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Systematic Revision of the Oligocene Billfishes (Istiophoriformes: Palaeorhynchidae) from Romania

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Abstract: This study revises †Palaeorhynchidae (Istiophoriformes), a rare and taxonomically disputed group within Romania's Oligocene ichthyofauna. Historically placed within Scombroidei, Istiophoriformes is now supported by molecular phylogenetics as a distinct lineage. However, prior Romanian fossil descriptions, often fragmentary, require critical revision to resolve their phylogeny, ecology, and biogeography. Outdated classifications must align with modern systematics. Our analysis confirms only two valid istiophoriform taxa in Romania's Oligocene: †*Homorhynchus colei*, previously misassigned to †*Palaeorhynchus longirostris* or †*P. glarisianus*, and †*Palaeorhynchus humorensis*. This clarifies long-standing taxonomic uncertainties and underscores the need for integrative approaches in paleoichthyology. The findings refine regional Oligocene biodiversity records and highlight the Eastern Carpathians' significance in understanding marine ecosystems of the epoch.

Keywords: Oligocene; billfishes; Piatra-Neamț; Gura Humorului; Romania

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1. Introduction

Billfishes are teleost fishes with elongated upper jaws (rostra) and, in some fossil forms, also elongated lower jaws. They include four extinct families (†Blochiidae, †Hemingwayidae, †Xiphiorhynchidae, and †Palaeorhynchidae) and two extant families (Istiophoridae and Xiphiidae) [1]. Taxonomically, they are traditionally classified as either within the suborder Scombroidei (order Perciformes), alongside mackerels, tunas, and relatives of the family Scombridae [2–5], or in the suborder Xiphioidei [6–9]. Fierstine [1] argues that certain morphological traits, particularly the rostrum and vertebral characteristics, are shared among the five billfish families. This supports their classification as a monophyletic group within the suborder Xiphioidei. However, he does not provide a definitive list of synapomorphies (shared derived traits) that specifically confirm their monophyly, as his emphasis is more on the fossil record and the taxonomic distinctions among the families. In our systematic palaeontology, we will provide a formal diagnosis to provide a solid context for our study.

Molecular phylogenetics [9–11] has redefined billfish relationships, now classified under a separate order, Istiophoriformes [11,12]. Wu et al. [13] indicate that billfishes have undergone convergent morphological evolution with Scombroidei, which is highlighted by the fact that modern billfishes share with tunas traits related to endothermy, even

though their molecular studies suggest that the lineages are not closely related. This implies distinct evolutionary paths despite their superficial similarities. The taxonomy of this group continues to evolve as new evidence emerges. While some fossil taxonomies have been updated, many still require careful reassessment to reflect current phylogenetic frameworks. De Gracia et al. [14] investigate the evolutionary relationships between fossil and living billfishes (Istiophoridae) in the Central Mediterranean during the Late Miocene, but the analysis does not include palaeorhynchids, as the focus is primarily on Istiophoridae, with some reference to Xiphiidae.

Presently, the fossil family †Palaeorhynchidae consists of four genera with about 23–25 species: †*Pseudotetrapturus* Danil'chenko, 1960 [15], with one species from the late Eocene of Russia; †*Palaeorhynchus* Blainville, 1818 [16], with nine to eleven species from the Eocene of Italy and Russia and the Oligocene of Croatia, France, Italy, Iran, Serbia, Germany, Romania, Russia, and Switzerland; †*Homorhynchus* Van Beneden, 1873 [17], with three species from the Eocene of France and Belgium and the Oligocene of Switzerland and Russia. Fierstine [1] also tentatively included with Palaeorhynchidae †*Aglyptorhynchus* Casier, 1966 [18], with about 11 species from the Eocene of Belgium and England, the Oligocene of Belgium, U.S.A., New Zealand [19], and the Miocene of the U.S.A. [1].

Fossilised remains of marine fish dating back to the Oligocene have been recorded in the Romanian Eastern Carpathians since the late 19th century, with notable occurrences near Piatra-Neamț [20–23]. The Oligocene fish fossil collection at the Natural Sciences Museum of Piatra-Neamț currently comprises over 50 species across various taxonomic groups. Among these fossils, palaeorhynchids are rare and poorly represented in the Piatra-Neamț Oligocene fauna and the broader Romanian Oligocene fish record (Suslănești, Gura Humorului). Their taxonomic classification has been primarily addressed by [22–24]. The primary objective of this study is to conduct a comprehensive re-examination and taxonomic redescription of the Palaeorhynchidae family from Oligocene deposits in Romania, to clarify morphological characteristics, update systematic classifications, and enhance our understanding of their paleoecological and biogeographical significance.

Geological Setting

Fossil fish remains have been documented in Oligocene organic-rich deposits across Central and Eastern Europe, including the Romanian Carpathians. Notably productive localities occur near Piatra-Neamț (Cozla, Pietricica Cernegura, Agârcia), Câmpulung Muscel (Suslănești), and Gura Humorului (Piatra Pinului) (Figure 1A), as described in previous studies (cited in the introduction).

Geologically, Cozla Mountain (Figure 1B) belongs to the Bistrița Half-Window, while the Piatra Pinului outcrop (Gura Humorului) is part of the Poiana-Făget-Isachia syncline within the Humor demi-window of the Vrancea Nappe (Marginal Folds Nappe; sensu [25]) in the Romanian Eastern Carpathians. The Vrancea Nappe is typically overlain by the Tarcău Nappe, exposed only as tectonic windows, demi-windows, or rabotage outliers [25–27]. Lithologically (Figure 1C), the Oligocene deposits of the Vrancea Nappe consist of the Lower Menilites, Bituminous Marls, Lower Dysodilic Shales, Kliwa Sandstone, Upper Dysodilic Shales and Menilites, and Gura Șoimului Formation [28]. The specimens related to this study were collected from the Dysodilic Shales Formation in Cozla Mountain (Piatra-Neamț) and Dysodilic Shale intercalations within the upper Kliwa Sandstone Formation (Piatra Pinului-Gura Humorului).

