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Anterior ossicone variability in *Decennatherium rex* Ríos, *et al.* 2017 (Late Miocene, Iberian Peninsula)

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ABSTRACT: The recovery of a new partial cranium of *Decennatherium rex* Ríos *et al.* 2017 bearing two anterior and two posterior ossicones from the Late Miocene deposits of the site Batallones-10 (MN-10, Cerro de los Batallones, Madrid Basin) sheds light on the complex variability of the cranial appendages of these extinct giraffids. The special features of the anterior ossicones of BAT10'18-C6-40, each formed by two bosses and separated by a septum increase the range of morphological variability found in the anterior ossicones of giraffids. Posterior ossicone variability has already been described in several sivatherine taxa as *Sivatherium maurusium* (Harris, 1974) but anterior ossicone variability has never been discussed for four-ossicone taxa. This new specimen accounts for the third morphotype found in *D. rex* anterior ossicones. BAT10'18-C6-40 is identified as an adult *D. rex* male on the basis of the development of the posterior ossicones. These are large and already show the first large bump which in this taxon is always located on the middle of the dorsal surface at a similar height on the right and left ossicones which agrees with Solounias (1988) who stated that these small irregular protuberances have a somewhat fixed position, suggesting a genetic basis. This new specimen represents a new example of cranial variability in *D. rex*, and makes it the extinct giraffid with the largest anterior ossicone variability found so far.

KEY WORDS: Cerro de los Batallones, development, Giraffidae.

1. Introduction

The genus *Decennatherium* was erected by Crusafont (1952) for the description of giraffid dental and postcranial material from the Vallesian Late Miocene deposits of Nombrevilla and Los Valles de Fuentidueña (MN9, Spain). He not only erected a new genus but also a new species *Decennatherium pachecoi* (Crusafont 1952; Ríos *et al.* 2016). The new addition to the genus, *Decennatherium rex* was described by Ríos *et al.* (2017) based on abundant skeletal material from the MN10 deposits of Cerro de los Batallones, specifically Batallones-10, that with more than a 60% of giraffid remains (Martín-Perea *et al.* 2021) constitutes one of the most complete samples of the giraffid fossil record. This abundance is reflected in the hundreds of *D. rex* remains found on the site, many of them in anatomical connection, allowing for the first description of giraffid vestigial metapodials and hyoid bones as well as the complete ontologenetic series of the skulls of the taxon.

The estimated height of *D. rex* to the cross is ~2 m and ~2.8 m to the top of the ossicones, and a body mass ranging from 776,7 to 1367,1 kg, very similar to the weight of an adult extant *Giraffa* and heavier than an adult *Okapia* (Ríos *et al.* 2017, Fig. 1). The results of the Ríos *et al.* (2017) cladistic analysis show *Decennatherium* as a basal offshoot of a clade containing the gigantic samotheres and sivatheres, characterised by the presence of a *Sivatherium*-like headgear among other features.

Decennatherium rex is the earliest example of the basic *Sivatherium*-like headgear (Ríos *et al.* 2017, figs 3–5 and 32–33). This consists of a four-ossicone pattern with two small anteriorly-oriented frontal ossicones plus two much larger, caudally-oriented and curved, fronto-parietal ossicones covered by numerous longitudinal ridges. The Iberian *Birgerbohlinia schaubi* from the Turolian of Piera and Crevillente-2 shows a larger version of *D. rex* ossicones, and the gigantic *Sivatherium hendeyi* from the Pliocene and *Sivatherium giganteum* and *Sivatherium maurusium* from the Pleistocene of Africa show the most extreme versions of this plan (Ríos *et al.* 2017, figs 32–33).

