ELOPTERYX REVISITED - A NEW BIRD-LIKE SPECIMEN FROM THE MAASTRICHTIAN OF THE HAŢEG BASIN (ROMANIA)

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Abstract – Putative bird remains were reported relatively early from the Maastrichtian continental beds of the Haţeg Basin. They were referred to as Elopteryx nopcsai Andrews, 1913 based on material collected by Nopcsa (femora, tibiotarsi), diagnosed as a large-size cormorant-like bird. Subsequently, the tibiotarsi were redescribed as belonging to two new taxa of large pelicans (Bradyornis draculai, Heptasteornis andrewsi).

More recently, several authors have contested the avian affinities of these remains, considering them as belonging to small non-avian theropods. The discovery of new bird-like remains is therefore remarkable, since they might potentially establish the presence of birds in the Haţeg ecosytem.

A distal right femur from the La Scoabă locality, Ţinpetru, is reminiscent in size and features of the femora described initially by Andrews, showing some resemblances to steganopod femora and corresponding in size to large Recent pelicans. However, several osteological details differentiate the specimen from other fossil and Recent steganopodes, suggesting that it does not, in fact, belong to a bird.

Several non-avian theropods have a distal femur reminiscent of the Ţinpetru specimen, showing an ectocoronydal crest and lacking a craniomedial crest. Among these, alvarezsaurids most closely resemble the La Scoabă femur. The new specimen is thus considered to belong to an alvarezsaurid, not to a steganopod bird; it represents the second indication of the presence of this peculiar late Cretaceous theropod clade in the Haţeg Basin.

Keywords – Haţeg Basin, Maastrichtian, Elopteryx nopcsai, Theropoda, Alvarezsauridae

INTRODUCTION

The Maastrichtian continental deposits of the Haţeg Basin (Fig. 1) contain a rich assemblage of vertebrates, representing all major groups from fishes to mammals (see Grigorescu & Csiki, 2002, for a recent review of the fauna).

Bird remains are extremely rare within this fauna. It is only recently that (as yet unsubstantiated) reports on the presence of enantiornithine birds appeared in the media (V. Codrea, press release, 2003). Possible bird remains were also discovered in the Fântânele microvertebrate fossil site (see Grigorescu et al., 1999) during the 2004 field campaign; these remains are still under study, and will not be discussed here.

However, a putative bird was among the first taxa described from the Haţeg Basin, given that Andrews (1913) erected the taxon Elopteryx nopcsai, based on two proximal femora. He also tentatively referred to this taxon a distal tibiotarsus, mostly because of its avian-like morphology and roughened surface texture which resembles that of the femora. (All the material was returned it to Bucharest, where the specimen was deposited in the collections of the Laboratory of Paleontology of the University of Bucharest (FGGUB R.1957). Due to its general avian-like morphology, FGGUB R.1957 might suggest the presence of steganopodes in the Haţeg Basin. It also invites comparisons with

Recently, an isolated distal right femur was discovered at Sînpetru as a loose element by one of the participants (Dulai Alfréd) on the fieldtrip of the Hungarian Paleontological Society annual meeting that took place in May 2005 at Haţeg. It was offered for study to the first author, who returned it to Bucharest, where the specimen was deposited in the collections of the Laboratory of Paleontology of the University of Bucharest (FGGUB R.1957). Due to its general avian-like morphology, FGGUB R.1957 might suggest the presence of steganopodes in the Maastrichtian of the Haţeg Basin. It also invites comparisons with Elopteryx and their possible relationships will be addressed in the present contribution. Moreover, the probable taxonomic affinities of the new specimen are also discussed.

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Institutional abbreviations: BMNH A PAL. – The Natural History Museum, London, Palaeontology Department Collections; FGGUB – Laboratory of Paleontology, Faculty of Geology and Geophysics, University of Bucharest; MAFI – Hungarian Geological Survey, Budapest

GEOLOGICAL SETTING

The Hațeg Basin is a small inter-montane basin situated in west-central Romania, in the Southern Carpathians (Fig. 1). It has a thick, but unevenly distributed, Permian to Quaternary sedimentary cover within which several sequences can be separated, bounded by regional unconformities (e.g. Grigorescu et al., 1990).

