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On the first occurrence of *Anoxypristis* (Pristidae, Elasmobranchii) in the Paleogene of Romania and southeastern Europe

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Abstract: This study provides the first record of the genus *Anoxypristis* in Romania and in the whole of southeastern Europe based on two isolated rostral spines discovered in Priabonian deposits of the Transylvanian Basin. Assessment of the validity of previously described Paleogene species of Pristidae emphasizes the need for more rigorous taxonomic criteria based on more than isolated rostral spines. The paleoecological implications of the Romanian *Anoxypristis* specimens, considering the habitat preferences of the extant species and the depositional environments represented by the fossiliferous strata, point to a coastal or estuarine setting.

Keywords:

- Pristidae;
- sawfish;
- Priabonian;
- Eocene;
- Transylvanian Basin

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Résumé : ***Sur la première occurrence d'*Anoxypristis *(Pristidae, Elasmobranchii) dans le Paléogène de Roumanie et d'Europe du Sud-Est***.- Cette étude, fondée sur la découverte de deux épines rostrales isolées dans des dépôts priaboniens du bassin de Transylvanie, constitue le premier signalement du genre *Anoxypristis* en Roumanie et en Europe du Sud-Est. L'évaluation de la validité des espèces de Pristidae du Paléogène décrites antérieurement met en évidence la nécessité de critères taxonomiques plus rigoureux, reposant sur davantage que de simples épines rostrales isolées. Les implications paléoécologiques des spécimens roumains d'*Anoxypristis*, en tenant compte des préférences d'habitat des espèces actuelles et des environnements de dépôt représentés dans les couches fossilifères, suggèrent un milieu côtier ou estuarien.

Motsclefs :

- Pristidae ;
- poissons-scies ;
- Priabonien ;
- Éocène ;
- bassin de Transylvanie

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1. Introduction

The paleoichthyological record has been historically underrepresented in Romania, with isolated teeth being often reduced to rare mentions in faunal lists or simply categorized as 'fish teeth.' Even in the extensively studied northwestern region of the Transylvanian Basin (see TRIF & CODREA, 2018, for a comprehensive review of prior research), ichthyolith occurrences have been rarely documented. This study provides the first record of *Anoxypristis*, a cartilaginous fish genus previously unknown from Romania, based on two isolated rostral spines. A very fragmentary fossil record of Elasmobranchii exists across a broad geographic area, stretching from Croatia to Greece and from Turkey to Bulgaria. The understanding of the Eocene elasmobranch assemblages has recently improved based on work conducted in Hungary and Ukraine (see KOVALCHUK *et al.*, 2023; SZABÓ, 2024), but *Anoxypristis* was until now unknown from this entire region.

2. Geological setting

The fossils discussed herein were collected from the northwestern part of the Transylvanian Basin. The Transylvanian Basin represents an Upper Cretaceous to Neogene sedimentary basin developed on top of a sequence of Paleozoic crystalline schist, ophiolites, volcanic deposits and sedimentary rocks spanning the Triassic to the mid-Cretaceous (CIUPAGEA *et al.*, 1970; SĂNDULESCU & VISARION, 1978; PARASCHIV, 1979; KREZSEK & BALLY, 2006). The stratigraphic architecture of the basin comprises four distinct tectonic and stratigraphic megasequences that date to the Late Cretaceous, Paleogene, Early Miocene, and Middle to Late Miocene, respectively (KREZSEK & BALLY, 2006). The specimens investigated were recovered from deposits belonging to the Paleogene megasequence. These deposits, located in northwestern Transylvania, display remarkable lateral facies variations, hence the delimitation of three depositional areas, namely, Gilău, Preluca and Meseș (Fig. 1.A-B). The *Anoxypristis* spines were derived from two localities in the Gilau and Meseș depositional areas.

Piscul Ronei (Turbuța): The Turbuța locality (Fig. 2.A) occurs within the Meseș depositional area. A prominent topographic feature, the Piscul Ronei is a 919-m-high peak sculpted by the erosion of a Paleogene monoclinal structure that dominates the landscape of the Turbuța-Jibou region. Here, the stratigraphic succession encompasses Paleocene to Eocene units, with minor occurrences of Pleistocene deposits. The following units are present at Piscul Ronei, in ascending stratigraphic order: the Jibou Formation (including the Rona Member of Thanetian-?Sparnacian age and the "upper red member" of Paleocene-Lutetian age), the Foidaș Formation (Lutetian), the Călata Group (including the lower Lutetian-Bartonian Căpuș Formation and the lower Priabonian Racoți Sandstone) and the Turbuța Formation (middle Priabonian) (PETRESCU *et al.*, 1975; MÉSZÁROS, 2000; CODREA & SĂSĂRAN, 2002). The Turea Group, represented by the Cluj Limestone (upper Priabonian), only crops out in the southern sector of Piscul Ronei.

