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# The antler-like appendages of the primitive deer *Dicrocerus elegans*: morphology, growth cycle, ontogeny, and sexual dimorphism

## *Los apéndices tipo asta del ciervo primitivo* Dicrocerus elegans: *morfología, ciclo de crecimiento, ontogenia y dimorfismo sexual*

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ABSTRACT

Males and many females of the primitive deer *Dicrocerus elegans* from Sansan (Middle Miocene, France) bore antler-like appendages consisting of a simple-branched protoantler growing from a rather long pedicle and are decorated with ridges and furrows. The protoantler capacity to be rejected and subsequently re-grow is clearly evidenced by the presence of both pedicle and protoantler cast specimens. The youngest appendage is a long, laterally flattened shaft whose apex is usually forked with no appreciable limit between the pedicle and the protoantler. In females, the anterior and posterior appendage margins form a more acute angle than that of males, and are more parallel when viewed laterally. After the first casting, the protoantler base is larger than the pedicle top and a coronet-like structure appears developed only around the medial side. With successive castings, the pedicles become shorter and their section is more circular, while protoantlers become much bigger, and have much longer and more separated branches. Branches of females are shorter than those of males, especially the anterior one, and appear in a straight line, instead of being bent. In oldest appendages, the branches are shorter and more similar in size. Accessory branches and irregularities of this basic morphology are common. The separation between both sex morphotypes appears clearly evidenced by Discriminant and Principal Component Analyses. Histological features point to important differences with true antlers and suggest that casting could not occur annually. A core of spongy bone trabeculae is not developed. Once growth is completed, the mineralization progress from the core to the periphery and when the final 'velvet' protoantler becomes completely petrified, the tissues dies and the velvet-like skin is cleaned. A high degree of both wear and polish of the branch apices evidence the hard, bare, dead protoantler phase before casting. Due to the complete growth cycle and the presence of the coronet-like structure, *Dicrocerus* protoantlers and antlers seem to be homologous appendages. Histological differences could be related to differences in hormonal cycle regulation that can be caused by the fact that *i*) *Dicrocerus* inhabited a tropical environment, and *ii*) females also developed protoantlers. It should not be overlooked that true antlers appear several million years later in time than the development of protoantlers and other cranial appendages in ruminants, and coinciding with the Middle Miocene Climatic Transition.

**Keywords:** Ruminantia, Miocene, Sansan, antlers, histology.

RESUMEN

Tanto los machos como muchas de las hembras del ciervo primitivo *Dicrocerus elegans* de Sansan (Mioceno Medio, Francia) poseían apéndices craneales de tipo asta que consisten en una protoasta bifurcada y ornamentada con surcos y crestas que es sustentada por un pedículo moderadamente largo. La capacidad de la protoasta de ser expulsada y regenerada es evidente a partir de los ejemplares de desmogue y también por las diferencias histológicas existentes entre la protoasta y el pedículo.

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El primer apéndice consiste en una vara larga, comprimida lateralmente, y con el ápice bifurcado, sin que se observe ningun límite apreciable entre la protoasta y el pedículo. En las hembras, el ángulo que forman los margenes anterior y posterior del apéndice es más agudo que en los machos (los márgenes son más paralelos en vista lateral). Tras el primer desmogue, la base de la protoasta es más amplia que la sección distal del pedículo, y se desarrolla una estructura similar a la roseta en la parte medial. Con los sucesivos desmogues, el pedículo se acorta y su sección se hace más circular, mientras que la protoasta es cada vez más grande y las ramas son más largas y parten más separadas desde la base sin interposición de un tramo basal. En las hembras, las ramas son más cortas, especialmente la anterior, y su trazado es rectilíneo en vez de curvo como en los machos. En los ejemplares seniles, las ramas son más cortas y de longitud más similar entre ellas. Es frecuente la presencia de ramas accesorias, así como irregularidades de este patrón básico. Los análisis discriminantes y de componentes principales realizados muestran una clara separación entre los morfotipos atribuidos a machos y a hembras. Existen importantes diferencias histológicas con las verdaderas astas que sugieren que el desmogue podría no haber sido anual. Se confirma que no se desarrolla hueso esponjoso y que la mineralización del protoasta progresa centrífugamente desde el centro hasta la periferia. El desmogue tiene lugar una vez que los tejidos están completamente mineralizados (muertos). A diferencia de otras protoastas, el ciclo en *Dicrocerus* era completo dado que están documentadas tanto la fase de muda del terciopelo, como la de exposición del hueso desnudo antes del desmogue. Dadas las similitudes en el ciclo de crecimiento, y dado que la base de la protoasta presenta parcialmente una estructura similar a la roseta, las protoastas de *Dicrocerus* y las astas parecen ser apéndices homólogos. Las diferencias histológicas podrían estar relacionadas con diferencias en el ciclo hormonal que regulaba su crecimiento. Diferencias que podrían guardar relación con el hecho que i) *Dicrocerus* vivió en ambientes tropicales, ii) las hembras también poseían protoastas. Cabe resaltar que las verdaderas astas aparecieron varios millones de años más tarde de que surgieran las protoastas y otros apéndices craneales en Ruminantia, y en coincidencia con la transición climática del Mioceno Medio.