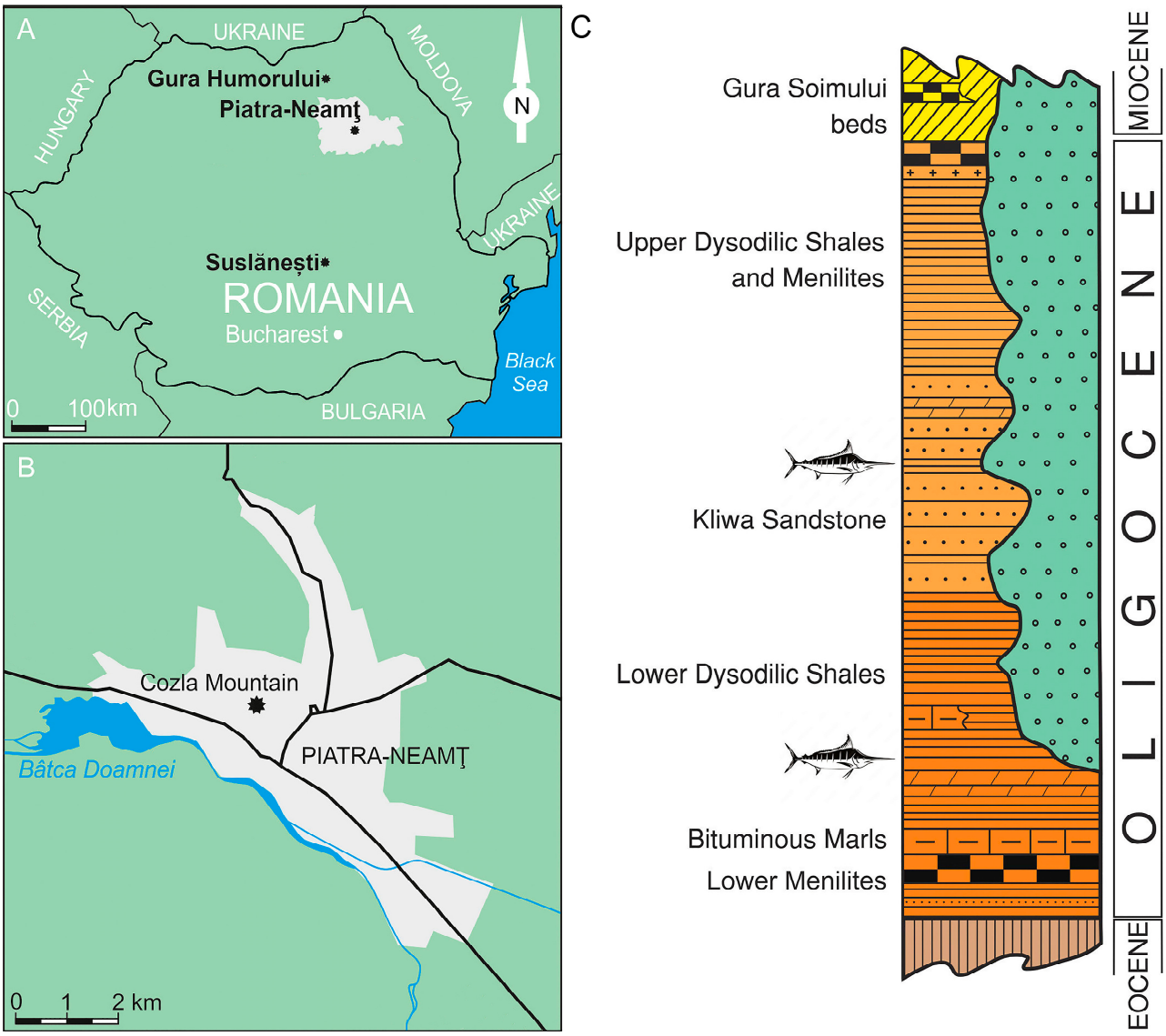

Figure 1. (**A**,**B**) Location of fossiliferous outcrops (Piatra-Neamț, Gura Humorului, Suslănești). (**C**) Lithostratigraphic column of the Vrancea Nappe from the central-northern part of the Eastern Carpathians (based on [29]).

2. Materials and Methods

In our systematic palaeontology, we follow the classifications of [11,12].

The studied material includes specimens housed in the Paleontological Collection of the Natural Sciences Museum of Piatra-Neamț and the Faculty of Geology and Geophysics, University of Bucharest collection. The specimens are included below within the systematic part.

Except for †*Palaeorhynchus humorensis* Brustur and Grigorescu, 1973 [24], the fossil specimens were studied using an Olympus SZX7 stereomicroscope. Photographs were captured using an Olympus OM-D EM 10 with a 60 mm macro objective.

Dagger symbol

We use the dagger symbol (†) for fossil representatives.

3. Systematic Paleontology

Superorder Acanthopterygii Rosen and Patterson, 1969 [30]

Order Istiophoriformes Betancur-R et al., 2013 [11]

Diagnosis: The following is condensed from the overview of [1]. Istiophoriformes have premaxillaries and maxillaries tightly bound in a non-protrusible, elongated rostrum. The body shape is described as slender fusiform [7], which means slender and elongated but not snake-like. Vertebrae are elongated and longer than they are deep. Neural and haemal spines are not simple but have various modifications, depending on the istiophoriform family. The caudal skeleton has a high degree of fusion, with two smaller hypural plates in †Hemingwaya. At the same time, other istiophoriforms have one massive hypural plate consisting of four or all five hypurals fused into one. The caudal fin is hypurostegic.

†Family Palaeorhynchidae Gunther, 1880 [31]
Diagnosis: The following is taken from [32]. Palaeorhynchidae have an enlarged and downturned maxillary flange, a continuous soft dorsal fin, which can be divided into two sections: an anterior one of longer ceratotrichia and a posterior one of shorter, more tightly packed rays. A fan-shaped pterygiophore bears each ray in the anterior section with three radiating ridges. The pterygiophores of the caudal section appear to be simple, wedge-like structures tapered away from the axial skeleton. The neural and haemal spines bear a caudal, ovoid-shaped extension.

†*Homorhynchus* Van Beneden, 1873 [17]
Type species: †*Homorhynchus bruxelliensis* van Beneden, 1873 [17], p. 207, by monotypy.
Composition: †*Homorhynchus deshayesi* (Agassiz, 1844) [33] from the Middle Eocene of France and Belgium and †*Homorhynchus colei* (Aggasiz, 1844) [33] from the Early Oligocene of Switzerland and Russia [1,32,34].
Diagnosis from [15,32,34]: The maximum body length reaches ~60 cm; length is 8–12 times the body height; rostrum markedly exceeds lower jaw; vertebrae: 50–55 in total; two pterygiophores per interneural spaces in anterior part of dorsal fin, respectively, per interhaemal spaces of the anterior section of the anal fin. Dorsal fin-ray (D1) count $\approx 2 \times$ vertebral count; there are no true D2 (second dorsal fin) and A2 (second anal fin), but the only continuous dorsal fin and only continuous anal fin are both divided in a long anterior section and short posterior one, surrounding the caudal peduncle. In the posterior section, there are more than two pterygiophores per interneural space or interhaemal space; hypurostegic caudal fin; pectoral and pelvic fins present.