A single *Anoxypristis* sp. rostral spine (BBUPSM 24018) was recovered from the Racoți Sandstone, alongside unidentified chelonian remains. The Racoți Sandstone (appearing in some publications under the alternative name of Rakoczy Sandstone) is a calcareous sandstone exhibiting a gradual increase in quartz content from south (Treznea region) to north (Turbuța), ultimately transitioning into a quartz sandstone (POPESCU, 1984).

Leghia: The Leghia locality (Fig. 2.B) is found approximately 45 kilometers northwest of Cluj-Napoca, in the Gilău depositional area (POPESCU, 1984). A specimen of *Anoxypristis* sp. (BBUPSM 24019) was recovered from the Valea Fânului quarry, south of the Leghia village. The Leghia area encompasses deposits belonging to the Călata Group, including the Căpuș Formation, the Inucu Formation, the Văleni Limestone and the Ciuleni Formation, all of which are overlain by Vișstea Limestone (RUSU, 1995).

The Leghia specimen was collected from the Vișstea Limestone, which in older geological literature was referred to as the "Lower Coarse Limestone" (see RUSU, 1987, 1995, for a comprehensive synonymy of this stratal package). This lithostratigraphic unit is assigned to the Lower Priabonian. The Vișstea Limestone represents deposition within an inner shelf environment characterized by warm water and a sandy substrate (RUSU, 1995; TRIF *et al.*, 2024). The Leghia Limestone and the Racoți Sandstone are time-equivalent (Fig. 2.C).

3. Material and methods

The two rostral spines described in the present paper are housed in the Paleontology and Stratigraphy Museum of Babeș-Bolyai University, Cluj-Napoca (BBUPSM). These specimens were photographed using a Nikon d5300 camera equipped with a Sigma 105 mm lens. The images were edited using GIMP, version 3.0.

4. Systematic paleontology

Subclass Elasmobranchii BONAPARTE, 1838

Order Rhinopristiformes NAYLOR et al., 2012

Family Pristidae BONAPARTE, 1838

Genus *Anoxypristis*
WHITE & MOY-THOMAS, 1941

***Anoxypristis* sp.**

Material: BBUPSM 24018 and BBUPSM 24019, two rostral spines in the BBUPSM collection (Fig. 3.a-h).

Occurence: Piscul Ronei, Turbuța locality, Racoți Sandstone (BBUPSM 24018); and Valea Fânului quarry, Leghia locality, Vișstea Limestone (BBUPSM 24019)