**Palabras clave:** Ruminantia, Mioceno, Sansan, astas, histología.

## Introduction

*Dicrocerus elegans* Lartet, 1837 is one of the earliest and best known ruminants bearing antler-like appendages. Deer antlers - structures developed as an outgrowth of the frontal bone - are unique among mammals. The branched distal part, or antler proper, is seasonally deciduous, the cycle and growth of which depend on the rise and fall of hormonal secretions. The deciduous nature can easily be recognized by the presence of cast specimens and by the coronet, a bony ring formed around the base of the regenerate antler. Because this structure is not clearly developed in Early-Middle Miocene deer, the deciduous nature of their antler-like appendages has been the subject for debate and, consequently, their relationships with the crown group of modern cervids still remain unclear. The deciduous nature can also be recognized by the fact that deer antlers change in size and complexity with age, so a lineal ontogenetic sequence can be designated. When Lartet (1837) first discovered this primitive deer from the Middle Miocene locality of Sansan (France), he used this latter argument supposing that the appendages were lifelong structures.

« Il n'est pas sans intérêt de rechercher pourquoi, dans ce groupe de cerfs de Sansan, que je propose de désigner par le nom sous-générique de *Dicrocères*, la forme des bois se montre constamment la même chez des individus d'âges très divers, ce qui, à défaut d'observation contraire (et il n'y en a pas jusqu'à ce jour), me ferait supposer que ces bois n'étaient point sujets à se renouveler comme le sont les cornes de nos cerfs actuels »

Also, being surprised by the different development of teeth, Lartet pointed out to environmental differences with the present-day climate in the area as the possible cause for the morphological and developmental changes.

«ces différences, qu'il est encore possible de constater, autoriseraient-elles à supposer des modifications équivalentes dans un autre ordre d'organes plus directement soumis à l'influence des agents extérieurs? Si l'on se rapporte à l'époque de ces temps anciens…. ont dû jouir d'une température au moins égale à celle de nos climat intertropicaux,……, et résultant de la chaleur propre du globe, et que l'on réfléchisse au dégagement considérable de gaz, particulièrement d'acide carbonique, qui devaient s'échapper d'un sol encore échauffé et de nombreuses sources thermales et sédimenteuses, il est difficile de croire que la composition de l'air ambiant fût exactement telle qu'elle l'est de nos jours.»

These suppositions attracted the attention of Geoffroy Saint-Hilaire, since, in the previous session of the Science Academy of Paris, he presented similar ideas on the influence that past environmental changes could well modify the animal form. In a later session, De Blainville (1837) refuted Lartet's asseveration by considering the appendages of

*Dicrocerus* to be quite similar to the deciduous antlers of extant muntjacs.

Nevertheless, Lartet had no clear idea about the taxonomy of Sansan's deer as he recognised three groups of dicrocers, named in 1851 using the latin names as *Dicrocerus elegans*, *Dicrocerus? crassum* and *Dicrocerus?? magnus*. Lartet rejoined in the second species several appendages consisting of longer pedicles and forked protoantlers with no burr or coronet at the base (these could correspond to juvenile *D. elegans*, or most probably to *Heteroprox larteti)*, and dentition and bones belonging to tragulids, while in the latter species he included dentition and bones belonging to Paleomerycids (Lartet, 1851).

In contrast, Filhol (1891) considered that *Dicrocerus* appendages were undoubtedly deciduous. However, he recognized such a great morphological disparity that described up to eight deer species, but none corresponding accurately to *D. elegans*. More recently, Stehlin (1928, 1937, 1939) clarified the systematics of primitive deer and assigned the Sansan's deer material to only two species: *Dicrocerus elegans* and *Heteroprox larteti*, thus recognising that most of the Filhol' species correspond to ontogenetic stages or aberrant specimens, and establishing the ontogenetical sequence for the appendages of both species. Stehlin (1939) also assumed a periodic cycle for the antler-like growth. This view has been generally accepted by Ginsburg (1963) and Ginsburg & Crouzel (1976).