†*Homorhynchus colei* (Agassiz, 1844) [33]
Figures 2–4
1833–1844 †*Palaeorhynchum colei* Agassiz: 85, p1.32, Figure 1 [33].
1833–1844 †*Palaeorhynchum microspondylum* Agassiz: 85, pl. 34a, Figure 2 [33].
1886 †*Hemirhynchus colei* (Agassiz, 1844), Wettstein, 78. [35]
1960 †*Homorhynchus colei* Danil'chenko, 161. p1. XV, Figure 2 [15].
1977 †*Palaeorhynchus longirostris* Agassiz, 1843, Ciobanu, p. 121, pl. XLII, Figure 1 [23].
1977 †*Palaeorhynchus glarisiaus* Blainville, 1818, Ciobanu, p. 122, pl. XLIII, Figure 1 [23].
2000b †*Homorhynchus colei* Ag., Monsch, p. 153, Figure 7.59 [34].
2010 †*Homorhynchus colei* (Agassiz, 1844), Bannikov, p. 149, pl. XXVI, Figure 2 [36].
2011 †*Homorhynchus colei* (Agassiz, 1844), Monsch and Bannikov, p. 291, Figure 42 [32].
Diagnosis from [15,32]: As for the genus, plus the body length is approximately 8–10 times the maximum body depth. The head length is about 3–3.5 times the body depth; the skull is shallow: depth about two-thirds of maximum body depth [37]. A total of 54–55 (26 + 28–29) vertebrae (25 + 28 in [15]. The dorsal fin originates adjacent to the first vertebra.
Note: The description in [34] expands on that in [15] of the neural and haemal spines, detailing simple spine-like structures (according to [15]) coming from constricted centra instead of spine-like structures with a full, plate-like extension.

Name in collection: †*Palaeorhynchus glarisianus* Blainville, 1818 [16]
Number: MSNPN-PC 154 (Figure 2).
Location in collection: Public exhibition.
General overview: Complete fish on slab.
Size: Length from distal tip of rostrum to last vertebra—375 mm.
General body features: The body is incompletely preserved due to bending but appears slender and almost snake-like, tapering posteriorly, similar to modern billfish, but somewhat slimmer. The body is covered in large cycloid scales.
Head: The relative head depth to body depth cannot be determined due to incomplete preservation in the anterior region. The skull roof is thick and ornamented with lines (shallow grooves). The rostrum is long and slender, though its full length is not entirely preserved. Preservation of the rostrum is poor, with much of its structure obscured by an irregular cavity filled in the restoration process. Small black structures in this area are likely artefacts from chemical reactions between the matrix and glue rather than teeth. The premaxillary flange is fragmented, with a small section overlapping the proximal dentary and angular. We infer that the original flange was considerably larger. The lower jaw is distinctly shorter than the rostrum.
Vertebral column: The vertebrae are hourglass-shaped, with pronounced constrictions and stout neural and haemal spines. The total vertebral count is uncertain due to poor anterior preservation, but we estimate at least 24 precaudal vertebrae (possibly more) and 28 caudal vertebrae (including the urostyle). Precaudal vertebrae lack parapophyses, with ribs articulating directly. These ribs are thick, robust, and curve posteriorly. Neural and haemal spines exhibit leaf- or trapezium-shaped caudal lamellae, which are poorly visible. Because of this, a false first impression of forked spines is created. The haemal spines of the first caudal vertebrae are obscured by the first 21 anal-fin pterygiophores, which are compressed into the body cavity. From the 13th caudal vertebra onward, neural and haemal spines become spatula-like, transitioning to slender trapezoidal shapes with posterior-pointing apices in the most caudal spines.
Unpaired fins: Both the dorsal and anal fins show two or three pterygiophores per interneural or interhaemal space. Their ceratotrichia are relatively short (shorter than maximum body depth, unlike †*Palaeorhynchus*). The dorsal fin preserves 71 rays, as the posterior section is missing and the anterior region is poorly preserved. The anal fin has four rays anterior to the first haemal spine, with a total of 29 rays preserved. In the caudal section, the anal fin appears compressed inward toward the vertebral column. The caudal fin complex is unclear; there may be one or two epurals, and the fifth hypural could be either autogenous or fused. Much of the hypural plate is concealed by the caudal fin. The caudal fin morphology is unclear due to displaced lepidotrichia, but we estimate ~23 rays.
Pectoral fin and girdle: The shoulder girdle is twisted and visible ventrally, with two partial pectoral fins (the best-preserved fin has 11 lepidotrichia, though the original number was likely higher).
The pelvic fin is not preserved.
Remarks: Ciobanu [23] mentioned the following meristics for this specimen: vertebrae: 52–54 (25 + 29); dorsal fin: 60?; anal fin: 40/40; pectoral fin: 12; pelvic fin: seven; caudal fin: 11/11.
Our meristic counts differ from Ciobanu's but correspond well on most points. In our opinion, the differences are caused by the difficulty of investigating poorly preserved specimens, which we overcame by examining the specimens by all of us and consulting with one another. We have not seen the pelvic fins with seven rays that Ciobanu reported. The meristic counts and other diagnostic characters still fit the diagnostic range of this species (see also Table 1), and the geographical and geological provenance correspond.

Although preservation is comparatively poor, we have no reason to believe this is another species other than the above-mentioned †*Homorhynchus colei*.

