon: Negro: Branco	MT671339	MT708512	MT356053

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Higher-level classification	Voucher data					GenBank Accession No.		
SUBORDER: Superfamily								
Family **Terminal taxon**	**Voucher museum and catalog no. when available**	**Voucher tag or other identifier**	**ANSP tissue reference number**	**Country**	**Basin: Sub-basins**	***rag 1***	***CO1***	***16S***
Platydoras hancockii (Valenciennes, 1840)	ANSP 179146	2369	t732	Guyana	Amazon: Negro: Branco	–	MT708511	MT356054
**Platydoras hancockii* (Valenciennes, 1840)	ANSP 179144	2032	t634	Guyana	Essequibo: Rupununi	KC555798	KC555679	KC555933
Platydoras helicophilus (Günther, 1868)	ANSP 187102	6980	t2266	Suriname	Maroni: Lawa	MT711299	MT712835	MT356055
Platydoras helicophilus (Günther, 1868)	ANSP 187102	6906	t1844	Suriname	Maroni: Lawa	MT711300	MT708510	MT356056
**Platydoras helicophilus* (Günther, 1868)	ANSP 187377	7050	t1285	Suriname	Maroni: Lawa	KC555799	KC555680	–
Platydoras sp. “Orinoco”	IAvH-P (GUA-YA18-P-16)	t8904	t15084	Colombia	Orinoco: Guaviare: Guayabero	MT671340	MT712836	MT356057
Platydoras sp. “Orinoco”	ANSP 198868	t4637	t12935	Venezuela	Orinoco: Arauca	MT671341	MT708509	MT356058
Platydoras sp. “Orinoco”	ANSP 198868	t4638	t12938	Venezuela	Orinoco: Arauca	MT671342	MT712837	–
Platydoras sp. “Orinoco”	ANSP 198868	t4639	t12937	Venezuela	Orinoco: Arauca	MT671343	MT712838	–
Platydoras sp. “Orinoco”	ANSP 198868	t4640	t12936	Venezuela	Orinoco: Arauca	MT711292	MT712839	MT356059
Platydoras sp. “upper Amazon”	ANSP 181047	P6053	t680	Peru	Amazon: Itaya	MT671344	MT712840	MT356060
Platydoras sp. “upper Amazon”	ANSP 191774	011	t4741	Peru	Amazon: Itaya	MT711297	MT712841	MT356061
Platydoras sp. “upper Amazon”	ANSP 191774	014	t4739	Peru	Amazon: Itaya	MT711298	MT712842	MT356062
**Platydoras* sp. “Xingu”	MZUSP 96336	7290	t14839	Brazil	Amazon: Xingu: Iriri	KC555800	KC555681	KC555934
Platydoras sp. “Xingu”	ANSP 194862	t0383	t8028	Brazil	Amazon: Xingu	MT711293	MT712843	MT356063
Platydoras sp. “Xingu”	INPA 40112	t0270	t7906	Brazil	Amazon: Xingu	MT711294	MT708508	MT356064
Pterodoras granulosus (Valenciennes, 1821)	ANSP 180883	A5100	t710	Argentina	Paraná: Guayquiraro	KC555802	KC555686	KC555939
Pterodoras granulosus (Valenciennes, 1821)	ANSP 181197	P6203	t1521	Peru	Amazon	KC555804	KC555684	KC555937
Pterodoras granulosus (Valenciennes, 1821)	ANSP 178350	1560	t758	Peru	Amazon: Yanuyacu	KC555801	KC555685	KC555938
Pterodoras rivasi (Fernández-Yépez, 1950)	MHNLS 20353	24220/CV002	t11300	Venezuela	Orinoco	KC555803	KC555687	KC555940
Pterodoras sp. “Nickerie”	ANSP 206841	–	t4949	Suriname	Nickerie	MT671345	MT712844	MT356065
**Rhinodoras armbrusteri* Sabaj, 2008	ANSP 179096	–	t599	Guyana	Amazon: Negro: Branco	KC555805	KC555688	KC555941
**Rhinodoras boehlkei* Glodek, Whitmire & Orcés V., 1976	ANSP 181044	P6059	t675	Peru	Amazon	KC555806	KC555689	KC555942
**Rhinodoras dorbignyi* (Kner, 1855)	LBP 3218	19423	t1785	Brazil	Paraná: Paraguai	KC555807	KC555690	KC555943
Rhinodoras gallagheri Sabaj, Taphorn & Castillo G., 2008	IavH-P	t8909	t15089	Colombia	Orinoco: Guaviare: Guayabero	MT671346	MT712845	MT356066
**Rhinodoras gallagheri* Sabaj, Taphorn & Castillo G., 2008	ANSP 191086	T09020	t1777	Venezuela	Orinoco: Apure	KC555808	KC555691	KC555944
Rhinodoras sp. “Xingu”	ANSP 196862	t2852	t10995	Brazil	Amazon: Xingu	MT671347	MT712846	MT356067
**Rhinodoras thomersoni* Taphorn & Lilyestrom, 1984	MCNG (field no. OC-09-006)	N021	t9504	Venezuela	Maracaibo: Santa Ana	KC555809	KC555692	KC555945
**Rhynchodoras woodsi* Glodek, 1976	ANSP 181042	P6052	t677	Peru	Amazon	KC555810	KC555693	KC555946
**Rhynchodoras woodsi* Glodek, 1976	ANSP 181042	P6061	t679	Peru	Amazon	KC555811	KC555694	KC555947
Rhynchodoras xingui Klausewitz & Rössel, 1961	ANSP 195903	t1483	t9126	Brazil	Amazon: Xingu	MT671348	MT712847	–
**Scorpiodoras bolivarensis* (Fernández-Yépez, 1968)	ANSP 182267	V183	t791	Venezuela	Orinoco: Ventuari	KC555812	KC555587	KC555845
**Scorpiodoras heckelii* (Kner, 1855)	AUM 42953	V5406	t1512	Venezuela	Orinoco	–	KC555696	KC555949
**Scorpiodoras heckelii* (Kner, 1855)	ANSP 182790	V5404	t792	Venezuela	Orinoco	KC555813	KC555695	KC555948

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Higher-level classification	Voucher data					GenBank Accession No.		
SUBORDER: Superfamily								
Family **Terminal taxon**	**Voucher museum and catalog no. when available**	**Voucher tag or other identifier**	**ANSP tissue reference number**	**Country**	**Basin: Sub-basins**	***rag 1***	***CO1***	***16S***
**Tenellus cristinae* (Sabaj, Arce H., Sousa & Birindelli, 2014)	ANSP 182744	P6096	t689	Peru	Amazon	KC555777	KC555655	KC555909
**Tenellus cristinae* (Sabaj, Arce H., Sousa & Birindelli, 2014)	ANSP 180551	4076	t773	Peru	Amazon: Madeira: Madre de Dios	KC555776	KC555654	KC555908
**Tenellus leporhinus* (Eigenmann, 1912)	MZUSP 96596	7082	t14830	Brazil	Amazon: Tapajós: Teles Pires	KC555773	KC555653	KC555907
**Tenellus leporhinus* (Eigenmann, 1912)	ANSP 182825	P4319	t795	Venezuela	Orinoco	KC555775	KC555652	KC555906
**Tenellus leporhinus* (Eigenmann, 1912)	ANSP 180297	V104	t780	Venezuela	Orinoco: Ventuari	KC555774	KC555651	KC555905
**Tenellus ternetzi* (Eigenmann, 1925)	ANSP 182852	CALH 56	t1525	Brazil	Amazon: Negro	KC555783	KC555661	KC555915
**Tenellus ternetzi* (Eigenmann, 1925)	ANSP 179203	T2451	t1527	Guyana	Amazon: Negro: Branco	KC555782	KC555660	KC555914
**Tenellus ternetzi* (Eigenmann, 1925)	ANSP 180177	2292	t766	Peru	Amazon: Nanay	KC555784	KC555662	KC555916
**Tenellus ternetzi* (Eigenmann, 1925)	ANSP 180905	4604	t798	Venezuela	Amazon: Negro: Casiquiare	KC555785	KC555663	KC555917
**Trachydoras brevis* (Kner, 1853)	MHNG 2650.062	GY04-091	–	Guyana	Essequibo: Rupununi	KC555814	KC555698	KC555951
**Trachydoras* cf. *paraguayensis* “Essequibo”	ANSP 179855	2211	t729	Guyana	Essequibo: Rupununi	KC555819	KC555699	KC555952
**Trachydoras gepharti* Sabaj & Arce H., 2017	ANSP 179866	2475	t767	Peru	Amazon: Nanay	KC555821	KC555705	KC555959
**Trachydoras gepharti* Sabaj & Arce H., 2017	ANSP 187373	T2293	t1517	Peru	Amazon: Nanay	–	KC555706	KC555960
**Trachydoras gepharti* Sabaj & Arce H., 2017	ANSP 185076	V021	t1544	Venezuela	Orinoco	–	KC555707	KC555961
Trachydoras microstomus (Eigenmann, 1912)	AUM 35800	T2100	t11214	Guyana	Essequibo	MT671349	MT712848	MT356068
**Trachydoras microstomus* (Eigenmann, 1912)	ANSP 179853	T2099	t1522	Guyana	Essequibo	KC555817	KC555702	KC555955
Trachydoras microstomus (Eigenmann, 1912)	MCNG ex. 53431	P4576	t865	Venezuela	Amazon: Negro	MT711290	MT712849	MT356069
Trachydoras microstomus (Eigenmann, 1912)	ANSP 203171	T09099	t15462	Venezuela	Orinoco	MT671350	MT712850	MT356070
**Trachydoras nattereri* (Steindachner, 1881)	ANSP 182593	P6313	t706	Peru	Amazon: Nanay	KC555816	–	KC555957
**Trachydoras paraguayensis* (Eigenmann & Ward, 1907)	ANSP 181011	A5134	t713	Argentina	Paraná	KC555818	KC555704	KC555958
**Trachydoras* sp. “mancha-caudal”	ANSP 182619	P6310	t705	Peru	Amazon: Nanay	KC555815	KC555703	KC555956
**Trachydoras steindachneri* (Perugia, 1897)	ANSP 178256	1673	t751	Peru	Amazon	–	KC555708	KC555962
**Wertheimeria maculata* Steindachner, 1877	MCP 43855	WM2	t14844	Brazil	Jequitinhonha	KC555822	KC555709	KC555963
**Wertheimeria maculata* Steindachner, 1877	MZUSP 88614	–	–	Brazil	Jequitinhonha	–	KC555710	KC555964

10 µl of Apex Taq DNA Polymerase Master Mix, 1.5 mM MgCl2 (Genesee Scientific), 0.5 µM of forward and reverse primer, 5–8 µl of distilled water and 1–4 µl of DNA template. Cycles of amplification were programmed accordingly: 95°C for 4 min (initial denaturation), 10 cycles of three steps, 50°C or 55°C for 30 sec (annealing, temperature decreased by 1°C after each cycle), 72°C for 2 min (extension) and 95°C for 1 min (denaturation); 30 cycles of three steps, 95°C for 1 min, 40°C or 44°C for 30 sec, and 72°C for 2 min; final extension step at 72°C for 10 min. Amplification of rag1 followed the protocol of Sullivan *et al.* (2006): 4 min at 95°C (initial denaturation), 35 cycles of three steps, 30 sec at either 50°C, 55°C or 59°C, 2 min at 72°C, and 30 sec at 95°C; final extension step for 4 min at 72°C. Amplifications were sent to Functional Biosciences, Inc. laboratories for purification and sequencing.

Molecular Data: sequence alignment and phylogenetic analyses. Sequences were edited and combined into contigs for each marker (rag1, co1, 16s) in Geneious 11.1.2 (Drummond *et al*., 2010). Complete gene sequences were aligned in MUSCLE 3.7 (Edgar, 2004) using default parameters. Alignments were refined manually, and sequences for the three markers were concatenated in Mesquite 3.40 (Maddison, Maddison, 2011). Translations of new sequences for co1 and rag1 were aligned in COBALT (Papadopoulos, Agarwala, 2007) to correct for frameshifts and to trim low-quality ends prior to DNA sequence alignment.

We analyzed combined nuclear and mitochondrial sequences using Maximum Parsimony (MP) and Bayesian Inference (BI), and employed the same parameters as Arce H. *et al.* (2013) for comparability. Analyses were performed on the combined dataset with terminals restricted to those represented by at least two loci (*i.e*., 218 specimens; Tab. 1). For MP analysis, the trees were generated using the "new technologies search" implemented in TNT (Goloboff *et al*., 2008) and 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; driven was set to reach the minimum length 50 times. The second step used the trees produced in the first search to perform a traditional TBR search. Gaps were treated as missing data and all characters had equal weights. Godman-Bremer support (Goodman *et al*., 1982; Bremer, 1988, 1994; Grant, Kluge, 2008) was calculated for each node and plotted on the consensus tree.

For Bayesian analyses, the concatenated gene matrix was divided into eight partitions: one for 16s, one for each nucleotide position per co1 codon, one for each nucleotide position per rag1 codon, and one for the rag1 intron. Bayesian analyses were conducted in MrBayes 3.1.6 (Huelsenbeck, Ronquist, 2001; Ronquist, Huelsenbeck, 2003) using the GTR + GAMMA model. We ran three heated chains and one cold chain for 60 million generations, sampling every 10,000th generation. To ensure sampling of the posterior distribution we discarded 0.25% of the trees.

Morphological Data. Specimens examined for morphological data were designated as alc (alcohol), sk (dry skeleton) or cs (cleared and stained following the methods of Taylor, Van Dyke, 1985). Data on the caudal skeleton were taken from cleared and stained specimens and dry skeletons while immersed in 90% glycerin and 75% ethanol, respectively, and viewed under a Wild M3C stereomicroscope. Immersion facilitated the removal of residual muscle tissue and assessment of sutures. Midlateral scutes were removed from both sides to facilitate clear observations of the caudal skeleton. Observations were made on adult specimens and juveniles at stages where the caudal skeleton was already mostly ossified. In a few cases, ontogeny was used to hypothesize fusion between elements (*e.g*., procurrent caudal-fin rays in some astrodoradins). But for the most part, fusions between elements (*e.g*., hypurals, parhypural) was presumed and not directly observed via ontogenetic series (*e.g*., Vaz, Hilton, 2020). Museum codes follow Sabaj (2020).

For descriptions of the caudal skeleton, we employed the diural scheme which considers the last vertebra to be a compound caudal centrum formed by the fusion of the posteriormost preural centrum (PU1) plus anteriormost ural centrum (U1) (Lundberg, Baskin, 1969; Grande, Shardo, 2002; de Pinna, Ng, 2004; Bird, Mabee, 2003; Bensimon-

Brito *et al*., 2012). In cases where a second ural centrum (U2) is visible, it is sometimes considered a fusion product of two or three originally distinct centra (Arratia, 2003; de Pinna, Ng, 2004; Bensimon-Brito *et al*., 2010, 2012). The compound caudal centrum (PU1+U1) supports the pleurostyle (PL), hypurals (HY) and parhypural (PH). We use the generic term pleurostyle for the elongate process that projects at an angle from the dorsal posterior corner of compound caudal centrum. Previous authors used the term uroneural (*i.e.,* modified ural neural arch) for this process in catfishes (*e.g.,* Lundberg, Baskin, 1969; Grande, Shardo, 2002; de Pinna, Ng, 2004); however, the homology and evolution of this process remains uncertain among ostariophysans (Cumplido *et al*., 2020). Hypurals are ventral bony elements separated into lower hypurals (HY1,2) and upper hypurals (HY3,4,5,6 in catfishes) by a diastema or gap for the passage of paired arterial and venous branches leading to and from the caudal fin (Desvignes *et al*., 2018). The parhypural represents the last haemal arch and spine, and the hypurals are considered modified haemal spines of the ural centra (Arratia, Schultze, 1992; Schultze, Arratia, 2013).

Lundberg, Baskin (1969) introduced a formula for describing various patterns of fusion and/or loss among the elements supported by the compound caudal centrum (PU1+U1). They used a plus sign (+) between adjacent elements that are presumably completely fused (*e.g*., PH+HY1+2), and a semicolon (;) between adjacent elements that remain separated or at least distinguishable, often by a long and continuous suture (*e.g*., PH; HY1; 2). Although the parhypural and ventral hypurals may appear separate and scored as such, these three elements are tightly associated or fused (continuous) proximally near their fusion to the compound caudal centrum from early developmental stages to adulthood in catfishes (Grande, Shardo, 2002; Adriaens, Vandewalle, 2003). When the sixth hypural was not distinguishable, it was presumed lost rather than fused, and thereby omitted from the formula.

For scoring individuals, we modified the formula of Lundberg, Baskin (1969) by using a hyphen (-) between elements that are only partially fused and retain features suggestive of independence such as distal or internal gaps and/or semitransparent windows of thin bone; figures in Grande, Shardo (2002) similarly employed hyphens. For scoring a taxon as a whole, a hyphen in the formula also might represent polymorphism where two elements may appear completely fused in some specimens, but separate in others. For completeness, we also included the pleurostyle (PL) and epural (EP) in the formula because those elements may fuse with each other or with the upper hypural plate in some taxa. Principal caudal-fin rays are reported as branched (Arabic numeral) or simple (lower case Roman numeral).