Despite this, A.B. Bubenik (1990) emphasized that *Dicrocerus* protoantlers have a highly active cortex (even if the appendage construction is completed) because mineralization progresses centrifugally and supposes that sequestration is produced when the tissues are still alive, as found in lagomerycid or procervuline protoantlers. Bubenik concluded the facultatively perennial nature for all these apophyseal appendages without a true coronet. This point of view is argued for the dicrocerine protoantler (Azanza, 1993) because a coronet-like structure is partially developed in *Dicrocerus* (as well as in the dicrocerines *Acteocemas infans* and *Stehlinoceros elegantulus*) and because the phases of the velvet-like skin cleaning and of the hard, bare, dead protoantler before casting, are documented in *Dicrocerus*. On the other hand, Ginsburg & Azanza (1991) evidenced the existence of two morphotypes considering that both males and females bore antler-like appendages. Thus, and given that specimens studied by Bubenik belong either to females (Bubenik 1990, fig. 18A and 18AS; also fig. 17A-left attributed to *Heteroprox*) or to the first young male appendage (A.B. Bubenik, 1990, fig. 1A-right, attributed to *Heteroprox*), his ideas are not sufficiently verified. It should be noted, non standing, that the sexual dimorphism in appendages of *Dicrocerus* is not recognized by Gentry *et al*. (1999) who attributed the morphotypes to a mere ontogenetical variability.

Both the features, coronet-like structure and velvet-like shedding, indicate a greater similarity between dicrocerine protoantlers and true antlers, and according to Azanza (1993) allow dicrocerines to be placed in an intermediate position between procervulines and the crown group of modern cervids. Moreover, the possibility that protoantlers may have given rise to the periodically shed cervid antlers was also pointed out by Azanza (1993) and Azanza & Ginsburg (1997).

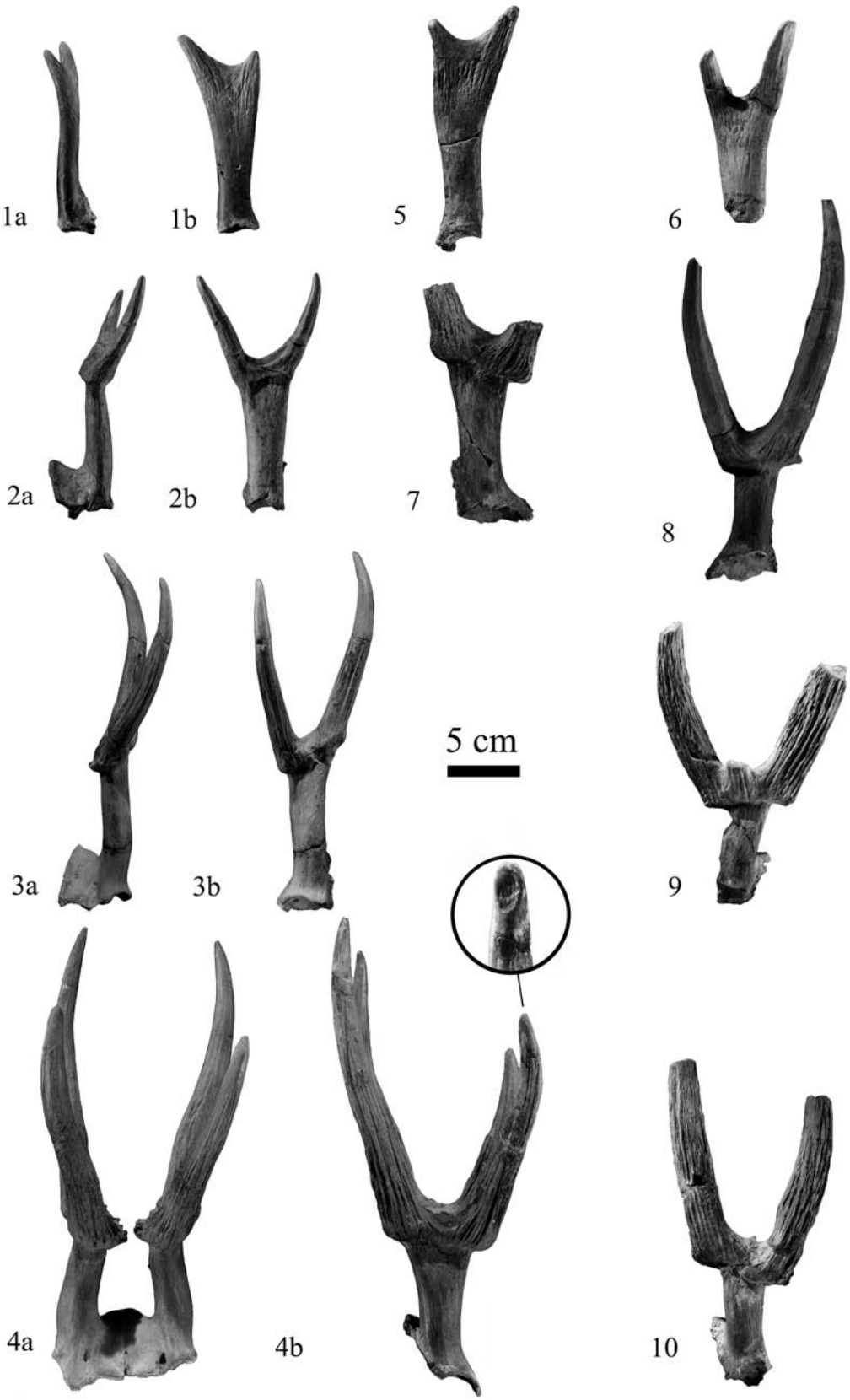
The nature and homology of cranial appendages should be based on comparisons of the details of the developmental processes and the inducing and contributing tissues, which is very speculative in fossil organisms. In this work, the morphology of *Dicrocerus* protoantlers is mega- and microscopically examined in order to determine their sexual dimorphism, cycle and growth patterns, and ontogenetical development, and thus their affinities, if any, to the periodically shed antlers.