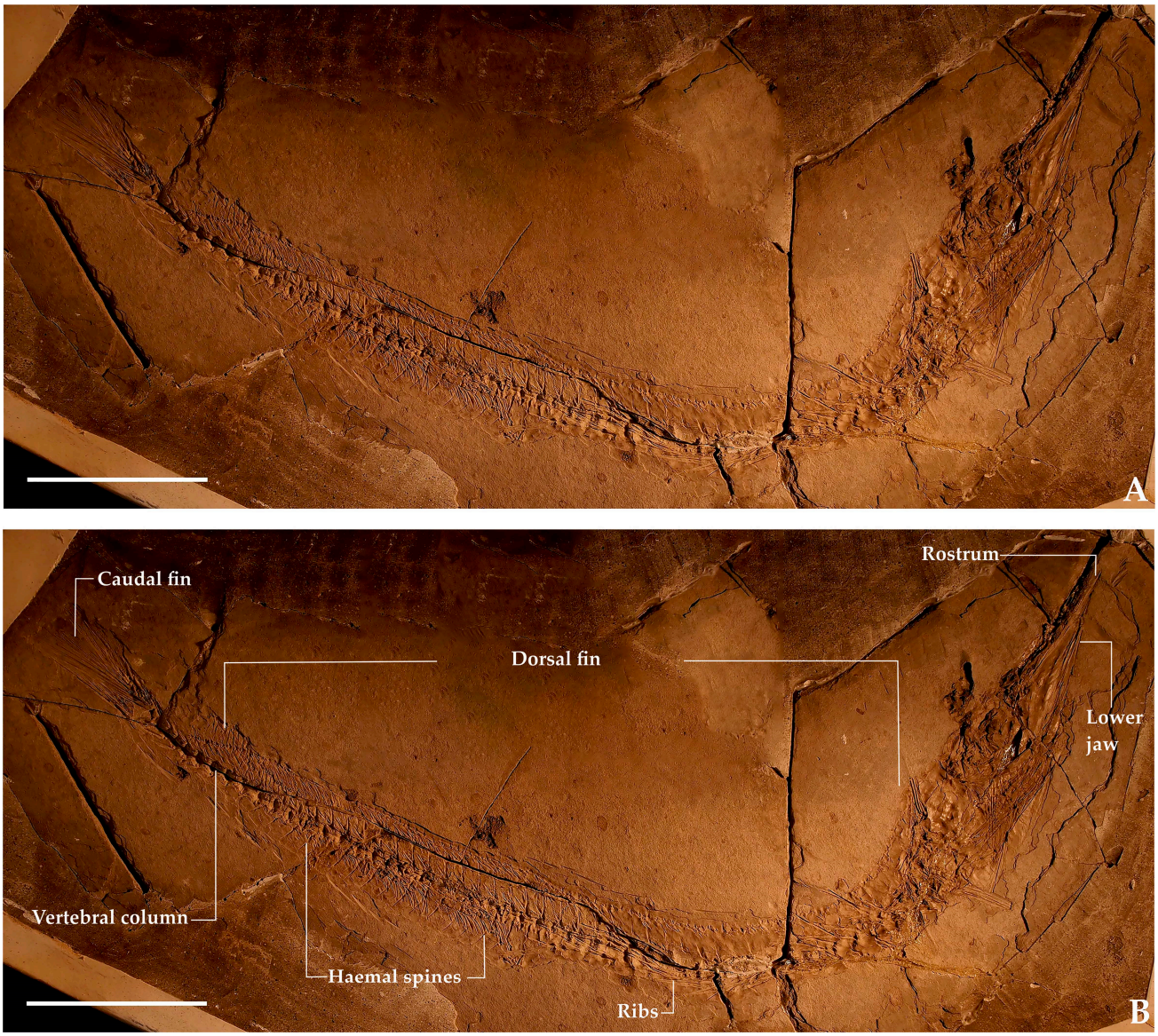

Figure 2. (**A**,**B**) †*Homorhynchus colei* (Agassiz, 1844) [33], MSNPN-PC no. 154, described and classified by [23] as †*Palaeorhynchus glarisianus*. Lower Dysodilic Shales Formation, Cozla Mountain, Piatra-Neamț. Scale bar: 5 cm.

Name in collection: †*Palaeorhynchus longirostris* Agassiz, 1843 [33]
Number: MSNPN-PC 155 (Figure 3).
Location in the collection: Depository.
General overview description: Complete fish on slab with caudal fin missing.
Size: Length from distal tip of rostrum to last preserved (50th) vertebra—610 mm.
General body features: The specimen is slender, elongated, and covered in large cycloid scales. Its rostrum is elongated, constituting approximately 64% of the total head length. A prominent premaxillary flange extends over the proximal and angular regions of the dentary. The lower jaw is significantly shorter than the rostrum, reaching only about 43% of the rostrum's proximal length.
Head: The head (incorporating branchiostegal rays) displays a depth of roughly two-thirds of the body's maximum depth (66%). The skull roof is robust but lacks surface ornamenta-

tion due to preservation limitations.

Vertebral column: The vertebrae are hourglass-shaped, featuring pronounced constrictions and sturdy neural and haemal spines. While poor preservation obscures the anterior vertebral column, 28 precaudal vertebrae are inferred. Of the caudal vertebrae, 22 remain intact, though the original count was likely greater. Precaudal vertebrae lack parapophyses, with ribs directly articulating to the centra. These ribs are thickened, robust, and posteriorly curved. Neural spines exhibit faint leaf-shaped caudal lamellae, weakly visible from the third caudal neural spine onward, superficially resembling forked spines. This is a false first impression because the preservation of the lamellae is relatively poor. Haemal spine lamellae and the caudal complex are absent due to preservation gaps.

Unpaired fins: Both dorsal and anal fins display two to three pterygiophores per interneural or interhaemal space. Their ceratotrichia are comparatively short (shorter than the body's maximum depth, distinguishing it from †*Palaeorhynchus*). The dorsal fin retains 77 rays, though the original number was higher due to missing posterior and degraded anterior sections. The anal fin preserves 39 rays, with seven positioned anterior to the first haemal spine; the complete count remains undetermined.

Pectoral fin and girdle: The shoulder girdle is ventrally exposed and distorted, with partial pectoral fins retaining nine lepidotrichia.

Pelvic fin elements are absent in the specimen.

Remarks: This specimen is catalogued in the Paleontological Collection of the Natural Sciences Museum of Piatra-Neamț as †*Palaeorhynchus longirostris* Agassiz, 1843 [33]. The collection records include no descriptions or additional information besides collecting data. While preservation quality limits detailed morphological analysis, the specimen's identification as †*Homorhynchus colei* remains strongly supported. Its meristic values align with the documented parameters of the species, and its geological setting and geographic origin are consistent with this taxonomic assignment.

Name in collection: †*Palaeorhynchus longirostris* Agassiz, 1843 [33]

Number: MSNPN-PC 197 (Figure 4).

Location in collection: Public exhibition.

General overview: Complete fish on slab.

Size: Length from distal tip of rostrum to last preserved vertebra—525 mm.

General body features: The specimen exhibits a slightly fusiform, slender, and elongated body, likely covered by large scales.