Character state mapping. For two characters associated with fusion patterns in the caudal skeleton, states were mapped on the Maximum Parsimony phylogeny generated in the current study for Aspredinidae, Auchenipteridae and Doradidae (*i.e*., Aspredinoidea). The first character was divided into two states: parahypural separate (1) or fused (2) with hypurals 1+2. The second character involved the upper hypurals (HY) and pleurostyle (PL) and exhibited three states treated as ordered: HY3+4; 5; PL (1), HY3+4+5; PL (2), and HY3+4+5-PL or HY3+4+5+PL (3). Next, each possible state was assigned to the common ancestor of the three families. Then, the number of transformations necessary to achieve the phylogenetic distribution of states in the terminal lineages was assessed by eye. The inferences from this exercise are presented in the Discussion.

RESULTS

Molecular Analyses. In our final analyses, 180 of the 218 specimens were represented by complete molecular data (all genes: rag1, co1, 16s; Tab. 1). Seven specimens were represented only by rag1 and co1 sequences, nine specimens were represented only by rag1 and 16s sequences, and 22 specimens were represented only by co1 and 16s sequences. The Maximum Parsimony (MP) analysis produced 144 most parsimonious trees of 9235 steps each. Under MP, the rag1 dataset consisted of 1861 total and 716 parsimony-informative base pairs for 196 specimens, the 16s dataset consisted of 583 total and 188 parsimony-informative base pairs for 211 specimens, and the co1 dataset consisted of 593 total and 246 parsimony-informative base pairs for 209 specimens. The combined dataset included 3037 total base pairs of which 1150 were parsimony informative for 218 terminals.

Trees produced by the Maximum Parsimony (MP) and Bayesian (BI) analyses were highly resolved and agreed on most intergeneric relationships (Figs. 4, **S1**, **S2**, **S3**) with a few notable exceptions. The largest disagreement between the MP and BI topologies involved the base of Doradidae. In the MP analysis, Acanthodoradinae was the first subfamily to diverge from the rest of Doradidae and Astrodoradinae was the second. BI reversed this topology with Astrodoradinae diverging first, followed by Acanthodoradinae. Relationships within Astrodoradinae also differed between the two analyses. Both identified *Anadoras* Eigenmann, 1925 as the first genus to diverge in Astrodoradinae. MP supported *Physopyxis* Cope, 1871 sister to *Astrodoras* + *Hypodoras* and *Amblydoras* Bleeker, 1862 sister to *Scorpiodoras* Eigenmann, 1925. BI placed *Physopyxis* sister to a clade composed of *Scorpiodoras* and *Amblydoras* (*Astrodoras* + *Hypodoras*).

Within the subfamily Doradinae, MP and BI differed in four major respects. In the parsimony analysis, *Doraops* + *Pterodoras* was the first group to diverge within Doradinae, followed by *Oxydoras* Kner, 1855. BI weakly supported (0.5 posterior probability) the reverse with *Oxydoras* as the first genus to split from the rest of Doradinae, followed by *Doraops* + *Pterodoras*. A second difference between MP and BI was placement of the clade *Centrodoras* (*Lithodoras* + *Megalodoras*). In the parsimony analysis, *Centrodoras* (*Lithodoras* + *Megalodoras*) was sister to the fimbriate-barbel doradids. Alternatively, BI supported a sister group relationship between *Centrodoras* (*Lithodoras* + *Megalodoras*) and *Centrochir* + *Platydoras*, and that clade was sister to the fimbriate-barbel doradids. Thirdly, MP supported the monophyly of *Doras* inclusive of *Doras punctatus* Kner, 1855 a species formerly assigned to *Ossancora* (Birindelli, Sabaj Pérez, 2011), and placed *Doras* sister to all other fimbriate-barbel doradids. In the BI analysis, *Doras carinatus* (Linnaeus, 1766; type species), *D. micropoeus* (Eigenmann, 1912), and *D. higuchii* Sabaj Pérez & Birindelli, 2008 formed a clade sister to all other fimbriate barbel taxa except *D. phlyzakion* Sabaj Pérez & Birindelli, 2008 and *D. punctatus*. Those two species, respectively, were successive sister taxa to the remaining fimbriate-barbel taxa. Finally, near the crown of the doradid tree, MP and BI disagreed on relationships within a clade composed of *Hassar* Eigenmann & Eigenmann, 1888, *Nemadoras* Eigenmann, 1925, *Tennellus* Birindelli, 2014 and *Hemidoras* + *Ossancora*. MP weakly supported two monophyletic clades, *Nemadoras* + *Tennellus* and *Hassar* (*Hemidoras* + *Ossancora*), each with a Godman-Bremer support value of 1 (Fig. **S2**). In the BI analysis, *Nemadoras* was the first genus to diverge and *Tennellus* + *Hassar* and *Hemidoras* + *Ossancora* formed reciprocally monophyletic clades (Fig. **S1**).

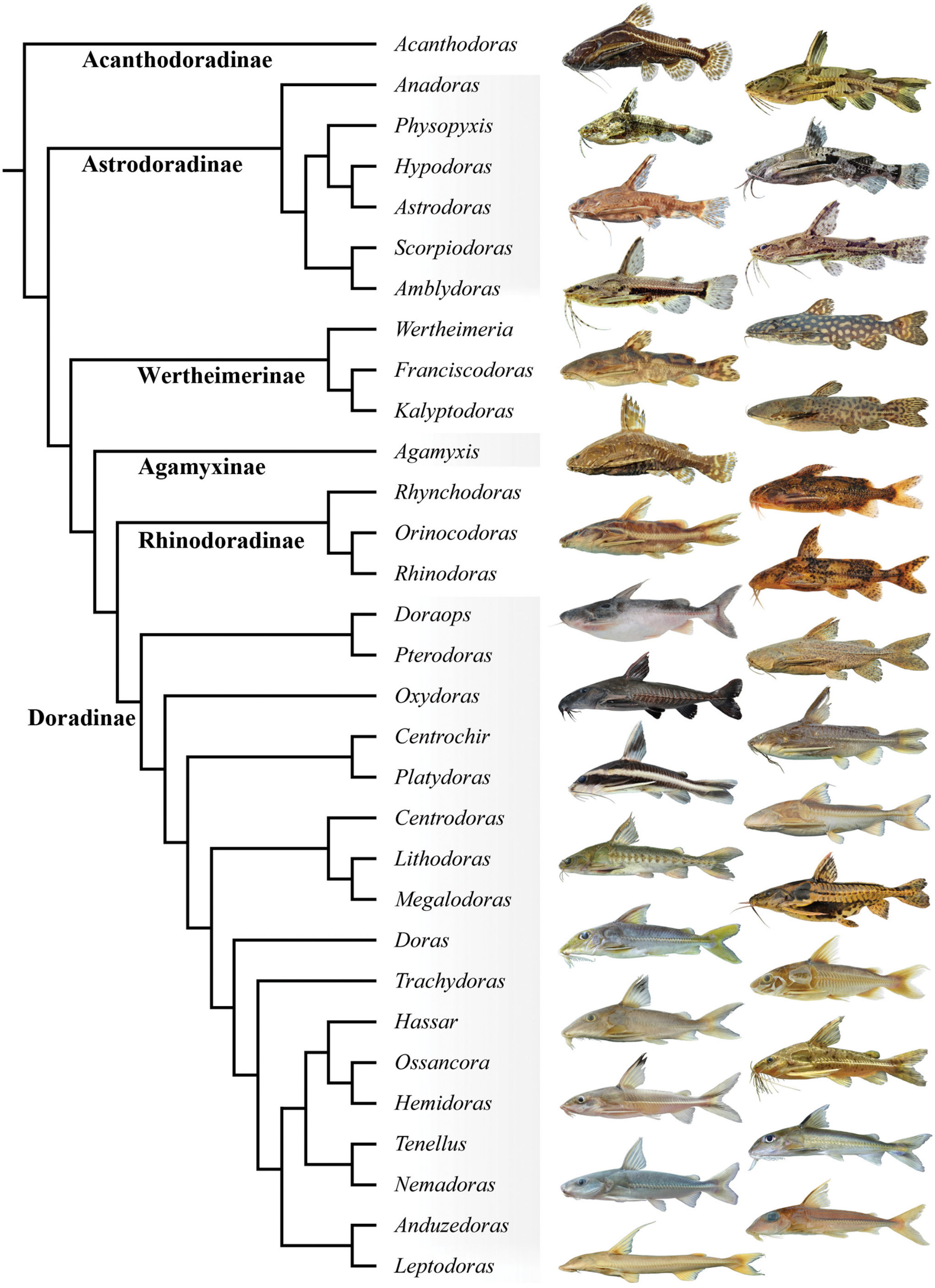


FIGURE 4 | Phylogenetic relationships among all genera and subfamilies of Doradidae inferred from Maximum Parsimony analysis of rag1, 16s and co1 DNA sequence data (strict consensus of 144 most parsimonious trees, each with 9235 steps).

Our revised classification of Doradidae (Tab. 2; Fig. 4) is based on relationships supported by the Maximum Parsimony analysis of the DNA sequence data. The results of the Bayesian analysis are consistent with our classification except for the monophyly of *Doras* which is supported only by MP. Except for Astrodoradinae and Doradinae, each subfamily is diagnosed by caudal-fin or other characteristics.

TABLE 2 | Revised classification of Doradidae Bleeker, 1858. Nominal species that remain questionable as valid preceded by "?" and listed under possible senior synonym. Totals exclude species that are questionably valid, and species introduced to or questionably present in a given basin. Asterisk denotes species included in molecular phylogenetic analyses.

			Amazonas			**Atlantic Coastal**			**La Plata**		
Subfamily Valid genus Valid species	**Caribbean** (west of Andes)	**Orinoco**	Upper (incl. Negro & Casiquiare)	Lower (incl. Madeira)	Tocantins	Guianas & Amapá, BR	Northern Brazil	Eastern Brazil	Uruguay & Yaguarón	Paraguay & Lower Paraná	Upper Paraná
Acanthodoradinae new subfamily											
Acanthodoras Bleeker, 1862											
1* *Acanthodoras cataphractus* (Linnaeus, 1758)		X	X	X		X					
2 *Acanthodoras depressus* (Steindachner, 1881)			X								
3 *Acanthodoras polygrammus* (Kner, 1853)		X	X	X		X					
? *Acanthodoras spinosissimus* (Eigenmann & Eigenmann, 1888)											
Astrodoradinae Higuchi, Birindelli, Sousa & Britski, 2007											
Amblydoras Bleeker, 1862											
4* *Amblydoras affinis* (Kner, 1855)			X	?		Essequibo					
? *Amblydoras insculptus* (Miranda Ribeiro, 1912)											
5 *Amblydoras gonzalezi* (Fernández-Yépez, 1968)		X									
6 *Amblydoras monitor* (Cope, 1872)			X	?							
7* *Amblydoras nauticus* (Cope, 1874)			X	?							
8* *Amblydoras nheco* (Higuchi, Birindelli, Sousa & Britski, 2007)										Paraguay	
9 *Amblydoras truncatus* Bleeker, 1863			Madeira								
Anadoras Eigenmann, 1925											
10* *Anadoras grypus* (Cope, 1872)			X	X							
11* *Anadoras weddellii* (Castelnau, 1855)				X	X	X				X	
? *Anadoras regani* (Steindachner, 1908)											
Astrodoras Bleeker, 1862											
12* *Astrodoras asterifrons* (Kner, 1853)			X	X							
Hypodoras Eigenmann, 1925											
13* *Hypodoras forficulatus* Eigenmann, 1925			X								
14* *Physopyxis ananas* Sousa & Rapp Py-Daniel, 2005		Upper	X	X		Essequibo					
15 *Physopyxis cristata* Sousa & Rapp Py-Daniel, 2005			Negro								

➡

TABLE 2 | (Continued)

			Amazonas			Atlantic Coastal			La Plata		
Subfamily Valid genus Valid species	**Caribbean** (west of Andes)	**Orinoco**	Upper (incl. Negro & Casiquiare)	Lower (incl. Madeira)	Tocantins	Guianas & Amapá, BR	Northern Brazil	Eastern Brazil	Uruguay & Yaguarón	Paraguay & Lower Paraná	Upper Paraná
16* *Physopyxis lyra* Cope, 1872			X	X							
Scorpiodoras Eigenmann, 1925											
17* *Scorpiodoras bolivarensis* (Fernández-Yépez, 1968)		X									
18 *Scorpiodoras calderonensis* (Vaillant, 1880)			Solimões								
19* *Scorpiodoras heckelii* (Kner, 1855)		X	Negro	X							
20 *Scorpiodoras liophysus* Sousa & Birindelli, 2011				Madeira							
Wertheimerinae Birindelli, 2014											
Franciscodoras Eigenmann, 1925											
21* *Franciscodoras marmoratus* (Lütken, 1874)								São Francisco			
Kalyptodoras Higuchi, Britski & Garavello, 1990											
22* *Kalyptodoras bahiensis* Higuchi, Britski & Garavello, 1990								Paraguaçu			
Wertheimeria Steindachner, 1877											
23* *Wertheimeria maculata* Steindachner, 1877								Pardo & Jequitinhonha			
Agamyxinae new subfamily											
Agamyxis Cope, 1878											
24* *Agamyxis albomaculatus* (Peters, 1877)		X									
25* *Agamyxis pectinifrons* (Cope, 1870)			X	X							
Rhinodoradinae new subfamily											
Orinocodoras Myers, 1927											
26* *Orinocodoras eigenmanni* Myers, 1927		X									
Rhinodoras Bleeker, 1862											
27* *Rhinodoras armbrusteri* Sabaj, 2008			Takutu			Essequibo					
28* *Rhinodoras boehlkei* Glodek, Whitmire & Orcés V., 1976			X	X	X						
29* *Rhinodoras dorbignyi* (Kner, 1855)									X	X	X
30* *Rhinodoras gallagheri* Sabaj, Taphorn & Castillo G., 2008		X									
31* *Rhinodoras thomersoni* Taphorn & Lilyestrom, 1984	Maracaibo										
Rhynchodoras Klausewitz & Rössel 1961											
32 *Rhynchodoras castilloi* Birindelli, Sabaj & Taphorn, 2007		Apure									
33* *Rhynchodoras woodsi* Glodek, 1976			X	X		Essequibo					
34* *Rhynchodoras xingui* Klausewitz & Rössel, 1961				Xingu	X						
Doradinae Bleeker, 1858											
Anduzedoras Fernández-Yépez, 1968											
35* *Anduzedoras oxyrhynchus* (Valenciennes, 1821)		X	Negro	X							
Centrochir Agassiz, 1829											

TABLE 2 | (Continued)

			Amazonas			Atlantic Coastal			La Plata		
Subfamily Valid genus Valid species	**Caribbean** (west of Andes)	**Orinoco**	Upper (incl. Negro & Casiquiare)	Lower (incl. Madeira)	Tocantins	Guianas & Amapá, BR	Northern Brazil	Eastern Brazil	Uruguay & Yaguarón	Paraguay & Lower Paraná	Upper Paraná
36* *Centrochir birindellii* (Sousa, Santana, Akama, Zuanon & Sabaj, 2018)				Xingu							
37* *Centrochir crocodili* (Humboldt, 1821)	Magdalena										
Centrodoras Eigenmann, 1925											
38* *Centrodoras brachiatus* (Cope, 1872)			X	X							
39* *Centrodoras hasemani* (Steindachner, 1915)			Negro								
Doraops Schultz, 1944											
40* *Doraops zuloagai* Schultz, 1944	Maracaibo										
Doras Lacepède, 1803											
41* *Doras carinatus* (Linnaeus, 1766)		Caroní				X					
42 † *Doras dioneae* Sabaj, Aguilera & Lundberg, 2007											
43* *Doras higuchii* Sabaj & Birindelli, 2008				X							
44* *Doras micropoeus* (Eigenmann, 1912)						X					
45* *Doras phlyzakion* Sabaj & Birindelli, 2008			X								
46* *Doras punctatus* Kner, 1853			X	X						X	
47 *Doras zuanoni* Sabaj & Birindelli, 2008					X						
Hassar Eigenmann & Eigenmann, 1888											
48* *Hassar affinis* (Steindachner, 1881)							X				
49* *Hassar gabiru* Birindelli, Fayal & Wosiacki, 2011				Xingu							
50* *Hassar orestis* (Steindachner, 1875)		X	X	X		Essequibo					
51 *Hassar shewellkeimi* Sabaj & Birindelli, 2013				Tapajós							
52* *Hassar wilderi* Kindle, 1895					X						
Hemidoras Bleeker, 1858											
53* *Hemidoras boulengeri* (Steindachner, 1915)			X	X							
? *Hemidoras morrisi* Eigenmann, 1925											
54* *Hemidoras morei* (Steindachner, 1881)		X	X			Essequibo					
55* *Hemidoras stenopeltis* (Kner, 1855)			X	X							
56* *Hemidoras stuebelii* (Steindachner, 1882)		X	X	X							
Leptodoras Boulenger, 1898											
57* *Leptodoras acipenserinus* (Günther, 1868)			X	Madeira							
58* *Leptodoras cataniai* Sabaj, 2005			X	X	X						
59* *Leptodoras copei* (Fernández-Yépez, 1968)		X	X	X							
60* *Leptodoras hasemani* (Steindachner, 1915)		X	X	X	X	Essequibo					
61* *Leptodoras juruensis* Boulenger, 1898			X	X							
62* *Leptodoras linnelli* Eigenmann, 1912		X	X	X		X					