## Material and methods

Our study is based on the huge collection of cranial appendages of *Dicrocerus elegans* recovered in the Middle Miocene deposits of Sansan (France), which probably constitutes the largest and extended of a Miocene deer. We have studied and measured over three hundred specimens stored in the MNHNP. Some of them are drawn in Filhol (1891), Stehlin (1939), A.B. Bubenik (1990) and Ginsburg & Azanza (1991). Also, we studied more than one hundred of specimens recovered in the nineties which are stored in the MHNT. This material was unpublished until now.

The appendage paleohistology is studied by means of transversal thin sections and radiographs. The sections and microphotographs were made at the Hard Rock and Microscopic Photography laboratories at Zaragoza University. The radiographs were made at the MNHNP. Cast antlers of *Cervus elaphus hispanicus* and *Capreolus capreolus* from Spain were also studied for comparison, as well as a cast antler belonging to *Muntiacus* sp. and recovered by L. Ginsburg in Thailand.

The morphometric study was based on 16 measurements of the pedicle and protoantlers using a digital Mitutuyo calliper (Appendix 1). Multivariate analyses for ascertaining the dimorphism in *D. elegans* were performed using SPSS 11.5. In order to obtain an ordination of the specimens as a function of their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2a
2b
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3a
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5 cm
9
4a
4b
10

Fig. 1.—Morphotype of cranial appendages that probably corresponds to the males of *Dicrocerus elegans* from the Middle Miocene deposits of Sansan (France). All specimens are stored in the MNHNP. Figures 1:1 to 1:4, and 1:9, compilling the ontogenetic sequence.
1: Sa10338. Frontal bone fragment bearing the complete cranial appendage. Element belonging to a juvenile *Dicrocerus*; first stage in which the protoantler was not still rejected; 2: Sa3323. Left frontal bone bearing the complete cranial appendage. Juvenile-subadult specimen; second stage in which the protoantler was regenerated; 3: Sa3486. Left frontal bone bearing the complete cranial appendage. Subadult specimen; third stage; 4: Sa3324 Left and right frontal bones bearing the complete cranial appendages. Adult specimen; fourth stage. Note that a coronet-like structure appears only developed on the medial side, and that the apices are polished (one of them is broken and its scar surface is also polished indicating that the bone was bared); 5: Sa3322. Left frontal bone fragment bearing the complete cranial appendage. Juvenile specimen; first stage in which the protoantler was not still rejected but was growing during more than one cycle; 6: Sa3364. Left cranial appendage. Juvenile specimen; first stage in which the protoantler was not still rejected but was growing during more than one cycle; 7: Sa3566. Right frontal bones bearing the complete cranial appendage. Adult specimen; fourth stage; 8: Sa3425. Left frontal bones bearing the complete cranial appendage. Adult specimen; fourth stage; 9: Sa3524. Left frontal bones bearing the complete cranial appendage. Adult-senile specimen; fifth stage. The pedicle is short and the protoantler basis is significantly larger than this structure. Note the presence of an external accessory branch; 10: Sa3388. Right frontal bones bearing the complete cranial appendage. Adult-senile specimen; five stage. Note that the protoantler basis is significantly larger than the pedicle.

size and morphology, Principal Component Analyses (PCA) were performed including jointly all the metric variables except the branch lengths. Finally, the scores of the specimens in the two first PCA factors were used to set them out in a bi-variated plot. Discriminant analyses were also employed to evaluate the ability of the sets of metric variables with the purpose of distinguishing between the two morphotypes and also to classify the uncertain cases according to the model derived.

