

New fossils of the early Miocene stem-cervid *Acteocemas* (Artiodactyla, Ruminantia) from the Iberian Peninsula shed light on the evolutionary origin of deer antler regeneration

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ABSTRACT

Acteocemas, a very poorly documented early Miocene stem-cervid, is one of the first ruminants bearing antler-like appendages, which has provided a ground for discussion on the origin of antlers. We describe a new and very complete appendage from the site of Sant Andreu de la Barca (Spain) together with some other unpublished specimens from the nearby Costablanca attributed to *Acteocemas* aff. *infans*, compare with fossils from elsewhere in Europe (including the *A. infans* holotype), and perform micro-CT scans. Findings provide new empirical data that *Acteocemas* protoantlers were able to be cast and re-grown. However, microstructural analyses suggest that the protoantler lifespan could be longer than that of modern antlers, preventing from assuming a similar cycle. Results support that increased seasonality associated to a drop in global temperatures played a role in the origin of antler regeneration, and that deciduousness (through bone shedding) was an efficient way for (male)deer to reduce the seasonal leftover of bone mass. The early evolution of deciduousness, as in the probable irregular protoantler cycle of *Acteocemas*, was limited by the warming ca. 17-15 Ma, whereas the emergence of antlers with coronet was concomitant with the second increase in seasonality associated to the cooling ca. 15-13 Ma.

KEYWORDS: Cervidae; Evolution; Antler; Palaeohistology; Palaeophysiology

Introduction

The abundant and large fossil record of antlers—the apophyseal branched bony cranial appendages of deer (Ruminantia, Cervidae) remarkable by their ability to be regularly shed and regenerated in an annual cycle—allows us to trace back the early evolution of cervids to the early Miocene (Azanza 1993a; Gentry 1994, 2000; Gentry et al. 1999; DeMiguel et al. 2014; Heckerberg 2017; Azanza and DeMiguel 2019; Rössner et al. 2021). Both the complexity and the singularity among mammals of antler replacement (Kierdorf and Kierdorf 2012; Li and Suttie 2012; Landete-Castillejos et al. 2019) in tandem with the well-established monophyly of the Cervidae (Gilbert et al. 2006; Hassanin et al. 2012; Chen et al. 2019) indicate a single origin for this structure within Ruminantia. Despite this, it has been a matter of discussion whether antlers derived from another type of cranial appendage or—taken into account the great differences in growth, development and microstructures among ruminant headgear—arose independently (Janis 1982; Bubenik 1983; Janis and Scott 1987; Morales et al. 1993; Gentry 1994; Davis et al. 2011; DeMiguel et al. 2014). Recently, Wang et al. (2019) pointed out that all ruminant cranial appendages probably share a common cellular origin in the neural crest stem cells. That means that the genetic / embryologic potential for developing cranial appendages is basally present at least in the crown-Pecora. However, the inclusion of fossils in phylogenetic analyses apparently contradicts the notion recently reinforced by Chen et al. (2019) and Wang et al. (2019), that the presence of cranial appendages is basal to crown-Pecora and that these structures were subsequently lost in several lineages, e.g. Moschidae (see e.g., Sánchez et al. 2015), but this seems not to be the case of the cervid *Hydropotes*. In any case, the hypothesis of antlers evolving from a pre-existent appendage appears to be now more feasible. Also, the genetic basis for antler regeneration has been recently provided and, interestingly, it seems to depend on genes in the oncogenic pathway in a group where the cancer risk is low, thus opening the possibility of a shared adaptive evolution with tumour suppressor genes in deer (Wang et al. 2019). However, despite all these recent efforts in antler research, the evolutionary origin of antler regeneration is still far from been fully understood. New research combining data from different (fossil and extant) taxa is required in order to gain new knowledge about one of the most unique mammalian anatomical developments.

Given the complexity and the physiological effort of the antler cycle—in which the regeneration process is involved—it has been assumed that deciduous antlers evolved from previous non-deciduous (Janis and Scott 1987; Gentry 1994) or facultative perennial (Bubenik 1990a) antler-like appendages. During the early Miocene, three Eurasian lineages (the two stem-cervids Procervulinae and Dicrocerinae, as well as the problematic Lagomerycidae, now placed very closely to Cervidae and considered to be its sister-group, if not a stem-cervid group) are known to have exhibited antler-like appendages that consist of long pedicles and branched protoantlers (Azanza 1993a; Azanza and Ginsburg 1997), leading to discussion on the process

of antlerogenesis (DeMiguel et al. 2014; Heckerberg 2017; Rössner et al. 2021). The absence of a true coronet or burr —i.e., a coarse bony rim developed at the base of the regenerated antler that starts to be recorded in the middle Miocene—, coupled with several differences in growth and bone histology with modern antlers, have been largely used to discard the deciduousness of these early Miocene protoantlers (Janis and Scott 1987; Bubenik 1983, 1990a; Gentry 1994), and hence their homology with antlers has been discussed (see for a review DeMiguel et al. 2014; Heckerberg 2017; Rössner et al. 2021). However, cast specimens have been recognised in all the early Miocene lineages recorded as early as MN3 (20 to 17 Ma, Larrasoña et al. 2006) sites (Ginsburg 1985a; Ginsburg and Bulot 1987; Azanza 1993a; Azanza and Ginsburg 1997; Azanza et al. 2011; Heckerberg 2017; Rössner et al. 2021). Thus, and although the death of protoantler tissues by ischemia has not been already demonstrated (Bubenik 1990a; Azanza and Ginsburg 1997) —except in the middle Miocene *Dicrocerus* (Azanza et al. 2011)—, a recent increasing knowledge of these cast protoantlers indicates that the casting process occurred by osteoclastic bone resorption in a similar way to modern-type antlers. By contrast, the protoantler bone regrowth is poorly evidenced (Rössner et al. 2021) and, hence, the regeneration process of these early Miocene antlers is still poorly documented despite being presumed as likely. Therefore, the deciduous nature could be inherent of the cervid headgear (DeMiguel et al. 2014; Heckerberg 2017; Rössner et al. 2021). Thus, two alternative hypotheses regarding the processes and mechanisms of regulation in the antler cycle have been proposed. On the one hand, some authors consider that these processes were acquired in a single step basally in cervid evolution (Rössner et al. 2021) while, on the other hand, others propose that they were acquired through two steps related to early-middle Miocene major climatic events (Azanza 1993a; Azanza and Ginsburg 1997; DeMiguel et al. 2014; Azanza and DeMiguel 2019).

Among early Miocene cervids, two different dichotomously forked antler-bearing lineages have been recognised in Western and Central Europe: *Procervulus* (Procervulinae) and *Acteocemas* (Dicrocerinae), with the distinction (both morphological and systematic) between them being not always clear. *Acteocemas* is a very rare genus whose protoantlers seem to show a coronet-like structure (Ginsburg 1985b, 2005b; Ginsburg et al. 1987), in contrast to the more commonly found *Procervulus* protoantlers. Current knowledge on *Acteocemas* has been mainly restricted to the type specimens of *A. infans* (Stehlin, 1939) (Chilleurs, France) and *A. beatrix* Ginsburg et al., 1987 (Chitenay, France) (Ginsburg 2005b). A set of appendages on a skull roof recently discovered in Switzerland has been also attributed to *Acteocemas* (Costeur et al. 2014; Rössner et al. 2014), but the study of this material is pending.

The presence of *Acteocemas* in the Iberian Peninsula has been very poorly documented and, consequently, it is highly rebuttable (Azanza 2000), with the clearest evidences coming from the Vallès Penedès Basin (Catalonia, Spain) (Crusafont et al. 1955; Azanza and Menéndez 1989/90). In this regard, a new and very complete appendage specimen recovered in the Baix

Llobregat sub-Basin, offers a unique opportunity to improve our knowledge of the processes and mechanisms of early antler deciduousness. Here we analyse (from morphological and histological viewpoints) this new specimen and compare it with other remains previously recovered in the nearby area and elsewhere in Europe, and outline the biochronological framework of *Acteocemas*. Also, we perform a microstructural study based on micro-CT scans to examine histological details and to discuss the histological properties of the appendage within the frame of antler deciduousness, in order to comprehend crucial questions on the early evolution of antler replacement.