TABLE 2 | (Continued)

	Caribbean (west of Andes)	Orinoco	Amazonas			Atlantic Coastal			La Plata		
Subfamily Valid genus Valid species			Upper (incl. Negro & Casiquiare)	Lower (incl. Madeira)	Tocantins	Guianas & Amapá, BR	Northern Brazil	Eastern Brazil	Uruguay & Yaguarón	Paraguay & Lower Paraná	Upper Paraná
63* *Leptodoras marki* Birindelli & Sousa, 2010				Xingu							
64* *Leptodoras myersi* Böhlke, 1970			X								
65* *Leptodoras nelsoni* Sabaj, 2005		X									
66* *Leptodoras oyakawai* Birindelli, Sousa & Sabaj, 2008				X							
67* *Leptodoras praelongus* (Myers & Weitzman, 1956)		X	X	X	X	Essequibo					
68 *Leptodoras rogersae* Sabaj, 2005		X									
Lithodoras Bleeker, 1862											
69* *Lithodoras dorsalis* (Valenciennes, 1840)			X	X	X	Amapá					
Megalodoras Eigenmann, 1925											
70* *Megalodoras guayoensis* (Fernández-Yépez, 1968)		X									
71* *Megalodoras uranoscopus* (Eigenmann & Eigenmann, 1888)			X	X	X	Essequibo					
Nemadoras Eigenmann, 1925											
72* *Nemadoras elongatus* (Boulenger, 1898)			X	X							
73* *Nemadoras hemipeltis* (Eigenmann, 1925)			X	X							
74* *Nemadoras humeralis* (Kner, 1855)			X	X	X						
75* *Nemadoras trimaculatus* (Boulenger, 1898)		X	X	X	X	Essequibo					
Ossancora Sabaj & Birindelli, 2011											
76* *Ossancora asterophysa* Birindelli & Sabaj, 2011			X	X							
77 *Ossancora eigenmanni* (Boulenger, 1895)			X	X							
78* *Ossancora fimbriata* (Kner, 1855)			X	X							
Oxydoras Kner, 1855											
79* *Oxydoras kneri* Bleeker, 1862										X	
80* *Oxydoras niger* (Valenciennes, 1821)			X	X	X	Essequibo		? São Francisco			
81* *Oxydoras sifontesi* Fernández-Yépez, 1968		X									
Platydoras Bleeker, 1862											
82* *Platydoras armatulus* (Valenciennes, 1840)		X	X	X	X					X	
83* *Platydoras brachylecis* Piorski, Garavello, Arce H. & Sabaj, 2008							X				
84* *Platydoras costatus* (Linnaeus, 1758)						X					
85* *Platydoras hancockii* (Valenciennes, 1840)		X	Negro			Essequibo					
86* *Platydoras helicophilus* (Günther, 1868)						Maroni					
Pterodoras Bleeker, 1862											
87* *Pterodoras granulosus* (Valenciennes, 1821)			X	X	X					X	Introduced
88* *Pterodoras rivasi* (Fernández-Yépez, 1950)		X									
Tenellus Birindelli, 2014											

TABLE 2 | (Continued)

	Caribbean (west of Andes)	Orinoco	Amazonas			Atlantic Coastal			La Plata		
Subfamily Valid genus Valid species			Upper (incl. Negro & Casiquiare)	Lower (incl. Madeira)	Tocantins	Guianas & Amapá, BR	Northern Brazil	Eastern Brazil	Uruguay & Yaguarón	Paraguay & Lower Paraná	Upper Paraná
89* *Tenellus cristinae* (Sabaj, Arce H., Sousa & Birindelli, 2014)		X	X	X							
90* *Tenellus leporhinus* (Eigenmann, 1912)		X	Negro	X	X	Essequibo					
91* *Tenellus ternetzi* (Eigenmann, 1925)											
Trachydoras Eigenmann, 1925											
92* *Trachydoras brevis* (Kner, 1853)			X	X		Essequibo					
93* *Trachydoras gepharti* Sabaj & Arce H., 2017		X	X	X							
94* *Trachydoras microstomus* (Eigenmann, 1912)		X	X	X		Essequibo					
95* *Trachydoras nattereri* (Steindachner, 1881)			X	X		Essequibo					
96* *Trachydoras paraguayensis* (Eigenmann & Ward, 1907)			? Solimões	X						X	Introduced
97* *Trachydoras steindachneri* (Perugia, 1897)			X	X							
	3	**31**	**57**	**53**	**16**	**25**	**2**	**3**	**1**	**8**	**1**
			69 (Amazonas)								

Caudal-fin shape. Most doradid caudal fins are separable into two shapes: evenly rounded *vs.* distinctly forked (Tab. 3; Fig. 4). An evenly rounded caudal fin is restricted to the monotypic Acanthodoradinae (*Acanthodoras*). Forked caudal fins are found in *Anadoras* (Astrodoradinae), Wertheimerinae and all members of the sister subfamilies Rhinodoradinae and Doradinae. In *Anadoras*, the caudal fin is shallowly to moderately forked with upper lobe often longer and lower lobe more broadly rounded. Among other doradids, caudal fins vary from shallowly forked with rounded or bluntly pointed lobes (*e.g.*, *Centrochir* Agassiz, 1829, *Platydoras*, *Oxydoras*, *Wertheimeria*) to deeply forked with pointed lobes (*Centrodoras* Eigenmann, 1925, *Doraops* Schultz, 1944, *Hassar*, *Hemidoras*, *Leptodoras* Boulenger, 1898, *Rhinodoras*).

Caudal-fin shapes in the remaining doradids occupy a spectrum of conditions between evenly rounded and distinctly forked. The monotypic Agamyxinae (*Agamyxis* Cope, 1878) generally has a truncate to emarginate caudal fin, the latter with gently rounded lobes. Among astrodoradins apart from *Anadoras*, the branched rays of the upper lobe are often longer, imparting an unevenly emarginate or obliquely truncate distal margin, especially among species of *Hypodoras* and *Physopyxis*. *Astrodoras* is somewhat unusual in that the upper lobe is relatively narrow and pointed and the lower lobe is broadly rounded, often imparting an uneven S-shape to the distal margin of the caudal fin.

Caudal-fin rays. Like most other catfishes, doradid caudal-fin rays are divided into principal rays (segmented) and procurrent rays (anterior ones unsegmented, posterior ones distally segmented). Principal rays include all distally branched rays and typically two unbranched (simple) rays, one adjacent to the dorsalmost and ventralmost branched ray, respectively. The dorsalmost principal ray is supported by the dorsalmost hypural

TABLE 3 | Summary of morphological differences in caudal-fin skeleton of Doradidae.

Subfamily Genus or species	Caudal-fin shape	Principal caudal-fin rays	Upper/lower procurrent rays	Total rays: upper / lower	Typical caudal-skeleton formula	Alternative conditions	Comments	Preparations examined (SL in mm)
Acanthodoradinae, new subfamily								
Acanthodoras Bleeker, 1862	evenly rounded	i,7/6-7,i	13–16/9–13	37–42: 21–24/16–20	PH+HY1+2; 3+4+5-PL; EP	upper hypural plate completely sutured to pleurostyle (3+4+5; PL) or completely fused to pleurostyle (3+4+5+PL)	upper hypural plate typically partially separated from pleurostyle via distal notch or incomplete suture	11: 4 alc, 2 sk (70-121.5), 6 cs (22.5–99)
Astrodoradinae Higuchi, Birindelli, Sousa & Britski, 2007								
Anadoras Eigenmann, 1925	shallowly to moderately forked with upper lobe usually longer and lower lobe more rounded	i,7/7,i	12–13/13–14	41–42: 20–21/21–22	PH-HY1+2; 3+4; 5; PL; EP	none observed	lenticular window of thin bone between PH and HY1+2 with associated suture obsolete or nearly so	11: 5 alc (71.5–114), 2 sk (84–85), 4 cs (44.7–71)
Hypodoras Eigenmann, 1925	truncate to unevenly emarginate with upper branched rays scarcely longer than lower	i,6/6,i	11/10–12	35–37: 18/17–19	PH+HY1+2; 3+4+5; PL; EP	hypurals 3+4 and 5 separate (3+4; 5) or sutured proximally, fused distally (3+4–5) in juveniles (<56 mm SL)	HY3+4+5 appears as singular plate with no evidence of sutures, open gaps or bony windows in adults (>86 mm SL)	9: 5 alc (75.9–103), 1 sk (87), 3 cs (26.4–55.5)
Physopyxis Cope, 1871	truncate to unevenly emarginate with upper branched rays distinctly longer than lower	i,7/4-5,i	13–18/11–16	38–47: 21–26/16–21	PH+HY1+2; 3+4; 5; PL; EP	parhypural and hypural 1+2 separated by distinct suture (PH; HY1+2); hypurals 3+4 and 5 sutured proximally, fused distally (3+4–5)		14 cs (11–30.3)
Amblydoras Bleeker, 1862	truncate to deeply emarginate with upper lobe sometimes longer	i,7/7,i	14–16/12–14	42–48: 22–25/20–23	PH+HY1+2; 3+4; 5; PL; EP	hypurals 3 and 4 separate (3; 4) or incompletely fused (3–4) in some juveniles (<24 mm SL)	small juveniles (<19 mm SL) exhibit 4–6 (*vs.* 7) branched rays in lower lobe	24: 4 alc (63–86), 20 cs (15.2–95.2)
Astrodoras Bleeker, 1862			10–13/9–12	35–40: 18–21/17-20		hypurals 3+4 and 5 sutured proximally, fused distally (3+4–5) in smallest specimen (49.3 mm SL)	anteriormost 1–3 dorsal and ventral procurrent rays flattened into plates	8: 4 alc (72.1–74.3), 4 cs (49.3–69.2)
Scorpiodoras Eigenmann, 1925			12–16/10–14	38–44: 20–23/18–21		hypurals 3 and 4 with suture or slit proximally, fused distally (3–4); hypurals 3+4 and 5 fused (3+4+5)	lower caudal-fin lobe rarely with 6 (*vs.* 7) branched rays	7: 2 alc, 5 cs (14.9–67)
Wertheimerinae Birindelli, 2014								
Franciscodoras Eigenmann, 1925	shallowly forked with lower lobe slightly more rounded	i,6–7/7,i	8–11/9–11	32–38: 15–19/17–19	PH; HY1+2; 3+4; 5; PL; EP	Birindelli (2014) reported that all hypural elements (PH, HY1 to 5) may be distinct in small juveniles	anteriormost 3–5 dorsal and ventral procurrent rays flattened into plates; Birindelli (2014:533) reported parhypural and hypural elements appearing distinct in small juveniles (*i.e.*, PH; HY1; 2; 3; 4; 5)	14: 10 alc (102.1–177.7), 2 sk (123.5–217), 2 cs (106–123)
Kalyptodoras Higuchi, Britski & Garavello, 1990		i,7/7,i	12–13/11–14	39–43: 20–21/19–22				2 alc (143.3–174.9)
Wertheimeria Steindachner, 1877			15/14	45: 23/22		hypurals 1 and 2 separated by lenticular bony window (HY1–2)		9: 6 alc (102.1–122.1), 2 sk (123.5–217), 1 cs (106)
Agamyxinae, new subfamily								
Agamyxis Cope, 1878	truncate to emarginate with rounded lobes	i,6/7,i	6–10/7–10	28–34: 13–17/14–18	PH-HY1+2; 3+4; 5; PL; EP	parhypural and hypural 1+2 completely fused (PH+HY1+2); hypurals 3+4 and 5 fused (3+4+5) in one specimen of *A. albomaculatus* (51.9 mm SL)	parhypural and hypural 1+2 typically fused distally, separated proximally by lenticular bony window that may include 1–2 open gaps and partial suture; bony window often completely occluded in larger specimens; anteriormost 4–8 dorsal and ventral procurrent rays flattened into plates	21: 5 alc (44–101.4), 16 cs (32.5–102.6)
Rhinodoradinae, new subfamily								
Orinocodoras Myers, 1927	forked with pointed lobes	i,7/8,i	9–11/10–11	37–38: 17–19/19–20	PH; HY1+2; 3+4; 5; PL; EP	Birindelli (2010:226) reported PH+HY1+2 in *R. thomersoni* (MHNLS 109, 60.9 mm SL, cs)	anteriormost 3–10 dorsal and ventral procurrent rays flattened into plates	6: 3 alc, 1 sk (193), 2 cs (41.9–52.4)
Rhinodoras Bleeker, 1862			14–17/14–16	45–48: 22–24/23–24				6: 4 sk (130.4–161.5), 2 cs (60.9–69.7)
Rhynchodoras Klausewitz & Rössel, 1961			16–19/17–19	50–55: 24–27/26–28				2: 1 sk (88), 1 cs (88.3)

➡

TABLE 3 | (Continued)

Subfamily Genus or species	**Caudal-fin shape**	**Principal caudal-fin rays**	**Upper/lower procurrent rays**	**Total rays: upper / lower**	**Typical caudal-skeleton formula**	**Alternative conditions**	**Comments**	**Preparations examined (SL in mm)**
Doradinae Bleeker, 1858								
Centrochir birindellii (Sousa, Santana, Akama, Zuanon & Sabaj, 2018)	shallowly forked with rounded lobes	i,7/8,i	10–17/10–14	37–48: 18–25/19–23	PH-HY1+2; 3+4; 5; PL; EP	none observed	parhypural and hypural 1+2 separated by partial suture visible proximally (obsolete distally) and set in or just dorsal to longer, lenticular, bony window; window occluded (but suture remnant persistant) in largest specimen	3: 2 sk (99.7–123.5), 1 cs (66.5)
Centrochir crocodili (Humboldt, 1821)	shallowly forked	i,7/8,i	13–14/12–13	42–44: 21–22/21–22	PH; HY1+2; 3+4; 5; PL; EP	parhypural and hypural 1+2 completely fused (PH+HY1+2) in one of five specimens	parhypural and hypural 1+2 typically separated complete suture set in lenticular bony window that may include small open gap; in largest specimen, suture obsolete, window occluded	6: 1 alc (149.3), 4 sk (119.9–140.5), 1 cs (133.9)
Platydoras Bleeker, 1862	shallowly forked with rounded lobes	i,7/8,i	11–13/9–11	37–41: 19–21/18–20	PH+HY1+2; 3+4; 5; PL; EP	parhypural and hypural 1+2 fused with lenticular bony window (PH-HY1+2)	parhypural and hypural 1+2 typically completely fused with suture obsolete; otherwise separated by bony window that may include open gap; anteriormost 3–5 dorsal and ventral procurrent rays flattened into plates	8: 7 sk (118–296), 1 cs (72.5)
remaining Doradinae	shallowly to deeply forked with pointed lobes	i,7/8,i	9–19/9–17	35–52: 17–27/18–26	PH; HY1+2; 3+4; 5; PL; EP	parhypural and hypural 1+2 sutured proximally, fused distally (PH–HY1+2); hypurals 3 and 4 sutured proximally, fused distally in some small juveniles	parhypural and hypural 1+2 typically separated by distinct and complete suture often just dorsal to sulcus or lenticular bony window that may include open gap; in some large specimens of *Doraops*, *Megalodoras* and *Pterodoras*, suture not visible distally and presumed obsolete (although the sulcus persists)	53: 18 sk (69–440), 35 cs (22.7–110)

plate (HY5) and easily distinguished even in small juvenile specimens (15–20 mm SL). It is typically about twice as long as the adjacent procurrent ray, which is supported by the pleurostyle. The ventralmost principal ray typically articulates near the distal junction of the parhypural on the compound caudal centrum (PU1+U1) and the haemal spine on preural centrum two (PU2); it may be supported by either or both processes.

Precise determination of the ventralmost principal rays can be problematic in small juveniles of some doradids (especially Astrodoradinae) because those rays are the last ones to branch and the transition between principal and procurrent rays is more gradual than in the dorsal caudal-fin lobe. For example, based on the criterion of simple *vs.* distally branched, the fused ventral plate (PH+HY1+2) in small *Amblydoras* (Astrodoradinae) may support only four branched rays (*vs.* seven in adults) and up to three simple rays (*vs.* zero, simple principal ray usually supported by haemal spine on PU2 in adults). Although lower counts of branched ventral principal rays are restricted to juveniles in *Amblydoras*, this condition persists in adults of *Physopyxis*, another astrodoradin (Tab. 3). Adult *Physopyxis* have only four or five ventral branched principal rays that are typically supported by the fused ventral plate (PH+HY1+2) and sometimes the haemal spine on PU2. The ventralmost principal ray is usually supported by the haemal spine on PU2, and the posteriormost ventral procurrent ray is supported by the haemal spine on either PU2 or PU3. *Physopyxis* also mature at the smallest size among all doradids with adults not exceeding 35 mm SL. Therefore, the reduced count of principal caudal-fin rays in *Physopyxis* appears to be a paedomorphic condition.