**Institutional abbreviations — MNHNP**, Muséum National d' Histoire Naturelle, Paris, France; **MHNT**, Muséum d' Histoire Naturelle, Toulouse, France;

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

## General morphology

*Dicrocerus* appendages are supported by the frontal bone but, in contrast to true antlers, the base is entirely on the supraorbital process without leaning on the braincase. As observed in deer appendages, we can also distinguish a proximal (basal) part or pedicle from a distal branched part, the protoantler properly. The size of the protoantler relative to that of the pedicle changes greatly according to the age. Thus, the relative protoantler length varies from 1/3 of the total length in juvenile specimens to 3/4 in adult ones (Fig. 1 and 2).

The pedicles are vertically oriented in lateral view, parallel to the sagittal plane in frontal view or converge inwards describing a weak curvature. The pedicle cross-section and length varies according to the age, from laterally flattened to rounded, but its base is less compressed transversally, and consequently the anterior and posterior margins diverge in lateral view, especially in the youngest individuals. The surface is smooth but very slight striations and shallow grooves are occasionally present.

The protoantler is inserted obliquely on the pedicle, and the basis is inclined forwards and outwards. It forks directly from the basis without any shaft gives access to the two branches, whose emplacements are situated lengthwise to the compression plane of the pedicle. The anterior branch is slenderer than the posterior one and points more outwards. Thus, the protoantler longitudinal plane converges posteriorly with the sagittal one. The branches can be subcircular or flattened in cross-section, some are curved while others are completely straight. However, the branch morphology and length varies greatly with age. An additional knob near of the base is observed in 50% of the specimens (Fig.2:3) Specimens with three branches are also frequent, the accessory branch usually points out from the base (Fig.1:9; Fig.2:12), but also from the posterior branch. Juvenile appendages have no appreciable limit between pedicle and protoantler. In adults, the protoantler base is larger than the pedicle top and a coronet-like structure appears developed only around its medial side. The protoantler surface is greatly decorated with ridges and furrows.

## Sexual dimorphism

Two morphotypes can be clearly recognized by both the morphology and the size of the pedicle and the protoantler (Fig. 1 and 2). In the smallest morphotype, the anterior and posterior pedicle margins form an acuter angle than that of the biggest morphotype (without being keeled) and are more parallel when viewed laterally (i.e. the difference