The exclusively continental, siliciclastic uppermost Cretaceous (Maastrichtian) – Lower Paleogene sequence, yielding a diverse vertebrate assemblage, is restricted to the central and western part of the basin. It was divided into two time-correlative lithostratigraphic units, the Sînpetru and Densuș-Ciula formations, differing mainly in the presence of volcanoclastic material in the latter (Grigorescu, 1992). Both represent an extensive episode of molasse deposition related to the uplift of the Southern Carpathians following the intra-Senonian (“Laramian”) orogenetic phase (e.g. main nappe formation and stacking during the uplift of the Southern Carpathians following the latter (Grigorescu, 1992). Both represent an extensive episode of molasse deposition related to the uplift of the Southern Carpathians following the intra-Senonian (“Laramian”) orogenetic phase (e.g. Willinghoffer, 2000).

The type section of the Sînpetru Formation, outcropping along the Sibișel valley, consists of a succession of mudstones with intercalated sandstone and conglomerate beds, reddish-brown coloured in the base, but dominantly dark grey in the top of the section. Sedimentological studies (Bojar et al., 2005, Therrien et al., 2002) suggest the deposits were laid down in a braided fluvial setting and represent floodplain and channel deposits, respectively. Up-section, an increase in transport energy, probably related to tectonic reactivation of the hinterland, as well as palaeoclimatic changes (to a more humid and colder climate) can be documented (Grigorescu, 1992; Therrien, 2004; Bojar et al., 2005). Magnetostratigraphic studies suggest that deposition of the Sînpetru section began in the latest part of Chron 32n and continued into Chron 31r (Early Maastrichtian) as Elopteryx nopcsai from this area. Unfortunately, no locality data, other than Sînpetru, is available for any of these specimens.

SYSTEMATICS

Theropoda Marsh, 1881
Tetanurae Gauthier, 1986
Avetheropoda Paul, 1988
Coelurosauria Huene, 1914
Maniraptoriformes Holtz, 1996
Maniraptora Gauthier, 1986
?Alvarezsauridae Bonaparte, 1991
Elopteryx Andrews, 1913
Elopteryx nopcsai Andrews, 1913

Holotype: BMNH A PAL.1234, proximal left femur

DESCRIPTION

FGGUB R.1957 represents the distalmost part of a small right femur (Fig. 2; see Table 1 for measurements) preserving the distal articular end, with incomplete condyles, as well as the distal part of the shaft. The surface of the bone is shiny, well-preserved and almost pristine, although the distal end is slightly eroded, exposing the porous inner structure of the condyles.

The distal part of the shaft is slightly triangular in cross-section. The cranial face is largely convex; the lateral face is flat, bordered caudally by a sharp ridge. The medial face is narrower, oblique medio-caudally with an angular caudo-medial edge; caudally, the shaft is broken, but was apparently flat. The cranial face of the shaft is smooth, while the lateral, medial and apparently the caudal faces are rugose, covered by a network of proximo-distally extending low, but distinct, anastomozed wrinkles. There is no mediodistal crest on the cranial face of the distal part.

The cross-section of the shaft reveals a thin layer of compacta (about 2 mm thick), surrounding...
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A large central cavity, suggesting the bone walls were thin.

The distal articular end is latero-medially expanded and relatively complex. The cranial face is largely rounded transversely. A slight concavity (representing probably a poorly defined cranial intercondylar groove) is developed only in the distalmost part, being bordered laterally and medially by low, robust protuberances raising from the edges of the corresponding condyles. In cranial view, these protuberances are also respectively laterally and medially bulging, giving the distal end an expanded outline.

