A Medium-Sized Robust-Necked Azhdarchid Pterosaur (Pterodactyloidea: Azhdarchidae) from the Maastrichtian of Pui (Haţeg Basin, Transylvania, Romania)

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A medium-sized robust-necked azhdarchid pterosaur (Pterodactyloidea: Azhdarchidae) from the Maastrichtian of Pui (Haţeg Basin, Transylvania, Romania)

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ABSTRACT

We describe a pterosaurian cervical vertebra collected from Maastrichtian sediments at the Pui locality in the Haţeg Basin, Romania. This specimen, a medium-sized, robust fourth cervical, is distinctive in morphology and represents a new, as yet unrecognized, azhdarchid pterosaur size class within the Haţeg Island fauna: it most likely belongs to a new taxon which we opt not to name here. The vertebra is referred to Azhdarchidae based on clearly preserved diagnostic features characteristic of this group and differs in proportions and anatomical details from the recently named azhdarchid *Eurazhdarcho langendorfensis* Vremir et al., 2013a, from the Sebeş region of the Transylvanian basin. We take issue with claims that all Maastrichtian Romanian azhdarchids (and other penecontemporaneous azhdarchids and azhdarchoids) should be uncritically assumed to be synonymous: it ignores anatomical characters that allow the specimens concerned to be differentiated and is based on an erroneous "one stratum, one species" philosophy contradicted by empirical data from other azhdar-

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choid assemblages. It has been suggested that the absence of small to medium-sized pterosaurs in Upper Cretaceous sediments is indicative of an evolutionary trend. However, evidence from the Haţeg Island fauna may indicate instead that smaller-sized pterosaurs were indeed present in this interval but remain underrepresented due to rare preservation and collection.

INTRODUCTION

The Upper Cretaceous (Maastrichtian) sediments in the Transylvanian and Haţeg regions of western Romania have become well known for their fossil vertebrates (e.g., Grigorescu, 2010; Weishampel and Jianu, 2011), with an increasing number of pterosaur specimens reported in recent years. To date, fossil remains have predominantly been referred to Azhdarchidae (Vremir et al., 2011, 2013a, 2013b; Jipa, 2012), an important group of long-necked, toothless pterodactyloids, which are thought to have dominated Late Cretaceous pterosaur assemblages. Azhdarchids are strongly associated with continental environments and, while some may have visited or even frequented marine environments, paleoenvironmental and ecomorphological data indicate that they were specialized for life in terrestrial settings (Witton and Naish, 2008, 2013). Recent discoveries also show that these animals are well represented in the upper Campanian and Maastrichtian deposits of Transylvania, especially in the Sebeş region (Transylvanian basin). Transylvanian basin pterosaurs collected thus far include the holotype specimen of *Eurazhdarcho langendorfensis*, known from an incomplete skeleton (Vremir et al., 2013a) but with a wingspan of ca. 3 m, the remains of a large, unnamed taxon of ca. 5 m wingspan (Vremir et al., 2014), and a contemporaneous giant azhdarchid that attained enormous size (wingspan up to 10 m) (Vremir, 2010; Vremir et al., 2013b).

This pterosaur size diversity is mirrored in collections from the famous Haţeg Basin, Romania. Fragmentary remains of individuals spanning a wide range of body sizes are known from sites in this region, contemporaneous with the gigantic *Hatzegopteryx thambema*, an azhdarchid that likely had a wingspan of 10–11 m (Jianu et al., 1997; Buffetaut et al., 2003; Csiki et al., 2009; Vremir, 2010; Weishampel and Jianu, 2011; Vremir et al., 2011, 2013a, 2013b; Dyke et al., in prep.).

Ongoing fieldwork and research on the Upper Cretaceous pterosaur material of the Transylvanian and Haţeg basins is providing new insights into azhdarchid anatomy, evolution, and paleoecology. Previous studies have pointed to the possibility of niche partitioning as a factor that allowed azhdarchids of differing sizes (and perhaps morphologies) to inhabit the same region and have also suggested close evolutionary links with older azhdarchids from Central Asia (Vremir et al., 2013a). Ongoing work also hints at unprecedented morphological diversity within Azhdarchidae, a group previously assumed to have been fairly conservative in anatomy and proportions (Witton and Naish, 2008, 2013).

We describe a near-complete neck vertebra collected from the Pui locality in the Haţeg basin (fig. 1) that is notable for its small size and distinctive morphology (figs. 2, 3). We interpret this vertebra as evidence for another novel component of the Late Cretaceous Haţeg Island pterosaur assemblage. Although cervical vertebrae have been considered highly diagnostic among and between taxa of azhdarchids, there is little agreement about which discrete morphological features can be used to distinguish taxa at the genus and species level. Although it is possible that some of the characters we discuss below (i.e., relative proportions vs. the morphology of the anterior articular region in respect to the anatomical position within the cervical series) could represent autapomorphies, we refrain from erecting a new name here (pending the results of ongoing fieldwork).

INSTITUTIONAL ACRONYMS

EME	Transylvanian Museum Society, Cluj-Napoca, Romania
LPB (FGGUB)	Laboratory of Fossil Vertebrates, Faculty of Geology and Geophysics, University of Bucharest, Bucharest, Romania
MAFI	Hungarian Geological Survey, Budapest, Hungary
MTM	Hungarian Museum of Natural History, Budapest, Hungary
OCP DEK/GE	Office Chérifien des Phosphates, Service Géologique, Khouribga, Morocco
TMM	Texas Memorial Museum, Texas Natural Science Center, University of Texas at Austin, Austin
TMP	Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada
UBBG	Babeş-Bolyai University, Faculty of Biology and Geology, Cluj-Napoca, Romania
ZIN	Zoological Institute of the Russian Academy of Sciences, St. Peters burg, Russia
ZMNH	Zhejiang Museum of Natural History, Hangzhou, China

SYSTEMATIC PALEONTOLOGY

Pterosauria Kaup, 1834
Pterodactyloidea Plieninger, 1901
Lophocratia Unwin, 2003
Azhdarchoidea Nessov, 1984 (sensu Unwin, 1992)
Azhdarchidae Nessov, 1984

Material: LPB (FGGUB) R.2395 (afterwards R.2395), a relatively small (89 mm in total length), mostly complete azhdarchid pterosaur midseries cervical vertebra, most likely cervical IV (figs. 2, 3). Our interpretation is that this specimen belongs to a medium-sized (wingspan ca. 3.5–4 m), relatively gracile, but comparatively short-necked azhdarchid.