The variability of the posterior ossicones is extensively described within this clade (Ríos *et al.* 2017; Ríos & Morales 2019) and has also been described in several sivatherine taxa

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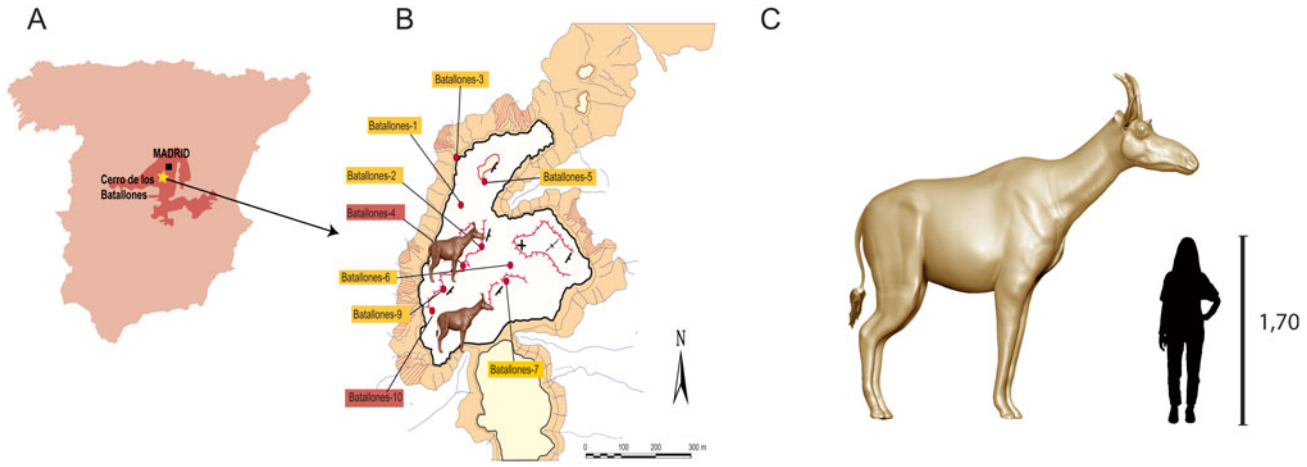

Figure 1. Location of Cerro de los Batallones.: (a) location of Cerro de los Batallones (yellow star) within Spain (modified from Calvo *et al*. 2013); (b) map of Cerro de los Batallones and location of the fossil sites bearing giraffid remains (modified from Calvo *et al*. 2013); and (c) size of *Decennatherium rex* (illustration by O. Sanisidro).

as *S. maurusium* (Harris 1974). There are both sexual and ontogenetic differences in *Decennatherium* ossicone development with two morphotypes described so far for both anterior and posterior ossicones, with males and older adults having larger, wider and more ornamented ossicones,

2. Geological background

The fossil site-complex of Cerro de los Batallones (Batallones butte) is located near the town of Torrejón de Velasco (Madrid province, Late Miocene, MN10, ca. 9.1 Ma), between the Jarama River Valley and the Prados-Guatén Depression in the central area of the Cenozoic Madrid Basin (Calvo *et al*. 2013). The fossil sites were found during mining operations at the butte (1991–2008) for the extraction of sepiolite. The fossil site-complex of Batallones comprises a system of nine, non-interconnected distinct sites located on the structural butte deposited in terrestrial environments during the early Vallesian (early Late Miocene, ca. 9 Ma) (Fig. 1a, b). Batallones-10, discovered in 2007, was the last fossil locality discovered in Cerro de los Batallones (Fig. 1b). Though all sites are Vallesian in age, there are slight differences in composition of micro-mammals and macro-mammals among the different fossil deposits that were attributed to minor temporal differences, indicating that Batallones-10 is older than the rest of the sites. The Cerro de los Batallones sites are hosted in cavities with an hourglass-shaped vertical profile, formed due to pseudokarstic processes in the Late Miocene (Pozo *et al*. 2004; Calvo *et al*. 2013). These cavities were scattered throughout a woodland landscape with wooded grassland patches (Domingo *et al*. 2013, 2016).