Geological framework, material and methods

Among the North Eastern Iberian basins, which are well known for their densely sampled record of Miocene mammals, the half-grabens of the Vallès-Penedès and Baix Llobregat Basins have delivered the early deer remains subject of this work (Figure 1a). While the Baix Llobregat Basin is mostly infilled by early Miocene continental and middle Miocene marine sediments which are discordantly covered by Early Pliocene layers (Casanovas-Vilar et al. 2011a), in the Vallès-Penedès Basin the sedimentation continued throughout the Miocene. The early Miocene layers form part of the Lower Continental Complexes lithostratigraphical unit and crop out in the south-eastern border where thickness is markedly lower (Cabrera 1981; Cabrera et al. 2004).

Acteocemas fossils from the Vallès-Penedès Basin come from Ca n'Obac (=Can Ubach) — an isolated finding in red lutites of the basal levels of the early Miocene in the Rubí area (Crusafont et al. 1955)—, and Costablanca (Azanza and Menéndez 1989/90). The site of Costablanca I is located in dark red lutites at the bottom of the Miocene formation (Crusafont et al. 1955) that crops out at the border between the municipalities of Castellbisbal and Martorell (Casanovas-Vilar et al. 2011a, 2011b) directly overlying the local basement of Paleozoic schists. Also, the fossiliferous marls and interbedded limolites of Costablanca II levels constitute the basal part of a thick succession of carbonates and lutites with a marked cyclicity (Crusafont et al. 1968; Casanovas-Vilar et al. 2011a, 2011b) that corresponded to short-lived shallow lacustrine systems intercalated with distal alluvial fan facies (Cabrera 1981). These levels also delivered a nicely preserved macroflora (Sanz de Siria 1981, 1994). The two mammal sites of Costablanca mainly delivered isolated macrovertebrate remains (Crusafont et al. 1955, 1968) with some micromammals. Casanovas-Vilar et al. (2011a, 2011b) correlate the micromammal assemblages with the “cricetid vacuum” faunas (Daams and Freudenthal 1989), generally regarded as belonging to MN3 (Figure 1b). The association of *Anchitherium*, *Andegameryx* and early deer (Casanovas-Vilar et al. 2011a, 2011b) is concordant with this age (Figure 1b). Two cervid mandibles and a single astragalus from Costablanca II were attributed to *Procervulus dichotomus* by Crusafont et al. (1968) but no antlers were recovered at this time. At least, one of the mandibles (which preserves a fragment of p1, whole p2, and a fragment of

p3) does not seem to correspond to an early deer. New magnetostratigraphical data indicate that the section begins with a long reversal interval that is correlated to chron C5Dr (Casanovas-Vilar, pers. comm.), so it could be older than the French locality of Beaulieu (C5Dn, Aguilar et al. 2013) and contemporaneous to MN3b localities from the Swiss Molasse (Kempf et al. 1997) that also yielded *Acteocemas* fossils (Costeur et al. 2014; Rössner et al. 2014). The early Miocene flora recovered indicates a seasonal tropical-subtropical climate under which forests of *Cinnamomum*, *Ficus* and *Sapindus* trees, beside palms of the genus *Sabalites*, were developed around swampy areas, while xerophytic plants (*Acacia*, *Cassia*) adapted to seasonal aridity grew far away from these areas (Casanovas-Vilar et al. 2011a).

In the Baix Llobregat sub-Basin, early deer fossils come from the site of Sant Andreu de la Barca, where a similar alternation of lutites and carbonates outcrops appears. According to Agustí (1981) two outcrops separated one from the other only a few meters are recognised (SPA-1 and SPA-2). Field work carried out at the site in 1996 delivered vertebrate microfossils in four superposed levels of lutites (Agustí and Galobart 1997). However, macrofossils have been also periodically collected from the surface (Agustí and Galobart 1997), including the *Acteocemas* appendage here described. Despite some difficulties for stratigraphic correlation, the rodent association characterised by the absence of cricetids (except the muroid *Melissiodon*), and the dominance of glirids and the eomyid *Ligerimys*, points out Sant Andreu de la Barca as belonging also to MN3 faunas. Furthermore, the record of *Anchitherium* and early deer at the site, the possible occurrence of *Andegameryx* —tentatively suggested by one m1—, together with the presence of the felid *Styriofelis turnauensis* and the first representatives of *Gomphotherium* (Agustí and Galobart 1997), reinforce this interpretation. In France, the first proboscideans are recorded at the top of the MN3, apparently after the disappearance of *Andegameryx* (Ginsburg 2005a) (Figure 1b). Accordingly, the assemblage of Sant Andreu de la Barca could be younger than that of Costablanca, and perhaps of Chilleurs-aux-Bois (type locality of *Acteocemas*) where both *Andegameryx* and proboscideans are absent (Ginsburg 2005a). Nevertheless, this is a tentative conclusion due to the limited sample and the possibility that the macromammal assemblage of Sant Andreu de la Barca could be mixed as a result of sampling from diverse levels. Finally, the outlined biochronological framework circumscribes *Acteocemas* to a short time span (about 1 Myr) immediately prior to the global warming between ~16.9–14.7 Ma (Steinthorsdottir et al. 2021) known as the Miocene Climate Optimum MCO (Figure 1b).

Studied material and comparative sample

This study focuses on a new, very complete left cranial appendage (IPS12180) from Sant Andreu de la Barca (latest Ramblian, MN3) that comprises the pedicle and the protoantler, the anterior branch of which is sectioned from its base. The labels of two branch fragments bear the

same collection number. The larger one seems to show some coincidences in sections and ornamentation, so it could belong to the anterior branch whereas the smallest one is an isolated distal fragment that probably belongs to another protoantler due to its larger basal section.

This specimen has been compared with the following remains from the sites of Costablanca (late Ramblian, MN3) —which were previously reported (Azanza and Menéndez 1989/90) but never figured or described—: a nearly complete protoantler (IPS14572); a small portion of an appendage (IPS22839) that preserved the basal part of the protoantler still attached to the pedicle top; and a small portion of a frontal bone (IPS22838) with the basal portion of the pedicle. All specimens are curated by the Institut Català de Paleontologia Miquel Crusafont (ICP) in Sabadell (Spain).

Also as comparative material, we included the holotype (NMB S.O.3126) of *Acteocemas infans* (Stehlin) 1939, one unpublished cast antler (NMB S.O.3895) from the locality-type (Chilleurs-aux-Bois, France) housed in the NMB-Naturhistorisches Museum Basel (Switzerland) and a plaster mold of the holotype and single specimen of *Acteocemas beatrix* Ginsburg et al. 2000 from Chitenay (France) housed in the Muséum d'Histoire naturelle de Blois (France).

Anatomical abbreviations

L: length; **La**: length measured on the anterior margin; **Lp**: length measured on the posterior margin; **DAP**: antero-posterior diameter; **DAPb**: antero-posterior diameter measured at the basis; **DAPd**: antero-posterior diameter measured distally; **DT**: transversal diameter; **DTb**: transversal diameter measured at the basis, **DTd**: transversal diameter measured distally; **Hbif**: height of the protoantler basis measured on the medial side at the mid-point of the bifurcation; **ped** pedicle; **pa**: protoantler; **br_a**: anterior branch; **br_p**: posterior branch.

Terminology, measurements and microstructural study

We follow Bubenik (1990) and Azanza and Ginsburg (1997) in using the term "protoantler" to refer to the branched distal part of an antler-like cranial appendage without a coronet delimiting its base that is capable of detaching itself from the permanent pedicle that grows upright from the orbital roof without leaning on the braincase. Accordingly, we distinguish it from the modern-type "antler" that shows a coronet around its base and that grows from a pedicle inclined backwards and supported on the braincase.

Measurements (Table 1) of pedicles and protoantlers were taken following Azanza et al. (2011) using a digital Mitutoyo sliding calliper to the nearest of 0.1 mm. All measurements are in millimetres.