Distally, the condyles are separated by a well-marked, deep and wide distal intercondylar groove; in its cranial part it is not continuous with the cranial intercondylar (extensor) groove, being separated from it by a low transverse ridge.

The caudal face is marked by a deep, triangular depression (the popliteal fossa), bounded by sharp ridges, the medial one being more angular. Distally, these are confluent with the distal margins of the medial condyle and ectocondylar ridge, respectively, while proximally they taper into the shaft and converge, almost meeting each other, toward the midline. From the caudal margin of the medial condyle, another angular crest arises and continues proximally on the caudo-medial edge of the shaft.

In the distal part, the popliteal fossa is closed by a transverse bridge formed by lateral and medial extensions of the medial and lateral condyles: we term this structure the infrapopliteal bridge. Whether this bridge was complete or not cannot be established, as the middle part is broken, but it appears to have originally been complete. At the base of the medial ridge bounding the popliteal fossa, a foramen pierces the infrapopliteal bridge, the canal apparently exiting on the lateral wall of the distal articular surface of the medial condyle.

As mentioned above, the condyles are eroded and incomplete; the lateral one seems to be better preserved. However, the transversely rounded medial condyle was originally apparently somewhat larger, with a roughly rectangular outline in distal view (the medio-distal corner is broken, giving it a false triangular shape). On the medial face of this condyle, a deep circular pit is present.

The lateral condyle projects more distally than the medial one; in cranial view, it is mediolaterally narrow and distally pointed. It shows a tripartite morphology. On the caudal face, a narrow, triangular ectocondylar tuber is developed (a precursor of, and corresponding to the crista tibiofibularis of birds, cf. Perle et al., 1994). It is separated from the lateral edge of the distal end by a shallow, rounded groove, the tibiofibular groove (sulcus tibiofibularis). Lateral to the sulcus tibiofibularis, the base of a prominence is preserved, corresponding to the external prominence of the lateral condyle described in Mononykus (Perle et al., 1994); cranio-distal to this, there is a circular pit on the lateral face of the distal end, also present in Mononykus (Chiappe et al., 1994: fig. 16E). The external prominence is relatively long proximo-distally. The distal articular face of the lateral condyle is complex. Caudally, the narrow crest of the ectocondylar tuber is confluent with the distal, articular part of the external prominence, while in the cranial part the articular surface is less distally extended, separated from the caudal part by a distinct step.

Table 1.

<table>
<thead>
<tr>
<th>Measurements of FGGUB R.1857</th>
<th>mm</th>
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<tr>
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</tr>
<tr>
<td>Estimated length</td>
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<tr>
<td>Width of lateral condyle</td>
<td>15.11</td>
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<tr>
<td>Breadth of lateral condyle</td>
<td>22.35</td>
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COMPARISONS AND DISCUSSIONS

The small size, thin bone walls and detailed morphology of FGGUB R.1957 indicate that it belongs to a theropod dinosaur.

Relationships to other theropods from the Haţeg Basin

The presence of several theropod taxa was reported in the past from the Haţeg Basin (see Grigorescu & Csiki, 2002 and Csiki & Grigorescu, 2003 for recent reviews). Most of these are represented only by isolated teeth (e.g. Csiki & Grigorescu, 1998, Codrea et al., 2002) with only a Saurornitholestes-like dromaeosaurid based on cranial bones (Weishampel & Jianu, 1996).

Postcranial remains of theropods are much rarer. The material described initially by Andrews (1913) and Lambrecht (1929) as Elopteryx was already mentioned; it includes two incomplete femora and three distal tibiotarsi; a distal femur referred by Grigorescu & Kessler (1981) to Eloperyx is probably misidentified and does not belong to a theropod (see below). A dorsal vertebral centrum of an unidentified middle-sized theropod was reported and figured by Smith et al. (2002) from Șăla-Vad. Several associated forelimb elements (humerus, ulna, metacarpal, phalanges), discovered at the Tuştea nesting site, were recently identified as probable caenagnathid oviraptorosaur by Csiki & Grigorescu (2005). However, neither of these specimens can be directly compared to FGGUB R.1957, due to lack of overlapping parts.