Geological Setting: The Pui vertebrate site is located in the lower section of the Bărbat valley, near Pui village in the eastern Haţeg basin (fig. 1). At this site, the Maastrichtian continental red deposits—known variously as the "Pui beds" or as the "Bărbat Formation" (Therrien, 2005)—are dominated by a coarse fluvial channel, occasional crevasse splay, and subordinated backswamp facies. Respectively, these sediments represent proximal and more distal floodplain units and comprise mostly red, calcareous silty claystones and paleosols (Csiki et al., 2010). Precise stratigraphic correlation with the other continental units of the Haţeg basin (e.g., Sînpetru and Ciula-Densuş forma-

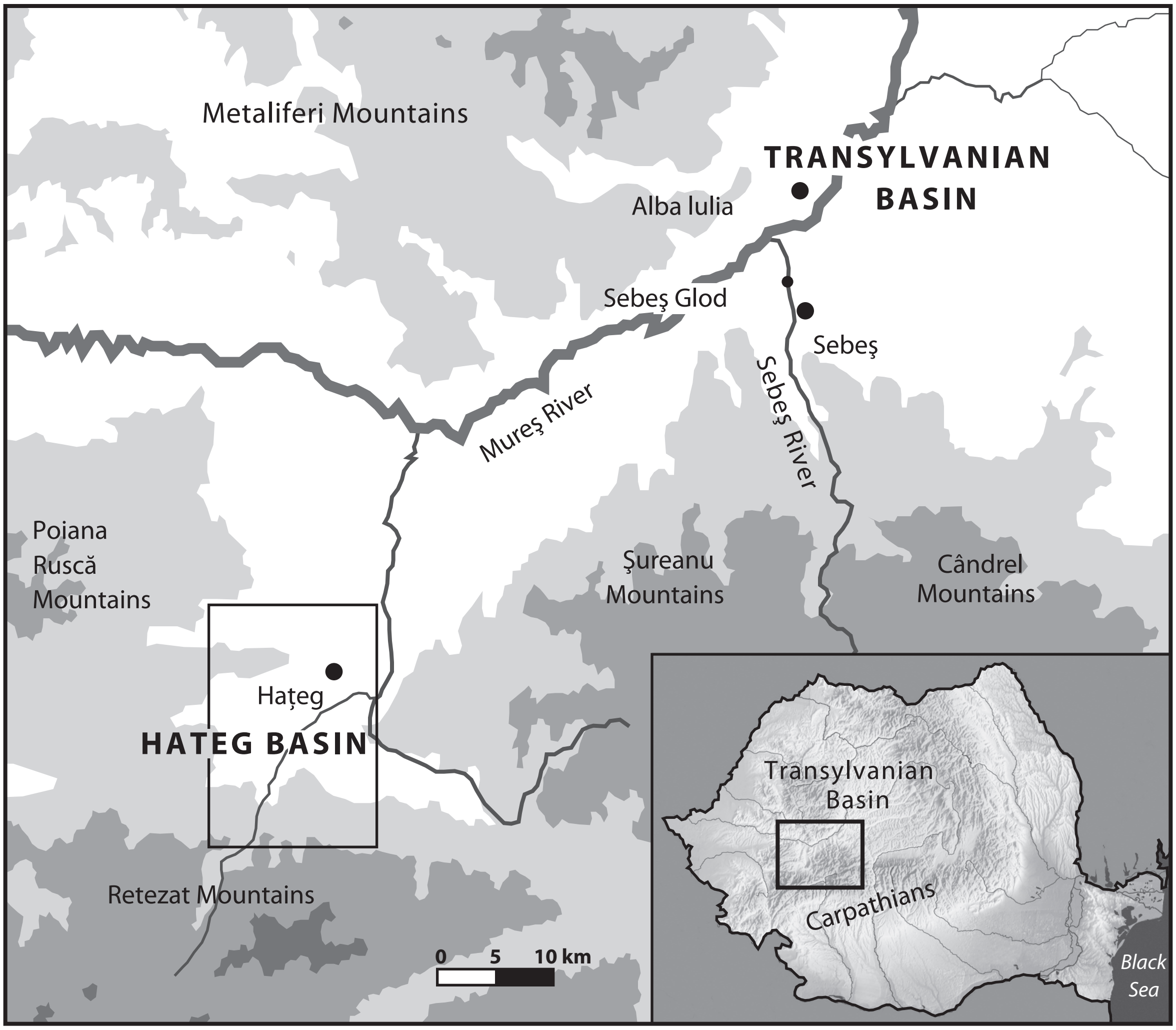

FIG. 1. Map of the Haţeg Island region, present-day Transylvania (Romania). The contemporaneous Transylvanian and Haţeg basins are indicated; the Pui locality is just a few kilometers from the town of Haţeg.

tions) is, however, currently unclear and a work in progress (Vremir and Dyke, unpublished data). Some detailed stratigraphic and sedimentological analyses and interpretations of the Bărbat river section are available (Van Itterbeeck et al., 2004; Therrien, 2005); based on palynological data, the Bărbat valley section (ca. 100 m in thickness) is within the Lower/Upper Maastrichtian boundary interval (van Itterbeck et al., 2004; Van Itterbeck et al., 2005), roughly synchronous with (or slightly younger than) the Sibişel valley type section of the Sînpetru Formation.

