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Elopteryx at Nălaţ-Vad: new theropod material described from the Haţeg Basin (Romania)

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Abstract. Being one of the first dinosaurs discovered in Romania, *Elopteryx nopcsai* is a Paravian dinosaur species whose described material is mainly based on proximal femur fragments. All the known remains assigned to this taxon have been collected from the latest Cretaceous (Maastrichtian) deposits of the Haţeg Basin. A similar fragment was collected from the Nălaţ-Vad locality and is herein described. It shares multiple similarities with specimens previously related to *Elopteryx* and fossils related to other taxa, such as Pengornithidae and Oviraptorosauria clades, mentioned herein. The tumultuous history of the systematic classification, its possible synonymy with other taxa, and some aspects regarding the paleoecology of this species are also included in this paper.

Keywords: *Elopteryx*, latest Cretaceous, Haţeg Basin, Romania.

Introduction

At the end of the 19th century, the famous paleontologist Ferenc (Franz) Nopcsa von Felső-Szilvás found a proximal fragment of a femur belonging to a small theropod dinosaur, nearby Sânpetru locality in the Haţeg Basin (Andrews 1913). This fossil, along with a multitude of other Cretaceous vertebrate remains discovered from this basin, have been purchased by the British Museum of Natural History. The British paleontologist Charles William Andrews received some limb bone fragments from Nopcsa, which the latter did not consider to be of "reptilian but rather avian in origin" (Andrews 1913). Andrews (1913) assigned the femur fragment to a new species named *Elopteryx nopcsai*. Since the initial description, more fossil material, especially femur fragments, has been discovered and assigned to this genus (Lambrecht 1929, 1933, Grigorescu & Kessler 1980, Kessler et al. 2005).

A fossil related to this genus has been discovered near the Nălaţ-Vad locality (Smith et al. 2002, 2022) by paleontologists at Babeş-Bolyai University of Cluj-Napoca. It is the proximal fragment of a right femur, which shares many characteristics with the *Elopteryx nopcsai* holotype.

Geological Setting and Ages

The morphology of the actual Haţeg Depression means nothing more than the legacy of a sedimentary basin that occurred at the end of the Cretaceous, today positioned between the Southern and Western Carpathians. These mountains are, in turn, the result of the Alpine evolution caused by compressive inter-plate interchanges between the European and African plates and the related microplates (Săndulescu 1984, 1994, Balintoni et al. 2014). Both specified Carpathian units were structured because of extensive shifts - e.g., Getic Nappe, Severin Nappe, Supra-Getic thrusted System - that occurred at the end of the Cretaceous in the 'Laramide' tectonic pulse (Săndulescu 1984, Csontos & Vörös 2004).

The sedimentary Haţeg Basin is a syn-orogenic basin that acted as a piggy-back basin in the latest Albian and early Campanian time span, later becoming a subsiding basin (Willingshofer et al. 2001). Volcanic inputs are recorded there, particularly in the northwestern area, where the sedimentary fill overlaps the metamorphic rocks of the Poiana Ruscă Mountains (Grellet-Tinner et al. 2012, Vornicu et al. 2023).

A tectonic evolution such as the one mentioned above caused the sedimentary fill of the basin to provide a transition from deep-sea sedimentary environments with flysch deposits, which subsequently became marine-littoral (Strei Formation), and then typically terrestrial with environments related to a fluvial plain (Melinte-Dobrinescu 2010), an evolution similar in some respects to that known from the SW or NW sides of the Transylvanian basin (Codrea & Dica 2005, Codrea & Godefroit 2008).