It is consequently difficult to establish whether FGGUB R.1957 belongs to one of the formerly described Haţeg theropods. Based on size correspondence with the holotype and referred femora and presence of a wrinkled surface texture (noted previously by Andrews, 1913 and Le Loeuff et al., 1992; see below) the Scoabă specimen is tentatively referred here to Elopteryx nopcsai Andrews, 1913. The general resemblance of FGGUB R.1957 to steganopod femora (see below), also noted by Andrews (1913) and Lambrecht (1929, 1933) in the case of Elopteryx, might, too, support this referral.

![Fig. 2. Elopteryx nopcsai, right distal femur (FGGUB R.1957), Scoaba locality, Sînpetru, in a – lateral, b – cranial, c – medial, d – distal and e – caudal views. c.i.c.g. – cranial intercondylar groove; d.i.c.g. – distal intercondylar groove; ec.t. – ectocondylar tuber; ect.c. – ectepicondyle; ipo.b. – infrapopliteal bridge; po.f. – popliteal fossa. Scale bar – 1 cm.](image-url)
Taxonomic history of *Elopteryx*

As mentioned above, *Elopteryx nopcsai* was erected by Andrews (1913) for two fragmentary femora and, tentatively, a fragmentary distal tibiotarsus, collected at Sînpetru and housed in the NHM (BMNH). Andrews (1913) designated the incomplete femur BMNH A PAL.1234 as the holotype of the new taxon. Of the other two specimens, BMNH A PAL.1235, the other femur, was referred to the same taxon due to its comparable morphology. However, the reason for referring the distal tibiotarsus (BMNH A PAL.4359) to *Elopteryx* was less reliable: Andrews noticed that the three bones apparently possess a similar roughened surface texture, which he regarded as suggestive of common taxonomic origin (op. cit.: p. 195, 196).

Subsequently, Lambrecht (1929) referred to *Elopteryx* two more specimens from Sînpetru two tibiotarsi collected by Nopcsa (BMNH A PAL.1528) and Lady Woodward (BMNH A PAL.1588). He included both *Elopteryx* and the Eocene taxon *Eostega lebedynskyi* Lambrecht, 1928, from Cluj (Transylvania, Romania) in the family Elopterygidae, a group classified in the ‘Pelecaniformes’ (Lambrecht, 1933).

Re-examination of this material by Harrison & Walker (1975) led to the removal of the tibiotarsi from *Elopteryx* and their referral to two new giant owl taxa: *Bradychneme draculae* and *Heptasteornis andrewsi*, for which the authors erected a new family (Bradychnemidae) within the Strigiformes. They accepted, however, the ‘pelecaniform’ affinities of the *Elopteryx* femora. Their interpretation of the material thus echoed the opinion of Andrews concerning the contradiction between the pelecaniform femora and the “running bird” tibiotarsi of *Elopteryx*.

More recently, an isolated fragmentary limb bone (FGGUB R.351) from Sînpetru was referred to *Elopteryx* by Grigorescu & Kessler (1981) and identified by them as a distal left femur. Csiki & Grigorescu (1998) reinterpreted it as a possible neoceratosaur distal femur. However, recent inspection of the vertebral material collected from the Hateg Basin and housed in the collections of the MAFI revealed the presence of a complete bone (MAFI Ob.3120a) in which the distal end is virtually identical in size and morphology to FGGUB R.351; it shows that this specimen represents instead the distal end of a moderately large metatarsal, belonging probably to a hadrosaur.