Our approach comprises the microstructural study of specimen IPS12180 using non-invasive methods. The appendage was scanned through high-resolution micro Computed Tomography

(CT) using a BioScan/Mediso Nano SPECT/CT scanner at the Instituto Aragonés de Ciencias de la Salud (IACS, Zaragoza, Spain). Scans were performed at 45 kV. The resulted voxel size is 0.07311 mm and the number of final slices is 1089. CT scans were processed using VSG-Avizo v. 7.0 (FEI Visualization Sciences Group, Hillsboro). Image thresholding was done automatically on the basis of changes in the Hounsfield units, that is, differences in the gray scale densities (Hounsfield 1973, 1976). Images of transversal, longitudinal or parasagittal, and cross sections at different locations were obtained to check how the internal tissues' densities change from the pedicle to the protoantler most distal peak. A physics color scale was applied to some images to better visualised the internal density changes of the fossil, ranging from dark blue (lowest density = air) to red (highest density). In order to interpret microstructural findings, we compared our results to available microstructural data of fossil protoantlers (Bubenik 1983, 1990; Vislobokova and Godina 1993; Azanza and Ginsburg 1997; Azanza et al. 2011; Rössner et al. 2021) and put in the context of current antler biology (Goss 1983; Bubenik 1990a, 1990b; Kierdorf and Kierdorf 2011, 2012, 2021; Li and Suttie 2012; Gomez et al. 2013; Kierdorf et al. 2013, 2021; Li 2013; Li et al. 2014; Landete-Castillejos et al. 2019) to be able to identify fundamental traits and/or patterns.

Results

Description of the specimens

Figure 2 depicts the two most important Iberian specimens: the nearly complete protoantler IPS14572 (Figure 2 a-c) and the very well-preserved left appendage IPS12180 from Sant Andreu de la Barca (Figure 2d-f) that consists of the nearly complete pedicle and most of the protoantler. According to the pointed morphology of the apices and the bone density of the surface, it is clear that the protoantler completed its growing in both specimens.

IPS12180 shows the pedicle broken just above the insertion on the frontal bone, as indicated by the medially enlarged basal section and the gentle curve at the bottom of its preserved anterior side (Figure 2e). The specimen IPS22838 from Casablanca—a small portion of the frontal bone with only the basal portion of pedicle preserved—clearly shows that the pedicle grows relatively upright from the orbit (i.e., the position on the skull is supraorbital)—. However, the preserved portion is not enough to unambiguously decide whether the pedicles are divergent in frontal view. Moreover, some doubts persist on the attribution of this specimen to *Acteocemas* due to its circular basal section.

The pedicle in IPS12180 is moderately long (about 40-45 mm, L/DAPd < 3.0) but much shorter than that seen in *Procervulus* (L/DAPd > 4,5), grows straight and is latero-medially compressed. Its section ranges from subtriangular at the bottom to elliptical at the top with rounded (i.e., without keels) anterior and posterior edges. The surface is smooth with only slight striations, especially at the top. However, there is a narrow groove on the medial side that

extends from the posterior part of the pedicle and immediately turns to the center, splitting when crossing the pedicle-antler transition area.

The protoantler has a simple, dichotomous construction with no shaft clearly developed, and it is obliquely inserted over the pedicle in IPS12180 (Figure 2d, f). There are clearly defined longitudinal grooves and ridges born just below the fork, indicating integumentary covering differences between the protoantler and the pedicle. This type of insertion is more evident in IPS14572 (Figure 2b). Another specimen badly preserved (IPS22839) shows the medial ridges beginning at a different level than the lateral ones, also indicating that the base is inclined relative to the longitudinal axis. Hence, the pedicle/protoantler transition is more clearly defined than in *Procervulus*.

The protoantler base is somewhat larger than the pedicle top. No coronet-like structure (or protocoronet) appears clearly developed in IPS12180, but some ridges show a basal swelling. This is well represented by a pronounced postero-medial ridge that appears prominently between two postero-medial and posterior wide grooves. In IPS14572, there is also a large ridge furrowing a branch (the posterior branch if a similar orientation to IPS12180 is assumed). However, the ridge development decreases suddenly from its middle part onwards. In IPS14572 a few aligned pearls following the outline of the protoantler base (Figure 2a, b) appear on the lateral side below the anterior branch (Figure 2a-b). On the medial side an irregular ridge (apparently formed by pearls) rises up from the basal part of the anterior branch (Figure 2c).

A wide channel appears on the anterior side of the protoantler base, especially on IPS14572 (Figure 2b). It is however smoother than that of the holotype of *Acteocemas* (Figure 3c, f). In IPS12180 the anterior side seems relatively flat, and the wide channel quickly splits because a ridge seems to begin more distally (though the anterior branch is sectioned from the base). A similar morphology is observed in IPS22839.

Palaeohistological results

The internal structure of IPS12180 (Figure 4, 5) shows that the appendage is composed of thick compact cortical bone and trabecular bone in the center. In the protoantler, the bone density is higher in the branch apices, but also in the medial/lateral sides of the bifurcation zone (Figure 4c) compared to the longitudinal mid-plane (Figure 4b). Interestingly, the bone density is also relatively high in the transition zone between the protoantler and the pedicle (Figure 4b), and decreases from the periphery to the center. Cross sections of the specimen (Figure 5) confirm how the trabecular bone in the center is being reduced to the longitudinal mid-plane in both the protoantler base (Figure 5b) and the pedicle top (Figure 5c). That is, the process of mineralisation seems to progress from lateral/medial to the longitudinal mid-plane, and not centrifugally as seen in *Dicrocerus* (Bubenik 1990a; Azanza et al. 2011).

Discussion

Acteocemas infans was described by Stehlin (1939) on the basis of a small incomplete appendage from the Chilleurs-aux-Bois (France; Loire Basin; Ginsburg 1990). The text-figure 11 of Stehlin (1939) reproduced this holotype (NMB S.O.3126) —a partial right frontal bearing the appendage whose branches are broken—. The specimen NMB S.O.3126 has the branches restored accordingly to this figure. It should be noted that restored parts on original antler material cannot be identified in replicas housed in the main European museums so the published drawings based on them (Azanza 2000, fig. 18; Ginsburg 2005b, fig. 1) probably distort the antler morphology. From the preserved base, the anterior branch of NMB S.O.3126 seems to be upright (i.e., parallel to the pedicle). However, the base of the posterior branch is not preserved, and consequently the reconstruction made by Stehlin (1939) is probably fictitious. It could be straight and not curved upwardly but oriented backwardly instead as in *Procervulus* or *Heteroprox*. From the pedicle top, a wide channel limited by two sharp ridges appears on the anterior side of the protoantler base, but its prolongation over the anterior branch could also be fictitious, because there is a ridge splitting this channel in two grooves that was not prolonged on the restored branch. *Procervulus* frequently has also a similar channel. Photographs of the holotype reproduced in Figure 3 (a-h) show its present state. Also, Rössner et al. (2021) (text-figs. 6a and 8i-j and online resource 15) reproduced a photograph in medial view joint to longitudinal and transversal radiographic sections based on a CT-scan.

Stehlin (1939) succinctly describes *A. infans* as possessing minute *Dicrocerus*-like protoantlers over compressed pedicles but very divergent one from another as seen in *Stephanocemas*. As a result, he named the species as *Stephanocemas infans*. Later on, Ginsburg (1985b) noted the differences between the European *S. elegantulus* and *S. infans* and the Asiatic forms included in *Stephanocemas*, thus proposing their taxonomical separation. For the smallest species Ginsburg (1985b) created the genus *Acteocemas* because its protoantler has a dichotomic construction instead of being multibranching or palmated as in the other *Stephanocemas* species.