Head: The head (including branchiostegal rays) is shallow, approximating 64% of the maximum body depth. The skull roof is thick and ornamented with lines (shallow grooves). The rostrum is elongated, measuring 67% of total head length. The premaxillary flange is prominent, partially obscuring the dentary, while the lower jaw is short, extending only to the midpoint of the rostrum.

Vertebral column: The vertebrae (total count: 27 + 28) are hourglass-shaped, with pronounced constrictions and stout neural and haemal spines. Precaudal vertebrae lack parapophyses, with ribs articulating directly; these are robust, caudally bent, and thick. Neural and haemal spines exhibit leaf-shaped caudal lamellae, though they are poorly preserved, creating a false impression of forked spines. The caudal complex is incompletely preserved, obscuring certain elements: there are possibly one to two epurals and ambiguity regarding the autonomy of the fifth hypural. The posterior hypural plate is fragmented.

Unpaired fins: The dorsal fin contains 107 preserved rays (incomplete), with two to three pterygiophores per interneural space. The ceratotrichia are relatively short (shorter than the maximum body depth, contrasting with †*Palaeorhynchus*). The anal fin has twenty-nine rays preserved, with four rays anterior to the first haemal spine; the total count is indeterminate due to fragmentation. The caudal fin is forked, near-semilunate (this shape

is more pronounced in smaller specimens), hypurostegic, with an estimated 30 rays.
Pectoral fin and girdle: The pectoral fin, with 13 preserved lepidotrichia, is likely incomplete.
The pelvic fin comprises two short lepidotrichia.
Remarks: The specimen was initially described as †*Palaeorhynchus longirostris* by [23], with the following meristic counts: vertebrae: 60–61 (34 + 27); dorsal fin: 94/94; anal fin: 40; pectoral fin: 14; pelvic fin: seven; caudal fin: 15/16. Our meristic counts again differ from Ciobanu's, probably because of the difficulty of investigating poorly preserved specimens, which we overcame by examining the specimens together. Subsequently, the specimen was reidentified as †*Homorhynchus colei* by Bannikov in [32], though without explicit morphological justification. Our analysis confirms this taxonomic assignment. At the same time, we note a minor discrepancy in vertebral count from the diagnosis in [32] (our 27 + 28 vs. 26 + 28–29 in [32]). All other diagnostic characters, including the identical geological provenance, support classification as †*H. colei*.

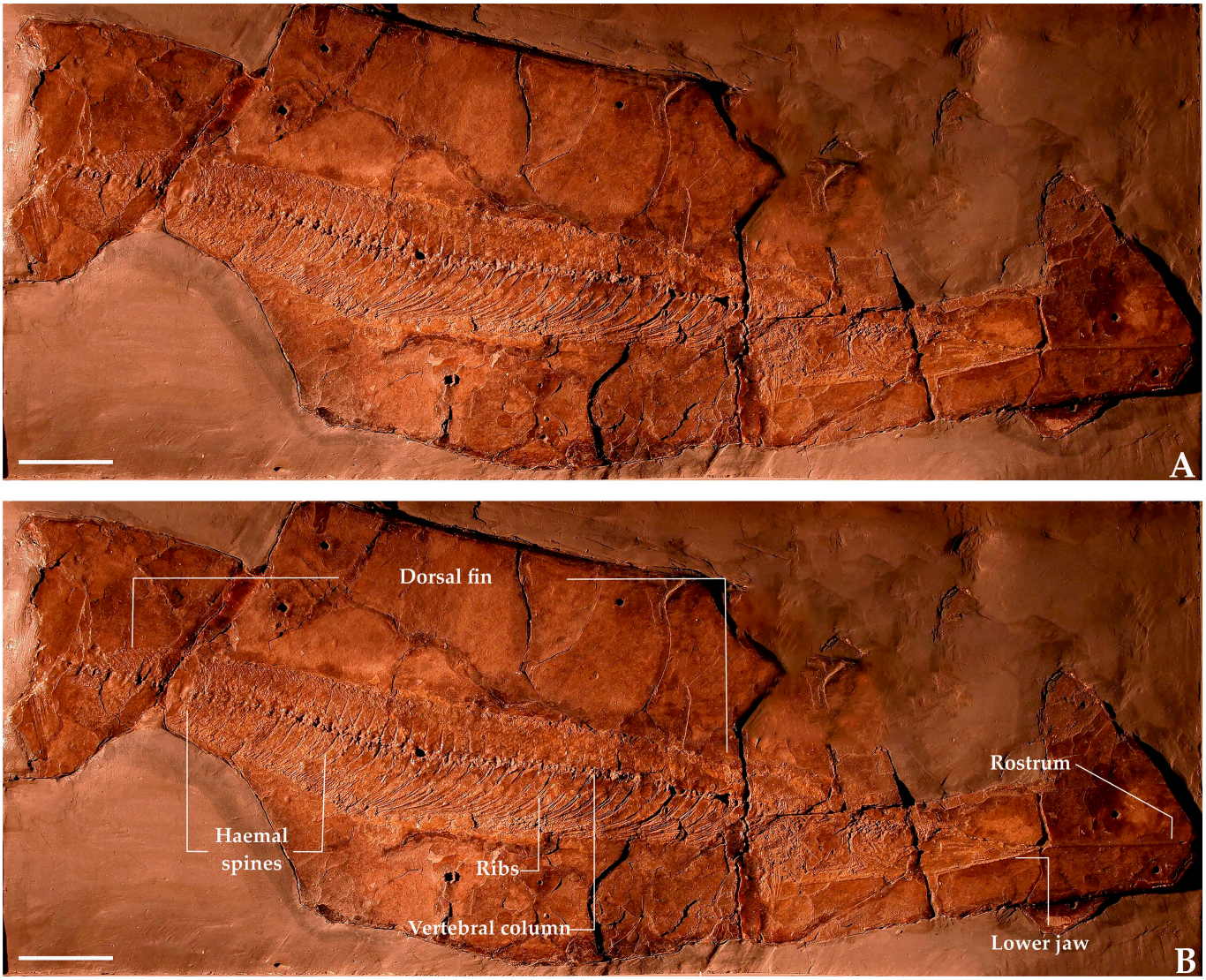

Figure 3. (**A**,**B**) †*Homorhynchus colei* (Agassiz, 1844) [33], MSNPN-PC no. 155, inventoried as †*Palaeorhynchus longirostris*. Lower Dysodilic Shales Formation, Cozla Mountain, Piatra-Neamț. Scale bar: 5 cm.