In the S-SE sides of the basin, the latest Cretaceous is represented by the Sânpetru Formation (Maastrichtian), formed by silty, grayish-green mudstone clays with red interbeds and numerous channel fills with lithoclasts of various origins (Therrien et al. 2002, Therrien 2005, Van Itterbeeck et al. 2004, Codrea & Solomon 2012, Solomon & Codrea 2015). The type section is located in the Sibişel Valley, but the same formation is exposed in outcrops along the Râul Mare riverbed at Toteşti (Codrea et al. 2002) and Nălaţ-Vad (Smith et al. 2002, see Fig. 1), as the discoverers of these sites (Vlad Codrea, Cristina Fărcaş, Paul Dica from Babeş-Bolyai University Cluj-Napoca) reported since the first published data (Codrea et al. 2002, Smith et al. 2002). This section continues also in the Unciuc area, but the arguments for a Cretaceous age of these deposits lack clear paleontological evidence. However, based on paleomagnetism, Panaiotu et al. (2011) related these sedimentary rocks to the uppermost part of the Chron C30n, i.e., near the K/T boundary. Subsequently, the possibility of belonging to another formation was expressed by Panaiotu et al. (2011), and Popescu et al. (2011), but no clear arguments could be put forward, except for some inputs of volcanogenic rocks reported inside the sedimentary succession of these localities. Some researchers, particularly paleontologists, have attempted to relate this succession to a distinct unit, striving to separate a stratigraphic entity that they called 'Râul Mare beds' (Brusatte et al. 2017), in which they included the entire succession between Nălaţ-Vad and Unciuc. The geological age of the Unciuc locality has the already mentioned blurriness. Such an approach probably arose because of the mention of a NE-SW trended fault that would be positioned between the Râul Mare and Sibişel Valley and another one in the same direction, a right strike-slip one north of Râul Mare. In this manner, a distinct block could be outlined (Bârzoi & Şeclăman 2010). However, the allocation to a formation or another of its Maastrichtian deposits remains an open question. We consider that the Sânpetru Formation is in question and not the Densuş-Ciula Formation. The geological age of the Nălaţ-Vad locality (Fig. 1) is considered Early Maastrichtian (Panaiotu & Panaiotu 2010), the oldest in the Râul Mare section.

The sedimentary sequences at the two localities from Râul Mare were studied and described in detail relatively soon after their discovery by Codrea et al. (2002), Smith et al. (2002), and Van Itterbeeck et al. (2004). At Nălaţ-Vad (Fig. 1), the fine overbank deposits refer in dominance to silt and clays. They are interbedded with layers of whitish calcretes. As pointed out by the mentioned geologists, they are the result of paleo groundwater levels, controlled by seasonality, in a subtropical climate.

Besides its spore-pollen association (Van Itterbeeck et al. 2005), the fossils collected from this locality (Fig. 1) are mainly composed of vertebrates: fishes, amphibians and small reptiles, turtles, crocodiles, dinosaurs (theropods, ornithopods, sauropods), pterosaurs, birds, mammals (e.g., Smith et al. 2002, 2022, Weishampel et al. 2010, Csiki-Sava et al. 2015, Venczel et al. 2016, Brusatte et al. 2017, Pérez-García & Codrea 2018, Mayr et al. 2020a,b, Martín-Jimenez et al. 2021, Mocho et al. 2023).

It is interesting to discuss the point that the reduced size of some of the dinosaurs, a dwarfing tendency, has led to interpretations related to the existence of an island realm in the eastern Tethys Ocean, known in references as the 'Haţeg Island' (e.g., Benton et al. 2010, Csiki-Sava et al. 2015). Of course, such interpolations base their reasoning on similar island models of more recent times (Van der Geer et al. 2011). However, such a restricted paleoenvironment to such an extent has nevertheless been questioned by some researchers (Krause et al. 2020), and the island model is perhaps oversimplifying.

Material and methods

One fragmentary proximal right femur (BBU-PSM V1009) is available for study. The fossil is curated in the Paleontology-Stratigraphy Museum of the Babeş-Bolyai University of Cluj-Napoca, Romania. This bone was found inside a concretion. It was prepared in the Paleotheriology and Quaternary Geology Laboratory of the Babeş-Bolyai University using an air-scriber and was cleaned by simple washing, using a soft brush and water. The bone was strengthened with Paraloid B-72 diluted in acetone (resulting in a solution of 5% concentration). The terminology follows Cau et al. (2015) and Mayr et al. (2020a).

The photographs were captured with a digital camera, a Sony Cyber-Shot DSC-RX100, on a professional tripod and processed using Adobe Photoshop CC 2017.