Associated vertebrate taxa within the Bărbat river section include (Therrien, 2005; Vremir and Dyke, unpublished data): fish (acipenseriforms and characids), anurans (*Eodiscoglossus* sp.), albanerpetonids (*Albanerpeton* cf. *inexpectatum*), Borioteiioidea and other lizards (*Bicuspidon hatzegensis* and a new, large-bodied taxon informally referred to as "*Puiodon*"), eusuchian crocodylomorphs (*Allodaposuchus precedens*), semiterrestrial meiolaniform (*Kallokibotion* *bajazidi*) and aquatic pleurodiran dortokid turtles, giant pterosaurs (cf. *Hatzegopteryx* sp.), ornithopod (*Zalmoxes robustus*, *Z.* cf. *sqhiperorum, Telmatosaurus transylvanicus*), sauropod (*Magyarosaurus dacus*), and theropod (indeterminate velociraptorine and troodontid-like forms) dinosaurs, and several multituberculate mammal species (*Barbatodon transylvanicum, Barbatodon* sp., and indeterminate cimolodontans).

R.2395 was collected in June 2012 from a relatively thick (ca. 1 m) brownish-red and occasionally pebbly, silty-sandstone layer at Pui. This upward-fining unit is interpreted as a shallow sandy channel fill deposit containing scattered, but well-preserved vertebrate fossils. Sediments are exposed in the Bărbat riverbed, about 800 m upstream from the main road into the Pui locality in the eastern Haţeg Basin.

R.2395 DESCRIPTION

R.2395 is a near-complete, midseries cervical vertebra preserved in a three-dimensional, almost uncrushed condition (figs. 2, 3) (although the posterior end is flattened and displaced slightly); it lacks the condyle, some of its posteroventral surface including the postexapophyses, and the right postzygapophysis. The left prezygapophysis is slightly damaged at its base on the dorsolateral side. Well-cemented sandy siltstone has filled the interior, and a partial internal mold of the posterior corpus section is visible on the ventral surface. This mold is perforated with small ellipses of white bone, which likely represent the trabeculae.

As preserved, R.2395 is 89 mm long (figs. 2, 3), but it was slightly longer when complete, perhaps reaching 97–100 mm prior to the loss of the condyle (fig. 3). At its widest preserved point (across the prezygapophyses) it is 44 mm across. The vertebra progressively tapers posteriorly to a narrow-waisted region on the centrum, which is 24 mm across as its narrowest point, and then abruptly broadens again at its postzygapophyseal section (the reconstructed postzygapophyseal width is ca. 42 mm). The specimen is 18 mm deep between the dorsal tip of the slightly damaged neural spine and the base of the centrum; it is likely that the specimen originally exceeded 20 mm in depth (anterior width/depth ratio: 2.2). The ventral surface of the centrum is slightly convex and lacks any unusual features. The reconstructed minimum elongation ratio (total length/prezygapophyseal width) of this vertebra is ca. 2.2 (preserved ratio = 2.0), whereas the maximum elongation ratio (total length/minimum corpus width) is ca. 4.1 (preserved ratio = 3.7).

R.2395 has prominent, elongate prezygapophyseal pedicles that enclose an angle of 35° with respect to the vertebral long axis and project anteriorly 10 mm from the dorsal rim of the cotyle and somewhat laterally from the vertebral body. This elongated aspect is created by its peculiar narrow and rather deep profile and also because it bears comparatively small dorsomedially oriented (mean inclination = 20° from horizontal plane), oval, convex articular facets (facet length = 10 mm; facet width = 8 mm; interprezygapophyseal width/articular facet width ratio = 5.5). The ventral surfaces of both prezygapophyses show a slight lateral swelling that probably represents the bases of the prezygapophyseal tubercles. The lateral and medial surfaces of the prezygapophyses are concave. No sign of the vertebral-costal canal, “foramen transversarium” (dorsally), or vestigial cervical rib (ventromedially) can be seen; however, dorsolaterally at the external base of the pedicel, a small elongated tubercle and a posteriorly oriented shallow depression are visible, which may represent vestigial states at least of the costal canal and transverse foramen.