Age: Priabonian

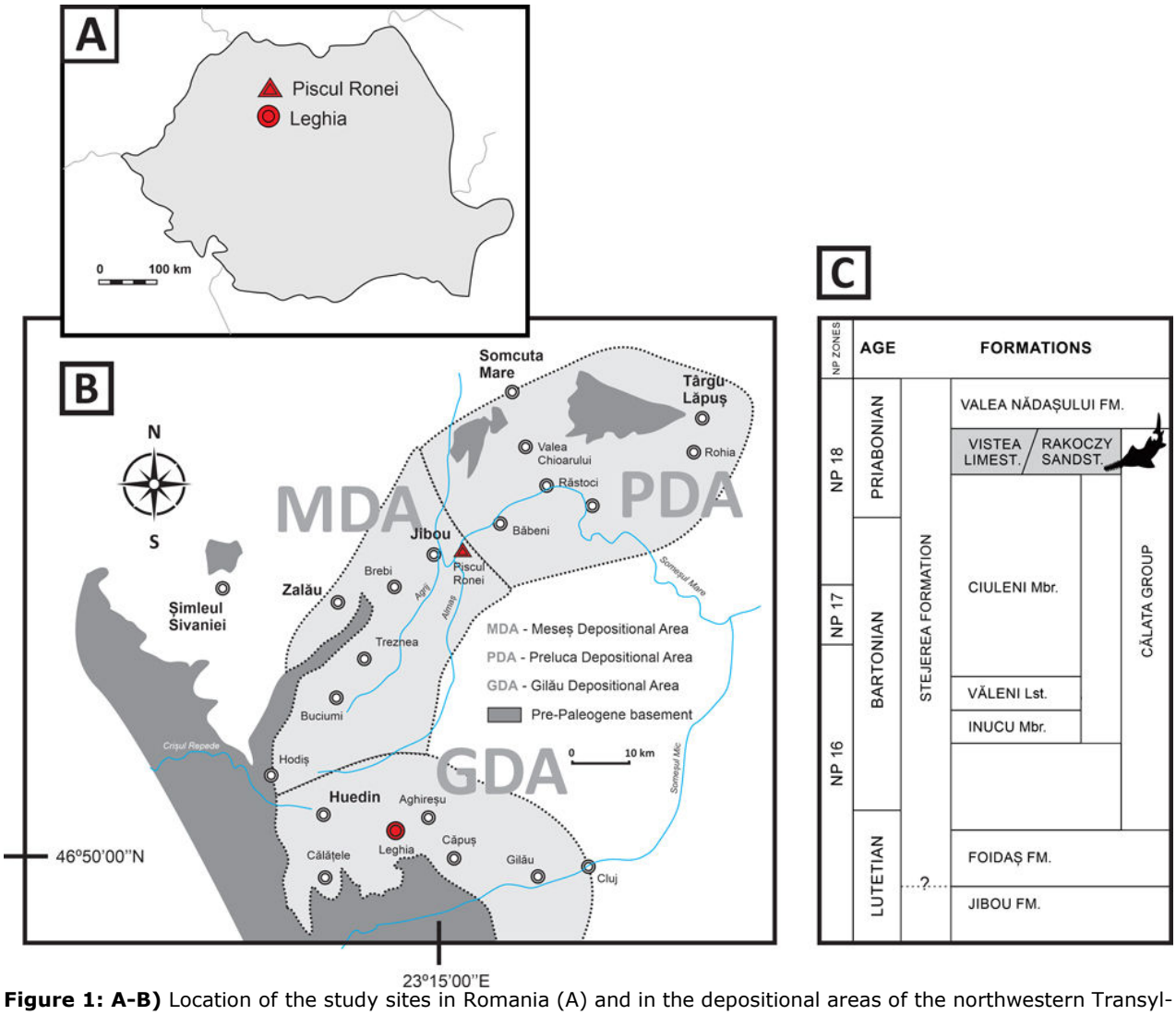

Figure 1: A-B) Location of the study sites in Romania (A) and in the depositional areas of the northwestern Transylvanian Basin (B). **C)** Simplified lithostratigraphic log of the Eocene deposits of the northwestern Transylvanian Basin [abbreviations: FM.=Formation, Mbr.=Member, Lst.=limestone; panel 1B after POPESCU (1984), simplified].

Description: The two rostral spines display a similar morphology. They are strongly dorsoventrally compressed and feature convex anterior and posterior edges. They are slightly curved posteriorly as well as ventrally. The posterior curvature is more pronounced on the Leghia specimen (BBUPSM 24019) compared to the one from Turbuța (BBUPSM 24018). The transverse section of the spines has a very thin, oval outline (Fig. 3.i). Both specimens exhibit faint longitudinal striations, but BBUPSM 24018 also displays raised transverse striations on its basal part (Fig. 3.e, g). The same specimen bears numerous striations on its the apical part, which are related to functional wear.

Discussion: The family Pristidae encompasses two extinct genera (*Peyeria* WEILER, 1935, and *Propristis* DAMES, 1883) and two extant genera (*Anoxypristis* WHITE & MOY-THOMAS, 1941, and *Pristis* LINCK, 1790). These taxa exhibit considerable morphological similarities with respect to the rostrum and associated rostral spines (CAPPETTA, 1987; WUERINGER *et al.*, 2009). The oral dentition of the family remains poorly documented in the fossil record, although a further genus of Pristidae, *Glaucopristis*, was recently erected based on teeth previously assigned to *Rhinobatos bruxelliensis* (REINECKE *et al.*, 2024). Given that extinct pristid genera have previously been established based solely on rostral spines, and considering the possibility that loose oral teeth may belong to any of the aforementioned genera, a conservative approach in proposing new genera of Pristidae based on oral teeth is advisable in order to avoid the growth of a parallel taxonomy.