Institutional abbreviations: BBU-PSM V– Paleontology-Stratigraphy Museum, Babeş-Bolyai University of Cluj-Napoca, Romania, Vertebrate collection; EME – Transylvanian Museum Society (Erdélyi Múzeum Egyesület), Cluj-Napoca, Romania; GMNH – Georgia Museum of Natural History, United States; IVPP – Institute of Vertebrate Paleontology and Paleoanthropology Beijing, China; MDE – Musée des Dinosaures, Espéraza, France; UBB V - Paleontology-Stratigraphy Museum, Babeş-Bolyai University of Cluj-Napoca, Romania, Vertebrate collection; ZCDM – Zhucheng Dinosaur Museum, Zhucheng, China.

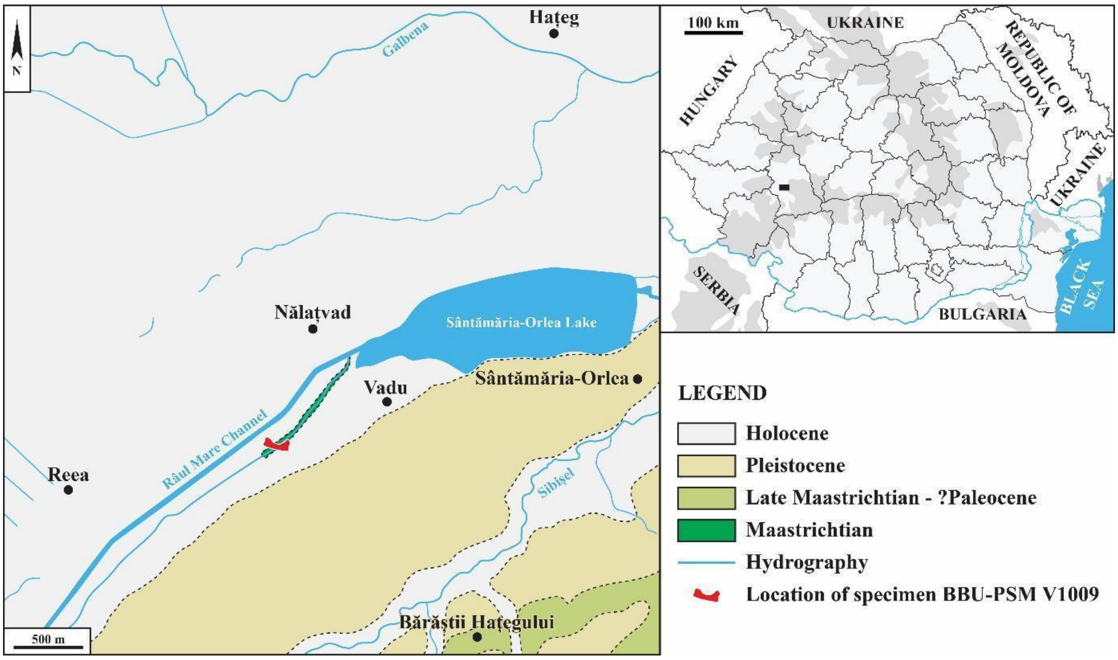

Figure 1. Geological map of the southwestern region of the Haţeg locality and its location in Romania (modified after Lupu et al. 2018).

Results

Systematic paleontology

Dinosauria Owen, 1842
Saurischia Seeley, 1888
Theropoda Marsh, 1881
    Maniraptora Gauthier, 1986
    Paraves Sereno, 1997
    Avialae Gauthier, 1986
        Elopteryx Andrews, 1913
        Elopteryx nopcsai Andrews, 1913