The total number of principal caudal-fin rays in doradids varies from 13–17 (Tab. 3). Seventeen (i,7/8,i) is the most common count and synapomorphic for Rhinodoradinae + Doradinae, which includes 71 of the 96 valid extant species. The subfamily Wertheimerinae and four of the six genera of Astrodoradinae (*Anadoras*, *Amblydoras*, *Astrodoras* and *Scorpiodoras*) typically have 16 primary caudal-fin rays (i,7/7,i). A typical of count of 15 (i,6/7,i) is diagnostic of the monotypic subfamily Agamyxinae. Acanthodoradinae has 15 or 16 primary caudal-fin rays, eight in the dorsal half and seven or eight in the ventral half (i,7/6-7,i). The astrodoradin genera *Hypodoras* Eigenmann, 1925 and *Physopyxis* are respectively diagnosed by the lowest counts, 14 (i,6/6,i) and 13–14 (i,7/4–5,i) primary caudal-fin rays.

The number of procurrent caudal-fin rays varies considerably from 6–19 dorsally and 7–19 ventally among the doradids examined here. The monotypic Agamyxinae routinely exhibits the lowest number of procurrent rays, with 6–10 dorsally and 7–10 ventrally. Other doradids with relatively few procurrent rays include *Franciscodoras* Eigenmann, 1925 (Wertheimerinae) with 8–11 dorsally and 9–11 ventrally, and a few members of the subfamilies Rhinodoradinae (*Orinocodoras eigenmanni* Myers, 1927) and Doradinae (*Hemidoras stuebelii* (Steindachner, 1882), *Ossancora* spp.) with 9–12 dorsally and 9–11 ventrally. The highest count of procurrent caudal-fin rays occurs in *Rhynchodoras* (Rhinodoradinae) with 19 dorsally and ventrally (this study) and up to 20 dorsally and 21 ventrally in *R. castilloi* Birindelli, Sabaj Pérez & Taphorn, 2007 according to Birindelli *et al*. (2007).

The total number of caudal-fin rays (principal + procurrent) varies from 26 to 55 among the doradids examined here. Agamyxinae usually has the fewest caudal-fin rays with a range of 28–34 (n = 19) and the modal count (31) is diagnostic of this monotypic subfamily. Only two genera exhibited ranges overlapping with that of Agamyxinae, the monotypic *Franciscodoras* (32–38) and *Ossancora* (34–40), members of Wertheimerinae and Doradinae, respectively. The highest counts (≥50) were recorded for individuals of *Rhynchodoras* (Rhinodoradinae) and the doradin genera *Anduzedoras* Fernández-Yépez, 1968, *Leptodoras* and *Oxydoras*.

Meristic data aside, doradids also varied in the morphology of the procurrent caudal-fin rays. In most doradids, the transverse width of the procurrent rays remains more or less consistent and the anteriormost ray originates well posterior to the base of adipose and anal fins, respectively (*e.g.*, Figs. 1A,B, 5E). In several unrelated taxa, however, anterior procurrent rays become gradually wider, forming procumbent plates with the anteriormost one originating at or near the base of adipose and anal fins, respectively (Fig. 6). Plate-like procurrent rays are found in all doradid subfamilies except the monotypic Acanthodoradinae, specifically: Astrodoradinae (*Anadoras*, *Hypodoras*, some *Astrodoras*), Wertheimerinae (*Franciscodoras*), Rhinodoradinae (all members), Doradinae (*Platydoras*, some *Ossancora*) and the monotypic Agamyxinae (*Agamyxis*). In *Agamyxis*, *Hypodoras* and some species of *Platydoras*, the plate-like procurrent rays are especially robust and contact the dorsal and ventral wings of the midlateral scutes, thereby encasing the caudal peduncle in bony armor. In *Anadoras*, *Franciscodoras*, Rhinodoradinae and some *Platydoras*, the plate-like procurrent rays are similarly robust, but do not contact the midlateral scutes and thereby frame the caudal peduncle dorsally and ventrally. In *Ossancora*, the anteriormost procurrent rays may become procumbent and plate-like (*i.e.*, elongate but relatively narrow) in larger adults.

Caudal-fin skeleton. The skeletal elements supporting the caudal fin are somewhat variable among doradids. Adults show little to no trace of ural centra beyond the terminal compound centrum (*i.e.*, Type 1 of de Pinna, Ng, 2004). However, an additional ural centrum ($U2^{+}$) was observed in the smallest juveniles available for clearing and staining (Fig. 5), specifically *Scorpiodoras bolivarensis* (Fernández-Yépez, 1968) (21.3 and 24 mm SL), *S. heckelii* (Kner, 1855) (14.9 mm SL), *Amblydoras affinis* (Kner, 1855) (15.2–18.6 mm SL) and *Hemidoras stenopeltis* (Kner, 1855) (22.7 mm SL) (see Discussion). There is only one epural and it remains detached from the compound caudal centrum.

The most common caudal-skeleton formula involves the least fusion among elements: PH; HY1+2; 3+4; 5; PL; EP (*e.g.*, Fig. 9D). In this condition, the parhypural and hypural 1+2 are continuous proximally near their fusion to the compound caudal centrum, but distinguishable distally by a long continuous plane suture (*i.e.*, butt joint). Hypural 3+4, hypural 5 and the pleurostyle are tightly associated, but distinguishable by complete plane sutures, and only the pleurostyle eventually fuses to the compound caudal centrum (see Discussion). This pattern is typical of Wertheimerinae and all members of Doradinae except *Platydoras* and *Centrochir birindellii* (Sousa, Chaves, Akama, Zuanon & Sabaj, 2018).

The second pattern is typical of Astrodoradinae, Agamyxinae, and doradins *Platydoras* and *Centrochir birindellii*: PH+HY1+2; 3+4; 5; PL; EP (*e.g.*, Figs. 5A–C). In general, the parhypural appears completely fused to hypural 3+4. Alternatively, the fusion is partial, in that a suture is generally not visible between the parhypural and hypural 3+4, but the intervening bone has small gaps and/or is thin to the point of translucence in juveniles and sometimes adults (*i.e.*, PH-HY1+2; see Figs. 7B, 8B,D).

The third pattern is unique to Acanthodoradinae and involves the highest degree of fusion: PH+HY1+2; 3+4+5-PL; EP (Figs. 7A, 8A). The parhypural and hypurals 1 and 2 are completely fused into a singular lower plate that typically supports seven principal caudal-fin rays including the ventralmost unbranched ray. Hypurals 3, 4 and 5 are likewise fused into a singular upper plate that supports eight primary caudal-fin rays including the uppermost unbranched ray. The upper hypural plate and pleurostyle may be separated by a suture, completely fused or partially fused with narrow distal gap. This gap marks the transition from the dorsalmost principal caudal-fin ray (supported by hypural 5) to the posteriormost dorsal procurrent ray (supported by the pleurostyle) of the evenly rounded caudal fin that is unique to Acanthodoradinae.

Classification of Doradidae. Based on our phylogenetic analyses of DNA sequence data for three genes (rag1, co1, 16s) we recognize six major lineages of doradids assigned here to three nominal subfamilies (Astrodoradinae, Doradinae and Wertheimerinae) and three new ones (Acanthodoradinae, Agamyxinae and Rhinodoradinae). When possible, the morphology of the caudal fin is used to diagnose each subfamily.

This study also proposes a number of species-level taxonomic changes based on the results of the molecular analyses and/or examination of specimens. We transfer *Platydoras birindellii* Sousa, Santana, Akama, Zuanon & Sabaj, 2018 to genus *Centrochir* Agassiz, 1829. *Doras punctatus* and *Oxydoras trimaculatus* are removed from *Ossancora* and *Tenellus*, respectively. *Doras punctatus* is tentatively restored to the genus *Doras*, and *Oxydoras trimaculatus* is transferred to the genus *Nemadoras*. Furthermore, *Doras helicophilus* Günther, 1868 is considered valid in *Platydoras*, and *Doras polygramma* Kner, 1853 is considered valid in *Acanthodoras* with *A. spinosissimus* (Eigenmann & Eigenmann, 1888) treated as a questionable synonym.

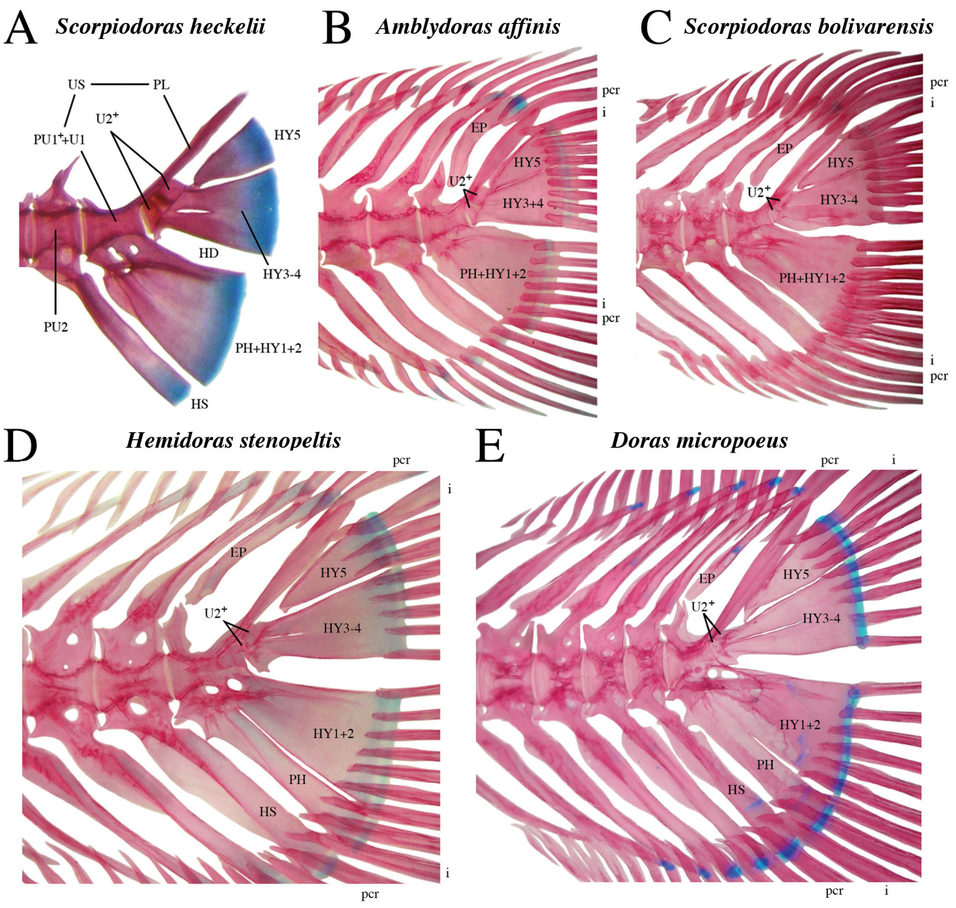


FIGURE 5 | Caudal skeletons in cleared and stained juveniles of Astrodoradinae (**A**–**C**) and Doradinae (**D**–**E**) showing ontogenetic fate of ural centrum 2 ($U2^+$). **A.** *Scorpiodoras heckelii* (ANSP 165801, 14.9 mm SL, PH+HY1+2; 3-4; 5; PL) with intervertebral joint evident between compound caudal centrum and $U2^+$; **B.** *Amblydoras affinis* (ANSP 179798, 15.2 mm SL, PH+HY1+2; 3+4; 5; PL) with partial intervertebral joint evident between caudal centrum and $U2^+$; one of three rays supported by HY5 is rudimentary (length half that of adjacent rays); **C.** *Scorpiodoras bolivarensis* (ANSP 165806, 21.3 mm SL, PH+HY1+2; 3-4; 5; PL) with narrow intervertebral joint evident between caudal centrum and $U2^+$, and hairline suture evident between bases of hypurals 3 and 4; **D.** *Hemidoras stenopeltis* (ANSP 189444, 22.7 mm SL, PH; HY1+2; 3-4; 5; PL) with $U2^+$ showing signs of fusion with base of hypurals 3 and 4; **E.** *Doras micropoeus* (ANSP 197119, 27.6 mm SL, PH; HY1+2; 3-4; 5; PL) with $U2^+$ fused to bases of hypurals 3 and 4, and tightly associated with posterior end of compound caudal centrum. Abbreviations: EP = epural, HS = hemal spine, HY = hypurals fused partially (-) or completely (+), HD = hypural diastema, i = outermost primary caudal-fin ray, pcr = procurrent caudal-fin ray, PH = parhypural, PL = pleurostyle, PU = preural centrum, $PU1^+$+U1 = compound caudal centrum, $U2^+$ = proximal and distal portions of ural centrum 2^+, US = urostyle.

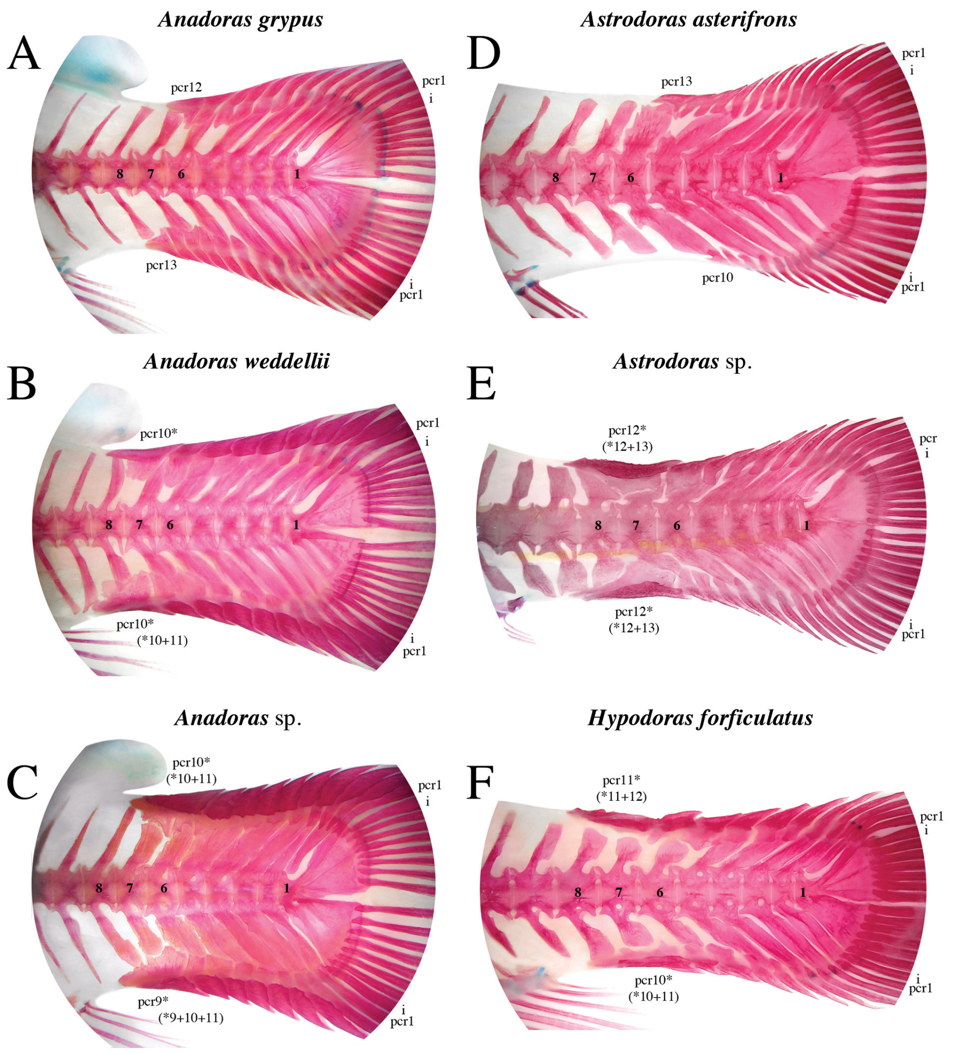
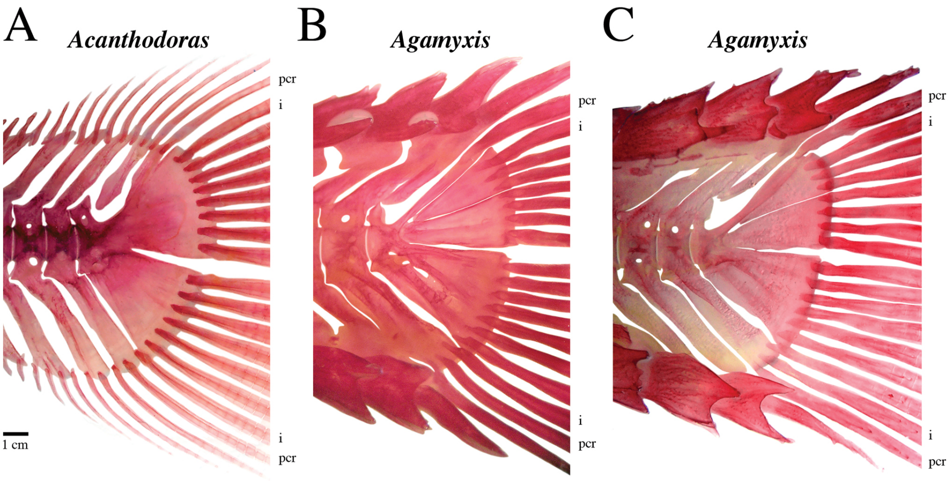


FIGURE 6 | Caudal skeletons in cleared and stained Astrodoradinae having anteriormost procurrent caudal-fin rays flattened into plates. **A.** *Anadoras grypus* (INHS 43663, 68.4 mm SL, PH-HY1+2; 3+4; 5; PL) having anteriormost procurrent elements weakly plate-like; **B.** *Anadoras weddellii* (MCP 20940, 68.9 mm SL, PH-HY1+2; 3+4; 5; PL) having multiple procurrent elements forming distinct plates with anteriormost dorsal one (pcr10*) possibly formed by fusion of two rays and anteriormost ventral one (pcr10*) evidently formed by fusion of at least two rays (10+11); **C.** *Anadoras* sp. (AUM 45441, 71 mm SL, PH+HY1+2; 3+4; 5; PL) having anteriormost dorsal procurrent plate (pcr10*) evidently formed by fusion of at least two rays (10+11) and anteriormost ventral one (pcr9*) formed by fusion of at least three rays (9+10+11); **D.** *Astrodoras asterifrons* (ANSP 177996, 67.1 mm SL, PH+HY1+2; 3+4; 5; PL). **E.** *Astrodoras* sp. (ANSP 187490, 49.3 mm SL, PH+HY1+2; 3+4-5; PL) having enlarged anteriormost procurrent plate evidently formed by fusion of two rays (12+13 dorsally and ventrally); **F.** *Hypodoras forficulatus* (ANSP 179009, 55.5 mm SL, PH+HY1+2; 3+4; 5; PL) having enlarged anteriormost procurrent plate evidently formed by fusion of two rays (11+12 dorsally and 10+11 ventrally). Caudal vertebrae numbered beginning with compound caudal centrum (1); i = outermost primary caudal fin ray, pcr = procurrent caudal-fin ray (* fusion possible or evident).