The oldest genus within the Pristidae family is *Peyeria*, represented solely by *P. lybica* WEILER, 1935, from the Cenomanian of Libya. CAPPETTA (1987) questioned the validity of this genus due to the existence a significant stratigraphic gap between *Peyeria* and the remaining genera, which only appeared in the Paleocene (CICIMURRI, 2007) or Eocene (CASE, 1994; CAPPETTA, 2012). In contrast, WUERINGER *et al.* (2009) regarded *Peyeria* as a potential ancestral lineage for the family Pristidae, suggesting a radiation event following the Cretaceous/Paleogene boundary. Notably, CAPPETTA (2012), in his comprehensive review of Pristi-

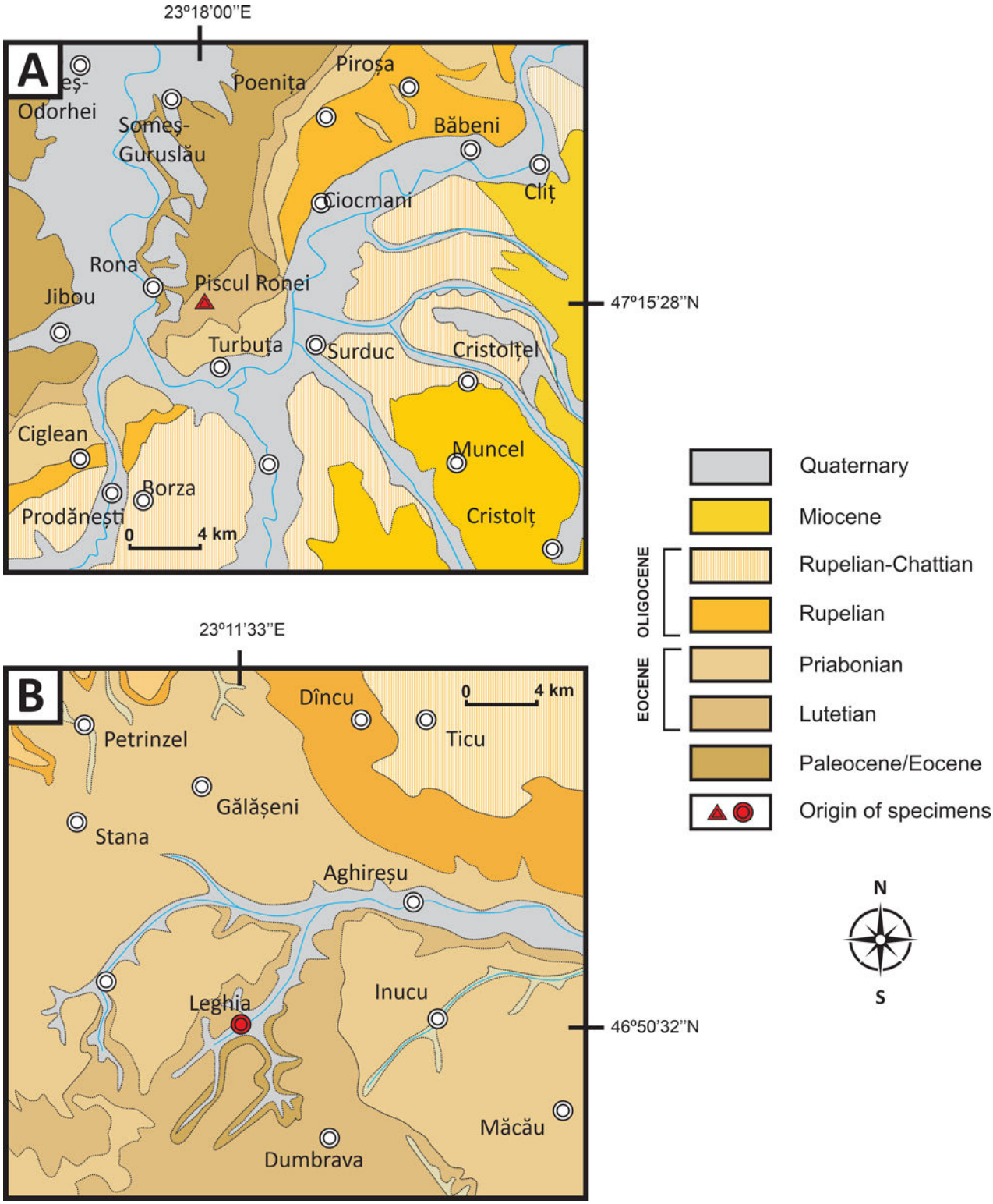

Figure 2: Geological maps of the (A) Piscul Ronei (Turbuța) and (B) Leghia localities, showing the find localities of the two pristid specimens dealt with herein [after the Geological Map of Romania, *folio* Cluj-Napoca, 1:200.000, SAULEA *et al.* (1967), modified and simplified].

dae, completely disregarded this genus without any acknowledgment of its prior assignment to the pristids.