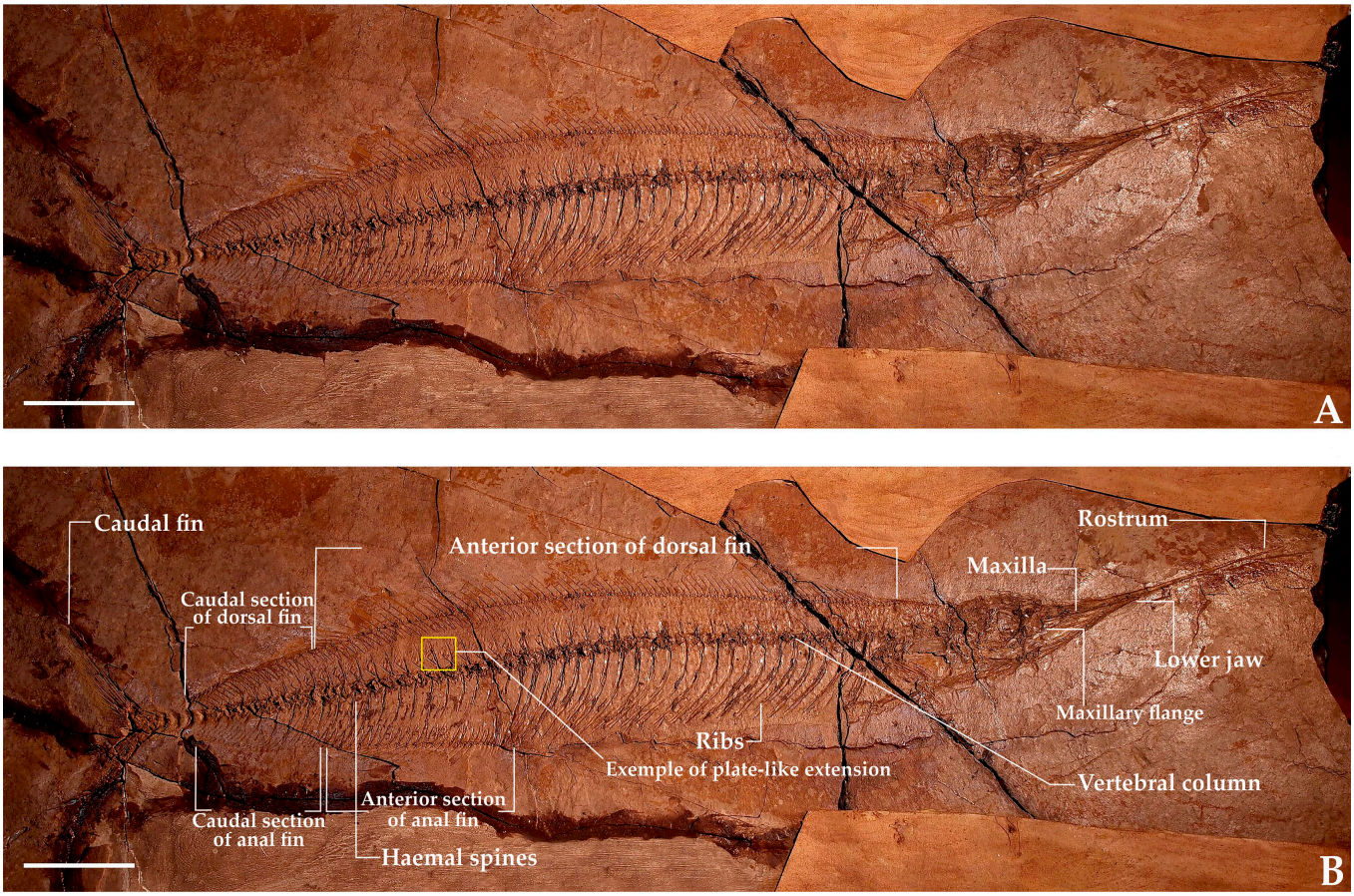

Figure 4. (**A**,**B**) †*Homorhynchus colei* (Agassiz, 1844) [33], MSNPN-PC no. 197, described and classified by [23] as †*Palaeorhynchus longirostris.* Lower Dysodilic Shales Formation, Cozla Mountain, Piatra-Neamț. Scale bar: 5 cm.

Table 1. †*Homorhynchus* species comparison.

Species Name	Vertebral Count	Key Morphological Features	Geographic Range	Age Range	References
†*H. colei*	26–28 + 28–29	None specifically, as other species are not well known. †*H. colei* is identified by its geographical and geological range.	Switzerland, Russia, Romania	Early Oligocene	[15,32]
†*H. bruxelliensis*	>21 caudal	Twenty caudal-fin rays. The species is poorly known. No other features are clearly described.	Belgium	Middle Eocene (early Lutetian)	[17]
†*H. deshayesi*	Not specified	Not specified.	France	Middle Eocene	[33]

†*Palaeorhynchus* de Blainville, 1818 [16]

Type species: †*Palaeorhynchum glarisianus* de Blainville, 1818, p. 314, [16], by monotypy.

Composition: We have recognised seven species, namely †*Palaeorhynchus zorzini* Fierstine, Bannikov, Monsch, 2008 [38] (Eocene of Italy); †*Palaeorhynchus senectus* Danil'chenko, 1962 [39] (Middle Eocene of Georgia); †*Palaeorhynchus parini* Bannikov, 1992 [40] (Mid-

dle Eocene of North Caucasus, Russia); †*Palaeorhynchus zitteli* (Kramberger, 1879) [41] (Oligocene of Poland, Romania, Russia); †*Palaeorhynchus glarisianus* de Blainville, 1818 [16] (Oligocene of France, Switzerland, Romania, possibly Germany, see [42]); †*Palaeorhynchus humorensis* Brustur and Grigorescu, 1973 [24] (Oligocene of Romania); †*Palaeorhynchus altivelis* Arambourg, 1967 [43] (Oligocene of Iran). Fierstine [1] mentioned nine to eleven species but did not mention them, so we do not know which taxonomy he applied; he also mentioned occurrences of this genus in the Early Oligocene of the former and possibly the Early Miocene of Germany and Switzerland.

Diagnosis from [32]: The upper and lower jaws are straight, elongated, and equal in length. The vertebrae number 50–60. Dorsal fin elements roughly match the number of vertebrae.