In recent years, the avian nature of the London *Elopteryx* material has been contested by many authors (Brodkorb, 1978; Elzanowski, 1983; Martin, 1983; Olson, 1985), and following them, by Grigorescu (1984), who referred to these specimens as indeterminate coelurosaur (i.e. small, cursorial non-avian theropods). Part or all of this material was regarded as being referable to Troodontidae by Norman (1985), Osmolska (1987: *Bradychneme* and *Heptasteornis*), Paul (1988: *Bradychneme draculae* and *Troodon? andrewsi*), Osmolska & Barsbold (1990: Troodontidae nomina dubia) and Houde & Milner (1993: *Heptasteornis*), although little supporting evidence was presented for these conclusions. Meanwhile Le Loeuff et al. (1992), synonymising both *Bradychneme* and *Heptasteornis* with *Elopteryx nopcsai*, identified it as a possible maniraptoran (i.e. either caenagnathid, dromaeosaurid or troodontid), most probable a dromaeosaurid. Finally, Csiki & Grigorescu (1998) suggested that the femora and tibiotarsi belong to different theropod taxa, “*Elopteryx*” being a derived maniraptoran, while “*Bradychneme*” might be a non-maniraptoran member of the Tetanurae.

The latest comprehensive compendium of the Dinosauria includes all these taxa, without further discussion, into the Troodontidae as *nomina dubia* (Makovicky & Norell, 2004). On the other hand, in a recent review of Mesozoic neornithine birds, Hope (2002) still listed *Elopteryx* (restricted to include only the femora, but giving an erroneous specimen number for the referred specimen, considered to represent the paratype) as a ‘pelecaniform’ bird, although she noted that the status of this material is still subject to controversy and requires further study. An avian affinity of *Bradychneme* or *Heptasteornis* is discarded by Hope (2002).

Finally, the most recent review of the London material by Naish & Dyke (2004) suggested that *Heptasteornis* (including only BMNH A PAL. 4359) might represent an alvarezsaurid, while *Bradychneme* represents an indeterminate maniraptoran, and *Elopteryx* (restricted to the holotype and referred femora) is either a troodontid or a non-ornithuromorphian pygostylian, but probably not an enantiornithine.

In order to assess whether FGGUB R.1957, here referred to *Elopteryx nopcsai*, supports one of the above hypotheses, a wider survey was conducted to establish its possible affinities within the Theropoda.

Affinities of FGGUB R.1957

Establishing the affinities of FGGUB R.1957 within the Theropoda is rather difficult, due to the fragmentary nature of the specimen. Although most theropod clades are diagnosed by a wealth of synapomorphies (see Chapters 3-11 in Weishampel et al., 2004), few of these are derived from the femur, and especially the distal femur. Some comparisons can be made, however, in order to elucidate the relationships of the specimen.

‘Ceratosaurian’ (including both Coelophysoidea and Neoceratosauromorpha) distal femora are characterized by a sharply separated tibiofibular crest (ectocondylar tuber) on the lateral condyle (e.g. Madsen & Welles, 2000); moreover, an infrapopliteal bridge is present in coelophysoids (Tykoski & Rowe, 2004), similar to the condition seen in FGGUB R.1957. However, these
Tetanurae is diagnosed, among other synapomorphies, by a prominent cranial intercondylar groove (rotular groove), a condition that has been reversed in several derived tetanuran clades (Holtz et al., 2004b). Since this feature is lacking in FGGUB R.1957, it is probably not member of any of the basal tetanuran groups. Tetanuran distal femora are also characterized by the presence of a prominent cranio medial muscle scar (for the M. tibialis cranialis) bordered by a cranio medial crest. The distribution of this character state (also present in more basal theropods) suggests it represents the plesiomorphic state for Theropoda, widely distributed in basal tetanurans. The absence of this character complex in the Hațeg femur also suggests it does not belong to a basal tetanuran.

Basally in Coelurosauria, compso gnathoids apparently possess a shallow cranial intercondylar groove, continuous with the distal intercondylar groove (e.g. Currie & Chen, 2001), while these are separated by a shallow bony bridge in FGGUB R.1957.