The Iberian material shares with NMB S.O.3126 —and not with *Procervulus*— the moderately long, laterally compressed pedicles, as well as a protoantler morphology that includes a base bigger than the pedicle top which forks without any shaft producing the branches. However, the holotype of *A. infans* shows a coronet-like structure (Figure 3e-h) around the medial and lateral sides. This structure (Figure 3e-h) is conformed on its medial side by a zigzagging ridge (Figure 3e) with some sharp crests growing upwards from the upper vertices and downwards from the lower ones. However, no pearls are observed (Figure 3e). In lateral view, this structure is abraded by taphonomic modification (Figure 3g) and the protoantler base is swollen in a lower position than the medial one (Figure 3f, h), suggesting that the protoantler base could be inclined with respect to the pedicle axis, as is observed in the

Iberian form as well. An inclined-type of insertion of the protoantler onto the pedicle is typical of dicrocerines (Azanza et al. 2011). Despite the presence of a few aligned pearls in the Costablanca specimen IPS14572 (Figure 2a-b), which are perhaps indicative of a partially developed proto-coronet, a clear difference between the Iberian form and the holotype of *A. infans* is the absence of the medial zig-zag ridge. Consequently, Azanza and Menéndez (1989/90) referred the Costablanca material to *Acteocemas* aff. *infans*, and we keep here this denomination for the Iberian form following a circumspect attitude.

The French site of Chilleurs-aux-Bois has provided another protoantler specimen (NMB S.O.3895, Figure 3i-l) —not published in Stehlin (1939)— which is abraded and perhaps also gnawed. The tips of the branches are not preserved. Both the size and the main features of the holotype described previously match this specimen. The largest branch (in anterior position assuming the same orientation as in the holotype) is oriented upright and curves slightly inwards. At the anterior side, its medial edge is abrupt and the lateral one shows a ridge at the basis (Figure 3i), with a flat surface between them (Figure 3j) —that may correspond to the anterior channel in the holotype—. The posterior branch is the smallest among all the specimens and points straight at 45° from the basal plane, as in the Iberian form. Also, as in the Iberian form, the posterior side is acute. The basal surface is concave and rough, indicating that the specimen is most probably a cast protoantler, and its outline is elliptical according to a medio-laterally compressed cross-section of the pedicle. The casting is apparently produced just below the fork, contrary to procervulines that have it produced more basally (see Heckerberg 2017 fig. 2; Rössner et al. 2021 figs. 3, 5a-b, 5g-I, 6b) —indicating that a shaft gives access to the branches—. Also, in *Procervulus*, the outline of the basal surface is more rounded according to a more circular cross-section of the pedicle. There is no coronet-like structure but the antler base is slightly swollen compared to the area where the casting has been produced (i.e., the periphery is bigger than the outline of the cast surface in frontal view, Figure 3j), contrary to that observed in *Procervulus*. Although no zig-zag coronet-like structure is developed, this specimen is here ascribed to *Acteocemas infans*, and shows greater resemblance with the Iberian form.

The presence of *Acteocemas* cf. *infans* in the Calatayud-Daroca Basin was proposed by Morales and Soria (1984) and Ginsburg et al. (1987) on the basis of a single protoantler from the site of Moratilla. Since there was no report of any coronet-like structure in the specimen, Azanza and Menéndez (1989/90) and Azanza (2000) referred this specimen to ?*Procervulus* sp., whereas Rössner (1995) attributed it to *Procervulus* cf. *praelucidus*. In the light of our new findings, the assignation of this specimen to *Acteocemas* is more plausible, as the protoantler base is enlarged respect to the pedicle top —despite the strong medio-lateral compression of the protoantler—. However, the small size of the pedicle cross-section is still an issue.

At this point, a small mention to *Acteocemas beatrix* Ginburg et al. 1987 is needed. *Acteocemas beatrix* was described after a single specimen from Chitenay (France). According to

Ginsburg et al. (1987), this specimen corresponds to a right appendage composed of a rounded pedicle and a very tiny spike protoantler with a coronet-like structure. Since Chitenay is stratigraphically older than Chilleurs (Figure 1), Ginsburg et al. (1987) consider *A. beatrix* as the ancestral form. Also, due to the very small size and simple construction of the protoantler, this specimen could correspond to an ontogenetically younger animal than the holotype of *A. infans* (even if the coronet-like structure discards that it was a yearling spike). However, the frontal bone is not preserved and its orientation is uncertain, even if it corresponds to the pedicle and protoantler. In antlers, if the branch apex is cracked but keeping its original orientation, the fracture healing line is accompanied by a swelling or bony ring around the region of the break (Goss 1983). This type of injury has been described for *Dicrocerus* (Azanza et al. 2011) and can be also observed in the Asian *Ligeromeryx complicidens* affecting to one of the branches of the holotype (Young 1964, fig.1). As Chitenay is the type locality for *Ligeromeryx praestans*, this specimen could be also interpreted as a damaged branch of its multibranching protoantler. However, the presence of a groove on the pedicle top that cross the coronet-like structure and is prolonged on the protoantler resembles the channel observed in the holotype of *Acteocemas*. Hence the current status of this species is uncertain.

The evolutionary origin of antler regeneration

Antlers are unique among mammal structures in their ability to be regularly dead (exposing the bare bone), dropped (antler casting) and regenerated in an annual cycle closely linked to the seasonal changes of plasma testosterone levels (Bubenik 1990b; Lincoln 1992). It has been a long debate if antlered deer shared a last common horned ancestor with other crown ruminants or evolved independently from a hornless ancestor. Early Miocene protoantlers have been a matter of such discussion, being interpreted either as lifelong protuberances, facultative perennial appendages, deciduous antler-like appendages, or early antlers. Hypotheses about early antler deciduousness have been stimulated by bone histological studies—based on radiographs, thin sections and CT-scans—for some of these protoantlers (Bubenik 1990a; Vislobokova and Godina 1993; Rössner 1995; Azanza and Ginsburg 1997; Azanza et al. 2011; Rössner et al. 2021), but only a few specimens of the oldest representatives are available. Interestingly, the new appendages here reported have the potential to shed light on the obscure evolutionary origin of the antler cycle in which the regeneration process is involved.

The most common morpho-functional hypothesis to explain antler deciduousness is based on their functionality as both display organs and weapons for intraspecific combat. Interestingly, the function as weapons occurs once the tissues are lifeless and the antler becomes bare bone, because velveted antlers are very sensitive (Goss 1983), and also because the mechanical properties of dry antlers that allow them to be used as weapons—drying takes place after the velvet shed—are superior to those of wet bone (Currey et al. 2009). Some studies emphasised

the difficulties in maintain stable the junction between living and dead tissues, as the body does not normally tolerate dead structures. When the dead antler is not cast (for instance, when casting is prevented by hormonal treatment, Kierdorf and Kierdorf 2012), the junction between the living pedicle and the dead antler bone can down the pedicle (the “die-back” process in Lincoln 1992) and, eventually, into the skull which is fatal (Kierdorf and Kierdorf 2012). This hypothesis alone does not explain why the antlers experience a re-grow. Another hypothesis refers to the need of maintaining antler functionality in the frequent case that they are broken or damaged when used in male to male disputes and fighting during the rutting period. Since no repair is possible to dead structures, annual replacement of dead antlers by a new set of living ones could be the better solution to ensure that the antlers are completely functional as weapons in each rutting period (Landete-Castillejos et al. 2019).

However, functionality as an effective weapon is compromised in protoantlers. The pedicle grows entirely from the orbital roof instead of being supported by the cranial vault—a better location for their use in male to male fighting (Bubenik 1983, 1990)—, as occurs in modern-type antlers. Also, we need to consider that early cervids also exhibited very large upper canines as functional intraspecific weapons. Accordingly, the following issues need to be addressed in order to assume that early Miocene protoantlers were lifeless before casting and that the antlers were regenerated later.

1) *Velvet-like shedding*. There is no evidence in early Miocene deer that mature protoantlers were bare bone and then used by the animal before casting. Most of the specimens are found with broken branches but this is most likely a result of taphonomical processes, instead of being used in life. The new Iberian specimens here figured have relatively well-preserved branches, and none of the partially preserved apices of IPS12180 show either signs of secondary polishing or wear by active use in life. On the other hand, the polishing of the entire surface in IPS14572 seems to be produced by taphonomical abrasion. The first unambiguous evidence of bare bone protoantler use still comes from the middle Miocene *Dicrocerus elegans* (Azanza et al. 2011).