Comparative Description

BBU-PSM V1009 is not as well preserved as the holotype (Fig. 2). The great trochanter is fragmentary (Fig. 2. A, D), and the circular fossa present on the femoral head of the holotype (Andrews 1913) is razed, as a consequence of its taphonomy and post-taphonomy events (Fig. 2. C, F). In both BBU-PSM V1009 and the holotype, the femoral head is well-developed and stands higher than the great trochanter (Fig. 2. A, D). In the proximal view, both specimens share a great trochanter of a slightly triangular outline, the anterior angle being the most acute (Fig. 2. B, E). The posterior angle is defined by the insertion of the obturator muscles (Andrews, 1913), taking the shape of a circular fossa in both the holotype and the new specimen (Fig. 2. B, C, E, F). In the medial view, a concave surface is present under the great trochanter and bears a small crest on the posterior side, indicating the emergence of the *linea aspera,* a feature present in both specimens (Figs. 2. C, F, 3. B). In UBB-PSM V1009, a second crest, which is slightly more prominent, is present on the very bottom of the medial surface, but it is likely to represent an artifact of preservation (Fig. 3. B). Ultimately, this fossil shares the general outline of the holotype, possessing diagnostic features described in Andrews (1913), enough to relate it to the *Elopteryx nopcsai* species. Furthermore, in cross-section, the reduction of the medullary cavity and the thickening of the cortical bone is obvious (Fig. 3. F). A thin, intermediate layer, marked by small holes surrounding the medullary cavity, is present, which could be indicative of the vascular canals of the medullary bone (Fig. 3. F). On the cranial portion, this intermediate layer has been completely replaced by a thickened cortical bone. The medullary cavity consists of two hemispheres that vary greatly in size and definition (Fig. 3. F). A similar configuration of the medullary cavity is also found in Pengornithidae (the cross-section of the femur IVPP-V15576 in O'Connor et al. 2018). In this specimen, the medullary cavity, whose hemispheres are similar in size and shape, is wider in proportion to the rest of the bone. It is also worth noting that the cortical bone in IVPP-V15576 is proportionally thinner than in BBU-PSM V1009. Acknowledging the fact that the bones of flightless birds generally possess thicker, more reinforced walls and less developed medullary cavities than those of flighted birds (Currey & Alexander 1985, Habib & Ruff 2008) and that Pengornithids were adapted for flight, the atrophied state of the medullary cavity and reinforcement of the cortical bone in *E. nopcsai* suggests that it was a secondarily flightless taxon while adapting to an exclusively terrestrial lifestyle.

Throughout the evolution of non-avian theropods, stability during locomotion was mainly maintained by a long, counter-balancing tail (Pittman et al. 2013). In the absence of a counter-balancing tail, avialans, especially the members of the Pygostylia clade, possess a very pronounced great trochanter, which serves as an attachment point for powerful iliotrocantericus muscles, which keep the femur sloped in a cranial position and bring the birds center of gravity forward, thus aiding in maintaining the balance of the organism (Gatesy 1999, Clifton et al. 2017). Pygostylians also have a very underdeveloped femoral head, breaking the trend seen in non-avian theropods, which have a very pronounced femoral head (Egawa et al. 2022) that stands taller than a poorly developed or absent great trochanter since these animals mostly relied on their tails for stability. Having a great trochanter, which is relatively comparable in height to the femoral head, the configuration seen in *Elopteryx* stands between what is seen in pygostylians and most non-avian theropods. A similar configuration to that seen in *Elopteryx* is also found in the Oviraptorosauria clade. Members of this clade, such as *Anomalipes zhaoi* (ZCDM V0020, Yu et al. 2018) and *Nankangia* sp. (GMNH F1000, Lü et al. 2013), have a very pronounced great trochanter, which is comparable to the femoral head in height (standing slightly taller). In proximal view, however, the great trochanter in Oviraptorosauria (*Anomalipes zhaoi* specimen ZCDM V0020, Yu et al. 2018) does not expose the same triangular outline as in *Elopteryx*, the posterior angle being especially underdeveloped, which indicates the likelihood of these similarities being convergent traits. Acknowledging the fact that oviraptorosaurs were also known for having unusually short tails, an intermediary between pygostylians and other non-avian theropods (Persons et al. 2013), this hints at a possibility that *Elopteryx* had a tail of similar length as oviraptorosaurs, an assumption which can only be confirmed following the discovery of more complete fossil material.