†*Palaeorhynchus humorensis* Brustur and Grigorescu, 1973 [24]

Figure 5

Name in collection: †*Palaeorhynchus humorensis* Brustur and Grigorescu, 1973 [24].

Number: CLPUB–LPB/II640.

Location in the collection: The Geology and Geophysics Faculty Hall, University of Bucharest.

Diagnosis after [24]: Elongated, fusiform body, with a maximum height of 8.2% of the body length excluding the caudal fin. The head length is 28% of the vertebral column length. The rostrum, formed by two elongated maxillaries, is 58% of the skull length. The large orbit, with nearly equal horizontal and vertical diameters, is 22.6% of the postrostral part length. There are 61 vertebrae, 21 of which are precaudal. The dorsal fin begins anteriorly, above the middle of the orbit, extending to the middle of the caudal peduncle. The anal fin is double; the first anal fin is more developed, with its anterior rays inserting opposite the 13th precaudal vertebra. The second anal fin is located behind the first, at a distance corresponding to the length of seven vertebrae. The body is covered with small cycloid scales.

Remarks: For a detailed analysis and description of the species, see [24]. The most notable distinction in †*P. humorensis* is the presence of a double anal fin, a feature undocumented in other †*Palaeorhynchus* species. This could represent either a specialised adaptation (e.g., for improved manoeuvrability) or a unique taxonomic characteristic. However, the apparent "double" fin might also result from misinterpretation or a fossil preservation artefact, as no other members of the †Palaeorhynchidae family exhibit this trait. Because it is not yet clear if the double fins are a true feature and because we have only one specimen, we cannot draw any conclusions on the function of this feature.

Additionally, †*P. humorensis* possesses 61 vertebrae, exceeding the typical range of 45–60 observed in other *Palaeorhynchus* species (see Table 2). This suggests either a more elongated body or a higher degree of segmentation. Detailed morphometric data for †*P. humorensis* (e.g., body height at 8.2%, rostrum length at 58% of total length) lack direct equivalents in other species descriptions, complicating comparative analysis. These proportions indicate a highly streamlined body shape, possibly reflecting distinct ecological or locomotory adaptations.

Table 2. †*Palaeorhynchus* species comparison.

Species Name	Vertebral Count	Key Morphological Features	Geographic Range	Age Range	References
†*P. altivelis*	53–54, of which 32–33 caudal	Anal fin originating under the penultimate precaudal vertebra	Iran	Oligocene	[43]
†*P. humorensis*	61, of which 40 caudal	Double anal fin (1st originating under 13th vertebra)	Romania (Gura Humorului)	Oligocene	[24]

Table 2. *Cont.*

Species Name	Vertebral Count	Key Morphological Features	Geographic Range	Age Range	References
†*P. glarisianus*	50–60, of which 35–36 caudal	Anal fin originating under the 18th precaudal vertebra	Switzerland, France	Early Oligocene	[44]
†*P. zitteli*	58–61 (?62) vertebrae, of which 33–35 caudal	Anal fin originating under 5th–7th before last precaudal vertebra	Poland, Russia, Romania?	Early Oligocene	[32]
†*P. parini*	58–60 vertebrae, of which 35–37 caudal	Anal fin originating under third or fourth before last precaudal vertebra	Northern Caucasus (Russia)	Middle Eocene	[32]
†*P. senectus*	50–60?	Elongated body, long rostrum, continuous dorsal fin	Georgia	Middle Eocene	[32]
†*P. zorzini*	50, of which 29 caudal	Fewer vertebrae (most primitive), long rostrum, continuous dorsal fin	Northern Italy (Bolca)	Late Early Eocene (Ypresian, ~50.5 Ma)	[38]