Among derived coeluro saurs, basal tyrannoraptoran theropods (tyran nosauroids, ornithomimosaurids) have distal femora showing a marked cranial intercondylar groove, a prominent cranio medial muscle scar (Tyrannosauroidea, Holtz, 2004) or a thin cranio medial crest (Ornithomimosauria, Makovicky et al., 2004). Lacking these characters, FGGUB R.1957 is probably not a member of any of these clades.

Among basal maniraptora ns, therizinosauroids (e.g. Zhang et al., 2001; Clark et al., 2004) have a more robust femur with a shallow cranial intercondylar groove, different from the condition seen in FGGUB R.1957. The popliteal fossa is unusually deep, but opens both proximally and distally, where it is confluent with the distal intercondylar fossa.

Oviraptorosaurs, meanwhile, approach the condition seen in the Hațeg specimen in several respects: in the presence of a well-marked tibiofibular crest, absence of a cranio medial adductor muscle scar and associated crest, and in the lack of a cranial intercondylar groove (the latter two apomorphically reversed in Oviraptoridae). Moreover, the lateral condyle projects more distally than the medial condyle, as in FGGUB R.1957; this character is identified as a synapomorphy of the Oviraptorosauria by Osmólska et al. (2004). A lateral epicondyle is also present in some oviraptorids. In the basal oviraptorosaur Microvenator celer the largely triangular shape of the popliteal area is reminiscent of that in FGGUB R.1957 (Makovicky & Sues, 1998). Absence of an infrapopliteal bridge differentiates, however, oviraptorosaur femora from the Hațeg specimen (e.g. Currie & Russell, 1988; Makovicky & Sues, 1998). An infrapopliteal bridge is apparently present in Avimimus portentosus (Vickers-Rich et al., 2002), but here the ectocondylar tuber is less well developed, the medial condyle extends more distally than the lateral condyle and there is no marked ectepicondyle.

Both troodontids (Makovicky & Norell, 2004) and dromaeosaurids (Norell & Makovicky, 2004) have femora similar to FGGUB R.1957 in that there is no cranial intercondylar groove or cranio medial crest and muscle scar. However, the popliteal fossa is open distally, unlike the condition seen in FGGUB R.1957, nor is there a defined ectocondylar tuber on the lateral condyle in dromaeosaurids (Ostrom, 1976).

In alvarezsaurids the distal femur shows several characters present in FGGUB R.1957, including absence of a well-marked cranial intercondylar groove, lack of a cranio medial crest and muscle scar, as well as presence of an ectocondylar tuber. Moreover, in Mononykus olecranus (Perle et al., 1994, Chiappe et al., 1996) and Patagonykys puertai (Novas, 1996, 1997), the lateral condyle is projected distal to the medial one and there is a prominent ectepicondyle. Finally, an infrapopliteal bridge is reported in Mononykus (Perle et al., 1994), and is also scored as present in Shuvuuia deserti (Clark et al., 2002), though it is missing in Patagonykys (Novas, 1996, 1997) and in Parvicursor remotus (Karhu & Rautian, 1996, Chiappe et al., 2002). The triangular shape of the popliteal fossa, bordered by proximally converging supracondylar ridges, is also shared by FGGUB R.1957 and Mononykus.

Among birds (Avialae), FGGUB R.1957 compares closely to stegano podes, both in general morphology and dimensions (it is similar to the large-sized pelican genera Pelecanus crispus and P. onocrotalus). However, several details differentiate it from all known fossil and Recent stegano pod taxa, such as the weak distal intercondylar groove and very superficial cranial intercondylar groove (in this respect, it is more similar to Phalacrocorax). The shallow ridge separating the cranial and distal inter condylar fossae is not present in the surveyed stegano podes. On the lateral condyle, both the crista tibiofibularis and the trochlea fibularis are weaker than in stegano podes. The medial condyle is narrower, with a smaller articular surface. The presence of a prominent patellar groove (corresponding to the cranial intercondylar groove of the theropods) is considered an unambiguous synapomorphy of Ornithurae (Neornithes + Hesperornithiformes) within the Maniraptora (e.g. Chiappe, 1995, Padian, 2004); the absence of this feature in FGGUB R.1957 suggests it is probably not a member of the Ornithurae.