History and Classification of *Elopteryx*

Andrews (1913) erected the new genus *Elopteryx*, based on a femur fragment and a tibiotarsus fragment discovered near the Sânpetru locality. These fragments have been initially compared by Andrews to the bones of Pelecaniformes. Showing very few similarities with the specified bones, Andrews suggests that *Elopteryx* had a more terrestrial lifestyle, and, despite these discrepancies, the British paleontologist still classified *Elopteryx* in the Pelecaniformes clade. The initial interpretation of *Elopteryx* as a terrestrial Pelecaniform remained undisputed until the discovery of a better-preserved femur fragment (Lambrecht 1933) that sported multiple similarities with paravian theropods (Csiki & Grigorescu 1998). In more recent papers, the systematics of *Elopteryx* has become more unclear. Osmólska & Barsbold (1990) placed *Elopteryx*, alongside multiple other Romanian genera known from fragmentary remains (i.e., *Heptasteornis* and *Bradycneme*), in the Troodontidae clade. This classification, however, has received some criticism in other following papers. The genus *Heptasteornis* is placed within the Alvarezsauridae clade (Naish & Dyke 2004), the genus *Bradycneme* is taken out of use (being considered a junior synonym of *Elopteryx*), and the phylogenetic position of the

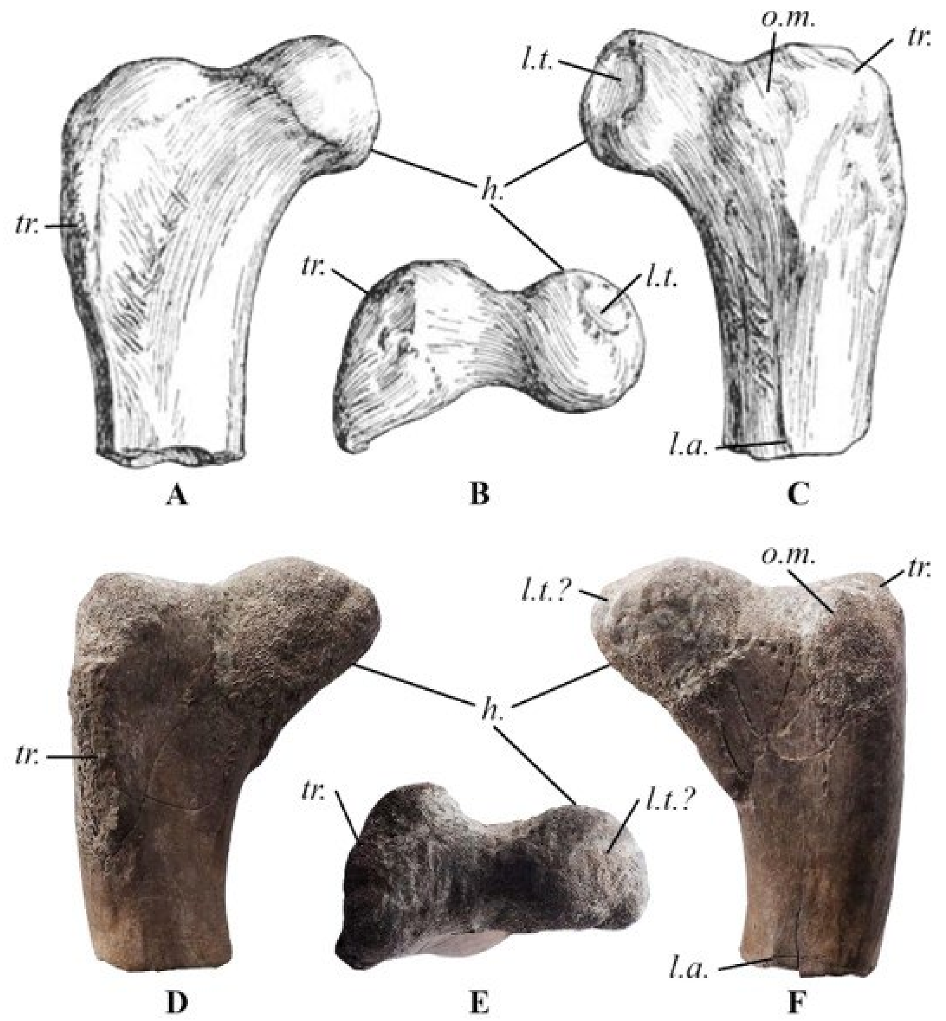

Figure 2. Comparison between the specimen described by Andrews (1913) (A, B, C; flipped illustrations) and specimen BBU-PSM V1009 (D, E, F). tr.- great trochanter, l.t.- ligamentum teres insertion hole, l.a.- linea aspera, o.m.- attachment point for the obturator muscles, h.- femoral head.

genus *Elopteryx* becomes a great subject of debate. Kessler et al. (2005) redescribed the fossil material attributed to *Elopteryx* and spotted some features seen in characteristics of Alvarezsauridae, but no conclusion is taken due to the fragmentary nature of the remains.