2) *Bone death*. Without evidence of velvet-like shedding, it is difficult to suppose that the bone of the protoantler died, as in extant cervids as soon as the velvet is shed the entire antler die off (Kierdorf and Kierdorf 2012, 2021; Gomez et al. 2013; Landete-Castillejos et al. 2019; Kierdorf et al. 2021), though it has been speculated whether the antler core could survive (Acharjyo and Bubenik 1983; Rolf and Enderle 1999). The tissues die by ischemia because the dense ossification and mineralisation (which is induced by a sharp rise in plasma testosterone levels just before the rutting season) cuts off the blood supply late in the growing antlers (Gomez et al. 2013). However, previous palaeohistological studies on early protoantlers have shown that the mineralisation process was different suggesting that the blood supply could not be completely

cut off and therefore the protoantler tissues could be still alive (Bubenik 1990a; Azanza and Ginsburg 1997).

If a cycle similar to that of modern-type antlers is assumed for protoantlers, the internal structure of IPS12180 would indicate an appendage in the latest growing phase. Hence, it would be expected that the protoantler tissues would die once the mineralisation of the protoantler-pedicle transition zone is completed by extending over the longitudinal mid-plane and reaching an intensity enough that the blood supply from inside the pedicle would result also completely cut off. Thus, the limit between the living bone and the dead one would be located at the pedicle top, i.e. where the protoantler detachment occurs according to the specimen NMB S.O.3895.

However, the internal structure of the earliest (MN3) appendages studied by Rössner et al. (2021) belonging to *Acteocemas infans* holotype (NMB S.O. 3126, Chilleurs-aux-bois, France), *Procervulus praelucidus* (SNSB-BSPG 1937 II 16841, Wintershof-west, Germany), and the large lagomerycid *Ligeromeryx praestans* (lectotype NMB S.O. 3020, Chitenay, France), do not match with that of IPS12180. All of them are also protoantlers still attached to the pedicle — i.e., corresponding to stages prior to a casting process—. In these appendages (Rössner et al. 2021, fig. 8 and online resources 15, 18 and 20), both the protoantler and the pedicle consist mainly of compact bone, with the consequent difficulty in locating the limit between the living bone and the dead one at the transition between protoantler and pedicle. To the contrary, pedicles of *Ligeromeryx* and *Procervulus* show a basal zonation with cortical tissue, intermediate trabecular tissue, and central medullary regions (Rössner et al. 2021), but very proximal relative to the zone where the detachment is produced according to the available cast specimens. Because this zonation is not clearly developed in the smaller species, Rössner et al. (2021) associate the absence of zonation in *Acteocemas* with an allometric effect. IPS12180 has a similar small size (Table 1) but it exhibits trabecular bone in the core, hereby rejecting this hypothesis. IPS12180 apparently corresponds to an earlier stage of bone mineralisation than the specimens referred above. If this is the case, the process of mineralisation seems to progress from distal to proximal along the pedicle, since this part in the holotype is also composed entirely of compact bone. That points to a more extended lifespan than modern-type antlers, but it is difficult to explain how a subsequent protoantler detachment could be produced at the pedicle top if the entire appendage is dying. Consequently, the tissues need to remain alive. The high porosity of the specimens (holotype of *Acteocemas* in particular; Rössner et al. 2021, figs. 6a and 8j and online resource 15) suggests that the blood supply running through external and internal vessels still could reach the entire appendage.

3) *Casting process*. Similarly to modern-type antlers, protoantlers underwent a casting process driven by osteoclastic resorption. Ginsburg (1985a) and Ginsburg and Bulot (1987) were the

first to observe that some isolated distal parts of procervuline and lagomerycid appendages show a concave basal surface that cannot be interpreted as a result of a fracture in life or alternatively by taphonomical processes. Accordingly, they interpreted these specimens as cast protoantlers. Azanza (1993), Azanza and Ginsburg (1997), and Azanza et al. (2011) observed some specimens with similar concave basal surfaces, evidencing that their rough texture probably derives from the development of bony spicules, remnants of the osteoclastic resorption, as it is the case in modern-type antlers. In these antlers, the detachment takes place when the bony spicules connecting pedicle and antler are so attenuated by the resorption process that become fractured under the weight of the antler (Goss 1983). Although recent histological studies of cast protoantlers (Heckerberg 2017; Rössner et al. 2021) have confirmed the osteoclastic resorption, available transversal or longitudinal thin sections of cast protoantlers (Azanza and Ginsburg 1997, plate 2, fig. 2; Rössner et al. 2021 figs. 5g, 6b) show that a protective basal bridge of compact bone (Bubenik 1990a; Rolf and Enderle 1999) was not developed, similar to that observed in castrated deer (see Goss 1983, fig. 142).

Osteoclastic resorption is induced in modern-type antlers by a drastic drop in plasma testosterone levels at the end of the rutting season, and occurs proximally to the junction between the dead and the living bone in the distal pedicle (Kierdorf and Kierdorf 2012). As dead bone is isolated and separated from living bone, casting of the dead antler is not an exceptional process (Kierdorf and Kierdorf 2012; Landete-Castillejos et al. 2019). However, that a distal part of a living appendage became cast is, by contrast, exceptional. The only mechanism that can be considered as similar is occasionally observed in velveted antlers of castrated temperate deer when they partly freeze (and then the frozen part becomes dead). However, this hypothesis cannot be applied for protoantlers since available palaeontological data show that early cervids inhabited tropical and subtropical environments. In addition, the size of early antlers is not comparable to that of extant temperate deer making tip freezing less probable. Interestingly, Kierdorf and Kierdorf (2021) illustrated in a red deer stag a case of bilateral, only incomplete velvet shedding and antler casting just above the coronet. The osteoclastic resorption follows a concave surface and is produced on both cortical and spongy bone (Kierdorf and Kierdorf 2021, fig. 4)—that is, without the protective basal bridge of compact bone—, as is observed in protoantlers. Kierdorf and Kierdorf (2021) assumed that the antlers were dead, but this needs a proper explanation, since the blood supply through the trabecular core from the pedicle could still be possible. Similar to the observations in castrated deer, Kierdorf and Kierdorf (2021) argued that this example is related to an abnormally lower and delayed rise of testosterone at the end of the antler growth period. Something similar has been proposed to occur in protoantlers (Azanza 1993; Azanza and Ginsburg 1997; Azanza et al. 2011; DeMiguel et al. 2014) because early deer evolved under tropical or subtropical conditions, and in tropical deer testosterone fluctuations are not so extreme as in temperate

species, and males remain fertile and able to breed at any time of year (Acharjyo and Bubenik 1983; Goss 1983; Bubenik 1990a, 1990b).

4) *Regeneration process*. Unusual double-head antlers, in which a renewed antler grows under the old hardened antler that fails to be cast, clearly evidence the fact that casting and regeneration are two independent processes (Goss 1983; Kierdorf and Kierdorf 1992). The coronet is a useful criterion to recognise a renewed antler, as the first set of antlers generally lack this structure (Goss 1983). However, the absence of coronet has been largely misinterpreted as an indication that the appendage had a lifelong persistence. It is difficult to interpret the type of structure that the medial zigzagging ridge of the holotype of *Acteocemas* may have been, since nothing like that can be observed in any other taxon and, as it is here proposed, it is not an exclusive diagnostical feature for *Acteocemas* (nor the presence of a medial proto-coronet in *Dicrocerus*, Azanza et al. 2011). It could thus represent a coronet-like structure in relation with the protoantler regeneration. In turn, the few aligned pearls in the specimen IPS14572 following the outline of the protoantler base could be interpreted as an incipient proto-coronet and, hence, it could be also in relation to the re-growth of the protoantler. Although the coronet has no apparent function in the casting process (Landete-Castillejos et al. 2019), a possible role in the process of regeneration has not been properly examined. The coronet is usually formed by pearls or knobs that enclose several branches of the superficial temporal artery that supply the regenerating antler. A possible function as a comb or bridge to organize and tighten the vessels and nerves of the growing velvet needs to be further investigated. Antlers with a true coronet appeared during the middle Miocene, and all deer bore this modern-type antler since the early late Miocene. That is, this structure emerged some million years after the casting process was clearly evidenced in early protoantlers, but that of *Acteocemas* seems to show the earliest precursor of this structure. In this line, it is worth to be mentioned that the coronet appears to be associated to a change in the pedicle orientation and position. The fossil record shows that the earliest antlers with coronet were supported by long pedicles growing lying on the frontal bone, whose basal position on the orbital roof soon migrated backwards and medially to overlap partially the braincase.