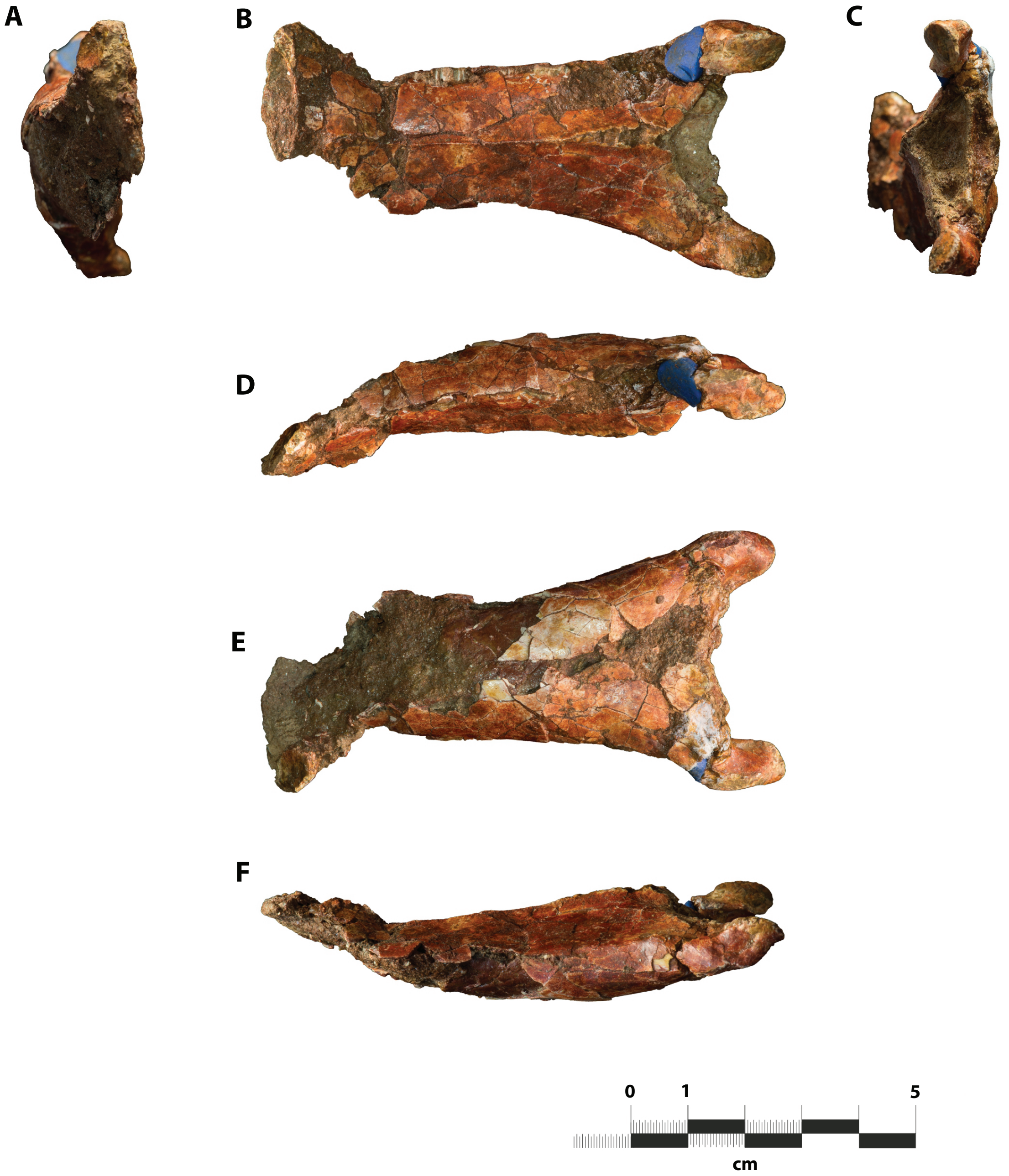

FIG. 2. Photographs of LPV (FGGUB) R.2395, almost complete cervical four from Pui, Haţeg basin, in anterior (**A**), dorsal (**B**), posterior (**C**), lateral (**D**), left lateral, inverted, (**E**) and right lateral (**F**) views.