The most important of the herbivore-dominated assemblages in Cerro de los Batallones is Batallones-10. This site was discovered in 2007 and contains several autochthonous multitaxic assemblages. A total of 15 large-mammal species are documented, including: hipparionine horses (*Hipparion* sp.) (Romano *et al*. 2017; Sanisidro & Cantalapiedra 2017; Domingo *et al*. 2018); giraffes (*D. rex*) (Ríos et al. 2017; Ríos & Morales 2019); proboscideans (Alberdi *et al*. 2017), rhinocerotids (Sanisidro & Cantalapiedra 2017); moschids (Sánchez *et al*. 2009, 2011; Pickford 2015); and medium-sized bovids and suids. Carnivore remains are scarce, including hyaenids (Fraile 2016, 2017), and mustelids and mephitids (Valenciano *et al*. 2015, 2020; Valenciano 2017; Valenciano & Govender 2020). There is also a rich assemblage of small mammals, including insectivores, rodents and lagomorphs (López-Antoñanzas *et al*. 2010; Alvarez-Sierra *et al*. 2017; Medina-Chevarrías *et al*. 2019). Other vertebrates identified at the Cerro de los Batallones sites include birds, fishes, amphibians, and reptiles, including large and small tortoises and lizards (Morales 2017). Mortality data, with abundant young individuals and the presence of pregnant females, indicate a catastrophic process of bone accumulation mainly driven by prolonged drought (Martín-Perea *et al*. 2021). The high proportions of partially preserved or fully-articulated skeletons, and absence of carnivore feeding marks on bones, suggest that carcasses were undisturbed by predation. Rapid desiccation of soft tissues kept many of the joints intact, resulting in a high proportion of articulated remains. During drought episodes, large mammalian herbivores congregated around a shrinking waterhole, depleting the local vegetation, such that weakened individuals died of starvation and miring rather than dehydration (Martín-Perea *et al*. 2021). Given that Batallones-10 was deposited in a small waterhole (Calvo *et al*. 2013), the working hypothesis is that the Batallones-10 assemblage conforms to an attritional model, where animals died of natural causes around the waterhole that they habitually visited (Martín-Perea *et al*. 2021). Therefore, the assemblage was the result of a gradual, attritional mortality profile often observed in sites frequented by taxa over long periods of time, such as watering holes (Agenbroad 1978; Barnosky 1985). The site is placed in the middle of the occurrence of the Vallesian Crisis, a period of profound faunal reorganisation related to global changes in climate seasonality (Domingo *et al*. 2014; Gómez-Cano *et al*. 2014; Azanza *et al*. 2017; Blanco *et al*. 2018, 2021) that may have affected the possibilities of survival in the area.

3. Materials and methods

3.1. Material

The description is based on a new partial cranium of *D. rex* bearing two anterior and two posterior ossicones from the Late Miocene deposits of the site Batallones-10 curated by the MNCN-CSIC (Madrid, Spain). The comparative material of *D. rex* also comes from the MNCN-CSIC collections. Comparative crania data of *Birgerbohlinia schaubi* come from Piera (Torrent dels Traginers, Piera, MN11) and from Crevillente-2 (Crevillente, Alicante, MN11), and are curated by the Institut Català de Paleontologia (Sabadell, Spain) and the Museo de Geologia de la Universidad de Valencia (Burjasot, Spain). Other cranial data were collected from material curated by the American Museum of Natural History (New York, USA), the

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Natural History Museum (London, UK), the Muséum national d'histoire naturelle (Paris, France), and the Naturhistorisches Museum Wien (Vienna, Austria).

3.2. Measurements

We mostly follow the measurements proposed by Ríos *et al.* (2017) for the skull Ríos *et al.* (2017: Online S1, Figs S1.1, S1.2). All measurements are presented in Table 1. We took all measurements with Mitutoyo digital calipers.

3.3. Nomenclature

For anatomical nomenclature of the cranial skeleton we follow Barone (1999), and the terminology proposed by Bärmann & Rössner (2011), and Azanza (2000) for the dentition.