There are other lines of evidence which allow to recognise that protoantlers underwent a process of regeneration: ontogenetical changes in size and morphology of both the pedicle and the protoantler with the successive cycles of cast and re-growth, and histological differences showing that the protoantler is made up of a more immature bone than the pedicle (Azanza et al. 2011). In dicrocerines, the first set of protoantlers grows from the pedicle having no size difference between the protoantler base and the pedicle top, but with the successive re-growth, the protoantler base is larger and it increases the size difference with the pedicle top (Azanza et al. 2011). IPS12180 and the other specimens attributed here to *Acteocemas infans* (or to a

closely related form), show protoantlers with a basal increased size respect to the pedicle top (that is, the basal dimensions clearly exceed the pedicle diameters). All of them seem to correspond to regenerated protoantlers. In a longitudinal radiographic section of the holotype specimen (Rössner et al. 2021, fig. 6a), a concave discontinuity of the Haversian tissue appears at the transition from the pedicle to the antler, which Rössner et al. (2021) interpreted as a kind of transverse seam indicating reinduced growth. However, this discontinuity fades out in another longitudinal radiographic section of the same specimen (Rössner et al. 2021, fig. 8j and online resource 15), with the consequent difficulty in interpreting what it really represents. Unfortunately, thin-sections are not available as all *Acteocemas* fossils are unique specimens, and regular computed tomography does not have the resolution required to determine from a histological viewpoint the maturity of the bone. However, it is worth noting that histological studies carried out in procervuline and dicrocerine protoantlers have indicated the widespread occurrence of secondary osteons (Azanza et al. 2011; Rössner et al. 2021). This remodelling activity indicates an extended lifespan of these protoantlers if compared to modern-type antlers (Azanza et al. 2011). This is consistent with the more prolonged mineralisation process extending from distal to proximal the protective bridge of compact bone —supposedly building in IPS12180— along the pedicle in the *Acteocemas* holotype as discussed above. A longer lifespan makes difficult to attribute an annual cycle similar to modern-type antlers.

The causal link between early antlers and extrinsic (climate-related) factors

Climate-related factors were already suggested to explain the sudden evolution of ruminant headgear around 19-17 Ma (DeMiguel et al. 2014). In particular, the origins of ruminant headgear were proposed to be associated with an increase of seasonality consequence of a significant drop in global temperatures (Janis 1982, 1990; Janis and Scott 1987; Azanza 1993a, 1993b; Morales et al. 1993; DeMiguel et al. 2014). The seasonality generated by the changes throughout the year of the environmental conditions (mainly temperature and/or rainfall) ultimately plays an important role in influencing the survival of organisms. Because of the morphophysiological constraints that the rumination imposed (Clauss et al. 2003), the increased seasonality of the early Miocene would have led to a major physiological stress during the season with scarce or low-quality food (Morales et al. 1993). Natural selection favours individuals that display behaviours, phenotypes, and physiological adaptations which allow them to maximise seasonally irregular resources. No organ is left out of the integration processes necessary to allow mammals to fulfil their physiological functions and the skeleton is an endocrine organ in itself (Karsenty 2012). This is not surprising considering the unique characteristics of bone and the energetic cost of coordinated regulation of bone mass or growth, energy metabolism, and reproduction (Karsenty 2006; Karsenty and Ferron 2012; Oury et al. 2011). Cranial bony appendages allowed bone storage without playing an active metabolic role

to cope with the increasing seasonal physiological stress (Morales et al. 1993), but the evolutionary response in each pecoran lineage was different according to specific physiological and developmental constraints.

Climate-related factors clearly affect the antler annual cycle of extant deer. Deer inhabiting temperate zones are concerned about summer versus winter, because this affects the survival of fawns (Goss 1983). The annual replacement of antlers, intrinsically controlled by fluctuating hormone levels (Bubenik 1990b) and coordinated with the reproductive cycle, is seasonally synchronised at middle-high latitudes, depending on extrinsic photoperiodicity (Goss 1983). Physiological functions have to help survival under difficult conditions, specifically the seasonal limitation of food intake, that is, of energy. Through bone shedding, deciduousness might be the better way for a male deer to reduce the seasonal leftover of bone mass (for females would be pregnancy), considering the high demand for calcium that bone antler mineralization requires (Gomez et al. 2013) and the highly energetic cost of regulating bone remodeling throughout adult life (Karsenty 2012).

The new histological evidences provided by the specimen IPS12180 allow us to reinterpret that the compact internal bone structure of the *Acteocemas* holotype is consistent with a longer protoantler lifespan than modern-type antlers, which makes difficult to assume a similar seasonal cycle. Then, it remains as an open question whether the cycle of the early protoantlers was aperiodic or irregular, either because the cycle was controlled by sex steroids in a way different from that of extant deer (e.g., see the effect of the administration of estrogens, Bubenik 1999; or antiandrogens, Kierdorf et al. 2021), or because the animal levels of sex steroids could vary little throughout the year and the antler casting often failed, as seen in tropical deer today.

An irregular cycle—that is, not necessarily each year and seasonally synchronized—has been proposed to explain the singularity of early Miocene antlers (Azanza 1993a, 1993b; Azanza and Ginsburg 1997; Azanza et al. 2011; DeMiguel et al. 2014) taking into account that: *i*) the development of such a complex and physiological process takes a long time and may be imperfect at first; and *ii*) the early Miocene climate was warmer than today (see Zachos et al. 2001; Hansen et al. 2013; Steinthorsdottir et al. 2021) and early deer evolved under tropical or subtropical conditions that were present in Eurasia north to the Alpine Mountain Belt (Heintz and Brunet 1982)—thus early cervids were more concerned about the rainy and dry seasons and less about summer and winter; and *iii*) protoantlers show some similarities with the antlers of castrated (Bubenik 1983, 1990a) or hormonal-treated male deer (Bubenik 1999; Kierdorf et al. 2021), and of tropical deer—following a non-seasonal annual cycle—, that could be related to less extreme fluctuations or low plasma testosterone levels.

The initial evolution of deciduousness, as seen in the probable irregular protoantler cycle of *Acteocemas* (ca. 18-17 Ma), was limited by the MCO warming event at ca. 17-15 Ma. The subsequent drastic middle Miocene Climatic Transition (MMCT ca. 15-13 Ma) cooling would

cause a new increase in seasonality of temperature that could well promote the hormonal changes necessary for the cycle becoming seasonal (Azanza 1993; Azanza et al. 2011; DeMiguel et al. 2014). Presumably, this was a result of selective pressures to concentrate breeding into specific seasons. The emergence of the antlers with coronet was concomitant with this second pulse (Azanza and DeMiguel 2019).

Conclusions

The small stem-cervid *Acteocemas* is one of the three earliest ruminants bearing antler-like appendages. *Acteocemas infans* has the features that an early relative of later antlered deer would be expected to exhibit, suggesting that deciduousness could be also inherent to antler-like appendages. Several diagnostic features are clear indication of protoantler regeneration, such as a coronet-like structure —or basal swelling, or aligned pearls— partially developed, and an enlarged base respect to the pedicle top. The specimen NMB S.O.3895, from the type locality and here ascribed to this form, demonstrates that the protoantler was able to undergo a casting process but, unlike *Procervulus*, the detachment occurs immediately below the bifurcation. The new Iberian appendage IPS12180 is at the latest growing phase, just before casting. It clearly shows that the protoantler has the central trabecular bone reduced to the longitudinal mid-plane, and that a protective bridge of compact bone at the transition zone with the pedicle is growing similar to the latest growing stage of modern-type antlers. However, it apparently corresponds to an earlier stage of bone mineralisation than the holotype NMB S.O.3126, in which the compact internal bone structure would be consistent with a longer protoantler lifespan than modern-type antlers, thereby discarding an allometric effect. Accordingly, it remains as an open question whether the protoantler cycle could be irregular in *Acteocemas*, as proposed for other early Miocene deer.