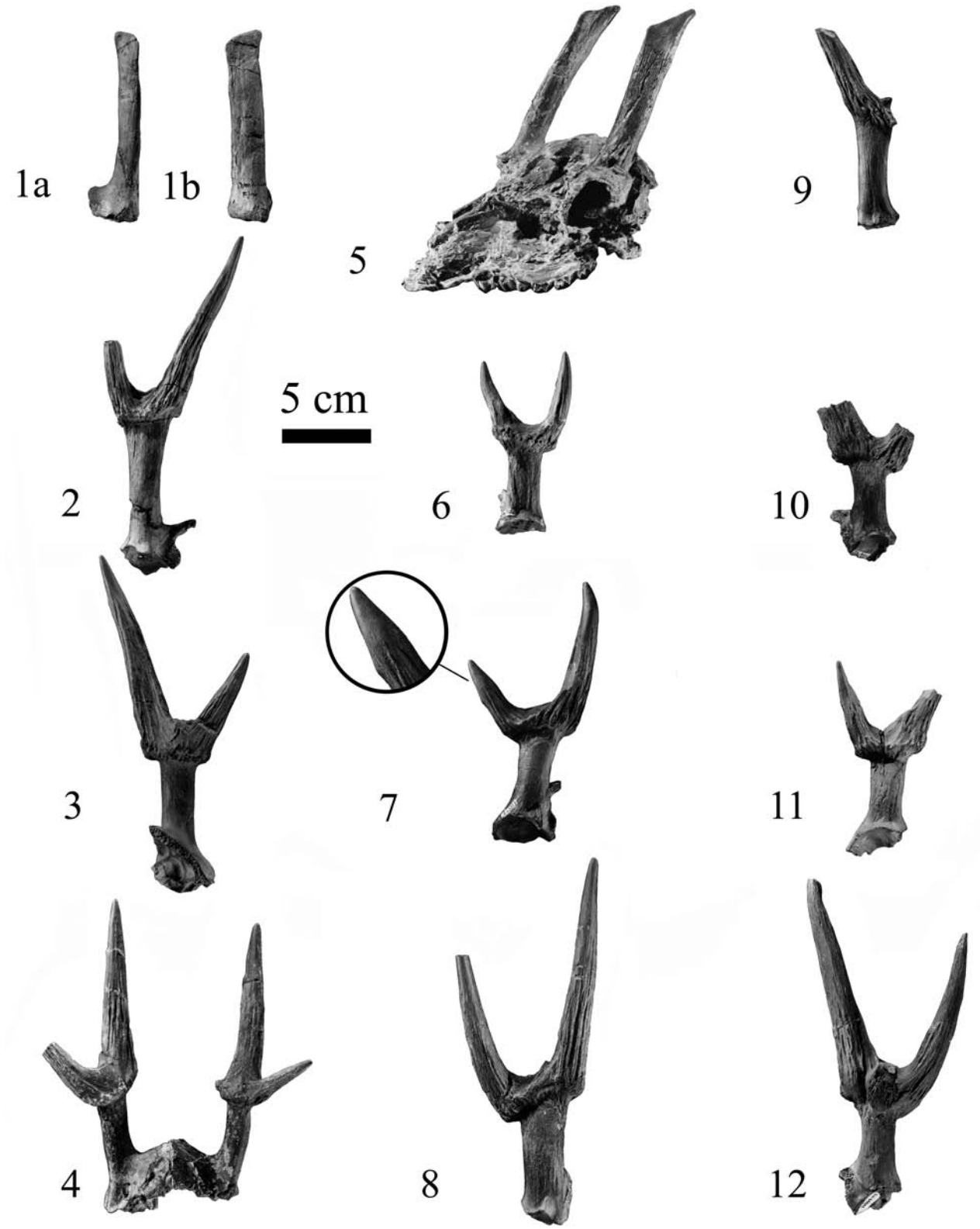
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Fig. 2.—Morphotype of cranial appendages that probably corresponds to the females of *Dicrocerus elegans* from the Middle Miocene deposits of Sansan (France). All specimens are stored in the MNHNP. Figures 2:1 to 2:4, and 2:12, compilling the ontogenetic sequence.
1: Sa3320. Left frontal bone fragment bearing the complete cranial appendage. Juvenile specimen; first stage in which the protoantler was not still rejected; 2: Sa3358. Left frontal bone bearing the cranial appendage (the anterior branch is broken). Juvenile-subadult specimen; second stage in which the protoantler was regenerated; 3: Sa3456. Left frontal bone bearing the complete cranial appendage. Adult specimen; third stage. Note that a coronet-like structure appears only developed on the medial side, and that apices are polished; 4: Sa10340. Left and right frontal bones bearing complete cranial appendages. Adult specimen; third stage. A coronet-like structure appears only developed on the medial side. There is a knob placed on the medial side between the branches. Note that the apices are polished; 5: Sa3567. Skull bearing the complete cranial appendages. The specimen could belong to a suadult *Dicrocerus*; first stage. The protoantler was not still rejected. Note that all upper check teeth are erupted; 6: Sa3326. Left frontal bone bearing the complete cranial appendage. Senile-aberrant specimen; fourth stage. Note that the apices are so worn and polished that the branches have acquired a similar length. The coronet-like structure is also on the external side; 7: Sa3329. Left frontal bone bearing the complete cranial appendage. Adult specimen; third stage. Note that the apices are worn and polished; 8: Sa3480. Left frontal bone bearing the cranial appendage (the apex of the anterior branch is broken). Adult specimen; third stage. Note the important development of the branches, specially the anterior one; 9: Sa3552. Left frontal bone fragment bearing the cranial appendage. Adult specimen; third stage. Note the aberrant morphology of the anterior branch; 10: Sa3444. Right frontal bone bearing the cranial appendage (the branches are broken). Adult-senile specimen; fourth stage. Note that the protoantler basis is significantly larger than the pedicle, and that the branches are greatly separated between them; 11: Sa3463. Left frontal bone bearing the cranial appendage (the posterior branch is broken). Adult-senile specimen; fourth stage. Note that the protoantler basis is significantly larger than the pedicle, and that the branches are greatly separated between them; 12: Sa10321. Right frontal bone bearing the cranial appendage (the apex of the posterior branch is broken). Adult-senile specimen; fourth stage. Note the presence of an external accessory branch placed between the other two.

between DAPb and DAPd is lower). Protoantlers have shorter branches in the smallest morphotype, especially the anterior one, and are placed in a straight line, instead of being bent. This variability is consistent with the presence of a somewhat sexual dimorphism similar to that observed in caribou and reindeer subspecies (*Rangifer tarandus*), the only extant deer in which females typically bear antlers. Contrary to the males, females of *Rangifer* bear smaller and simpler antlers with a more offensive pattern (Bubenik, 1975). The alternative hypothesis, the presence of two *Dicrocerus* species, does not seem feasible. Besides *Dicrocerus*, there is another deer in Sansan fossil site, the procervuline *Heteroprox larteti*. Given that in this epoch the group was barely radiating, the simultaneous occurrence of three very similar sized cervids, being two sympatric species, does not seem feasible (Ginsburg & Azanza, 1991). Thus, these authors proposed that males of *D. elegans* supported the biggest morphotype of appendage, whereas females bore the smaller one. Nonetheless, this point of view was not accepted by Gentry (1994) and Gentry *et al*. (1999), who attributed these morphological differences to an ontogenetical variability.