4. Systematic palaeontology

MAMMALIA Linnaeus, 1758
CETARTIODACTYLA Montgelard *et al.* 1997
RUMINANTIA Scopoli, 1777
PECORA *sensu* Webb & Taylor, 1980
GIRAFFIDAE Gray, 1821
Genus *Decennatherium* Crusafont, 1952
D. rex Ríos *et al.* 2017
(Fig. 2)

4.1. Etymology

Rex, Latin for king.

4.2. Emended diagnosis

A large giraffid with two pairs of ossicones. Smaller anterior pair located above the orbits and anteriorly oriented, and variable as it can show a single ossification point or that each be formed by two bosses and separated by a septum. Larger posterior pair located posterior to the orbits and posteriorly oriented. Posterior ossicones curved, showing a high number of ridges on their surface. Middle indentation of the hard palate slightly posterior to the M3. Broad occipital. Long premaxillae. Elongated diastema. p3 lacking mesolingual conid. Slightly molarised p4. Cervical vertebrae of medium length. Scapula with acromion. Robust postcranial skeleton. Metacarpals of medium length showing a medium depth palmar trough. Differs from *Decennatherium pachecoi* in: p3 with an isolated wall-like mesolingual conid structure; anterior stylid and conid of the p3 always present; and more robust metapodials.

4.3. Holotype

BAT10'13-E2-69, skull with ossicones and mandible.

4.4. Paratypes

The remaining referred material from Batallones-10.

4.5. Locality, age and horizon

Batallones-10, Cerro de los Batallones, late Vallesian, MN 10, local zone J, Madrid province, Spain. (ca. 9 Ma) (Fig. 1).

4.6. Material

BAT10'18-C6-40, partial cranium bearing two anterior and two posterior ossicones (Fig. 2).

Table 1. Comparative measurements of *Decennatherium rex* ossicones

Species	Locality	Country	Epoch	Museum	Specimen number	Morphotype	Element	1	2	5	6
D. rex	**Batallones-10**	**Spain**	**MN10**	**MNCN**	**BAT-10'18-C6-40**	**II**	**Posterior Right**	**333**	**326**	**250**	**80**
D. rex	**Batallones-10**	**Spain**	**MN10**	**MNCN**	**BAT-10'18-C6-40**	**II**	**Posterior Left**	**345**	**340**	**240**	**80**
D. rex	**Batallones-10**	**Spain**	**MN10**	**MNCN**	**BAT-10'18-C6-40**	**II**	**Anterior Right**	**10**		**170**	
D. rex	**Batallones-10**	**Spain**	**MN10**	**MNCN**	**BAT-10'18-C6-40**	**II**	**Anterior Left**	**13**		**175**	
D. rex	Batallones-10	Spain	MN10	MNCN	BAT-10'13-E2-69	II	Posterior Left	382	332	260	75
D. rex	Batallones-10	Spain	MN10	MNCN	BAT-10'13-E2-69	II	Posterior Right	360	305	260	82
D. rex	Batallones-10	Spain	MN10	MNCN	BAT-10'13-E2-69	II	Anterior Left	65	70	150	65
D. rex	Batallones-10	Spain	MN10	MNCN	BAT-10'13-E2-69	II	Anterior Right	30	50	112	65
D. rex	Batallones-4	Spain	MN10	MNCN	BAT-04'00-37	II	Posterior Left	400	324	290	97
D. rex	Batallones-4	Spain	MN10	MNCN	BAT-04'00-37	II	Posterior Right	410	333	295	95
D. rex	Batallones-4	Spain	MN10	MNCN	BAT-04'00-37	II	Anterior Right	25	40	130	47
D. rex	Batallones-4	Spain	MN10	MNCN	BAT-04'00-37	II	Anterior Left	20	20	120	
D. rex	Batallones-10	Spain	MN10	MNCN	BAT-10'08-G3-91	I	Posterior Right	237	215	192	38
D. rex	Batallones-10	Spain	MN10	MNCN	BAT-10'08-G3-91	I	Posterior Left	225	195	228	43
D. rex	Batallones-10	Spain	MN10	MNCN	BAT-10'08-G3-91	I	Anterior Right	15	19	81	24
D. rex	Batallones-10	Spain	MN10	MNCN	BAT-10'08-G3-91	I	Anterior Left	18	22	71	22
D. rex	Batallones-10	Spain	MN10	MNCN	BAT-10'09 F3-102	I	Posterior Right			218	
D. rex	Batallones-10	Spain	MN10	MNCN	BAT-10'09 F3-102	I	Posterior Left	245	220	206	37
D. rex	Batallones-10	Spain	MN10	MNCN	BAT-10'09 F3-102	I	Anterior Right		8	95	
D. rex	Batallones-10	Spain	MN10	MNCN	BAT-10'09 F3-102	I	Anterior Left	13	10	72	