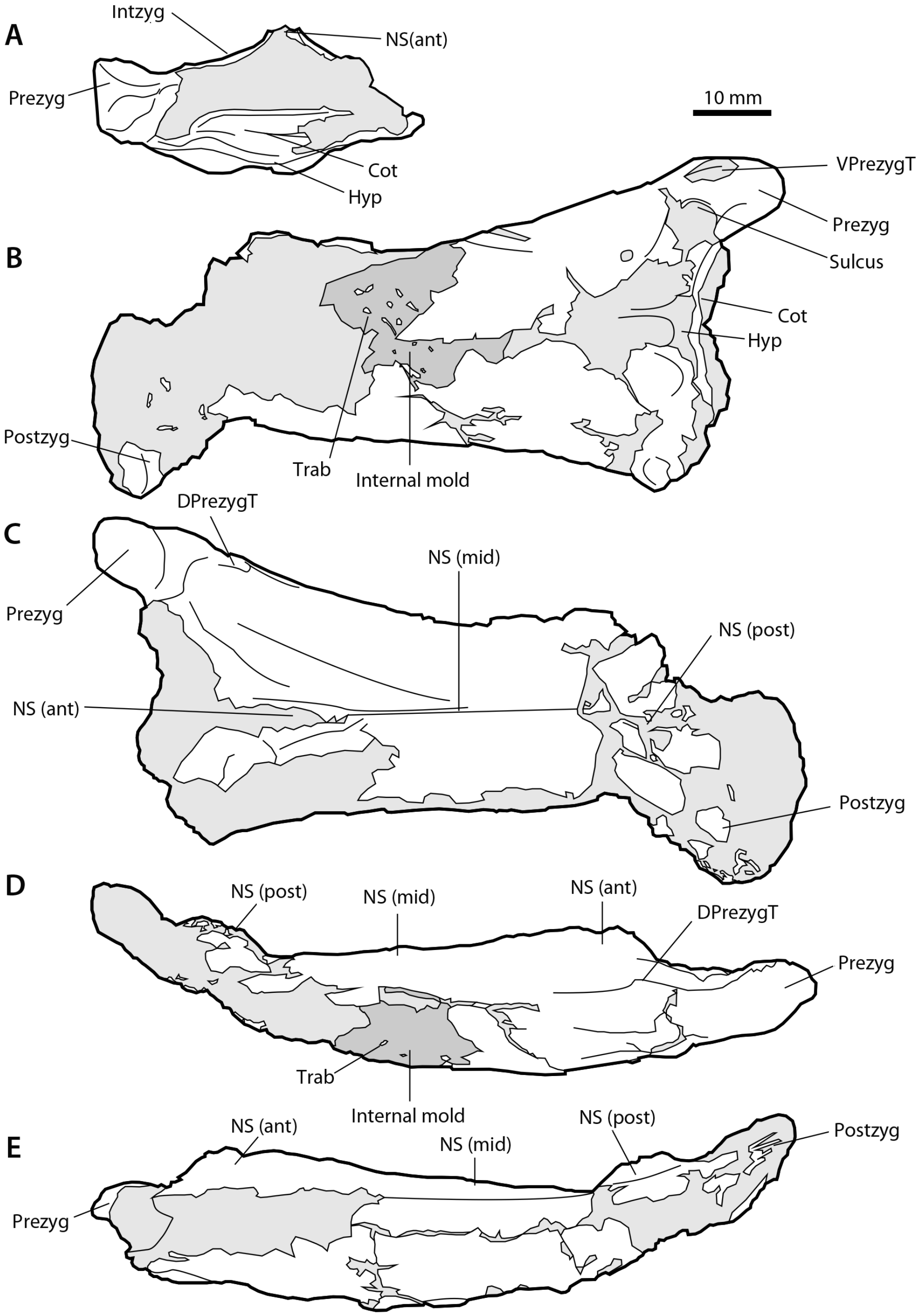

FIG. 3. Interpretative drawing of LPV (FGGUB) R.2395, almost complete fourth cervical from Pui, Haţeg Basin in anterior (**A**), ventral (**B**), dorsal (**C**), and right (**D**) and left lateral (**E**) views. Abbreviations: **Cot,** cotyla; **DPrezygT,** dorsal prezygapophyseal tubercle; **Hyp,** hypapophysis; **Intzyg,** interzygapophyseal area/space; **NS,** neural spine; **Prezyg,** prezygapophysis; **Trab,** trabecula; **VPrezygT,** ventral prezygapophyseal tubercle.

The anterior face of the neural arch was unaffected by compressive forces and maintains a low, triangular profile measuring 23 mm wide and 11 mm tall. The interzygapophyseal ridge is well developed and indented in a V-shape that points posteriorly, enclosing an angle of 110°. The anterior neural canal opening is relatively large and subcircular (6.5 mm in diameter) and entirely occupies the space between the interzygapophyseal ridge and the supracotylar shelf. On both sides, the neural canal is bordered by much smaller and circular pneumatic foramina (2–2.5 mm in diameter; about three times smaller than the neural canal), situated low in the lateral corners of the neural arch.

The cotyle has been slightly crushed dorsoventrally. It retains a shallow concavity of elongated oval shape, 20.5 mm wide and 5 mm in height (preserved width/depth ratio = 4; estimated original width/depth ratio = 3). On the weathered anteroventral margin, the cotylar base is prominent, marking the site of a small hypapophysis. Partial preservation of an internal mold and spongiose bone suggest that the hypapophysis was continuous with a short, ventral ridge along the anterior body of the centrum.

The vertebral corpus of R.2395 is relatively elongate and dorsoventrally compressed; as a result, the neural arch is depressed into the centrum for much of its length. The corpus tapers posteriorly to form a distinct "waist" in the posterior corporeal region. Each dorsolateral face of the corpus is slightly concave, whereas the lateral and ventral surfaces appear convex. The well-preserved neural spine is low (vestigial) along much of the length of the corpus, and in the midsection is almost entirely absent. The neural spine attains its greatest height at its anterior end, although slight wear on its dorsal surface prohibits measurement of its actual height. We expect that this portion of the spine remained fairly low even when complete, however, due to the low angle of the adjacent dorsolateral faces and relatively narrow area of weathering. The anterior region of this spine meets the medial apex of the interzygapophyseal ridge. The midlength of the spine is represented by a very low ridge, which expands somewhat laterally and dorsally at the posterior end into a low spine. This posterior spine is much smaller than the anterior, extending for only 9 mm along the centrum (11% of preserved centrum length) compared to ca. 18 mm (22%) anteriorly.

The posterior end of R.2395 is incomplete, but retains the left postzygapophysis. The posterior region has been slightly crushed and rotated dorsally. The left postzygapophysis is relatively broad (12 mm), acutely diverged from the adjacent postzygapophysis and shorter than the prezygapophyses, extending only 4 mm posteriorly from the centrum, and enclosing an angle of 45° with respect to the long axis. The posteriorly tapering dorsal and ventral surfaces of the zygapophysis remain visible as does the lateroventrally oriented oval articular surface (10 mm long; 7 mm wide). Because of postdepositional deformation, it is not possible to determine the original inclination of the articular face, but this was probably less than 30° from the horizontal plane.

The bone walls of R.2395 are extremely thin, measuring no more than 0.5–1.0 mm across broken compacta surfaces at the midlength of the specimen. Several rounded, submillimeter pieces of bone can be seen in the internal vertebral mold revealed by the broken ventral surface. We interpret these structures as broken shafts of trabecular bone crossing the void space within the vertebra. Further evidence of internal structures, in the form of spongiose bone, can be seen in weathered surfaces across the specimen. The bone surface texture across most of the specimen is extremely smooth, but weathered portions of bone have a fibrous appearance.

R.2395 COMPARISONS

R.2395 possesses an anatomy typical of a midseries azhdarchid cervical vertebra and thus can confidently be referred to this group (figs. 2, 3). Azhdarchid cervicals can be distinguished from those of other pterodactyloids on the basis of a well-established combination of characteristics, including their extremely reduced neural spines, incorporation of the neural arch into the centrum, hornlike supports for the prezygapophyses and elongate centrum (e.g., Howse, 1986; Kellner, 2003; Unwin, 2003; Witton and Naish, 2008). All of these features are visible in R.2395 (figs. 2, 3).

Determining the further significance of R.2395 is reliant on ascertaining which part of the cervical series it represents. Complete, or near-complete, neck skeletons are known for several azhdarchid taxa, including *Zhejiangopterus* (Cai and Wei, 1994), *Phosphatodraco* (Pereda Suberbiola et al., 2003, but note that the bone identifications of this specimen are controversial; see Kellner, 2010), *Azhdarcho* (Averianov, 2010; 2013) and *Quetzalcoatlus* sp. (Witton and Naish, 2008). From the nearby Transylvanian basin of Romania, the cervicals III and IV of *Eurazhdarcho* are also known (Vremir et al., 2013a). Azhdarchid cervicals have clear characteristics corresponding to their position within the cervical series: as a result, well-preserved isolated elements can be allocated specific vertebral numbers. Many of these identifying features were first noted by Averianov (2010: 277) and include proportions of the neural arch and cotyle, hypapophysis development, and neural spine condition.