The second extinct genus, *Propristis*, made its appearance in the Eocene and is represented by a single valid species, *P. schweinfurthi* DAMES, 1883. This genus is morphologically distinct from *Pristis* and *Anoxypristis* by featuring short rostral spines that are notably wide anteroposteriorly and have predominantly sharp carinae. Also, the length of the part inserted into the rostrum (*i.e.*, the 'root') is much shorter in *Propristis* than in *Anoxypristis* or *Pristis*.

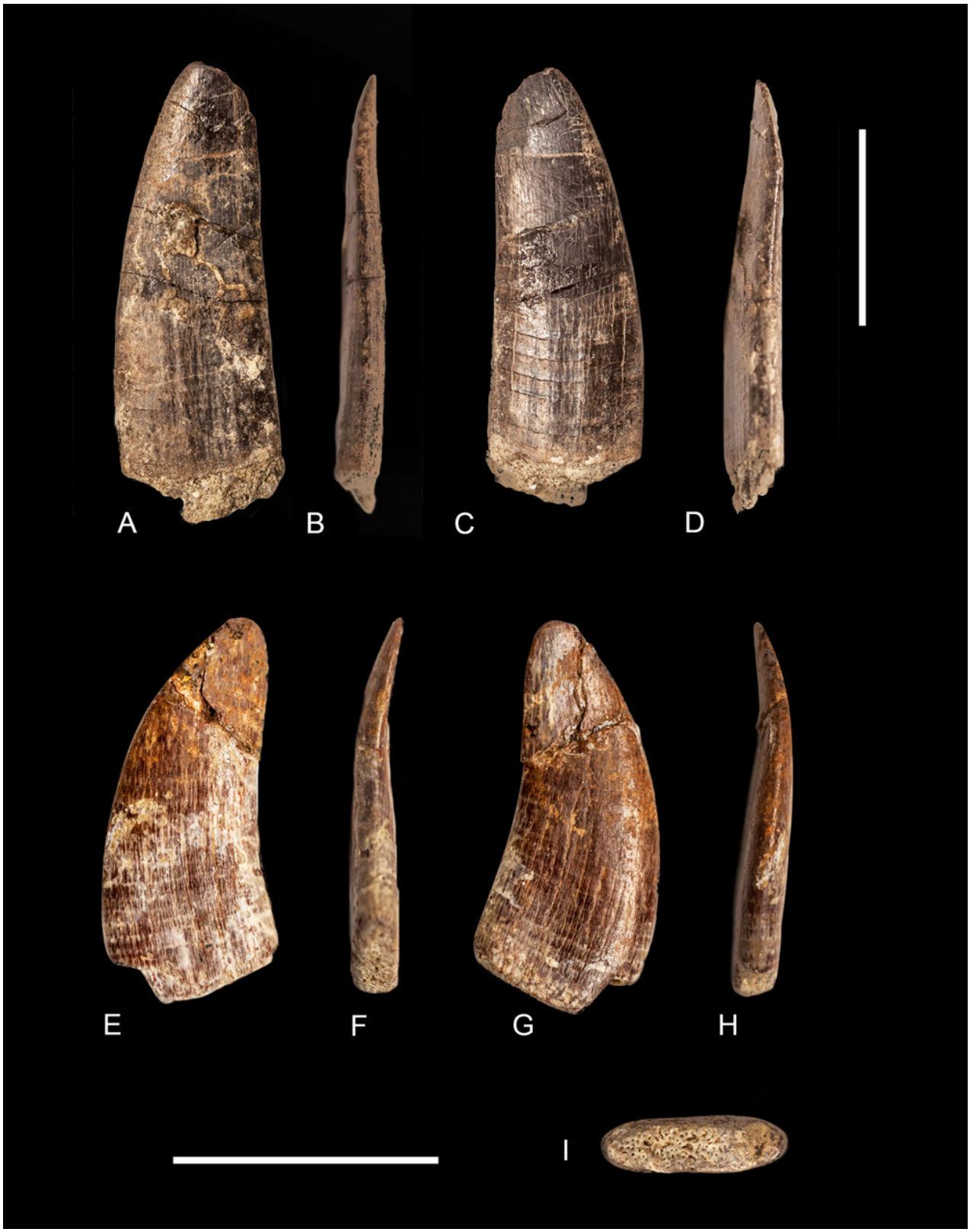

Figure 3: Rostral spines of *Anoxypristys* sp. from (A-D) Leghia [specimen BBUPSM 24019] and (E-I) Piscul Ronei (Turbuța) [specimen BBUPSM 24018]. A, E - dorsal views; B, F - posterior views; C, G - ventral views; D, H - anterior views; I - basal view. Based on their dorsoventral curvature, both spines likely come from the right side of the rostrum. Scale bars = 10 mm.

More recently, the taxon *Mesopristis osonensis* FARRES, 2003, was erected based on a single rostrum that purportedly represents an intermediate morphology between *Pristis* and *Anoxypristis*. However, CAPPETTA (2012) synonymized *Mesopristis* with *Anoxypristis* without providing any supporting justification. A highly apomorphic character of *Mesopristis* is the way in which the rostral spines

attach to the rostrum, with the hollowed spine base articulating on a tongue-like projection of the rostrum, forming an interlocking mechanism of mortise-and-tenon type. This morphological character is not present in the spines from Romania, nor in any other spines known in the literature.

The two extant genera, *Pristis* and *Anoxypristis*, are typically readily distinguishable through the morphology of their rostral spines. *Pristis* is characterized by elongated, pointed spines exhibiting a ventral curvature. In dorsal view, these spines are either straight or display a slight posterior curvature, with the anterior margin generally sharp and the posterior margin concave (Cappetta, 2012, p. 394), though the latter can occasionally be straight or roughly "D-shaped" in cross section. The sharpness is usually restricted to the distal end of the spine. Conversely, *Anoxypristis* is distinguished by strongly dorsoventrally compressed spines possessing either sharp or rounded anterior and posterior cutting edges (Cappetta, 2012, p. 393). It is crucial to acknowledge that heavily worn rostral spines of *Pristis* may be superficially similar to those of *Anoxypristis*. Consequently, making taxonomic assignments beyond the family level (Pristidae indet.) in case of worn or juvenile rostral spines is to be avoided.