Boldface type mentioned as new studied material.
[1]Length of the ossicone (dorsal).
[2]Length of the ossicone(ventral).
[3]Anteroposterior diameter (APD) at the ossicone base.
[4]Transverse diameter (TD) at the ossicone base.
[5]Circumference at the ossicone base.
[6]Circumference at the ossicone tip.
[7]APD at the ossicone tip.
[8]TD at the ossicone tip.
[9]Perpendicular height; of the ossicone from skull roof to tip.
[10]TD at the middle of the ossicone.
[11]APD at the middle of the ossicone.
[12]Distance between tips of anterior ossicones/distance between tips posterior ossicones.
[13]Distance between bases of anterior ossicones/distance between bases of posterior ossicones.
[14]Distance between bases of anterior and posterior ossicones of the same side.

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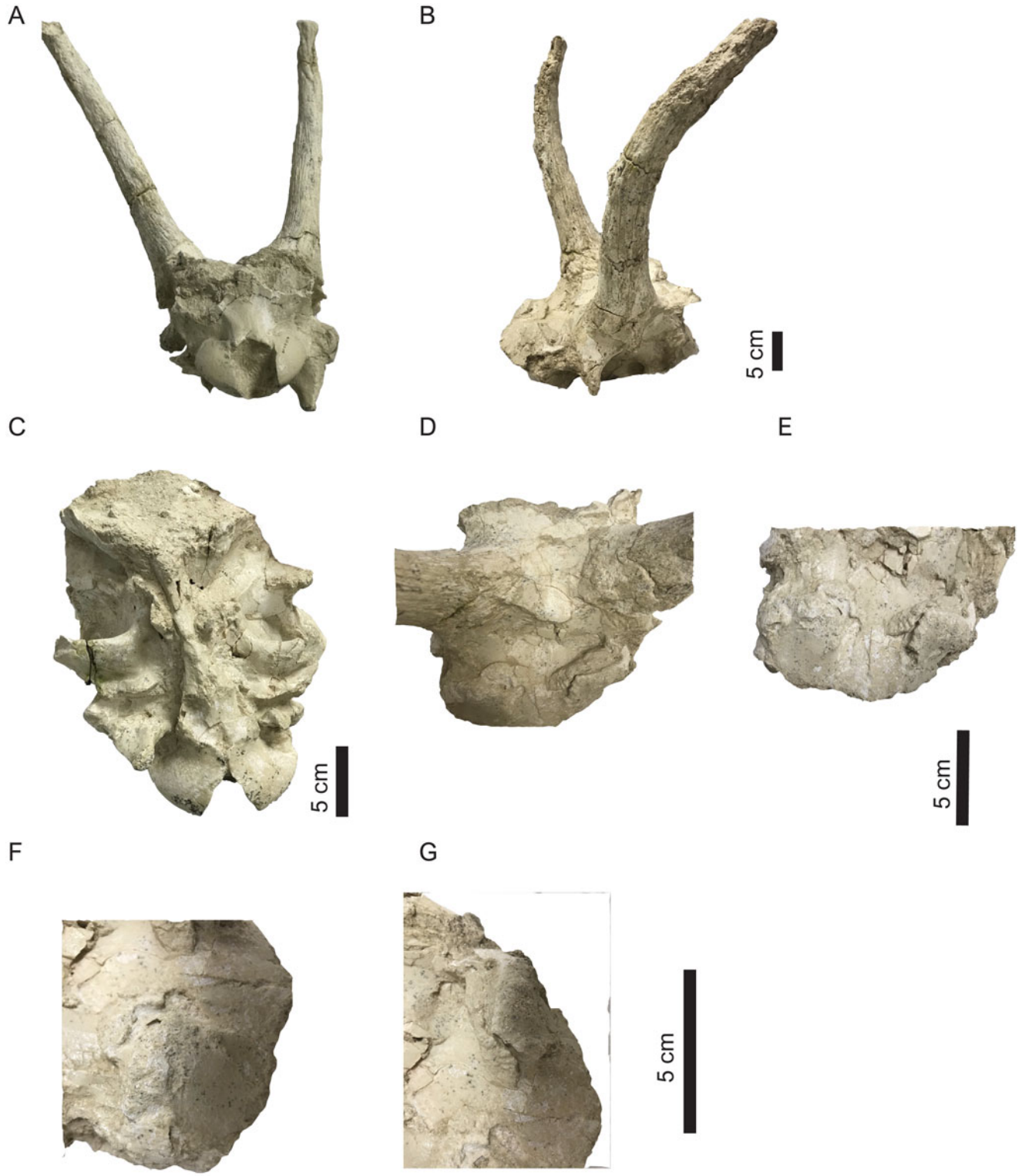