PH+HY1+2; 3+4+5-PL PH-HY1+2; 3+4; 5; PL PH+HY1+2; 3+4; 5; PL

FIGURE 7 | Caudal skeletons in cleared and stained specimens of monotypic subfamilies Acanthodoradinae (**A**) and Agamyxinae (**B, C**). **A.** *Acanthodoras* sp. "shallow scute" (ANSP 161507, 57.6 mm SL) showing distal gap between partially fused hypural 5 and pleurostyle; **B.** *Agamyxis albomaculatus* (ANSP 134781, 37 mm SL) showing proximal gap in bony window between partially fused parhypural and hypurals 1+2; **C.** *Agamyxis albomaculatus* (INHS 30084, 72.4 mm SL) showing parhypural completely fused to hypurals 1+2.

Aspredinoidea Adams, 1854

Included taxa: Aspredinidae Adams, 1854; Auchenipteridae Bleeker, 1862; Doradidae Bleeker, 1858.

Diagnosis. Calegari *et al.* (2019) diagnosed the clade Aspredinidae (Auchenipteridae + Doradidae) on the basis of 29 DNA sequence and four morphological synapomorphies: (1) anterior fontanel elliptic, (2) proximal extremity of pleural ribs twisted, (3) hyomandibula articulated to neurocranium via sphenotic and pterotic, and (4) compound centrum including up to fifth vertebra. Those authors noted that synapomorphies (1) and (2) are exclusive for the clade, but reversed in some members of Auchenipteridae + Doradidae; synapomorphy (3) is convergent in some *Pimelodus* (Pimelodidae); and synapomorphy (4) is highly homoplastic within the group. The clade Aspredinidae (Auchenipteridae + Doradidae) also is supported by other phylogenetic analyses of molecular sequence data (Sullivan *et al.*, 2006, 2008; Lundberg *et al.*, 2007; Arcila *et al.*, 2017; Betancur-R. *et al.*, 2017).

Remarks. Auchenipteridae and Doradidae historically composed the superfamily Doradoidea (*e.g.*, de Pinna, 1998; Birindelli, 2014; Calegari *et al.*, 2019) or informal "doradioids [*sic*]" (Mo, 1991). In a broader sense, auchenipterids, doradids and the African family Mochokidae have been grouped together in the suborder Doradoidei (de Pinna, 1998), superfamily Doradoidea (Chardon, 1968; Diogo, 2003), or informal "doradoids" (Lundberg, 1993; Friel, 1994). Friel (1994) also proposed a sister group relationship between his "doradoids" and Aspredinidae based on his phylogenetic analysis of morphological data. Calegari *et al.* (2019) removed Mochokidae from the clade first proposed by Friel (1994) and employed the subordinal name Doradoidei for Aspredinidae (Auchenipteridae + Doradidae).

We use the name Aspredinoidea at the superfamilial level for the clade Aspredinidae (Auchenipteridae + Doradidae) for four reasons: (1) it is premature to subdivide Siluriformes into more than the three commonly recognized suborders, Loricarioidei, Diplomystoidei and Siluroidei, (2) the composition of Doradoidea varies among recent authors (*e.g.*, Diogo, 2003 *vs.* Birindelli, 2014 and Calegari *et al*., 2019), (3) a group composed exclusively of Aspredinidae, Auchenipteridae and Doradidae has not been proposed at the family-group level (*i.e*., no history of prevailing use as a superfamily), (4) Aspredinidae Adams, 1854 has priority over Auchenipteridae Bleeker, 1862 and Doradidae Bleeker, 1858 in a family-group name exclusive to those taxa.

Doradidae Bleeker, 1858

Included taxa: Acanthodoradinae, new subfamily; Astrodoradinae Higuchi, Birindelli, Sousa & Britski, 2007; Wertheimerinae Birindelli, 2014; Agamyxinae, new subfamily; Rhinodoradinae, new subfamily; Doradinae Bleeker, 1858.

Diagnosis. Birindelli (2014) identified three synapomorphies unique to the family: midlateral scutes present; ligament present between Müllerian ramus and lateral line; and infranuchal ligament (between posterior nuchal plate and the first long-formed rib) ossified.

Distribution. Doradidae is endemic to South America where it occurs on both sides of the Andes Mountains, but is limited to systems draining into the Atlantic Ocean (Tab. 2). One subfamily, Wertheimerinae, contains three monotypic genera endemic to rivers draining the Atlantic Shield of eastern Brazil. The middle to lower reaches of the largest of those rivers, the São Francisco, may have recently included *Oxydoras*, a member of the subfamily Doradinae. *Doras humboldti* Spix, Agassiz 1829, currently a junior synonym of *Oxydoras niger* (Valenciennes 1821), was based on a specimen about 55.5 cm long reportedly from the rio São Francisco at or near Januária (Koerber, 2021). Furthermore, the Museu de História Natural Louis Jacques Brunet in Recife has a dry stuffed specimen of *Oxydoras* (MHN-LJB 0016) that is associated with other 19th Century specimens from the lower São Francisco (Flávio Bockmann, 2021, pers. comm.). *Oxydoras*, however, does not currently inhabit the São Francisco Basin and the historical records may have been based on specimens transported from the Amazonas Basin (Flávio Lima, 2021, pers. comm.).

Wertheimerinae aside, representatives of the other five subfamilies are preserved in the faunas of the Orinoco and Amazonas basins, although the latter is far more diverse with approximately 69 species (*vs.* 31 in the Orinoco). The doradid fauna of the Essequibo lacks the monotypic Agamyxinae, but includes an impressive 25 species distributed among four subfamilies. Compared to the other major cis-Andean river basins, the La Plata is relatively depauperate with only eight species representing three subfamilies (Astrodoradinae, Rhinodoradinae, Doradinae).

Three species representing two subfamilies (Doradinae + Rhinodoradinae) inhabit river systems draining into the southwestern Gulf of Mexico west of the Andean divide. *Centrochir crocodili* (Humboldt, 1821) (Doradinae) occurs in the Magdalena Valley between the Cordillera Central and Cordillera Oriental of the northern Andes. *Doraops zuloagai* Schultz, 1944 (Doradinae) and *Rhinodoras thomersoni* Taphorn & Lilyestrom, 1984 (Rhinodoradinae) occur in the smaller Catatumbo basin between the two major branches of the Cordillera Oriental, namely the Cordillera de Perijá to the west and Cordillera de Mérida to the east. These three species are not closely related to each other, but sister to other taxa widely distributed east of the Andes.

Rhinodoras thomersoni is the first species to diverge in its genus and the remaining ones are widely distributed in the Orinoco, Amazonas, Essequibo and Paraná basins. *Rhinodoras* also includes the only doradid species native to the upper Paraná basin above Iguaçu Falls. The monotypic *Doraops zuloagai* is sister to the genus *Pterodoras* which has a distribution pattern similar to cis-Andean species of *Rhinodoras*. Notable differences include the expansion of *Pterodoras* to coastal drainages east of the Essequibo (*i.e.*, Corantijn-Nickerie) and its absence from the upper Paraná basin. The two lineages, *Rhinodoras* and *Doraops* + *Pterodoras*, are in separate, but sister subfamilies, Rhinodoradinae and Doradinae, respectively. It is not unreasonable to suspect that the same vicariant event, the uplift of the Mérida Andes beginning as early as Eocene-Early Miocene (Cediel, 2019), isolated *Rhinodoras thomersoni* and *Doraops zuloagai* from their respective, cis-Andean sister clades.

Centrochir was previously considered to be monotypic and sister to *Platydoras* (Birindelli, 2014), a cis-Andean genus that expands upon the *Pterodoras*-distribution pattern to include coastal drainages east of the Nickerie (*i.e.*, Suriname, Maroni) and east of the Amazonas Delta (*i.e.*, Mearim, Pindaré, Itapecuru, Parnaíba) (Piorski *et al*., 2008). Perhaps the biggest surprise of the current study was the discovery of a second, cis-Andean species of *Centrochir*. *Centrochir birindellii* was originally described in *Platydoras* (Sousa *et al*., 2018) and is endemic to the Xingu basin above the river's departure from the Brazilian Shield where it co-occurs with a species of *Platydoras*. The occurrence of sister species in a major right bank tributary to the lower Amazonas (cis-Andean) and Magdalena Basin (trans-Andean), respectively, is mysterious.

Acanthodoradinae, new subfamily

urn:lsid:zoobank.org:act:A6A7B0AA-EB1D-412F-9566-2F11025B0C3C

Included taxa: *Acanthodoras* Bleeker 1862 [type genus] with three nominal valid species, *Acanthodoras cataphractus* (Linnaeus, 1758), *A. depressus* (Steindachner, 1881) and *A. polygrammus* (Kner, 1853). The status of *Acanthodoras spinosissimus* (Eigenmann & Eigenmann 1888) as a valid species or a synonym of *A. polygrammus* remains uncertain.

Diagnosis. Acanthodoradinae is morphologically diagnosed by two characteristics that are unique among Doradidae: caudal fin symmetrically rounded (*vs.* unevenly rounded/emarginate, truncate or forked) and adults typically with a single upper hypural plate that incorporates fused hypurals 3–5 and usually the pleurostyle to some degree (*vs.* pleurostyle entirely separate from upper hypurals).

Remarks. *Acanthodoras* is the only doradid and the only member of the clade Doradidae + Auchenipteridae with an evenly rounded caudal fin (Birindelli, 2014; Calegari *et al*., 2019; this study). The most closely related taxa with a similarly rounded caudal fin are found in Aspredinidae, the sister family to Doradidae + Auchenipteridae. Among doradids, *Acanthodoras* exhibits the highest degree of fusion among elements supporting the caudal fin (Figs. 7A, 8A). The three upper hypurals are always fused into a solid plate (HY3+4+5) that may be partially or completely fused to the pleurostyle or remain separated from the pleurostyle by a complete suture. Other doradids (*Agamyxis*, *Hypodoras*, *Scorpiodoras*) sometimes exhibit complete fusion of hypurals 3–5, but the pleurostyle remains separated by a complete suture. In *Acanthodoras*, the two lower hypurals and parhypural are always fused into a solid plate (PH+HY1+2). Fusion of hypurals 1+2 with the parhypural is common in Astrodoradinae and occasional in Agamyxinae.

Astrodoradinae Higuchi, Birindelli, Sousa & Britski, 2007

Included taxa: *Amblydoras* Bleeker, 1862 (synonyms *Zathorax* Cope, 1871, *Merodoras* Higuchi, Birindelli, Sousa & Britski, 2007), *Anadoras* Eigenmann, 1925, *Astrodoras* Bleeker, 1862, *Hypodoras* Eigenmann, 1925, *Physopyxis* Cope, 1871, and *Scorpiodoras* Eigenmann, 1925 (synonym *Autanadoras* Fernández-Yépez, 1950).

Diagnosis. Astrodoradinae is not currently diagnosable by any morphological characters uniquely derived within Doradidae and unreversed within the subfamily (Higuchi *et al*., 2007; Birindelli, 2014; this study). Nevertheless, the monophyly of this clade is strongly supported by phylogenetic analyses of DNA sequence data (Arce H. *et al*., 2013; this study). Several spermatic characters may be uniquely diagnostic, but require evaluation for all astrodoradins. For example, *Anadoras* and *Amblydoras* are the only doradids in which spermatozoa have a bell-shaped nucleus and two flagella (Quagio-Grassiotto *et al*., 2011). Both conditions are similarly found in *Pseudobunocephalus amazonicus* (Mees, 1989) (Aspredinidae) and the latter condition also occurs in the catfishes *Nematogenys inermis* (Guichenot, 1848) (Nematogenyidae), *Malapterurus electricus* (Gmelin, 1789) (Malapteruridae) and *Cetopsis coecutiens* (Lichtenstein, 1819) (Cetopsidae) (Quagio-Grassiotto *et al*., 2011).

Remarks. Among doradid subfamilies, Astrodoradinae exhibits by far the most variation in the caudal fin. Its shape varies from forked (*Anadoras*) to truncate (*Hypodoras*) or unevenly rounded with upper lobe longer than lower (*Physopyxis*). Counts of principal rays vary from 13 or 14 (*Physopyixs*) to 14 (*Hypodoras*) or 16 (*Amblydoras*, *Anadoras*, *Astrodoras* and *Scorpiodoras*). Hypural 5 may be completely fused with hypural 3+4 (*Hypodoras*, sometimes *Scorpiodoras*) or partially so (sometimes *Physopyxis*). The parhypural is typically fused to hypurals 1 and 2 (PH+HY1+2), but separated by a lenticular window of thin bone in *Anadoras* (PH-HY1+2).

The procurrent caudal-fin rays grade anteriorly into procumbent plates in *Anadoras*, *Astrodoras* and *Hypodoras* (Figs. 6, 8B,C). In some species, the anteriormost procurrent elements become fused into an enlarged plate that looks singular from an external viewpoint. This fusion is inferred from ontogenetic changes and comparisons among congeners. For instance, the development of procurrent plates varies among species of

Anadoras. *Anadoras grypus* (Cope, 1872) (Fig. 6A) exhibits a condition that is similar to most other doradids. The anteriormost procurrent element is only weakly plate-like and slightly larger than its neighbor. The anteriormost dorsal procurrent plate is supported by the neural spine on the 7th preural centrum (PU7) and has laterally paired ventral processes that occupy the gap between neural spines on PU6 and PU7. The anteriormost ventral procurrent plate lies below and just posterior to the distal end of the haemal spine on PU8 and has laterally paired dorsal processes that occupy the gap between haemal spines on PU7 and PU8. In *Anadoras weddellii* (Castelnau, 1855) (Fig. 6B), the procurrent caudal-fin elements form multiple distinct plates. The anteriormost dorsal plate is enlarged, supported by two neural spines on PU7 and PU8, respectively, and has a large ventral keel that occupies the gap between those two neural spines. Although displaced anteriorly by one centrum, the enlarged dorsal procurrent plate in *A. weddellii* resembles the overall shape and position of the two anteriormost procurrent elements in *A. grypus*. Also, procurrent elements typically articulate with only one neural spine. Since the enlarged dorsal procurrent plate in *A. weddellii* articulates with two neural spines, it likely represents a fusion of the two anteriormost plates.

The anteriormost ventral procurrent plate in *A. weddellii* also is enlarged, contacts the haemal spines on PU8 and PU9, respectively, and has a large middorsal crest that occupies two successive gaps between the haemal spines on PU7, PU8 and PU9, respectively. In this case, the shape and articulation of the enlarged plate resembles those of the 2–3 anteriormost plates in the unmodified condition of *A. grypus*. The fusion of 2–3 procurrent elements ventrally (*vs.* two fused dorsally) is corroborated by meristics. In *A. grypus*, there is typically one more procurrent element in the ventral series. In *A. weddellii*, the counts of dorsal and ventral procurrent elements are equal (or sometimes one greater in the dorsal series). Counts of procurrent caudal-fin elements are higher in *A. grypus* (12–14 dorsally and 13–15 ventrally) *vs. A. weddellii* (10–11 dorsally and 10 ventrally), again suggestive of plate fusion in *A. weddellii*.