In contrast to the relatively straightforward determination of the pristid genera, species-level identifications are challenging based on rostral spine morphology alone. Even with respect to the extant taxa, an accurate species assignment requires a comprehensive approach that integrates morphological observations with statistical morphometric analyses of both the spines and rostrum (see the extensive discussions in Seitz & Hoover, 2017, and Trif & Vonica, 2018). Unfortunately, this multifaceted approach is largely inapplicable to fossil materials.

Within the fossil record, rostral spines are the most commonly reported pristid remains, while rostra are exceedingly rare. While oral teeth are likely more represented than hitherto reported in the fossil record, their morphology remains poorly understood, hindering their reliable identification as belonging to pristids (Cappetta, 1987, 2012; Dica, 2006), though this is beginning to change (Reinecke *et al.*, 2023). Beyond considerations of size, establishing a connection between oral teeth and rostral spines necessitates a comprehensive examination of these structures in extant species before morphological traits can be reliably applied to fossil specimens.

Systematic examination of all the published records of Pristidae reveals that no less than 42 nominal fossil species have been described and included in the family, 27 of which are Eocene, or presumed to be Eocene in age. Most of them are assigned to the genus *Pristis*, including *P. lathami* Galeotti, 1837, *P. hastingsiae* Agassiz, 1841, *P. bisulcatus* Agassiz, 1843, *P. acutidens* Agassiz, 1843, *P agassizi* Gibbes, 1847, *P. contortus* Dixon, 1850, *P. parisiensis* Gervais, 1852, *P. curvidens* Leidy, 1855, *P. amblodon* Cope, 1869, *P. brachyodon* Cope, 1869, *P. bassanii* Zigno, 1882, *P. ingens* Stromer, 1905, *P. fajumensis* Stromer, 1905, *Eopristis reinachi* Stromer, 1905, *Oxypristis ferinus* Böhm, 1926, *P. mucrodens* White, 1926, *P. hamatus* White, 1926, *P. priemi* Leriche, 1933, *P. wateleti* Leriche, 1933, *P. imhoffi* Leriche, 1933, *P. propinquidens* Casier, 1949, *P. praecursor* Casier, 1949, *P. brevis* Casier, 1949, *P. brayi* Casier, 1949, *P. olbrechtsi* Dartevelle & Casier, 1959, *P. pickeringi* Case, 1981. Potentially included in *Pristis* is also *M. osonensis* Farres, 2003.