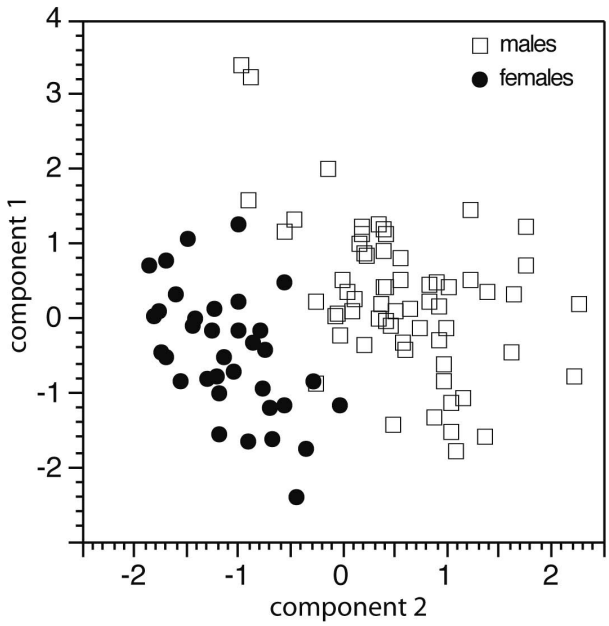


Fig. 3.—Scatter plots of the scores for the first two principal components, which capture the 79,95% of the variance. The PCA was carried out using twelve appendage measurements (branch lengths were excluded).

The separation between both morphotypes is clearly confirmed by the morphometric study. Figure 3 and table 1 show the results of the Principal Component Analysis. The first two components capture the 79,95% of the variation. The loading of all variables is positive, except in the pedicle length, with values greater than 0,7 on the first component which explains the 68,33% of the variation. The pedicle measurements load greatly on the second principal component which explains the 11,61% of the variation, in particular the length and the distal antero-posterior diameter. Plotting the scores for these two components (fig. 3) shows two groups of specimens with very little superposition

Table 1.—**Percentage of actual variation (% of the total variance) explained and factor loadings on the first two components of the PCA on the twelve appendage measurements (branch lengths were excluded)**

| | Component 1 | Component 2 |
|---|---|---|
| Variance explained | 68,334 | 11,616 |
| Factor loadings | | |
| L_ped | 0,318 | 0,886 |
| DAPb_ped | 0,900 | 0,200 |
| DTb_ped | 0,904 | -0,320 |
| DAPd_ped | 0,810 | 0,509 |
| DTd_ped | 0,897 | -0,217 |
| DAPb_pa | 0,922 | 0,046 |
| DTb_pa | 0,800 | -0,398 |
| Hbif_pa | 0,716 | -0,176 |
| DAPb_br_a | 0,924 | -0,009 |
| DT_ br_a | 0,915 | 0,007 |
| DAPb_br_ p | 0,789 | -0,259 |
| DTb_br_p | 0,835 | -0,052 |

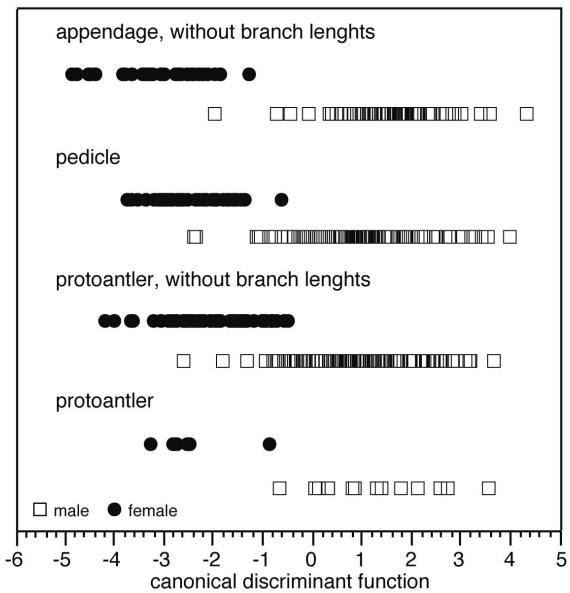


Fig. 4.—Univariate plot of scores for the discriminant function of the four discriminant analyses performed on appendage measurements of putative male (open squares) and female (closed circles) individuals.

between them that correspond to the predefined morphotypes.

In order to evaluate the ability of the sets of metric variables with the purpose of distinguishing between the two morphotypes, four discriminant analyses were realized. Figure 4 and tables 2 and 3 display the results obtained. The percentage of accurate classification was higher than 90% in all data sets (table 2), i.e. the separation between the predefined morphotypes can be made using only the pedicle or protoantler measurements, but results are better if the complete set of measurements is used (fig. 4). It should be noted that, despite to display the highest percentage of correct classification (100%), the analysis performed using the protoantler measurement set is based on very few specimens.