Fusion of anteriormost dorsal and ventral procurrent elements also was observed in a cleared and stained adult of an undescribed species of *Anadoras* from the rio Tocantins Basin (Fig. 6C). The anteriormost dorsal plate is extremely enlarged and contacts three neural spines on PU6, PU7 and PU8, respectively. Its ventral keel appears weakly divided into three sections, one articulating with PU6 neural spine, the second articulating with PU7 neural spine and the third directed towards the gap between PU7 and PU8 neural spines. In this case, the anteriormost dorsal plate is almost certainly formed by the fusion of at least two procurrent elements. The anteriormost ventral plate has a large dorsal crest that articulates with three haemal spines on PU6, PU7 and PU8, respectively. Accordingly, the anteriormost ventral plate appears to be a fusion of at least three procurrent elements.

In some species of *Astrodoras* and its monotypic sister genus *Hypodoras*, the anteriormost procurrent plate is more than twice the size of its neighbor, with a noticeable increase in transverse width (*vs.* width of anteriormost procurrent plates more uniform in *Anadoras*). The dramatic enlargement of the anteriormost procurrent plate also provides evidence for fusion of procurrent elements. As in *Anadoras grypus*, the anteriormost procurrent element is only weakly plate-like in some species of *Astrodoras* (Fig. 6C). The anteriormost dorsal procurrent plate has laterally paired ventral processes that articulate with the distal margin of neural spine on PU6 (*vs.* PU7 in *A. grypus*). The anteriormost ventral procurrent plate has laterally paired processes that project dorsally and articulate with the ventroposterior end of the haemal spine on PU6. In other species of *Astrodoras* (Fig. 6E), the anteriormost dorsal procurrent plate is greatly enlarged and has a long ventral keel supported by two neural spines on PU7 and PU8, respectively. The supporting neural spines are shortened (PU7) or have a downwardly sloped distal margin (PU8) to accommodate the large keel. Likewise, the anteriormost ventral procurent plate is greatly enlarged and has a pronounced crest that articulates with similarly modified ends of haemal spines on PU7 and PU8, respectively. As in *Anadoras*, species of *Astrodoras* with enlarged procurrent plates have fewer procurrent elements than those lacking such plates. Therefore, the enlarged anterior plates in *Astrodoras* are likely due to the fusion of at least two procurrent elements.

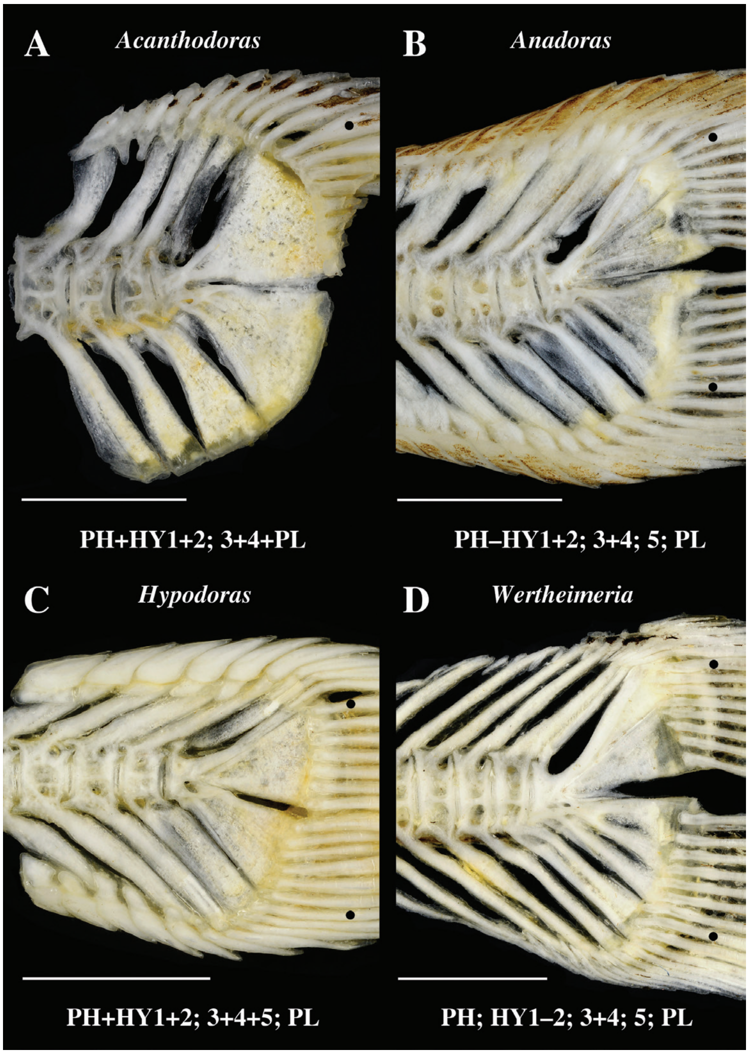


FIGURE 8 | Caudal skeletons typical of Acanthodoradinae (**A**), Astrodoradinae (**B, C**) and Wertheimerinae (**D**). **A.** *Acanthodoras polygrammus* (ANSP 179421, 121.5 mm SL) with pleurostyle fused to hypural 5; **B.** *Anadoras grypus* (ANSP 179170, 84 mm SL) with parhypural partially fused to hypural 1+2 via thin bony window (no suture); **C.** *Hypodoras forficulatus* (ANSP 182630, 87 mm SL) with parhypural fused to hypural 1+2 and hypural 3+4 fused to 5; **D.** *Wertheimeria maculata* (ANSP 189489, 123.5 mm SL) with hypurals 1 and 2 partially fused via thin bony window (no suture). Black dots indicate outermost primary caudal-fin rays. Scale bars = 1 cm.

Similar fusion seems to hold true for *Hypodoras*, a monotypic genus in which the anteriormost dorsal and ventral procurrent elements also are dramatically enlarged into a procumbent plate. In a small (26.4 mm SL) cleared and stained juvenile, the two anteriormost dorsal procurrent elements are plate-like and each one bears a shallow, ventral keel that articulates with the neural spine on PU7 and PU8, respectively. The two anteriormost ventral procurrent elements also are plate-like and articulate with the haemal spines on PU7 and PU8, respectively. In larger cleared and stained specimens (36 and 55.5 mm SL; Fig. 6F), a single enlarged plate spans the distal ends of the PU7 and PU8 neural spines, and has a shallow keel that ends opposite the distal margin of the more posterior spine. Likewise, the anteriormost ventral plate articulates with the expanded haemal spines on PU7 and PU8, respectively. Therefore, in adult *Hypodoras* the enlarged anteriormost procurrent plate appears to be a fusion of two procurrent elements.

Wertheimerinae Birindelli, 2014

Included taxa: *Franciscodoras* Eigenmann, 1925, *Kalyptodoras* Higuchi, Britski & Garavello, 1990, and *Wertheimeria* Steindachner, 1877 [type genus].

Diagnosis. Wertheimerinae can be diagnosed from all other doradid genera by the following unique combination: parhypural typically sutured to hypural 1+2 (*vs.* completely or partially fused with hypural 1+2) and caudal fin typically with i,7/7,i principal rays.

Remarks. Birindelli (2014) established the subfamily Wertheimerinae for two genera, *Kalyptodoras* and *Wertheimeria*, that shared a uniquely derived synapomorphy: hyomandibular crest well-developed for insertion of the *m. levator arcus palatini* (*vs.* absent, rudimentary or weakly developed in all other doradids). In *Franciscodoras*, Birindelli (2014) treated the hyomandibular crest as absent to rudimentary. *Franciscodoras* also differs by having procurrent rays grading anteriorly into procumbent plates (*vs.* all procurrent rays rod-like in *Kalyptodoras* and *Wertheimeria*). Nevertheless, molecular phylogenetic analyses support not only the inclusion of *Franciscodoras* in Wertheimerinae, but nests it in a sister group relationship with *Kalyptodoras*. Furthermore, cytogenetic data show a high similarity between *Franciscodoras*, *Kalyptodoras* and *Wertheimeria* (Takagui *et al.*, 2019). In *Franciscodoras*, Birindelli (2014:533) noted that the parhypural and hypural elements may be distinct in small juveniles (*e.g.*, 29.4 mm SL): PH; HY1; 2; 3; 4; 5 (*vs.* PH; HY1+2; 3+4; 5 in adults).

Agamyxinae, new subfamily

urn:lsid:zoobank.org:act:B6EAAB63-8F43-4763-9F26-D94861FACBD6

Included taxa: *Agamyxis* Cope, 1878 [type genus] with two nominal valid species, *Agamyxis albomaculatus* (Peters, 1877) and *A. pectinifrons* (Cope, 1870).

Diagnosis. Agamyxinae is diagnosed by two characters that are both unique within Doradidae: total number of caudal-fin rays extremely low, modally 31, range 28–34 (*vs.*

32–38 in *Franciscodoras* and 34–55 in all other doradids), and external bony surfaces and fin rays extremely spiny, ornamented with numerous small to large accessory spines (*vs.* accessory spines absent or present with limited distribution and entirely absent from anal and pelvic fins).

Remarks. *Agamyxis* is the thorniest of thorny catfishes. Conspicuous accessory spines occur on the posterior cleithral process, midlateral plates and the plate-like procurrent rays of the caudal fin. Much smaller spines occur along the free margins of bones of the nuchal shield and cranium including the infraorbitals. Accessory spines are also conspicuous along the lateral surfaces of the dorsal-fin spine and along the dorsal and ventral surfaces of the pectoral spine. Smaller spines occur along the rays of the anal and caudal fins, and minute spines are visible on the dorsal- and pelvic-fin rays (spines lacking from pectoral-fin rays). Accessory spines are present in other doradids, especially *Acanthodoras* and most members of Astrodoradinae, but consistently lacking from the anal and pelvic fins.

The caudal fin formula of *Agamyxis* is summarized as PH-HY1+2; 3+4; 5 due to variation in contact between parhypural and HY1+2. In most specimens, the distal portion of the parhypural and HY1+2 are fused (suture lacking), but the proximal portion retains evidence of a gap that may be partially open and/or occluded by a window of thin bone (Fig. 7B). Alternatively, parhypural and HY1+2 may be completely fused (PH+HY1+2; Fig. 7C) or separated by a complete suture (PH; HY1+2). The upper hypural plate invariably supports seven principal caudal-fin rays with HY5 supporting the upper unbranched ray as well as one branched ray. The lower hypural plate typically supports eight caudal-fin rays with one specimen having only seven. The lower unbranched principal ray is typically supported by the haemal spine on PU2 (or nearly so), and exceptionally supported by the parhypural in the one specimen with seven lower principal caudal-fin rays.

Rhinodoradinae, new subfamily

urn:lsid:zoobank.org:act:8CBB768E-912E-43F0-B299-B5BA54363E7E

"Rhinodoradini".—Quagio-Grassiotto *et al*., 2011:09 [unavailable; authors used in reference to "informally named tribe"].

Rhinodoradini.—Arce H. 2015:244 [unavailable; author did not explicity indicate nominal taxon as intentionally new (see van der Laan *et al*., 2014:08, Article 16.1)].

Included taxa. *Orinocodoras* Myers, 1927, *Rhinodoras* Bleeker, 1862 [type genus], and *Rhynchodoras* Klausewitz & Rössel, 1961.

Diagnosis. With respect to the caudal fin, Rhinodoradinae is diagnosed from all other doradids by the unique combination: principal caudal-fin rays i,7/8,i, procurrent rays grade anteriorly into procumbent plates and parhypural typically separated from hypural 1+2 by complete suture. Rhinodoradinae also is diagnosed by two characters unique within Doradidae as proposed by Birindelli (2014) for his "*Rhinodoras* clade": posterior limit of autopalatine approximately at vertical through the middle of orbit (*vs.* finishing anterior to orbit), and hyomandibular with crest for attachment of portion of the *m.*

adductor mandibulae (*vs.* crest absent). Unlike Birindelli (2014), we do not consider the triangular posterior cleithral process to be a third exclusive character as suggested by the author. Arce H. (2015) identified another character unique to Rhinodoradinae among doradids: portion of the *m. extensor tentaculi* inserting ventrally on the autopalatine (*vs.* insertion limited to dorsal surface of autopalatine). This may be associated with the autopalatine character described by Birindelli (2014).

Remarks. Based on Birindelli's (2014) phylogenetic analysis of morphology, members of Rhinodoradinae formed a monophyletic clade nested within his Doradinae as the sister group to *Oxydoras* + fimbriate-barbel doradids. Phylogenetic analyses of molecular data (Arce H. *et al*., 2013; this study) support the removal of rhinodoradin taxa from Doradinae. In all species of Rhinodoradinae, the procurrent rays of the caudal fin grade anteriorly into 3–10 plates that frame the caudal peduncle dorsally and ventrally. This character, however, is homoplastic as it is also found in the subfamilies Astrodoradinae (some *Astrodoras*), Wertheimerinae (*Franciscodoras*), Agamyxinae (*Agamyxis*), and Doradinae (*Platydoras*).

Doradinae Bleeker, 1858

Included taxa. *Anduzedoras* Fernández-Yépez, 1968, *Centrochir* Agassiz, 1829, *Centrodoras* Eigenmann, 1925, *Doraops* Schultz, 1944, *Doras* Lacepède, 1803 [type genus] (synonym *Mormyrostoma* Miranda Ribeiro, 1911), *Hassar* Eigenmann, Eigenmann, 1888, *Hemidoras* Bleeker, 1858 (synonym *Opsodoras* Eigenmann, 1925), *Leptodoras* Boulenger, 1898, *Lithodoras* Bleeker, 1862, *Megalodoras* Eigenmann, 1925 (synonyms *Hoplodoras* Eigenmann, 1925, *Deltadoras* Fernández-Yépez, 1968), *Nemadoras* Eigenmann, 1925, *Ossancora* Sabaj Pérez & Birindelli, 2011, *Oxydoras* Kner, 1855 (synonyms *Pseudodoras* Bleeker, 1858, *Hildadoras* Fernández-Yépez, 1968), *Platydoras* Bleeker, 1862 (synonym *Cataphractus* Edwards, 1771 [unavailable]), *Pterodoras* Bleeker, 1862 (synonyms *Apuredoras* Fernández-Yépez, 1950, *Parapterodoras* Risso & Morra, 1964, *Sachsdoras* Fernández-Yépez, 1968), *Tenellus* Birindelli, 2014, and *Trachydoras* Eigenmann, 1925.

Diagnosis. As recognized here, Doradinae is not diagnosable by any unambiguous morphological synapomorphies. Molecular analyses (Arce H. *et al*., 2013; this study) support the current composition of Doradinae divided into five subclades: *Pterodoras* + *Doraops*, *Oxydoras*, *Centrochir* + *Platydoras*, *Centrodoras* (*Lithodoras* + *Megalodoras*) and the fimbriate-barbel taxa (crown group). All doradins have i,7/8,i principal caudal-fin rays, a count shared with its sister subfamily Rhinodoradinae. Doradins typically have a caudal-fin formula of PH; HY1+2; 3+4; 5 (Figs. 5D,E, 9), a condition shared with Rhinodoradinae and Wertheimerinae (Fig. 8D). However, within the clade *Centrochir* + *Platydoras* the parhypural and hypural 1+2 are often completely fused in *Platydoras* (Fig. 9B), partially so in *Centrochir birindellii* (Fig. 9A) and rarely so in *C. crocodili* (see Tab. 2). In some large doradins (*e.g*., *Doraops*, *Megalodoras*, *Pterodoras*), the distal portions of parhypural and hypural 1+2 may appear secondarily fused (Fig. 9C). In nearly all doradins, the procurrent caudal-fin rays are typically rod-like, not flattened into plates as in Rhinodoradinae. *Platydoras* is the only doradin wherein the anteriormost procurrent caudal-fin rays become flattened into plates that either frame the caudal peduncle or encase it by contacting the midlateral scutes (Fig. 9B).

Remarks. The Doradinae of the current study is composed of the same taxa as in Birindelli (2014) minus members of Rhinodoradinae.