Based on original species descriptions, a significant proportion of characters purportedly distinguishing these taxa from one another are in fact plesiomorphic within the family Pristidae. Conversely, truly autapomorphic characters diagnostic of *Anoxypristis* are relatively few. Furthermore, many among the aforementioned species lack detailed descriptions or remain entirely undescribed. Several taxa are known only from fragmentary remains such as isolated rostral fragments (*e.g.*, *P. propinquidens*, *P. bisulcatus*) or rostral spines only (*e.g.*, *P. imhoffi*). The widely recognized species *P. lathami*, which is frequently cited for Eocene rostral spines, also exemplifies another problematic, or at least tenuous, taxonomic assignment, as it was originally described for a fragmentary rostrum devoid of articulated rostral spines. Spines were subsequently recovered from calcareous sands proximal to the limestone matrix containing the rostrum, raising concerns regarding their definitive association: "... à côté de ce bloc gisaient, dans le sable calcarifère, deux pointes osseuses sourcent sans doute de ce museau ..." […aside of this block, lying in the calcareous sand, were two bony spikes that undoubtedly originated from this snout…] (Galeotti, 1837, p. 46).

Observations on an extant rostrum of *Pristis* sp. housed in the Zoological Museum of Babeș-Bolyai University, Cluj-Napoca have revealed a significant extent of morphological variability among the rostral spines. While proximal spines (*i.e.*, those closer to the rostrum apex) often lack the characteristic posterior concavity observed in this genus, the remaining spines exhibit considerable variations without discernible patterns or morphological trends. At seemingly random intervals, rostral spines deviate from the typical morphology, losing the posterior concavity and displaying a reduced dorsoventral compression as well as a straight posterior margin, or even a convex edge like that characterizing the anterior face (Fig. 4).