To conclude, the incomplete nature of FGGUB R.1957 makes rather tentative its referral to one of the theropod clades. However, this survey shows it is most closely comparable to the Late Cretaceous
alvarezsaurids, although similarities with other derived maniraptorans (especially non-oviraptorid oviraptorosaurs) are also present.

Alvarezsaurids in Europe?
The alvarezsaurids are a clade of derived theropods with a peculiar, unique morphology (especially in the forelimb), many bird-like traits and an unusual biogeographic distribution. There were first allied with avialians (e.g. Perle et al., 1994, Chiappe, 1995, Chiappe et al., 1996, Novas, 1996), but more recently have been regarded as closely related to, but outside of the bird clade (sister-taxon of Aves, cf. Chiappe et al., 2002 or basal members of Avialae, cf. Padian, 2004), as a sister-taxon of Eumaniraptora (Troodontidae, Dromaeosauridae and Avialae; Holtz & Osmólska, 2004), as a basal maniraptoran clade, only distantly related to birds (Novas & Pol, 2002) or even as outside of Maniraptora, as a sister-group to Ornithomimidae (e.g., Sereno, 1999). Although there is no current agreement on their systematic relationships, their inclusion within the Maniraptora seems well established.

If FGGUB R.1957 is indeed referable to Elopteryx, then Elopteryx most probably represents an alvarezsaurid, even a mononykine, as its distal femur presents autapomorphic features of that clade (well-developed ectocondylar tuber and ectepicondyle, presence of an infrapopliteal bridge). Naish & Dyke (2004) suggested that, although Heptasteornis might represent an alvarezsaurid, the holotype material of Elopteryx shows a character combination that apparently excludes its membership from that clade. Two possibilities can be taken into account: either Elopteryx is a peculiar, autapomorphic alvarezsaurid with a posterior trochanter or FGGUB R.1957 is referable to Heptasteornis instead of Elopteryx, in which case the presence of two similar-sized small theropod taxa should be accepted in the Haţeg fauna, both with a peculiar wrinkled surface texture, to our knowledge not yet reported in other theropods.

The palaeogeographic distribution of previously known alvarezsaurids shows an interesting, but easily understandable, pattern (see below). However, the implications of the presence of European alvarezsaurids are far-ranging, and their potential to test previous evolutionary scenarios is great.

The oldest (and most basal) members of the clade, Alvarezsaurus calvoi and Patagonykus puertai (e.g. Chiappe et al., 2002) are restricted to South America, where they occur in Turonian-Santonian deposits (e.g. Makovicky et al., 2005). Derived members of the family (the mononykines: Mononykus olecranus, Parvicursor remotus and Shuvuuia deserti) are known from the Campanian-Maastrichtian of Central Asia; a possible mononykine was also reported from the Maastrichtian of North America (Hutchinson & Chiappe, 1998). This distribution suggests an endemic South American radiation of the clade, followed by a latest Cretaceous dispersal into Asiamerica (North America and Asia; e.g. Novas, 1996, Hutchinson & Chiappe, 1998).

The presence of alvarezsaurids in the latest Cretaceous of Europe was suggested previously by Naish & Dyke (2004) in the case of Heptasteornis, and is further supported (although tentatively) by FGGUB R.1957. As it now stands, all reported European alvarezsaurid remains are restricted to the Hateg area (possible alvarezsaurid remains from the Upper Cretaceous of France are waiting for description; D. Naish and G. Dyke, pers. comm. 2005). Moreover, both Naish & Dyke (2004) and the present study suggest that these remains are referable to derived alvarezsaurids, being most similar to Mononykus and Shuvuuia. The presence of a mononykine in Hateg is at odds, however, with the above palaeobiogeographic scenario, which implies presence of alvarezsaurids outside South America in the Campanian at earliest.