Figure 2. BAT10'18-C6-40, skull fragment of *Decennatherium rex* bearing four ossicones: (a) posterior view; (b) medial/lateral view; (c) ventral view of the basioccipital region; (d) dorsal view; (e) close-up of the right anterior ossicone; and (f) close-up of the left anterior ossicone.

5. Description

BAT10'18-C6-40 (Figs 2, 3), is a partial skull bearing two anterior and two posterior ossicones. The anterior ossicones are frontal and each of them is formed by two asymmetrical bosses. Each one is separated by a deep septum that reaches the skull roof and runs diagonally to the sagittal skull plane (Fig. 3). They reach a vertical height of 13 mm. The anterior boss is larger occupying three-quarters of the total anterior ossicone area. The posterior ossicones are long, reaching 345 mm in length, and are located posterior to the orbits over the parietals. They are oriented posteriorly and slightly outwards. The posterior ossicones are curved, ornamented by numerous surface ridges, which run longitudinally from the base to the tip of the ossicone. There is a large swelling located dorsally on the middle of the ossicone at a similar height on the right and left ossicones. The apices are blunt. The surface of the ossicones is very porous, similarly to the surface of the ossicones of extant *Giraffa*. This may indicate that even with their large size they were covered in hair, irrigated by the cornual artery. There is no development of the frontal sinus to hollow the ossicones.

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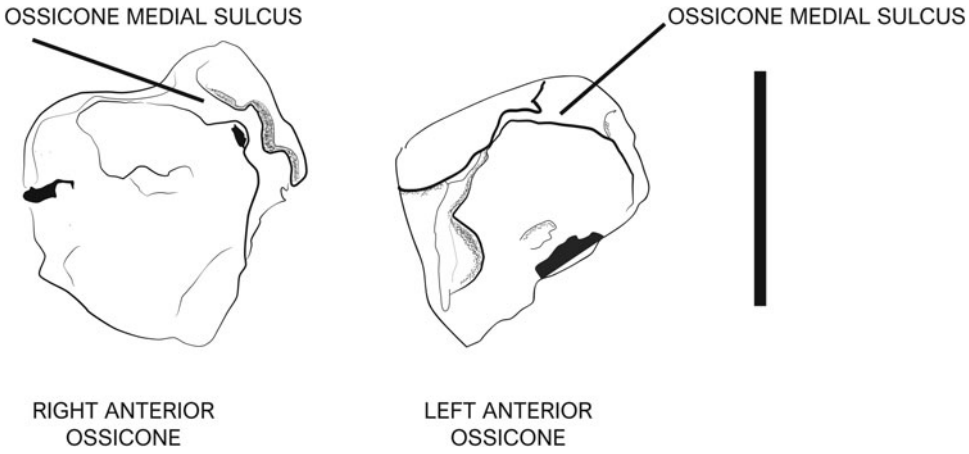

Figure 3. BAT10'18-C6-40: anterior ossicones interpretative drawing showing the medial sulcus.