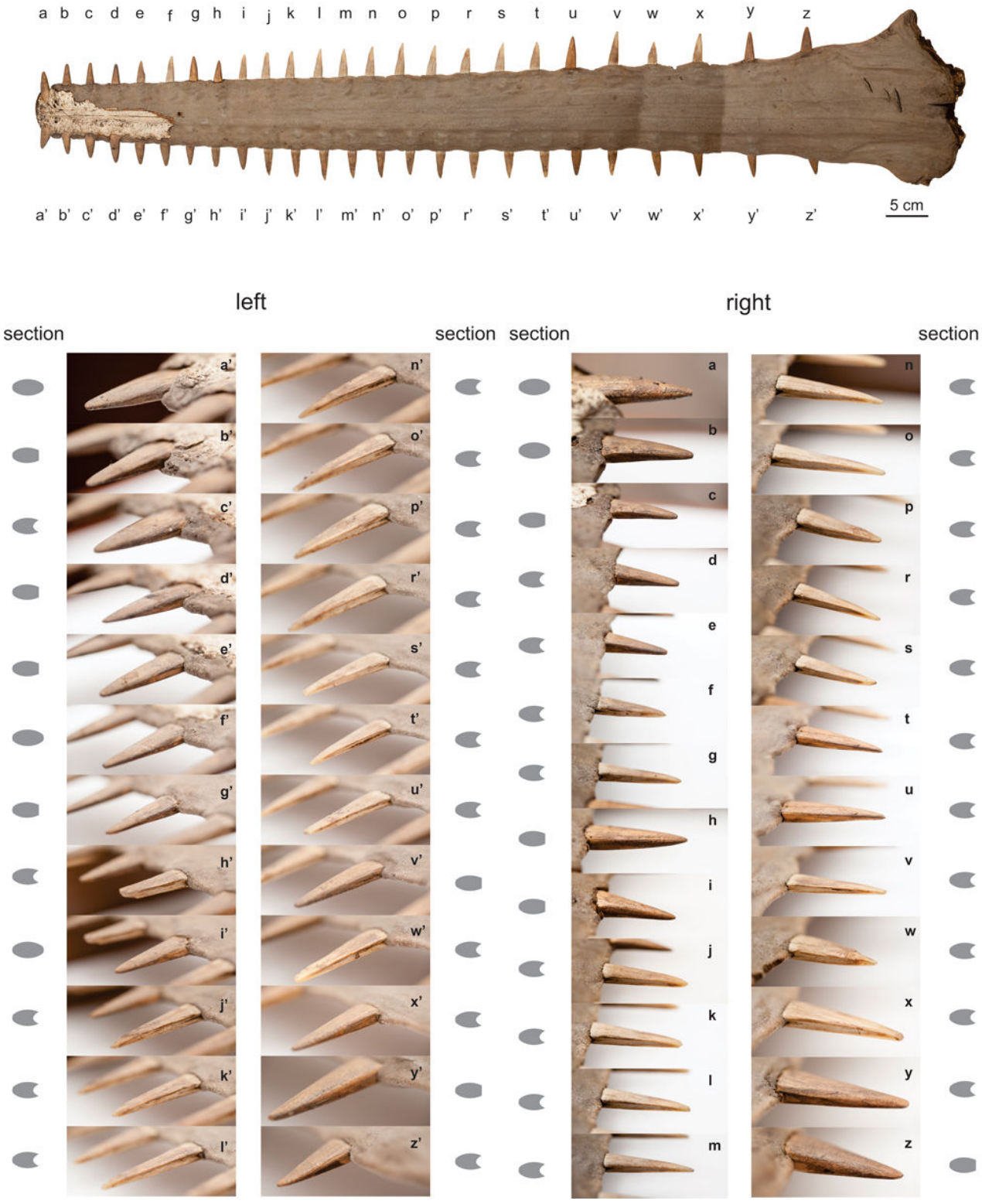

Figure 4: Variability of cross-section profiles in the rostral spines of *Pristis* sp. (specimen from the Zoological Museum of Babeș Bolyai University, Cluj-Napoca - no inventory number). The label only indicates that the specimen originated in the Mediterranean Sea (note that *Pristis* is no longer part of the Mediterranean fauna).

Although the ambiguities in the definition of some of the fossil species of Pristidae were sometimes pointed out as early as in the 19th and early 20th centuries (Dames, 1883, p. 138; Woodward, 1889, p. 73; Stromer, 1905, p. 46), taxonomical identification of pristid fossils to the genus level have only become more widespread recently, especially in the case of finds consisting of isolated rostral spines (Cappeta, 2012; Carrillo-Briceño *et al.*, 2015). In light of these considerations, the morphology of the Romanian spines dealt with herein, in the context of the variability of extant pristid spines, are best assigned to the *Anoxypristis*. These fossils represent the first

record of this taxon from Romania as well as from the whole of southeastern Europe. Fossil *Anoxypristis* spines have previously been reported from the Eocene of Morocco (CAPPETTA, 2012), Belgium (CASIER, 1949), Uzbekistan (CASE *et al.*, 1996), Mexico (GONZÁLEZ-BARBA, 2003), Egypt (ZALMOUT *et al.*, 2012), USA (EBERSOLE *et al.*, 2019, 2025) and Austria (ADNET *et al*., 2021). Included in this list are only those instances where the morphology of the transversal section of the rostral spine could be verified from published photographs or from comprehensive descriptions.

The inferred habitat preferences of the fossil *Anoxypristis* is based on that of the only extant species in the genus, namely, *A. cuspidata* (LATHAM, 1794). *Anoxypristis cuspidata* is a benthopelagic amphidromous fish found in tropical and subtropical, coastal-marine and estuarine waters, with a depth range of 0-40 m. It mainly occurs in inshore coastal waters, estuarine environments and river deltas (PEVERELL, 2005; RADKHAH & EAGDERI, 2019). These observations are consistent with the depositional environment inferred for the Vișstea Limestone and the Racoți Sandstone, the two stratigraphic units from which the specimens in question were recovered.

5. Conclusions

This study contributes to the understanding of the paleobiodiversity of the southeastern European region by documenting the first occurrence of *Anoxypristis* in Romania. The discovery of *Anoxypristis* in the Transylvanian Basin provides valuable insight into the paleoecology of the area, confirming the local occurrence of coastal-marine or estuarine environments during the Priabonian. In addition, the considerable morphological variability of the rostral spines, coupled with the fragmentary and isolated nature of most pristid fossils, present significant challenges in accurately identifying the fossil members of Pristidae at the species-level.

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