Csiki et al. (2010) have published a thorough description of one relatively well-preserved specimen collected near the Sebeş-Glod locality from Early Maastrichtian aged rocks, introducing the new taxon name *Balaur bondoc*. The thoracic and caudal vertebrae, one shoulder girdle, one pelvis, and multiple leg bones (paradoxically, both femurs - left and right - are missing) have been discovered. By far, the most striking feature of this animal are the very large first and second toe on each foot, adorned with hypertrophied, hook-like talons, the main reason *Balaur bondoc* was initially classified as a dromaeosaurid. In a more recent paper by Cau et al. (2015), multiple features uncharacteristic of the Dromaeosauridae, such as the atrophied third finger, the fused metatarsus, and scapulocoracoid and the co-ossification of the pelvic bones, were identified in *Balaur*. These features are very unusual for most theropods but prove to be common in Avialae, especially in the basal members. Thus, *Balaur bondoc* is reclassified as a basal member of Avialae, being placed outside of Pygostylia. Under this new interpretation, even the distinct foot morphology makes more sense, as the hypertrophied first toe is characteristic of Avialae. More features identified by Cau et al. (2015), such as the atrophic condition of the hand articulation, a very wide and spacious pelvic canal, and a robust metatarsus, clash with the initial image of *Balaur* as an active predator, as these features are only found in herbivorous animals. Apart from being used in restraining their prey (Fowler et al. 2011), it is likely that the hypertrophied recurved talons characteristic of dromaeosaurids would also aid these animals in climbing (Manning et al. 2006), which is why Cau et al. (2015) suggested that the unusual foot morphology characteristic of *Balaur bondoc,* especially its very dromaeosaur-like sickle claws, were likely an adaptation to a partially arboreal lifestyle, assisting the relatively robust animal while climbing. It is also worth mentioning that Cau et al. (2015) point out that