In ventral view the foramen magnum is rounded and deep with a deep intercondylar groove. The retroarticular process expansion is not fused to the bullae, which are not very developed. The auditory meatus is rounded and laterally oriented. The basioccipital muscular tubercles of the occipital are very prominent. Measurements are detailed in Table 1.

6. Discussion

6.1. Ontogenetic state

BAT10'18-C6-40 corresponds to *D. rex* Morphotype II (Fig. 4) as it shows a higher development in both anterior and posterior ossicones than Morphotype I (Ríos *et al*. 2017). Morphotype II most likely corresponds with adult males (Ríos & Morales 2019). BAT10'18-C6-40 only has the first swelling or bump that appears in *D. rex* males' ontogenetic process as a consequence of secondary bone deposition, indicating that it was not too advanced in its ontogenetic development – older males show a much higher number of dorsal ventral and lateral swellings resulting from this secondary bone may be related to the age of the individual. This agrees with Solounias *et al*. (1988) who stated that these small irregular protuberances have a somewhat fixed position, suggesting a genetic basis.

6.2. Anterior ossicone variability

Posterior ossicone variability has already been described in several sivatherine taxa as *S. maurusium* (Harris 1974) and *D. rex* (Ríos *et al*. 2017; Ríos & Morales 2019) (Fig. 3), but anterior