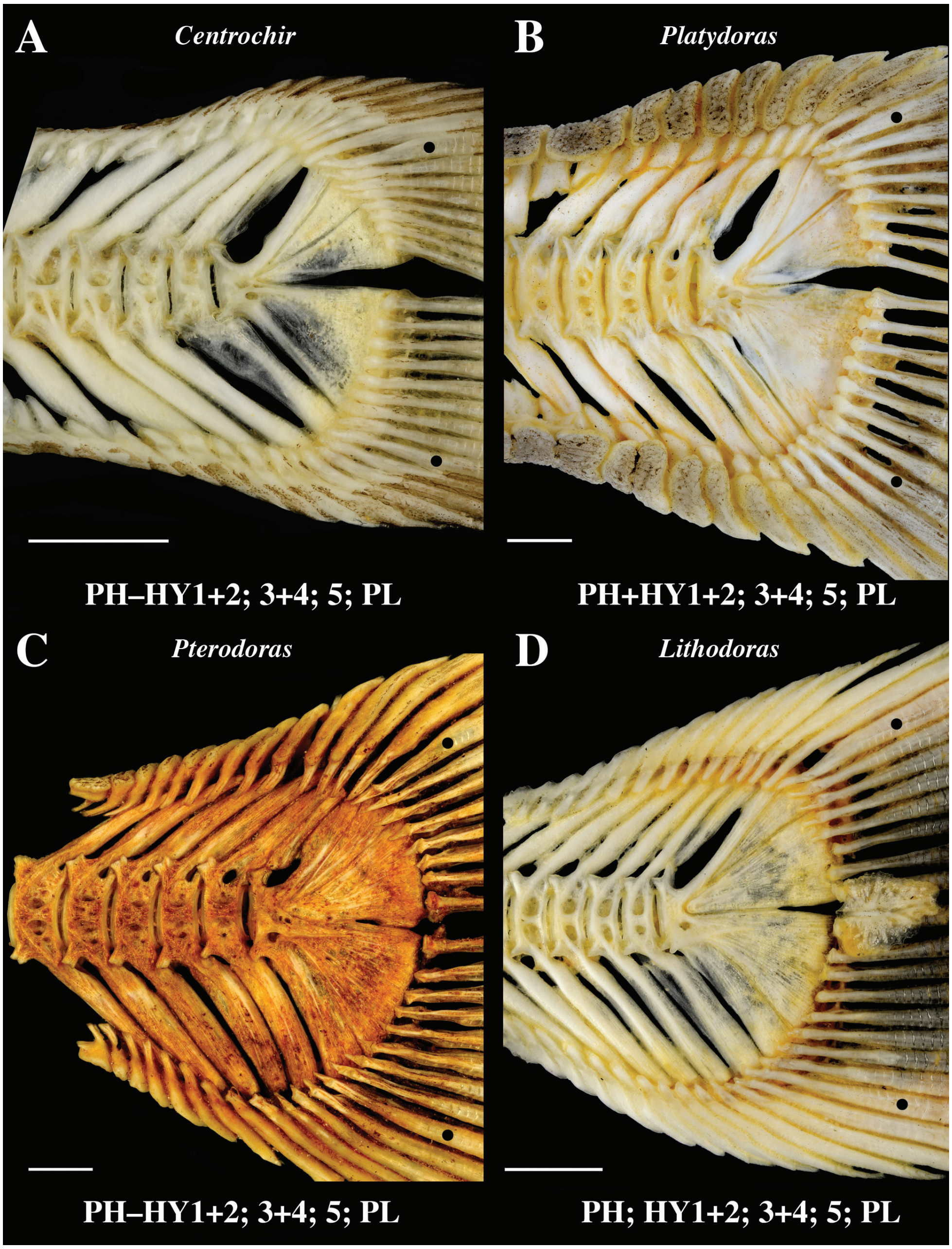


FIGURE 9 | Caudal skeletons typical of Doradinae. **A.** *Centrochir birindellii* (ANSP 197107, 123.5 mm SL) with parhypural partially fused to hypural 1+2 via proximal bony window containing hairline suture; **B.** *Platydoras hancockii* (ANSP 180286, 296 mm SL) with parhypural completely fused to hypural 1+2; **C.** *Pterodoras granulosus* (ANSP 179244, 297 mm SL) with scarcely evident suture between parhypural and hypural 1+2; **D.** *Lithodoras dorsalis* (ANSP 187376, 212 mm SL) with clearly evident suture between parhypural and hypural 1+2. Black dots indicate outermost primary caudal-fin rays. Scale bars = 1 cm.

DISCUSSION

Impact of sampling on molecular topologies. There are two major differences between the molecular datasets analyzed here and previously so by Arce H. *et al.* (2013): density of ingroup sampling and age of outgroup. Both studies included representatives of all 31 valid doradid genera, and Arce H. *et al.* (2013) analyzed 86 species-level taxa representing about 76% of the estimated species-level diversity (*i.e.*, ~96 nominal valid species plus ~17 undescribed species-level taxa). The current study analyzed 100 species-level taxa or about 88% of the estimated total diversity. The current study also included 174 doradid individuals compared to 130 in Arce H. *et al.* (2013). With respect to outgroups, Arce H. *et al.* (2013) included 10 species representing nine genera of Auchenipteridae and three species and genera of Aspredinidae based on other molecular studies that supported Aspredinidae sister to Auchenipteridae + Doradidae within the large catfish suborder Siluroidei. The current study expanded the number of auchenipterids to 25 species in 16 genera (*sensu* Calegari *et al*., 2019) and aspredinids to nine species in eight genera. More importantly, this study included two species of Cetopsidae, the first family to diverge in Siluroidei, and one species of Diplomystidae, the sister group to Siluroidei (Sullivan *et al*., 2006; Lundberg *et al*., 2007; Nakatani *et al*., 2011; Arcila *et al*., 2017; Betancur-R. *et al*., 2017).

To test the effects of the older outgroup, we performed a Maximum Parsimony (MP) analysis on the current (expanded) ingroup using the younger, more limited outgroup of Arce H. *et al.* (2013) (Fig. **S3**, Tab. 4). The younger outgroup had the greatest impact on the deeper nodes. For example, Doradidae was non-monophyletic when the younger outgroup was used in Arce H. *et al.* (2013) and the current study. However, whereas Astrodoradinae was sister to Auchenipteridae + remaining doradids in Arce H. *et al.* (2013), Acanthodoradinae + Auchenipteridae was sister to the remaining doradids in the MP analysis of the expanded ingroup with the restricted, younger outgroup. Therefore, increasing the age of outgroup in the current study established a deep and novel node supporting the monophyly of Doradidae (Godman-Bremer support 5). Also, Godman-Bremer support for the node joining subfamilies Wertheimerinae, Agamyxinae, Rhinodoradinae and Doradinae decreased from 13 (Arce H. *et al*., 2013) to 11 with the younger outgroup (but expanded ingroup), but increased to 16 with the older outgroup. With respect to the monophyly of subfamilial nodes shared with Arce H. *et al.* (2013), Godman-Bremer support decreased for Acanthodoradinae, Wertheimerinae and Doradinae and increased for Astrodoradinae, Agamyxinae and Rhinodoradinae in the current study (increases greater for Astrodoradinae and Rhinodoradinae when using the older outgroup). Godman-Bremer support for the monophyly of genera more often increased in the current study and by similar amounts between the older and younger outgroups. In the most dramatic increases, Godman-Bremer support rose by five for both *Oxydoras* and *Platydoras*. The latter genus had the highest increase in species and individuals added to the current study, two and 16, respectively.

The addition of one ingroup taxon, *Doras phlyzakion*, to the current study had a significant effect on the placement of another taxon, *Doras punctatus*, in the Maximum Parsimony (MP) analysis. Birindelli, Sabaj Pérez (2011) included *D. punctatus* in their new genus *Ossancora*, its members sharing maxillary barbel long with smooth elongate fimbriae, teeth present on dentary and premaxilla and posterior coracoid and posterior

TABLE 4 | Comparison of taxon sampling and Godman-Bremer support values (GBS) for monophyly of genera and higher-level relationships based on Maximum Parsimony analyses performed in Arce H. *et al.* (2013) and current study. With 2013 Outgroup: Aspredinidae (3 genera and species) and Auchenipteridae (9 genera, 10 species). With Current Outgroup: Diplomystidae (*Diplomystes nahuelbutaensis*), Cetopsidae (*Cetopsis coecutiens*, *Helogenes marmoratus*), Aspredinidae (8 genera, 9 species), Auchenipteridae (16 genera, 25 species, 32 individuals). Not supported (ns); not tested (nt); no change (–). **Centrochir* including *C. birindellii*. ***Doras* including *Doras punctatus*. ****Ossancora* minus *Doras punctatus*.

Subfamily	**Arce H. *et al.* (2013)**			Current study		GBS Change for Current Ingroup	
Genus/Relationship	Species	Individuals	GBS	Species added	Individuals added	2013 Outgroup	Current Outgroup
Acanthodoradinae new subfamily	**2**	**5**	**52**	**1**	**1**	**-19**	**-13**
Astrodoradinae	**15**	**16**	**30**	**–**	**–**	**+1**	**+4**
Amblydoras	5	5	4	–	–	-1	+1
Anadoras	3	3	25	–	–	+3	+4
Astrodoras	2	2	6	–	–	-3	–
Physopyxis	2	2	48	–	–	–	-11
Scorpiodoras	2	3	14	–	–	-5	-3
Astrodoras + Hypodoras	3	3	13	–	–	–	+2
Wertheimerinae	**3**	**7**	**31**	**–**	**–**	**-4**	**-2**
Franciscodoras	1	2	12	–	–	+1	+1
Kalyptodoras	1	3	20	–	–	-3	-1
Wertheimeria	1	2	9	–	–	–	–
Franciscodoras + Kalyptodoras	2	5	6	–	–	-1	-2
Agamyxinae new subfamily	**2**	**5**	**35**	**–**	**–**	**+1**	**+1**
Rhinodoradinae new subfamily	**7**	**8**	**17**	**2**	**3**	**+2**	**+3**
Rhinodoras	5	5	5	1	2	–	–
Rhynchodoras	1	2	76	1	1	-29	-28
Orinocodoras + Rhinodoras	6	6	26	1	2	-5	-5
Doradinae	**57**	**89**	**6**	**11**	**40**	**-1**	**-1**
*Centrochir**	1	2	nt	1	2	+3	+3
Centrodoras	2	3	6	–	1	–	–
*Doras***	4	7	ns	1	2	+2	+2
Hassar	3	3	21	1	1	–	–
Hemidoras	3	3	10	1	1	-4	-4
Leptodoras	12	16	3	2	12	+3	+3
Megalodoras	2	2	2	1	1	–	–
Nemadoras	4	11	1	–	–	+1	+1
*Ossancora****	2	4	3	–	–	-2	-2
Oxydoras	3	3	22	–	1	+5	+5
Platydoras	6	6	8	2	16	+5	+5
Pterodoras	2	4	16	1	1	-1	-1
Tenellus	3	9	3	–	–	+1	+1
Trachydoras	7	12	16	1	1	-3	-3
Anduzedoras + Leptodoras	13	18	4	2	12	+1	+1
Centrochir + Platydoras	7	8	3	3	18	+1	+1
Centrodoras + Lithodoras + Megalodoras	5	6	22	1	2	+3	+3

TABLE 4 | (Continued)

Subfamily	**Arce H. *et al.* (2013)**			Current study		GBS Change for Current Ingroup	
Genus/Relationship	Species	Individuals	GBS	Species added	Individuals added	2013 Outgroup	Current Outgroup
Doraops+ Pterodoras	3	5	13	1	2	+4	+4
Hemidoras + Ossancora	5	7	11	1	2	-3	-3
Lithodoras + Megalodoras	3	3	8	1	1	-1	-1
fimbriate-barbel doradids	39	67	23	6	17	-2	-1
Higher-level relationships							
Rhinodoradinae + Doradinae	64	97	3	13	43	–	-2
Agamyxinae + Rhinodoradinae + Doradinae	66	102	15	13	43	–	-1
Wertheimerinae + Agamyxinae + Rhinodoradinae + Doradinae	69	109	13	13	43	-2	+3
Acanthodoradinae + Wertheimerinae + Agamyxinae + Rhinodoradinae +Doradinae	71	114	2	14	44	ns	ns
Astrodoradinae + Wertheimerinae + Agamyxinae + hinodoradinae +Doradinae	84	125	ns	14	43	+2	+2
Doradidae	86	130	ns	14	44	ns	+5

cleithral processes finishing near the same vertical line. In the study by Arce H. *et al.* (2013), Bayesian and maximum likelihood analyses placed *D. punctatus* sister to a clade composed of three species of *Doras*, but the MP analysis placed *D. punctatus* sister to a clade of all remaining fimbriate-barbel doradids. The addition of *Doras phlyzakion* to the current study provided new support for placing *D. punctatus* in *Doras* (Godman-Bremer support 2 regardless of outgroup) and for a sister group relationship between the two species (Godman-Bremer support 5 regardless of outgroup). Oddly enough, this addition had the opposite effect on the Bayesian analysis. The new Bayesian topology did not support *Doras* as monophyletic, but had *D. phlyzakion*, *D. punctatus* and a clade of three other *Doras* species as successive sister groups to a clade composed of all other fimbriate-barbel doradids.

The phylogeny of Doradidae is clearly sensitive to ingroup density and outgroup age when Maximum Parsimony is used to analyze three genes, one nuclear (rag1) and two mitochondrial (co1, 16s). The question remains whether adding more genes and more ingroup species to the analysis will reinforce the nodes established in this study, or result in a new topology.

Caudal-fin shape in doradids. Caudal-fin shapes in Doradidae (evenly rounded, forked, evenly or unevenly truncate/emarginate) are loosely correlated with habitat and behavior. Doradids with caudal fins that are evenly rounded (Acanthodoradinae) or truncate/emarginate (Agamyxinae, Astrodoradinae except *Anadoras*) are generally benthic and occupy shallow, lentic habitats with ample structure such as woody debris, leaf litter and aquatic vegetation. Such habits are common to lakes, backwaters and river margins as well as floodplain creeks during the low-water season. During the day, *Acanthodoras* and *Agamyxis* are commonly found wedged in cavities in submerged logs. Many astrodoradins (*e.g.*, *Amblydoras*, *Hypodoras*, *Physopyxis*) partially bury themselves in sand or mud.

Doradids with forked caudal fins occupy a wide variety of benthic and pelagic habitats in lakes, rivers and creeks. *Anadoras* is the only astrodoradin with a distinctly forked caudal fin (upper lobe often longer than lower). Like other astrodoradins, *Anadoras* occupies shallow lentic habitats with woody debris and may bury in loose substrates or wedge themselves in wood; but, species also frequent midwater habitats with aquatic vegetation (*e.g.*, floating meadows). Benthic taxa that hide in cavities in rock or wood during the day (*Centrochir birindellii*, *Platydoras*) often have shallowly forked caudal fins. Benthic taxa that frequent open substrates of sand or silt in large rivers (*e.g.*, *Anduzedoras*, *Doras*, *Hassar*, *Hemidoras*, *Leptodoras*) typically have deeply forked caudal fins with pointed lobes, as do benthic taxa associated with rocky rapids (*Rhinodoras*, *Rhynchodoras*). Benthic taxa that occupy more sluggish waters such as floodplain lakes (*e.g.*, *Megalodoras*, *Oxydoras*) generally have moderately forked caudal fins with more rounded lobes. Midwater taxa that occupy large rivers and lakes (*e.g.*, active swimmers *Doraops zuloagai* and *Pterodoras*) also have deeply forked caudal fins with pointed lobes.

Caudal-fin skeleton developmental morphology. Our interpretations for doradids stem from the developmental morphology of the caudal skeleton in the ictalurid catfish *Ictalurus punctatus* (Rafinesque, 1818) as described by Grande, Shardo (2002) and in the zebrafish as described by Bird, Mabee (2003), Bensimon-Brito *et al.* (2010, 2012) and Desvignes *et al.* (2018). Those studies are summarized as follows with notes on contrasting views taken from Cumplido *et al.* (2020).

The compound caudal centrum is initally composed by the first preural centrum ($PU1^+$) anteriorly and the first ural centrum (U1) posteriorly. $PU1^+$ is thought to be formed by PU1 and an extra centrum (+) despite the absence of a physical separation between these centra (Bensimon-Brito *et al.*, 2010). Both $PU1^+$ and U1 begin as chordacentra, the products of direct mineralization from within the notochord sheath, generally in a ventral to dorsal direction. U1 appears first and $PU1^+$ usually follows as a anteroventral extension of U1 due to a continuous and uniform mineralization process (*i.e.*, no internal boundaries visible between $PU1^+$ and U1). On rare occasions, $PU1^+$ and U1 develop as two separate elements with subsequent fusion in a dorsal to ventral direction. As the fused chordacentra ($PU1^+$+U1) become fully formed, a perichordal layer of bone is deposited outside of the mineralized notochord sheath. Bone formation begins as two separate rings at the anterior and posterior edges of the compound centrum and progresses towards the central part of the centrum, thereby forming the autocentrum. In contrast, Cumplido *et al.* (2020) considered the compound caudal centrum to be initially composed of ural centra 1 and 2 (U1+U2) because of their association with the proximal ends of hypurals 1 and 2, respectively, and the absence (loss) of the preural centrum 1 (PU1) near the base of the parhypural during early stages of development.

Shortly after the first ural chordacentrum (U1) becomes visible, the more posteriorly placed second ural centrum ($U2^+$) forms separately within the notochord sheath. Similar to the first preural centrum ($PU1^+$), $U2^+$ is considered to be a compound structure formed by the fusion of multiple urals during the chordacentrum stage. Bensimon-Brito *et al.* (2012) reported an inner dark line running perpedicular to the notochord and separating $U2^+$ into anterior and posterior halves. The dividing line was clearly associated with mineralized notochord tissue (*vs.* notochord sheath). This internal zone of mineralization expands as $U2^+$ eventually fuses with the compound caudal centrum ($PU1^+$+U1). Prior to that fusion, the narrow space between $PU1^+$+U1 and $U2^+$ may appear as a partial intervertebral joint interrupted dorsally by bone. After fusion, PU1^{+}+U1+U2^{+} is collectively termed the urostyle (*sensu* Bird, Mabee, 2003), a structure that also eventually incorporates the first pair of uroneurals (*i.e.*, pleurostyle). In contrast, Cumplido *et al.* (2020) treated the U2^{+} of Bensimon-Brito *et al.* (2012) as the third ural (U3) which remains as a chordacentrum unfused to the compound caudal centrum.