A preliminary analysis of the palaeobiogeographical significance of the Hateg fauna (Csiki, unpubl. Ph. D. thesis) suggests that it descends from a late Early Cretaceous generalized fauna, with a few immigrant taxa from western Europe, introduced during the Late (but not latest) Cretaceous, most probably before the Campanian.

If Heptasteornis and/or Elopteryx (if FGGUB R.1957 belongs to this later taxon) indeed represent alvarezsaurids, their presence in the distinctly endemic Hateg fauna can be explained by one of the following alternative hypotheses:

1) alvarezsaurids represent a group originating in and being endemic to South America, dispersing from there northwards, as proposed by Novas (1996), but their dispersal took place earlier than suggested previously. However, inter-American continental connections during the Late Cretaceous seem to have been restricted to the latest Cretaceous (e.g. Bonaparte, 1984);

2) alvarezsaurids had a wide geographic distribution before the Late Cretaceous, being present in both Gondwana and Laurasia. The proposed phylogenetic relationships of the Hateg alvarezsaurids is consistent with the presence of a Laurasian alvarezsaurid clade (the mononykines). The phylogenetic relationships of the alvarezsaurids within Coelurosauria (in any of the hypotheses outlined above) is also consistent with such a early wide distribution, since all derived coelurosaurian clades had their earliest occurrence in the Barremian at the latest (see reviews in Weishampel et al., 2004), suggesting a long hidden evolutionary history of the Alvarezsauridae;

3) alvarezsaurids are indeed of South American origin, and their dispersal towards (western) North America occurred in the Santonian-Campanian (as suggested by Novas, 1996), from where they were introduced rapidly to Europe, either directly or via Asia. However, current palaeobiogeographic reconstructions do not show continental connections of Europe with either of these
landmasses after the Cenomanian - Turonian (e.g. Smith et al., 1994), nor were there close biogeographic relationships between their respective faunas (e.g. Le Loeuff, 1991, 1997, Holtz et al., 2004a; but see Martin et al., 2005, for an alternative view).

Finally, it should be noted that Holtz et al. (2004b, p. 100) have suggested that Rapator ornitholestoides from the Albain of Australia might be an alvarezsaurid. If their suggestion is correct (the published figures of the specimen, a probable manual digit, show it is reminiscent of those of Mononykus and Patagonykus), then alvarezsaurids may have been more widely distributed prior to the Late Cretaceous. This early and unexpected paleobiogeographic occurrence supports an early origin of the alvarezsaurids (at least by the early Late Jurassic), being concordant with hypothesis (2) listed above.

CONCLUSIONS

A small distal femur, discovered recently at Sînpetru, is shown to belong to a theropod, and is possibly referable to Elopteryx nopcsai Andrews, 1913, a purported steganoopid bird, but is most probably a derived maniraptoran. Interestingly, it presents a character combination reminiscent of the condition reported in derived alvarezsaurids, the mononykines.

If the specimen indeed belongs to a mononykine alvarezsaurid, it would be the second report of this group in the Maastrichtian Hâţeg fauna, after Heptasternos andrewsi (Naish & Dyke, 2004). Whether it is referable to Elopteryx, as is suggested here, or to Heptasternos (the presence of two different alvarezsaurid taxa, besides that of a non-alvarezsaurid Elopteryx is a less parsimonious hypothesis, and is disregarded for the moment), it strengthens the idea of the presence of the alvarezsaurids in the latest Cretaceous of Europe (specifically the highly endemic Hâţeg fauna).

The presence of alvarezsaurids in Europe, if confirmed, challenges current hypotheses of the palaeobiogeography and evolution of the clade and requires alternative scenarios to be explained. Further skeletal remains are needed to finally establish the presence of alvarezsaurids in Europe and to understand their relationships to other members of the clade. New discoveries, integrated into a large-scale palaeobiogeographic study of Late Cretaceous faunas, are also necessary to choose between the palaeobiogeographic scenarios suggested by the recognition of European alvarezsaurids.

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REFERENCES


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