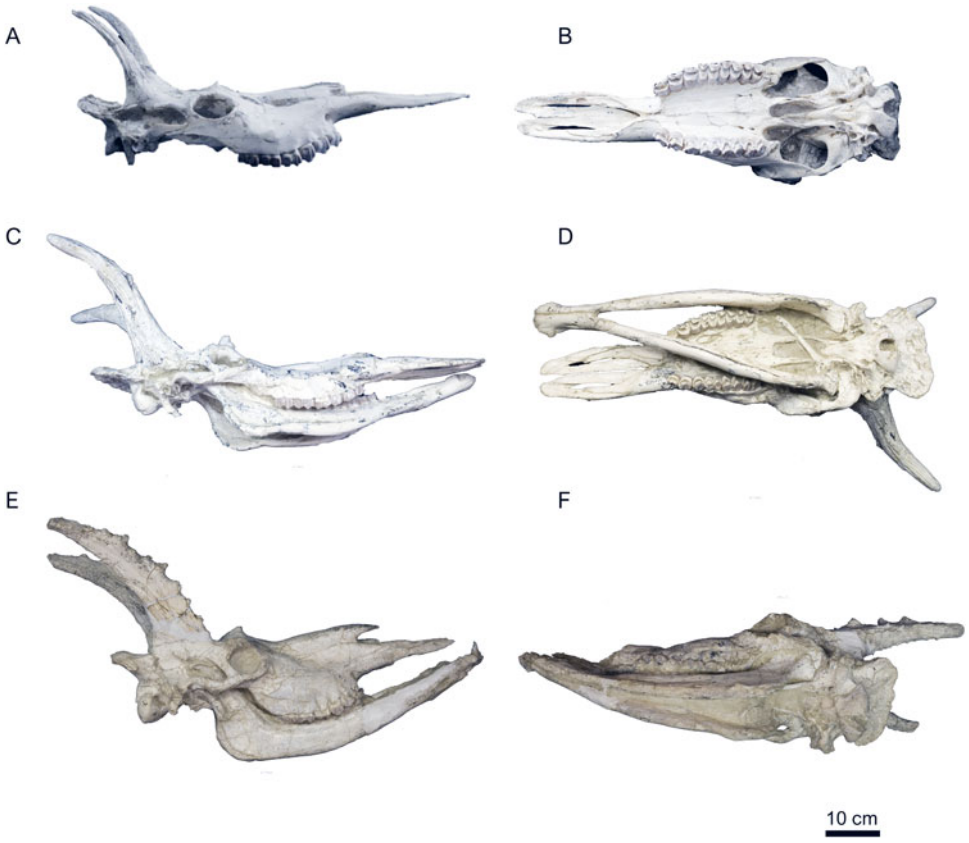

Figure 4. *Decennatherium rex* skulls showing ossicone variability: (a, b) BAT-10'08-G3-91, morphptype I (female) skull in (a) medial/lateral view; (b) ventral view; (c, d) BAT10'13.E2-69, morphptype II (male) skull in (c) medial/lateral view; (d) ventral view; (e, f) BAT-04'00-37, morphptype II (old male) skull in E medial/lateral view; and (f) ventral view.

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ossicone variability has never been discussed for four-ossicone giraffid taxa. All anterior ossicones found in both previously described *D. rex* morphotypes arise from a single osteological base; however, BAT10'18-C6-40 accounts for a third morphotype found in *D. rex* anterior ossicones (Ríos *et al.* 2017; Ríos & Morales 2019). BAT10'18-C6-40 is identified as an adult *D. rex* male not very advanced in age on the basis of the development of the posterior ossicones and the development of the middle dorsal swelling. However, its anterior ossicones differ, as usually the smaller anterior pair in males is more developed, conical, and is anteriorly oriented forming an angle with the skull roof of approximately 60°, while reaching 65 mm in height. Morphotype I (females) anterior and posterior ossicones are less developed than in BAT10'18-C6-40 and the anterior ossicones are reduced to unattached little circular discs with a pointy projection in the middle, and the slenderer posterior ossicones range from 225 mm to 270 mm in length. The distance between the bases of the anterior and posterior ossicones in morphotype II also differs, doubling morphotype II in comparison to that of morphotype I (~80 mm vs ~40 mm). According to Harris (1974), his disparity in size and development of the bumps in giraffid posterior ossicones may represent individual variability, but it is also possible that the amount of secondary bone apposition, in the form of ornamentation, may be a function of the age of the individual. However, the morphological disparity of the anterior ossicones of BAT10'18-C6-40 clearly accounts for a third anterior ossicone morphotype in *D. rex*, specifically a second variant of morphotype II. This new morphotype and this high degree of anterior ossicone variability may be related to the specimen being a male (which deposit more secondary bone) as well as the ontogenetic state of the individual. This new specimen represents a new example of cranial variability in *D. rex*, and makes it the extinct giraffid with the largest anterior ossicone variability found so far in the fossil record.

7. Conclusions

The recovery of a new partial cranium of *D. rex* Ríos *et al.* 2017, bearing two anterior and two posterior ossicones from the Late Miocene deposits of the site Batallones-10 (MN-10, Cerro de los Batallones, Madrid Basin), sheds light on the complex variability of the cranial appendages of these extinct giraffids. The special features of the anterior ossicones of BAT10'18-C6-40, each formed by two bosses and separated by a diagonally placed septum, increase the range of morphological variability found in the anterior ossicones of giraffids. Posterior ossicone variability has already been described in several sivatherine taxa but anterior ossicone variability has never been discussed for four-ossicone taxa. This new specimen accounts for the third morphotype found in *D. rex* anterior ossicones (Ríos et al. 2017; Ríos & Morales 2019). BAT10'18-C6-40 is identified as an adult, but not elderly, *D. rex* male on the basis of the development of the posterior ossicones. These are large and already show the first large bump, which in this taxon is always located on the middle of the dorsal surface at a similar height on the right and left ossicones (Ríos *et al.* 2017), agreeing with Solounias *et al.* (1988) on the hypothesis of these small irregular protuberances having a genetic basis for their fixed position. This new specimen represents a new example of cranial variability in *D. rex*, and makes it the extinct giraffid with the highest anterior ossicone variability found so far.

8. Acknowledgements

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9. Competing interest statement

None.

10. References

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