We argue that R.2395 is most likely not a third cervical. The third cervicals of *Eurazhdarcho*, *Quetzalcoatlus, Azhdarcho,* and (possibly) *Phosphatodraco* differ from this element in several ways, including lacking large hypapophyses and having neural spines, which extend along the entire corpus with relatively wide bases. Their corporal margins are also largely parallel sided without a posteriorly displaced "waist," and their dorsolateral corporeal faces are convex, creating a tubelike cross section without the pinched dorsal region seen in other azhdarchid cervicals. The neural spines of the third cervicals of *Azhdarcho* and *Eurazhdarcho* are continuous and elevated in their midsection, not subdivided into anterior and posterior sections. These features strongly contrast with those of R.2395, suggesting it is not a third cervical. We note that the relatively short length of R.2395 is reminiscent of third cervicals in other azhdarchids, however. These cervicals are among the shortest in the neck skeleton, with much lower minimum elongation ratios (ER, measured as total vertebral length against width across the prezygapophyses) than most of the other midseries vertebrae (see below). The minimum ER for the third cervical of *Azhdarcho* (ZIN PH 131/44) is 2.13, *Eurazhdarcho* (EME 312/2) measures 2.34 and *Quetzalcoatlus* sp. (TMM 42422-24) is 3.65. The ratio recorded for R.2395 is 2.0 (perhaps approaching 2.2 when complete), which more closely approximates the values for cervical III than any other element of the azhdarchid cervical midseries.

It is likely that R.2395 is also not a sixth cervical, nor an eighth or ninth. The sixth cervicals of azhdarchids are poorly known, but the neural spine on cervical VI of *Azhdarcho* possesses a very tall posterior region, contrasting with the diminutive posterior neural spine component in R.2395. The sixth cervicals of *Azhdarcho* (ZIN PH 147/44), *Zhejiangopterus* (ZMNH M.1329), *Quetzalcoatlus* (TMM 42422-20), and (possibly) *Phosphatodraco* (OCP DEK/GE 111) are also relatively elongate compared with R. 2395, with minimum ERs of 2.32, 3.53, 4.5, and 3.11, respectively. We therefore think it unlikely that R. 2395 represents cervical VI, and also conclude that it is not an eighth or ninth cervical, which are usually much shorter (Averianov, 2010; 2013). These vertebrae have higher cotyles, relatively diminutive zygapophyses, well-developed hypapophysis and wide centra without posteriorly displaced "waists." However, the neural arch of R.2395 is about two times taller than the preserved cotyle, lacks a large hypapophysis, and bears well-developed prezygapophyses. The neural spines of the seventh cervicals in *Azhdarcho* (ZIN PH 138/44) and (possibly) *Phosphatodraco* also seem rather larger and broader than that present in R.2395.

Morphologies closer to those of R.2395 are seen in the fourth and fifth cervicals of some azhdarchid taxa (Averianov, 2010; 2013). These vertebrae have relatively lower cotyles, moderately developed hypapophyses, very low neural spines with particularly reduced middle sections, posteriorly displaced corporeal "waists," flattened or concave dorsolateral corporeal faces, and relatively large zygapophyses. These features are all present in R.2395, suggesting that it too represents a cervical IV or V. Distinguishing between cervicals IV and V can be difficult, but we note that R.2395 has only very small sulci beneath its prezygapophyses, more reminiscent of those in cervical IV of *Azhdarcho* (ZIN PH 144/44) than cervical V (Averianov, 2010). This may indicate that R. 2395 represents cervical IV rather than V, but the possession of obvious prezygapophyseal sulci in fourth cervicals of *Quetzalcoatlus* (TMM 41544.8) and *Eurazhdarcho* (EME 312/1) indicate that this character is only a tentative guide to position. The rather stunted nature of R.2395 may corroborate its identification as a cervical IV, however. The fifth cervicals of azhdarchids are consistently longer than all other bones in their necks, and sometimes considerably so (e.g., Wellnhofer, 1985; Frey and Martill, 1996; Bennett, 2001; Unwin, 2003). The length: width ratio of cervical V is 6.09 in *Quetzalcoatlus* (TMM 42422-32), while that of *Arambourgiania* is at least 7.47. These conditions contrast markedly with those of R.2395 and we therefore conclude that R.2395 is most likely cervical IV.

R.2395 differs from cervical IV of *Azhdarcho lancicollis* (ZIN PH 144/44) in that it is proportionally shorter and wider (see above) and has a truncated and wider "waisted" corporeal region (Averianov, 2010). The neural spine morphology is also broadly similar between R.2395 and ZIN PH 144/44, but the anterior and posterior spine elevations are of similar lengths in the latter, which differs from the condition in R.2395 where the posterior is much shorter than the anterior. The anterior neural spine projection also occupies more of the centrum in R.2395 than it does in *Azhdarcho*. The articular faces of the prezygapophyses may also be inclined somewhat more dorsally in R.2395, and *Azhdarcho* lacks tubercles on the dorsal face of the prezygapophyseal base. R.2395 is also similar to ZIN PH 144/44 in bearing only small ventral prezygapophyseal sulci.

Cervical IV of *Quetzalcoatlus* sp. (TMM 41544.8) is proportionally much longer and narrower than R.2395, with relatively prominent prezygapophyseal sulci. TMM 41544.8 also bears broader prezygapophyses that comparatively reduce the width of its neural arch compared to that of R.2395 (Witton and Naish, 2008). The lateral margins of the anterior region project at a more acute angle in TMM 41544.8 than those of R.2395. The ventral surface of TMM 41544.8 also seems to possess a slight ridge, which is absent in R.2395. TMM 41544.8 is rather poorly preserved and distorted, however, and this feature may be an artifact of preservation, along with absence of the dorsal prezygapophyseal tubercle.