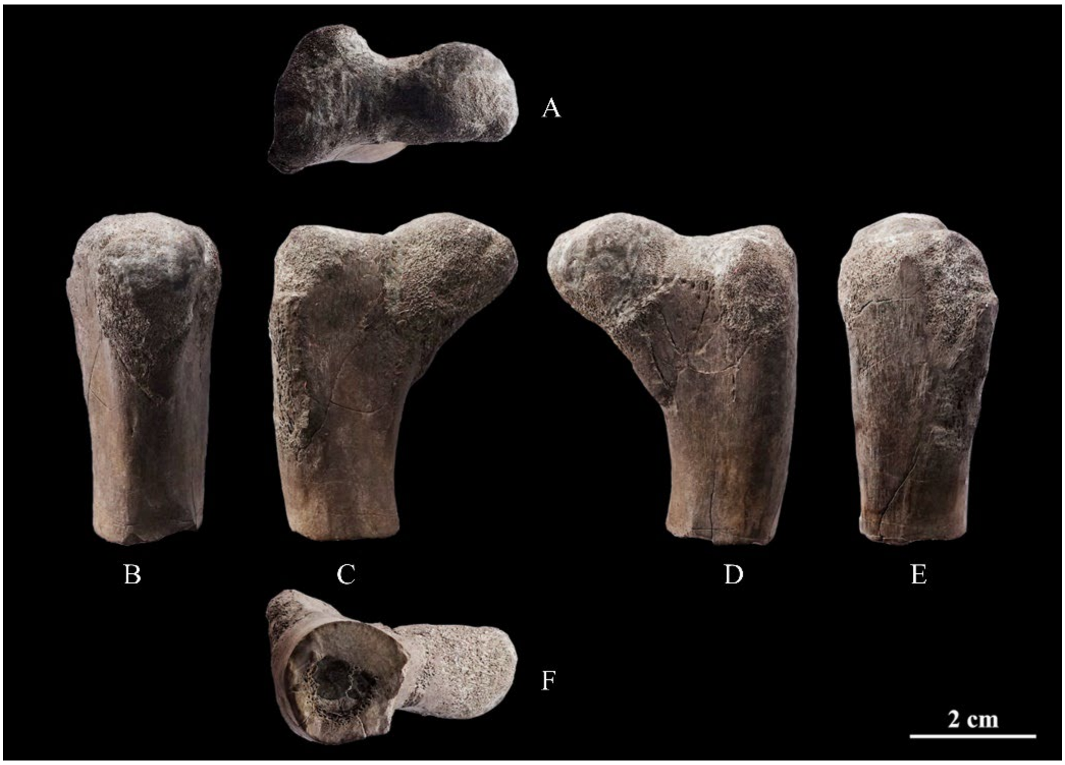

Figure 3. Specimen BBU-PSM V1009 in: A - proximal, B - medial, C - anterior, D - posterior, E - lateral, and F – distal views.

the articular joints of the hallux would have made this digit highly mobile, an adaptation that could have further aided *Balaur* in climbing and perhaps a rudimentary form of perching.

Buffetaut & Le Loeuff (1998) reported a large pelvic bone and a proximal femur fragment from some Maastrichtian rocks of southern France and coined a new genus, *Gargantuavis*. The pelvis has a very pronounced antitrochanter, and the acetabulum is placed next to the fourth sacral vertebra. Moreover, the pelvis is notably wide and unlike what is seen in semi-aquatic flightless Mesozoic birds such as *Hesperornis*, which suggests *Gargantuavis* had a terrestrial lifestyle. The proximal femur fragment, which is poorly preserved, has a rounded trochanteric crest, similar to what is seen in modern Palaeognathae (Buffetaut & Le Loeuff 1998). The clear absence of the fourth trochanter from the femur, precisely the attachment of the caudofemoralis muscles, suggests this animal lacked a bony tail, the main reason for its initial placement within the Pygostylia clade. Following these observations, Buffetaut & Le Loeuff (1998) suggest that *Gargantuavis* is likely the largest Mesozoic avialan for which we have concrete fossil evidence. The subsequent unearthing of a second, more well-preserved femur (Buffetaut et al. 2019) only backs the initial classification of *Gargantuavis* as a Pygostylian.

Mayr et al. (2020a) have described a pelvis bone from Nălaţ-Vad locality. The specimen, UBB-V649, bears many similarities with the pelvis reported from southern France. The small discrepancies between the two bones, such as the smaller size of UBB-V649 and its placement of the acetabulum next to the fifth sacral vertebra, can be explained by the fact that these two specimens were discovered in relatively distant geological formations and from rocks of different ages. An intriguing aspect covered in Mayr et al. (2020a) is the fact the femur fragments that were attributed to *Elopteryx* fit very nicely in the UBB-V649 acetabulum, suggesting the Nălaţ-Vad pelvis could also belong to this genus. Mayr et al. (2020a) also point out that the femur fragments discovered in southern France were erroneously attributed to the genus *Gargantuavis* due to the isolated and unarticulated nature of the fragments.