While the processes and mechanisms that allow the cast and re-growth could be acquired basally in Cervidae, the regulation mechanisms (hormonal control linked to the reproductive cycle and seasonally synchronized) may have been not necessarily basal. The initial evolution of deciduousness, as in the probable irregular protoantler cycle of *Acteocemas* (ca 18-17 Ma), was limited by the MCO warming event at ca. 17-15 Ma. The subsequent drastic cooling of the MMCT (ca. 15-13 Ma) caused a new increase in seasonality that probably led to specific hormonal changes necessary for the cycle became seasonal. The appearance of the antlers with coronet were concomitant with this second pulse.

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Figure captions

Figure 1. a) Geographical location and simplified geological map of the Vallès-Penedès Basin and the Baix Llobregat sub-Basin highlighting the main *Acteocemas*-yielding early Miocene mammal localities (modified from Casanovas- Vilar et al. 2016a). Locality acronyms: CBL = Costablanca; COB = Ca n'Obac; SAB = Sant Andreu de la Barca. b) Biochronological framework for *Acteocemas*. Biochronological correlation and available magnetostratigraphic dating constraint *Acteocemas* biochronological range between 18-17 Ma, just before the Miocene Climatic Optimum (MCO; ~16.9–14.7 Ma). Climate curve based on estimate surface temperature by Hansen et al. (2013). Life reconstruction of *Acteocemas* by Flavia Strani.

Figure 2. *Acteocemas* aff. *infans* from the Iberian Peninsula (late Ramblian, early Miocene, MN3). a-c) IPS14572, nearly complete protoantler from Costablanca (Vallès-Penedès Basin); a) lateral, b) anterior, and c) medial views. Note that there is no clear coronet-like structure but there are instead clear aligned pearls at the basis. d-f) IPS12180, left dichotomous protoantler on pedicle, from Sant Andreu de la Barca (Baix Llobregat sub-Basin); d) anterior, e) medial, and f) posterior views. Note the enlarged base of the protoantler and the oblique insertion on the pedicle top.

Figure 3. *Acteocemas infans* (Chilleurs-aux-Bois, France, early Miocene, MN3). a-h) NMB S.O.3126, holotype, left dichotomous protoantler on pedicle; a) posterior, b) medial, c) anterior and d) lateral complete views; e) medial, f) anterior, g) lateral and h) posterior detailed views of the transition between protoantler and pedicle (note the coronet-like structure. i-l) NMB S.O.3895, cast of a left dichotomous protoantler; i) lateral, j) anterior, k) medial, and l) ventral views (note the absence of concave basal surface indicating casting process).

Figure 4. Internal architecture of IPS12180 from Sant Andreu de la Barca. a) location of the radiographic sections on posterior view, b) radiograph following the longitudinal mid-plane of the protoantler, and c) radiograph following the longitudinal mid-plane of the pedicle. A physics colour scale was applied to some images to better visualize internal density changes in the fossils, ranging from dark blue (lowest density = air) to red (highest density).

Figure 5. Internal architecture of IPS12180 from Sant Andreu de la Barca on cross (a-e) and transversal (f-h) sections. The location of the radiographic sections is indicated on lateral view. The trabecular bone in the center is reduced to the longitudinal mid-plane in both the protoantler base (b) and the pedicle top (c). Note also how the protoantler is enlarged compared to the pedicle top in transversal radiographs (f-h).

Tables

Table 1. Protoantler measurements (in mm) of the studied Iberian specimens and *Acteocemas infans* from the type locality.

| Sigle | L | DAPb_ped | DTb_ped | DAPd_ped | DTd_ped | Hbif | DAPb_pa | DTb_pa | Lp_br_a | DAPb_br_a | DTb_br_a | La_br_p | DAPb_br_p | DTb_br_p |
|---------------------|-------|----------|---------|----------|---------|-------|---------|--------|---------|-----------|----------|---------|-----------|----------|
| Chilleurs | | | | | | | | | | | | | | |
| S.O.3126 (holotype) | 43,61 | 12,6 | 9,72 | 13,28 | 9,78 | 7,39 | | 12,01 | | 10,26 | 9,37 | | | |
| S.O.3895 | | | | | | 14,32 | 18,54 | 12,12 | >35 | 12,21 | 10,18 | >24 | 11,09 | 9,05 |
| SAB | | | | | | | | | | | | | | |
| IPS 12180 | > 40 | 14,69 | 12,59 | 16,26 | 9,94 | 17,05 | 17,77 | 11,74 | | 12,42 | 9,09 | | | |
| CBL | | | | | | | | | | | | | | |
| IPS CBL 22826 | | | | 16,17 | 12,44 | ±14 | 20,5 | 13 | >31 | 9,77 | 9,88 | ±49 | 11,33 | 12,08 |
| IPS CBL 22839 | | | | 11,23 | 10,46 | ±12 | 18,43 | 16,36 | | 10,14 | 10,26 | | | |
| IPS CBL 22838 | | 12,77 | 14,33 | | | | | | | | | | | |