Comparisons with the *Phosphatodraco mauritanicus* holotype (OCP DEK/GE 111) are complicated by disagreements regarding the identification of the cervical vertebrae in this specimen.

While Pereda Suberbiola et al. (2003) suggested that the holotype specimen preserves cervicals V–IX, Kellner (2010) concluded in contrast that they represent III–VIII with the broken, alleged cervical V of OCP DEK/GE 111 in fact parts of cervicals III and IV. If Kellner (2010) is correct, then OCP DEK/GE 111 includes overlapping material that can be compared with the presumed cervical IV R.2395. Even if this is the case, however, comparisons between R.2395 and this material are still limited because OCP DEK/GE 111 has been significantly crushed, and its cervical IV is only visible in a relatively uninformative lateroventral view. Thus, other than suggesting that *Phosphatodraco* may have a slightly longer and more tubular cervical IV than R.2395, we cannot provide meaningful comparison between these specimens. Similar constraints are found when comparing the cervical remains of *Zhejiangopterus linhaiensis* with R.2395. Several relatively complete skeletons of this azhdarchid are known, but all are extremely crushed and many anatomical details are absent or obscured (Cai and Wei, 1994). However, it can still be seen that the fourth cervicals of *Zhejiangopterus* are considerably more elongate than R.2395.

To our knowledge, no other definitively identified azhdarchid cervicals IV are known. Averianov (2010) suggested that MTM Gyn/448, a partial cervical vertebra possibly from the azhdarchid *Bakonydraco galaczi*, may be a fourth cervical. However, although this cervical is not well preserved, it is clearly proportionally longer and bears more obvious prezygapophyseal sulci than R.2395 (Ősi et al., 2005). Averianov (2010) also suggested that two azhdarchid cervicals from Canada, TMP 92.83.7 and TMP 89.36.254, may also represent fourth cervicals. The latter compares poorly with R.2395 in that it is much more slender and possesses large prezygapophyseal sulci, but TMP 92.83.7 is rather short (length: width ratio of 2.6) and bears reduced sulci similar to R.2395 (Godfrey and Currie, 2005). TMP 92.83.7 differs, however, in lacking a waisted region along its corpus, having a slightly shorter anterior section of the neural spine, and in being proportionally longer, despite its generally squat proportions compared to other azhdarchids.

Although, as we have noted, R.2395 is morphologically very similar to presumed fourth cervicals in other azhdarchids, it differs in having a somewhat lower minimum ER. The same ratio is consistently higher in the fourth cervicals of other azhdarchids, and sometimes exceedingly so: the fourth cervicals of *Eurazhdarcho* (EME 312/1), *Azhdarcho* (ZIN PH 144/44), *Quetzalcoatlus* (TMM 41544.8), and *Zhejiangopterus* (ZMNH M1329) are (at least) 2.6, 2.6, 3.67, and 4.56 longer than wide, respectively (Cai and Wei, 1994; Witton and Naish, 2008; Averianov, 2010; Vremir et al., 2013a). It is therefore possible that R.2395 represents an animal with a relatively short and robust neck compared to other azhdarchids. If true, then a shorter neck in the R.2395 animal may reflect ontogenetic influences. Pterosaur cervical vertebrae increase in length during growth with clear positive allometry (Wellnhofer, 1970), suggesting the compact shape of R.2395 may reflect a young individual with short neck vertebrae. The external bone texture of R. 2395 suggests that this individual had finished growing. External surfaces of pterosaur bone exhibit a smooth, polished texture once growth ceases, reflecting the deposition of an avascular layer over the external bone wall (Bennett, 1993). Smooth textures can be seen across unweathered bone surfaces in R. 2395. The absence of fibrous bone cannot be attributed to a preservational artifact either, as fibrous bone can clearly be seen on weathered bone where the avascular layer has been stripped away. Further corroboration of this hypothesis comes from the sharply defined tubercles and articular faces seen on the specimen, which likely represent the enhanced ossification present in adults (e.g., Bennett, 1995).

DISCUSSION

The vertebra we present in this paper expands our knowledge about the ever-growing record of Romanian latest Cretaceous pterosaurs and may also shed light on the idea of niche portioning in Haţeg Island pterosaurs (Vremir et al., 2013a, 2013b). The "Haţeg Island" pterosaur fauna (comprising records from both the geologically distinct Haţeg and Transylvanian basins) is now known to be relatively diverse and comprises the giant *Hatzegopteryx thambema* (Buffetaut et al., 2002; 2003), another unusually robust *Hatzegopteryx*-like form (Vremir, 2010; Vremir et al., 2013b) currently under description (Dyke et al., in prep.), and the relatively small *Eurazhdarcho langendorfensis* (Vremir et al., 2013a). The last-mentioned taxon has seemingly "typical" azhdarchid proportions, including a proportionally long neck (estimated at 497–516 mm). Although incomplete, we suggest that R.2395 most likely belongs to a new, moderately sized azhdarchid with a shorter, stouter neck (352–419 mm; 23%–41% shorter than *Eurazhdarcho*). Indeed, R.2395 probably does pertain to a new taxon, but we have opted not to name it in this contribution due to the extremely fragmentary material that is currently known.

It should be noted that Averianov (2014) argued that *Eurazhdarcho* is merely a juvenile of *Hatzegopteryx thambema* and that all characters proposed as diagnostic for the former are erroneous. We are happy to admit that, ideally, superior discoveries are required before we can adequately test the possibility that the sympatric azhdarchids discussed here and elsewhere (Vremir et al., 2013a; Vremir et al., 2014; Dyke et al., in prep.) are individual variants or age classes of the same taxon, However, we do not agree with Averianov's (2014) primary assumptions: that sympatric azhdarchids should be assumed to be conspecific by default and that small and midsized specimens must automatically be assumed to be juveniles of the giant taxa found in the same strata. Averianov's (2014) philosophical approach to taxonomic lumping is demonstrated both by his adoption of Martill and Naish's (2006) now abandoned and very much out of date proposal that *Thalassodromeus sethi*, *Tupuxuara longicristatus,* and *Tup. leonardii* are synonymous, and by his assumption that scattered azhdarchid remains recovered from diverse horizons and localities should all belong to the same species (*Azhdarcho lancicollis*), despite differences in morphology and size. In any case, it should be recognized that our hypotheses concerning the taxonomic validity of the azhdarchids we describe (*Eurazhdarcho* and R.2395) revolve around the observation of anatomical criteria (including vertebral proportions) that allow these specimens to be distinguished as putative taxa.