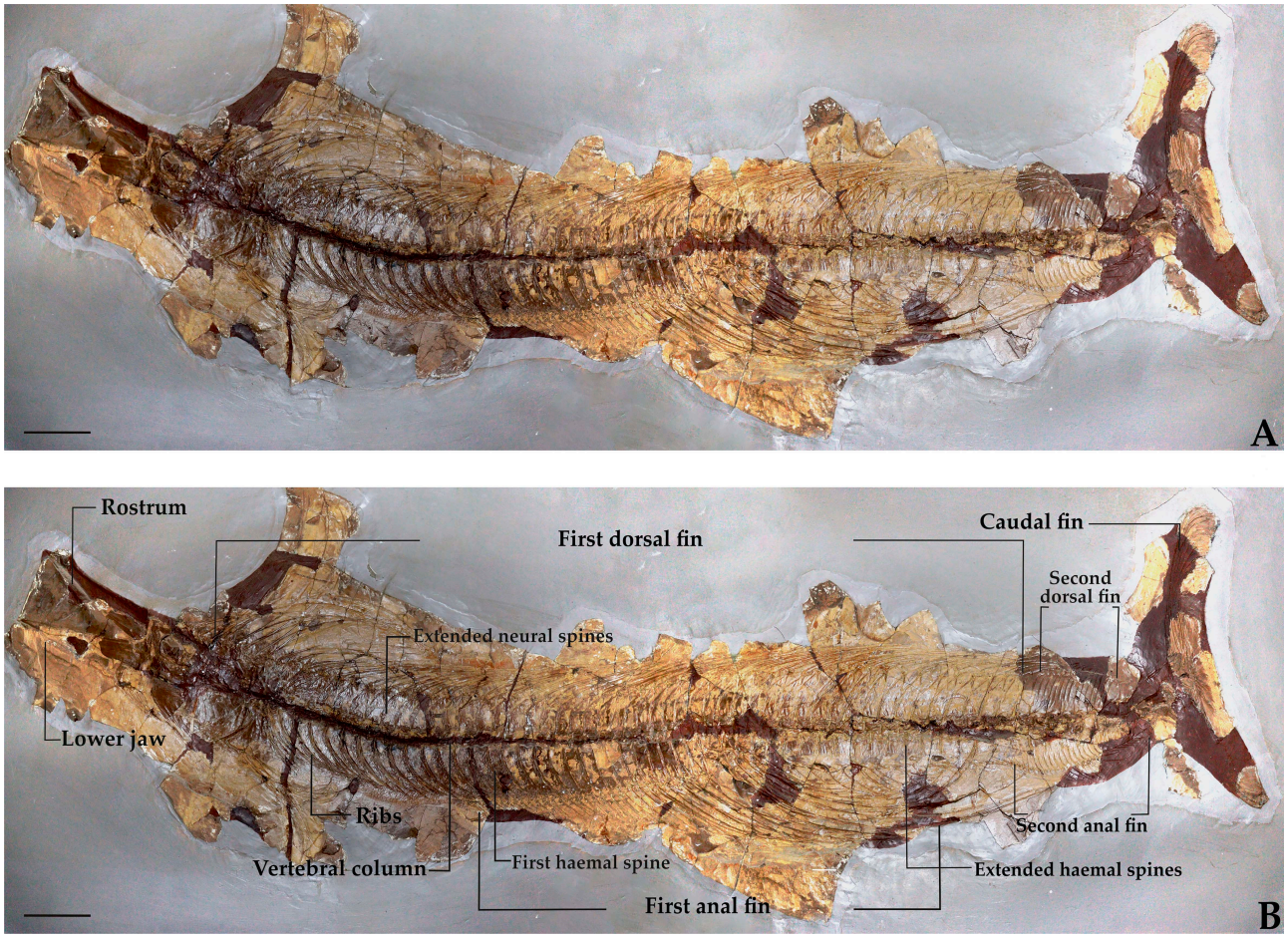

Figure 5. (**A**,**B**) †*Palaeorhynchus humorensis* Brustur and Grigorescu, 1973 [24], CLPUB–LPB/II640, Dysodilic Shale intercalation from the upper part of the Kliwa Sandstone Formation (Piatra Pinului, Gura Humorului). Scale bar: 10 cm.

4. Discussion

The well-documented fossil record of the family Palaeorhynchidae provides insights into its temporal, geographic, and evolutionary dynamics. Palaeorhynchids, from the Eocene to the Oligocene epochs, have primarily been found in Europe [16,33], with additional records from regions such as Russia [15], Iran [43], North America [1], and New Zealand [19]. This distribution reflects a wide paleobiogeographic spread in ancient marine environments, particularly within the Tethys and Paratethys Seas.

The fossil record of this family not only sheds light on the diversity and morphology of these elongated, rostrum-bearing fish but also offers clues about paleoenvironmental conditions and the preservational biases that occurred during the Paleogene period. The oldest known fossils of the Palaeorhynchidae family are attributed to †*Palaeorhynchus zorzini*, which was described from the late Early Eocene, found at the Monte Postale and Pesciara localities in Bolca, Northern Italy [38]. This species, possessing around 50 vertebrae, is considered the most primitive within the genus, suggesting that the diversification of Palaeorhynchidae began in the warm, tropical waters of the Tethys Sea [45,46]. Slightly younger records include †*Palaeorhynchus senectus*, which has been reported from the Middle Eocene of the Dabakhansk Formation in Georgia [39]. Additionally, the discovery of Eocene species such as †*Palaeorhynchus parini* from the Upper Eocene Kuma layer in the Northern Caucasus [40] highlights the early geographic spread of this family across the Paratethys region.

Most Palaeorhynchidae fossils are found in Oligocene deposits, indicating either a peak in species diversity or enhanced preservation due to favourable sedimentary conditions. The type species, †*Palaeorhynchus glarisianus*, was first described from Early Oligocene deposits in Glarus Canton, Switzerland [16,33]. This species is characterised by its elongated body, long rostrum, and a continuous dorsal fin that extends from behind the skull to near the tail. It is a well-documented family with many well-preserved specimens. The distribution of †*P. glarisianus* extends to Alsace, France [44], indicating a widespread presence during the Rupelian stage of the Oligocene. The abundance of †*P. glarisianus* fossils found in fine-grained marine sediments could suggest that these organisms were deposited in low-energy, deep-water environments.

In Eastern Europe, †*Palaeorhynchus zitteli* is recognised as the earliest member of the Palaeorhynchidae family, which was found in the Oligocene deposits of Poland, Romania, and Russia. In Romania, this species was described by Paucă [22] from the Suslănești area in the Eastern Carpathians. Unfortunately, the current location of the specimen is unknown, which complicates further research, which is also why we did not include a description. Additional fossil records from Romania's Oligocene period include †*Palaeorhynchus humorensis*, identified in the dysodilic shales near Gura Humorului [24] in the Carpathian Basin. These discoveries indicate that the Palaeorhynchidae family inhabited diverse marine environments during the Oligocene, from coastal zones to deeper basinal settings.

In this paper, we present, for the first time, an assessment of the morphological characters that identify †*Homorhynchus colei* specimens, which were previously assigned by [23] to †*Palaeorhynchus glarisianus* and †*Palaeorhynchus longirostris* from the Oligocene formations of Piatra-Neamț. However, the taxonomic status of †*Homorhynchus* remains problematic. The assignment of our specimens to †*H. colei* is the diagnostic criteria established by [15,32]. The geological provenance of our specimen, consistent with Early Oligocene deposits, corroborates findings from [15,32]. Our attempt to compare †*H. colei* to other species of †*Homorhynchus*, however, shows insufficient morphological data in the original descriptions of †*H. deshayesi* and †*H. bruxelliensis*. While the Oligocene †*H. colei* is well defined, the other two species from the Eocene are not, and we find it impossible to state how they

differ from †*H. colei.* Furthermore, the lack of clear diagnostic traits separating †*H. deshayesi* from †*H. bruxelliensis* raises the possibility of their synonymy.

To resolve these taxonomic uncertainties, a comprehensive revision of existing specimens, supplemented by additional material, is necessary. Future studies should prioritise detailed comparative analyses to establish robust morphological distinctions and clarify species boundaries within †*Homorhynchus.*

5. Conclusions

This study establishes taxonomic clarifications for Romanian Palaeorhynchids through morphological re-examination. Notably, material previously attributed to †*Palaeorhynchus* from Piatra-Neamț has been reassigned to †*Homorhynchus colei*, resolving prior ambiguities. This provides new insights into the evolutionary diversity of billfish-like fishes. Additionally, †*P. humorensis* exhibits a peculiar double anal fin and elevated vertebral count-features; however, since the presence of double fins remains uncertain and we have only one specimen, we cannot conclusively determine their function. Comparative studies with extant and extinct billfishes could determine whether this morphology is autapomorphic or convergent. Our study advances the fossil record documentation of †Palaeorhynchidae, offering critical evidence for reconstructing Paratethyan marine ecosystems and climate dynamics during the Oligocene.

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Abbreviations

The following abbreviations are used in this manuscript:

MSNPN-PC	Palaeontological Collection of the Natural Sciences Museum Piatra-Neamț;
CLPUB–LPB	Palaeontological Collection of the Geology and Geophysics Faculty Hall, University of Bucharest.

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