Initially, mostly due to the lack of corresponding material, the synonymy between *Elopteryx* and *Balaur* was revoked (Brusatte et al. 2013). However, Mayr et al. (2020a) highlight multiple similarities between UBB-V649 and the pelvis attributed to the genus *Balaur* (specimen EME.VP313), such as the pronounced antitrochanter and the same number of sacral vertebrae. Although the discovery of UBB-V649 did not end this debate, it is undoubtedly a crucial piece of evidence that highlights the very possible synonymy between *Elopteryx*, *Balaur* and this fossil, but a conclusion could be based only on more better-preserved fossils.

Discussion

The analysis of the *Elopteryx nopcsai* specimen BBU-PSM V1009 and the pointed-out similarities between it and other fossil material add to what little is currently known of this problematic taxon. The comparisons strongly indicate that the owner of this bone was a secondarily flightless bird that lacked a pygostyle, sporting instead a bony tail in life. This interpretation of BBU-PSM V1009 aligns smoothly with the osteological conditions described in *Balaur bondoc* specimen EME PV.313 in Cau et al. (2015) and thus supports the possible synonymy between *Balaur* and *Elopteryx* suggested by Mayr et al. (2020a). While not being its focus, this analysis also indicates a correlation between the size and height of the great trochanter (in comparison to the femoral head) and the tail length in theropod dinosaurs, thus providing more insight into reconstructing taxa known from more fragmentary and incomplete remains, and so will have to be looked further into in future publications.

If the fossil remains initially attributed to *Elopteryx nopcsai* and *Balaur bondoc* would prove to be representative of a single taxon, as Mayr et al. (2020a) suggested, we could be addressing an animal with a very peculiar lifestyle. The fused scapulocoracoid in EME PV.313 and the thickened layer of cortical bone found in BBU-PSM V1009 strongly indicate that the animal in question was secondarily flightless. Moreover, the bizarre foot morphology that is present in EME PV.313, believed to be a climbing adaptation (Manning et al. 2006, Cau et al. 2015), makes it tempting to hypothesize that as some of the Cretaceous avialans were losing their ability to fly, whether it was before or after these animals became isolated on the so-called 'Haţeg Island', they retained their adaptations for an arboreal lifestyle, only making them more suited for sustaining a larger, more robust climber. It is also worth noting that in early flighted birds, long bony tails were selected against in favor of shorter ones, a trait more efficient in providing lift, braking, and turning while flying (Rashid et al. 2014). The presence of a long bony tail in the ancestors of *Elopteryx* would have decreased their flight efficiency, which likely predisposed the population to lose this ability under the constraints of an external factor such as an isolated environment.

The similarities between UBB-V649, the pelvic material of EME PV.313 and the *Gargantuavis philoinos* holotype MDE C3-525, initially assessed in Mayr et al. (2020a) suggest a more recent common ancestry between *Gargantuavis* and *Elopteryx* than previously assumed, which may hint at the possibility that the Romanian taxon is a member of Gargantuaviidae. This interpretation clashes, however, with the initial belief presented in Buffetaut et al. (2019) that *Gargantuavis*, and thus Gargantuaviidae as a whole, were a family inside Pygostylia, therefore a more basal position within Avialae will have to be reassessed for this grouping if that is found out to be the case in future papers. Unluckily, these taxa are known from very incomplete and fragmentary remains, which makes for a very limited analysis that can fortunately be added upon with future discoveries of more complete fossil material.

Conclusions

Documented especially on proximal femur fragments, *Elopteryx* is a latest Cretaceous paravian dinosaur from 'Haţeg Island.' The femur fragment discovered in Nălaţ-Vad bears many similarities with the *Elopteryx nopcsai* holotype discovered at the end of the 19th century by Nopcsa and later described by Andrews (1913). Although this more recently found proximal femur fragment morphologically and anatomically fits in with the recently described UBB-V649 pelvis discovered from the same locality, more clarification will have to be conducted in the future for the systematic classification of this specimen. An ample systematic revision is necessary in the future, and if UBB-V649 and *Balaur bondoc* prove to be junior synonyms of *Elopteryx*, the priority of the name will have to be taken into account.

For instance, due to the fragmentary state of the fossils attributed to *Elopteryx*, interpretations of its physiognomy, paleoecology, and systematic position are difficult. The finding of better-preserved specimens is the single way to close the debates.

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