In addition to azhdarchids, supposed records of pteranodontid pterosaurs (estimated wingspan <1 m) have also been reported from Maastrichtian deposits at Sînpetru in the Haţeg basin (Jianu et al., 1997; Weishampel and Jianu, 2011). Further work is required to determine the affinities of these specimens in light of newly collected elements from across Haţeg Island, but if they are pteranodontids they are significant in demonstrating the presence of this lineage in Maastrichtian sediments (Pteranodontidae is otherwise unknown in sediments younger than those of the lower Campanian) and would imply additional niche partitioning within this pterosaur assemblage.

An even smaller (reported as possibly young juvenile) azhdarchid was identified in the Oarda de Jos-Sebeş (OdA) microvertebrate assemblage on the basis of two small edentulous jaw fragments, (Jipa, 2012). Additionally, an alleged fifth component of the Haţeg Island pterosaur fauna was also presented based on a fragmentary cranial crest allocated to an "anachronistic" medium-sized azhdarchoid identified as representing the new thalassodromid species "*Thalassodromeus sebesensis*" (Grellet-Tinner et al., 2013; Grellet-Tinner and Codrea, 2014). In fact, this fragmentary specimen is not from a pterosaur at all but, a partial plastron of the stem-turtle *Kallokibotion* (Dyke et al., 2014). Finally, additional small to medium-sized pterosaur specimens have also been collected from upper Campanian and Maastrichtian sediments in the Sebeş area, notably from the Petreşti-Arini, Oarda de Jos, and Şard vertebrate localities (Vremir et al., in press).

Regarding Nopcsa's elusive small pterosaur remains from the Haţeg basin, previously referred to ?*Ornithocheirus* (Nopcsa, 1926), only one incomplete notarium has so far been relocated (Jianu et al., 1997; Ösi and Fözy, 2007; Weishampel and Jianu, 2011). This specimen (MAFI Ob.1948) was collected by Hungarian geologist Gyula Halaváts in the early 1890s in the eastern Haţeg basin (Nopcsa, 1899), but its true identity was only recently recognized: it is a fragmentary sacrum of a maniraptoran theropod dinosaur (Ösi and Fözy, 2007). Various ornithocheirid-like pterosaur teeth have also been mentioned from the Haţeg basin (Nopcsa, 1914; Csiki et al., 2009), but we consider these to most likely belong to small titanosaurian sauropods (Vremir et al., 2011). The other remaining pterosaurian bones mentioned by Nopcsa are apparently lost. The only other small (wingspan 2–3 m) pterosaur specimen known to date from the Haţeg basin is a fragmentary distal wing phalanx (UBBG Bo1), collected by one of us (M.V.) from the Ciula-Densuş Formation of the Boiţa locality (Vremir et al., 2011). This specimen is not accessible to us for study.

Our current limited dataset does not permit detailed insight into the specific paleoecological differences between the Haţeg Island pterosaurs, but we speculate that the shorter, proportionally wider R.2395 (presumably representing part of the neck that was proportionally shorter and wider overall than the necks of other azhdarchids) may have been offered greater mechanical strength than the more elongate and slender necks of other azhdarchid taxa. This, along with its larger size, may have facilitated the capture of larger prey or the use of a more stressful foraging mechanism than that present in its contemporary *Eurazhdarcho*, thus preventing direct competition for resources (cf. Vremir et al., 2013a). More fossils, and particularly cranial material, are clearly needed to corroborate these speculations.

Finally, our inferred small body size for the R.2395 animal is of further significance when considered within the context of pterosaur body-size evolution. As discussed above, both the bone texture of this element and its well-defined tubercles strongly suggest that it comes from a morphologically mature individual. It has been argued that small pterosaurs are largely or entirely absent from the Late Cretaceous (e.g., Butler et al., 2013; Benson et al., 2014), a factor that may have played a part in pterosaur extinction at the end of the Mesozoic (Unwin, 2006; Witton, 2013). R.2395 augments the 3 m wingspan (or smaller) *Eurazhdarcho* and the 2.5 m span *Montanazhdarcho minor* (McGowen et al., 2002; Vremir et al., 2013) from the Campanian-Maastrichtian, suggesting that smaller pterosaurs may not be as rare in this interval as has been suggested (Benson et al., 2014). Moreover, in the latest Cretaceous deposits of Romania, pterosaur fossils belonging to medium or small size classes are actually more abundant than are very large or giant ones, with the latter comprising less than 30% of the sample of more than 50 confidently identified specimens (Vremir et al., 2011; Dyke et al., in prep.). We subsequently question whether the increasing rarity of smaller pterosaurs throughout the Cretaceous is actually a taphonomic effect caused by an apparent increase in the terrestrialization of pterosaur faunas (Buffetaut et al., 1997;

Butler et al., 2013; Benson et al., 2014). If true, this taphonomic artifact may imply the existence of many small pterosaur species in habitats usually not conducive to fossilization of their thin-walled bones. Benson et al. (2014) analyzed pterosaur size distribution across time and reported evidence for Cope's rule (a trend towards ever-larger body sizes). While the evidence for this trend is based on a preponderance of evidence and would not be destroyed by one or two additional data points, the existence of nongigantic pterosaurs in the Late Cretaceous would be noteworthy in view of the general trend otherwise reported.

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