The sequence of development of the vertebral centra is preceded by that of the modified neural and haemal arches and spines. The appearance of those epaxial (neural) and hypaxial (haemal) structures help to infer homologous landmarks along the notochord and incipient vertebral column. The haemal elements (parhypural and hypurals) appear first. The parhypural (PH) and hypural 1 (HY1) are closely associated with the ventral face of the compound caudal centrum (PU1^{+}+U1) in the region of the first preural centrum (PU1^{+}). This association helps define PU1^{+} as a compound element formed by PU1 and an extra centrum (*sensu* Bensimon-Brito *et al*., 2010, 2012). Hypural 2 (HY2) is associated with the posterior portion of the compound caudal centrum in the region of the first ural centrum (U1). Subsequent hypurals (HY3–5 or 6) are associated with more distal urals (if present), presumably in a one-to-one ratio. A physical gap, or hypural diastema, occurs between HY2 and HY3.

The dorsal-lateral surface of the urostyle (PU1^{+}+U1+U2^{+} in zebrafish) is closely associated with uroneurals and epurals (epaxial elements). A uroneural is a modified neural arch of an ural vertebra (Schultze, Arratia, 2013). A single uroneural may arise as a bilateral pair of bone slivers along the dorsal-lateral surface of the urostyle and extend from PU1^{+} to the tip of the notochord. This same uroneural eventually fuses to the urostyle to form the pleurostyle according to some authors (*e.g*., Grünbaum *et al*., 2003). Epurals develop slightly above the urostyle and are interpreted as neural spines detached from their neural arches. The anteriormost epural is sometimes interpreted as a neural spine detached from the neural arch vestige projecting dorsally from the PU1^{+} region of the urostyle.

In Doradidae, the compound caudal centrum appears to be composed of the first preural centrum plus an extra centrum (PU1^{+}) and the first ural centrum (U1), as in zebrafish (setting aside the contrasting view by Cumplido *et al*., 2020). Posterior to the compound caudal centrum, we observed an additional element interpreted as the second ural centrum (Fig. 5). This element seems to eventually fuse to base of hypurals 3 and 4 as similarly described by Lundberg, Baskin (1969) and supported (at least in part) by Grande, Shardo (2002). Based on their developmental study of the ictalurid catfish *Ictalurus punctatus*, Grande, Shardo (2002) agreed that a structural unit does form between ural centrum 2 and hypurals 3 and 4, but noted that in rare cases U2 fuses with the compound caudal centrum as in zebrafish (*sensu* Bird, Mabee, 2003; Bensimon-Brito *et al*., 2012).

Our interpretations are based on observations of cleared and stained juveniles of doradins (*Doras* and *Hemidoras*) and astrodoradins (*Amblydoras*, *Physopyxis*, *Scorpiodoras*) including a growth series of *Amblydoras affinis* (Fig. 5). In the two smallest juveniles examined (14.9 and 15.2 mm SL for *Scorpiodoras* and *A. affinis*, respectively), the posterior end of the compound caudal centrum (PU1^{+}+U1) is followed by an elongated element that occupies the space and angle of the dorsally flexed terminus of the notochord. This element lies between and is in tight contact with the proximal end of the pleurostyle and the bases of hypurals 3 and 4, respectively. The elongated element is unevenly mineralized and longitudinally separable into proximal, middle and distal portions. The proximal portion has a conical articular surface (*sensu* de Pinna, Ng, 2004) separated from the posterior end of the compound caudal centrum (PU1$^+$+U1) by a distinct gap resembling an intervertebral joint. The distal portion resembles a longer tube. A similar element is clearly visible in the cleared and stained specimen of *Physopyxis cristata* Sousa & Rapp Py-Daniel, 2005 (11 mm SL) figured by Sousa, Rapp Py-Daniel (2005:634, fig. 8a). We treat this element as ural centra 2$^+$ because of its resemblance to the compound ural centrum (U2$^+$) described by Bensimon-Brito *et al.* (2012:121, figs. 3D, G, H) in zebrafish.

In *Amblydoras affinis*, the proximal, conical portion second ural centrum (U2$^+$) becomes smaller and more triangular in juveniles 17.1–17.7 mm SL, is scarcely visible by 18.6 mm SL, and indistinguishable at 23.7 mm SL as it fuses to the ventral base of hypural 3+4. The distal, tube-like portion of U2$^+$ remains distinguishable at 23.7 mm SL. At 24.8 mm SL, the adult condition is nearly achieved wherein the second ural centrum (U2$^+$) appears fully fused to the base of hypural 3+4. In adults, the proximal end of this structural unit (U2$^+$+HY3+4) becomes tightly wedged into the concavity formed in part by the posterior facet of the compound caudal centrum and fused pleurostyle (*i.e*., urostyle).

The juvenile doradids examined here were already at a stage that was too advanced to observe the ontogeny of the epaxial and hypaxial caudal elements. Paired vestiges of a neural arch project from the dorsal surface of the urostyle in the PU1$^+$ region, and remain separate from their corresponding neural spine (epural). The proximal end of the uroneural appears to be fused to the compound caudal centrum (PU1$^+$+U1) at an early stage (thus forming the pleurostyle).

Caudal-fin skeleton in adult catfishes. Doradidae is a member of the suborder Siluroidei, one of the three major lineages of catfishes: Loricarioidei and Diplomystoidei + Siluroidei (Arcila *et al*., 2017). Within the Loricarioidei, fusion is common among skeletal elements supporting the caudal fin, and at least two hypurals are fused (Lundberg, Baskin, 1969). The highest degree of fusion among loricarioids occurs in the families Loricariidae and Scoloplacidae. In most loricariids, the epural, pleurostyle and upper hypurals are fused into a single plate, the lower hypurals and parhypural are fused into a second plate, and a bony bridge between the two plates reduces the diastema to a shallow distal notch: PH+HY1+2; 3+4+5+PL+EP (Lundberg, Baskin, 1969:44, fig. 9). In the monotypic Scoloplacidae, fusion of the caudal skeleton is taken a step further as there is no demarcation between the upper and lower hypurals: PH+HY1+2+3+4+5+PL+EP (Lundberg, Baskin 1969 [as "*Bunocephalus* sp."]; Schaefer, 1990:191, fig. 17). At the opposite extreme within Loricarioidei is the monotypic Nematogenyidae, the first family to diverge within the suborder. In *Nematogenys* Girard, 1855, only hypurals 1 and 2 are fused, hypurals 3, 4 and 5 remain separate from each other and the pleurostyle, and the parhypural remains separate from the lower hypurals: PH; HY1+2; 3; 4; 5; PL (Lundberg, Baskin, 1969:43, fig. 8). The epural also persists and is fully developed in *Nematogenys vs.* lost in some Loricarioidei, the family Trichomycteridae in particular (Lundberg, Baskin, 1969).

The caudal skeleton in the monotypic suborder Diplomystoidei represents the most dissociated condition in catfishes. In *Diplomystes* Bleeker, 1858, the hypurals are represented by six separate elements, the upper hypurals are unfused to the compound caudal centrum (PU1⁺+U1) and separated from the lower hypurals by a distinct diastema, the pleurostyle and parhypural remain separated from hypurals, and the epural is fully developed and detached from its neural arch: PH; HY1; 2; 3; 4; 5; 6; PL; EP (Lundberg, Baskin, 1969). A few members of Siluroidei share this extremely dissociated condition, including most species of Cetopsidae (Lundberg, Baskin, 1969; de Pinna, Ng, 2004), the oldest extant family in the suborder (Arcila *et al*., 2017). A few siluroids also have an extremely consolidated caudal skeleton such as Chacidae and some plotosids wherein the pleurostyle, hypurals and parhypural are completely fused into a singular plate that lacks a diastema: PH+HY1+2+3+4+5+PL (Lundberg, Baskin, 1969).

Within the Siluroidei, the caudal skeleton in Aspredinoidea [Aspredinidae (Auchenipteridae + Doradidae)] exhibits close to the full range of conditions known for catfishes. All members of Aspredinoidea have five hypurals (*vs*. six in some siluroids). Furthermore, hypurals 1 and 2 and hypurals 3 and 4, respectively, are almost always fused. Within Aspredinoidea, the highest degree of fusion occurs in Aspredinidae, the oldest of the three families. In Aspredinidae, the parhypural is fused to hypurals 1 and 2 (PH+HY1+2) and the three dorsal hypurals are fused into a solid plate (HY3+4+5) (Lundberg, Baskin, 1969; Friel, 1994; de Pinna, Ng, 2004; Friel, Carvalho, 2016; MHS, pers. obs.). In two genera, *Hoplomyzon* Myers, 1942 and *Pseudobunocephalus* Friel, 2008, the pleurostyle and epural are incorporated into the upper plate: PH+HY1+2; 3+4+5+PL+EP (Friel, 1994; MHS, pers. obs.). *Hoplomyzon* also has a bony bridge between the upper and lower plates that reduces the diastema to a distal notch, as in some loricariids. In Auchenipteridae, the caudal skeleton is relatively conserved. Nearly all auchenipterids share the pattern PH+HY1+2; 3+4; 5; PL (Lundberg, Baskin, 1969; Birindelli, 2014; Calegari *et al*., 2019; MHS, pers. obs.). In at least two species, *Pseudauchenipterus jequitinhonhae* (Steindachner, 1877) and *Tatia strigata* Soares-Porto, 1995, the three upper hypurals are fused into a singular plate (Calegari *et al*., 2019).

In Doradidae, the skeletal elements supporting the caudal fin generally fall into one of three patterns. In the most common one, three hypural plates are distinguishable (HY1+2, 3+4, 5) and the parhypural is separate, though tightly associated with HY1+2. In the second pattern, the fusion between the parhypural is complete (PH+HY1+2) or partial (PH-HY1+2). The third pattern involves the highest degree of fusion and is unique to the monotypic Acanthodoradinae. The parhypural and hypurals 1 and 2 are fused into a solid ventral plate and hypurals 3–5 are fused into a solid dorsal plate that generally incorporates the pleurostyle to some degree (HY3+4+5-PL).

Caudal-fin skeleton evolution in Aspredinoidea. Among catfishes, Lundberg, Baskin (1969:45) noticed a “trend from the primitive condition of six separate hypurals to the most advanced condition of complete fusion of caudal elements”. This trend is consistent with conditions observed in the first lineages to diverge within each of the two major clades of catfishes, Loricarioidei and Diplomystoidei + Siluroidei. The first lineage to diverge within Loricarioidei, *Nematogenys*, exhibits the least degree of fusion among hypural elements (HY1+2). The highest degree of fusion among caudal elements in Loricarioidei is found in the crown clade Scoloplacidae (Astroblepidae + Loricariidae). In Astroblepidae, the parhypural is fused to hypurals 1 and 2 and the upper hypurals are fused to the pleurostyle (PH+HY1+2; 3+4+5+PL). In Loricariidae, the upper plate fuses to the epural but remains distinguishable from the lower plate (PH+HY1+2;

3+4+5+PL+EP), and in Scoloplacidae the upper and lower plates are indistinguishable (PH+HY1+2+3+4+5+PL). As mentioned above, diplomystids have the plesiomorphic formula with six separate hypurals. This formula similarly occurs in first family to diverge among siluroids, Cetopsidae, but is restricted therein to the subfamily Cetopsinae. In the other cetopsid subfamily, Helogeninae, fusions occur between hypurals 1 and 2 (HY1+2) and 3 and 4 (HY3+4), respectively, and the sixth hypural (HY6) is lost (Lundberg, Baskin, 1969:42, fig. 7).

The evolutionary trend from hypural elements separate (ancestral) to fused (derived) is not observed in the superfamily Aspredinoidea based on the optimization of transformations for two caudal-skeleton characters mapped onto the Maximum

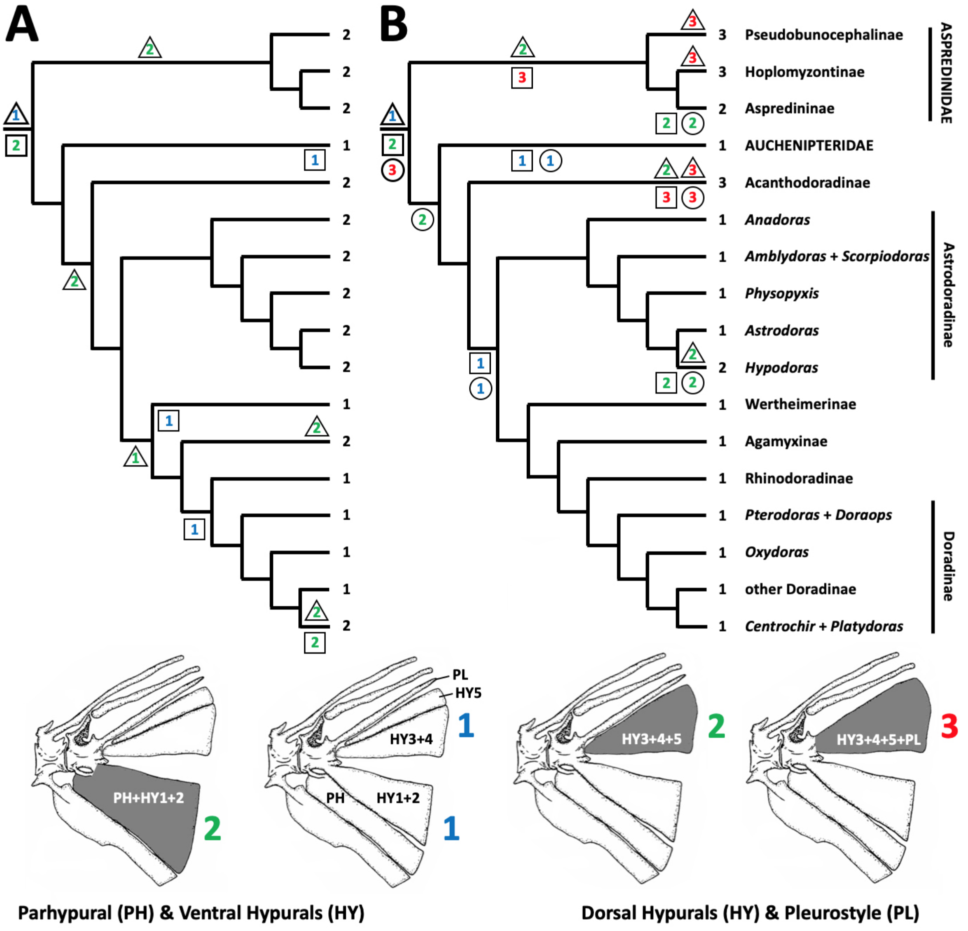


FIGURE 10 | Scenarios for evolution of fusion patterns observed in ventral (A) and dorsal (B) elements of the caudal-fin skeleton in Aspredinoidea mapped onto Maximum Parsimony phylogeny generated in this study. Character states (ordered): 1 = PH; HY1+2 (ventral) or HY3+4; 5; PL (dorsal); 2 = PH+HY1+2 (ventral) or HY3+4+5; PL (dorsal); 3 = HY3+4+5-PL or HY3+4+5+PL (dorsal only). Transformation series distinguished by state assumed for common ancestor: 1 (triangles), 2 (squares), 3 (circles); each symbol represents one transformation (except for bolded symbols representing common ancestor). Illustrations adapted from Lundberg, Baskin (1969:42, fig. 7A).

Parsimony tree generated in this study (Fig. 10). With respect to the ventral elements, the most parsimonius traversal of the tree begins with a common ancestor having a greater degree of fusion, PH+HY1+2 (*vs.* PH; HY1+2). From this starting point, it takes only four transformations to account for the phylogenetic distribution of character states among extant Aspredinoidea. If the parhypural is treated as separate in the common ancestor of Aspredinoidea, five steps are needed to achieve the same distribution for extant Aspredinoidea. With respect to the dorsal hypural plate, the condition for the common ancestor of Aspredinoidea is ambiguous. Six transformations are needed to achieve the diversity of fusion patterns among extant Aspredinoidea whether their common ancestor exhibited the least, most or an intermediate degree of fusion among the dorsal hypurals and pleurostyle.

Generally speaking, aspredinoid catfishes with rounded, truncate and emarginate caudal fins tend to exhibit greater degrees of fusion among the caudal supporting elements (parhypural, hypurals, pleurostyle) and occupy relatively shallow, lentic habitats with ample structure (*e.g.*, floodplain creeks and lakes, quiet backwaters and margins of rivers). Skeletal elements supporting the caudal fin are more separated in taxa with moderately to deeply forked tails that occupy lotic habitats in medium to large river channels.

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Mark Henry Sabaj: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing-original draft, Writing-review and editing.

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