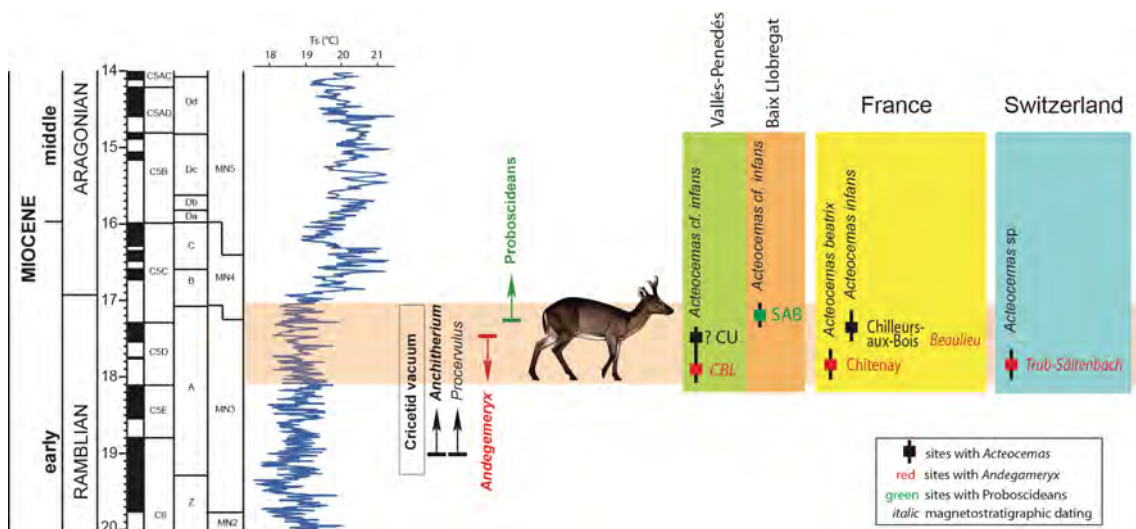


Figure 1

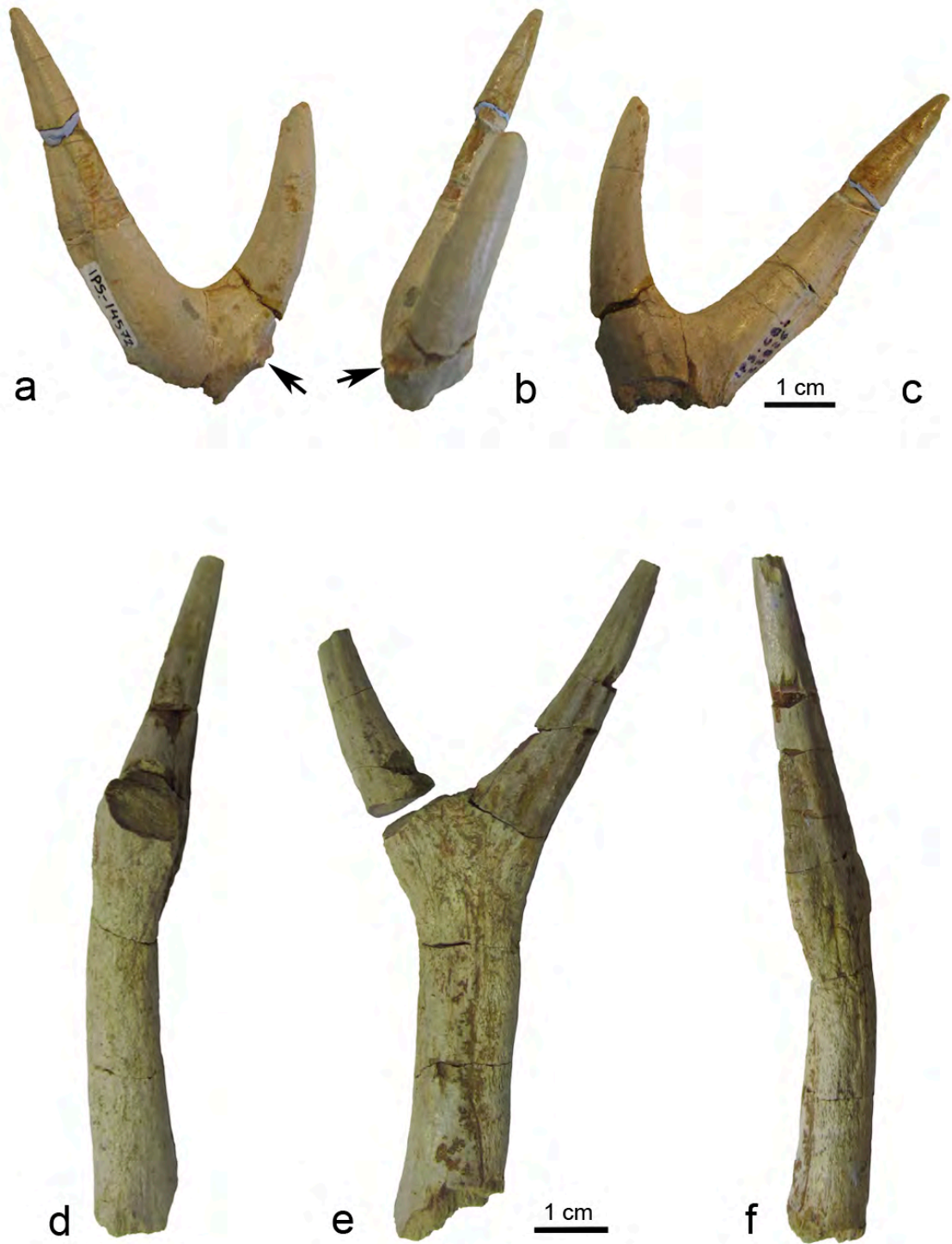


Figure 2



Figure 3

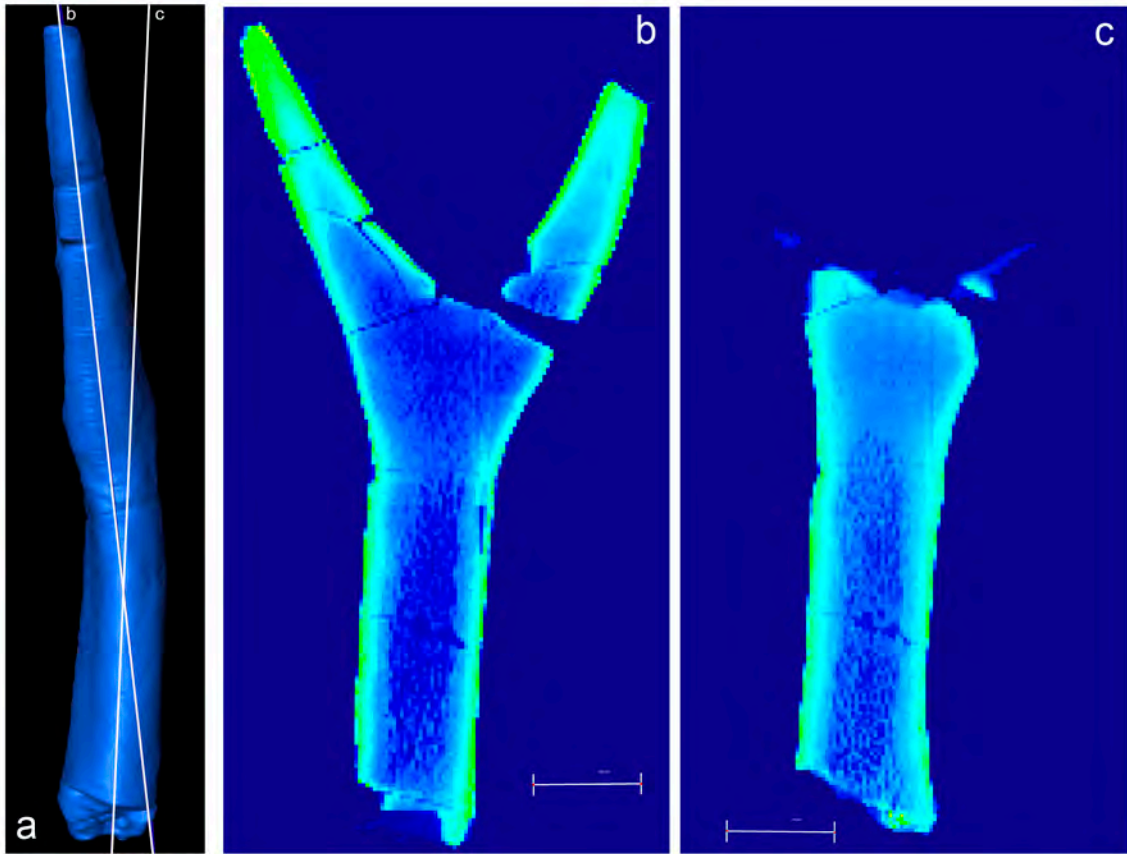


Figure 4

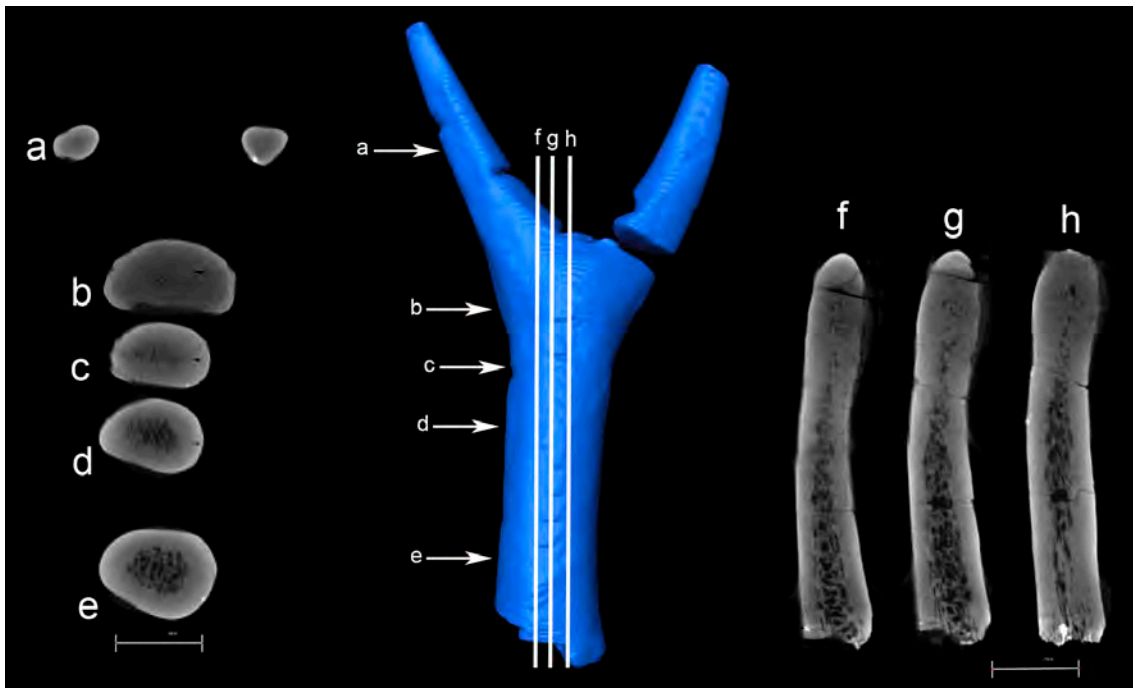


Figure 5