Following the criteria of Ginsburg & Azanza (1991), specimens were distributed in two sex-morphotype groups thus obtaining a sex ratio of 2:1, which is not a plausible ratio in a natural population. A possible explanation to this fact could be that not all females bore appendages, as occurs with *Rangifer*. The frequency of antlered females in caribou and reindeer varies considerably among herds, and over time within a herd (Bergerud, 1971; Thing *et al*., 1986; Reimers, 1993; Schaefer & Mahoney, 2001; Cronin *et al*., 2003). For this reason, we attributed a fragment of a skull to a putative hornless female (Sa10308, Fig.5:8). This specimen clearly belongs to *D. elegans,* since it shows the diagnostic wide protruding sagittal crest. There are two buttons or knobs placed on the supraorbital processes, suggesting that the appendage growth was inhibited. Similar buttons are also observed in two skulls of *Procervulus dichotomus* that were attributed to females by Ginsburg & Bulot (1987). They are also observed in antlerless females of *Rangifer (*Thing *et al*., 1986; fig. 2C). In females of caribou, the fact to be antlered is not a permanent condition in the individual and pedicles may be reabsorbed (Thing *et al*., 1986; fig. 2D). However, it should be noted that the very occasional absence of antlers in males of woodland caribou has also been reported (Goss, 1983). Thus, the possibility that the skull remains Sa10308 belongs to a male cannot be fully discarded.

## Casting process

The deciduous nature can be easily recognized by the presence of cast specimens and by the coronet, a bony ring formed around the base of the regenerate antler. Moreover, there are other lines of evidence such as histological differences between the pedicle and the antler, or changes in size and morphology that both pedicle and antler undergo

Table 2.—**Classification rate obtained in the discriminant analyses performed on each of the four sets of appendage measurements. Table showing the percentage of both original and cross-validate (in parenthesis) grouping of cases. N; number of valid cases (specimens) used for the analysis**

| | | | % accurate classification | | |
|---|---|---|---|---|---|
| Discriminant analysis | | N | all | male | female |
| Appendage, without branch lenghts | | 100 | 99,0 (97,0) | | |
| | male | 66 | | 98,5 (97,0) | 1,5 (3,0) |
| | female | 34 | | 0,0 (2,9) | 100 (97,1) |
| Pedicle | | 159 | 95,0 (94,3) | | |
| | male | 110 | | 93,6 (92,7) | 6,4 (7,3) |
| | female | 49 | | 2,0 (2,0) | 98,0 (98,0) |
| Protoantler, without branch lenghts | | 159 | 93,1 (93,1) | | |
| | male | 103 | | 91,3 (91,3) | 8,7 (8,7) |
| | female | 56 | | 3,6 (3,6) | 96,4 (96,4) |
| Protoantler | | 23 | 100 (69,6) | | |
| | male | 15 | | 100 (66,7) | 0,0 (33,3) |
| | female | 8 | | 0,0 (25,0) | 100 (75,0) |

Table 3.—**Summary results and data of the discriminant function obtained in the discriminant analyses**

| | | Appendage without branch lenghts | Pedicle | Protoantler without branch lenghts | Protoantler |
|---|---|---|---|---|---|
| M of Box | | | | | |
| | p | 0,002 | 0,000 | 0,000 | — |
| Lambda of Wilks | | | | | |
| | p | 0,000 | 0,000 | 0,000 | 0,022 |
| Standarized coefficients | | | | | |
| | L_ped | 0,545 | 1,035 | | |
| | DAPb_ped | 0,685 | -0,165 | | |
| | DTb_ped | 0,542 | 0,542 | | |
| | DAPd_ped | 0,166 | 0,178 | | |
| | DTd_ped | -0,330 | 0,589 | | |
| | DAPb_pa | -0,477 | | 0,396 | 0,235 |
| | DTb_pa | 0,268 | | -0,107 | 0,211 |
| | Hbif_pa | -0,033 | | 0,204 | -0,258 |
| | DAPb_br_a | -0,285 | | 0,084 | -0,073 |
| | DT_ br_a | 0,790 | | 0,761 | 0,448 |
| | Lp_b_ a | | | | 3,960 |
| | La_br_a | | | | -3,315 |
| | DAPb_br_ p | -0,185 | | -0,303 | -0,110 |
| | DTb_br_p | 0,019 | | 0,038 | 0,512 |
| | La_br_ p | | | | -0,086 |
| | Lp_br_p | | | | -0,495 |
| Centroid function value | | | | | |
| | male | 1,578 | 1,003 | 1,019 | 1,252 |
| | female | -3,064 | -2,253 | -1,873 | -2,347 |

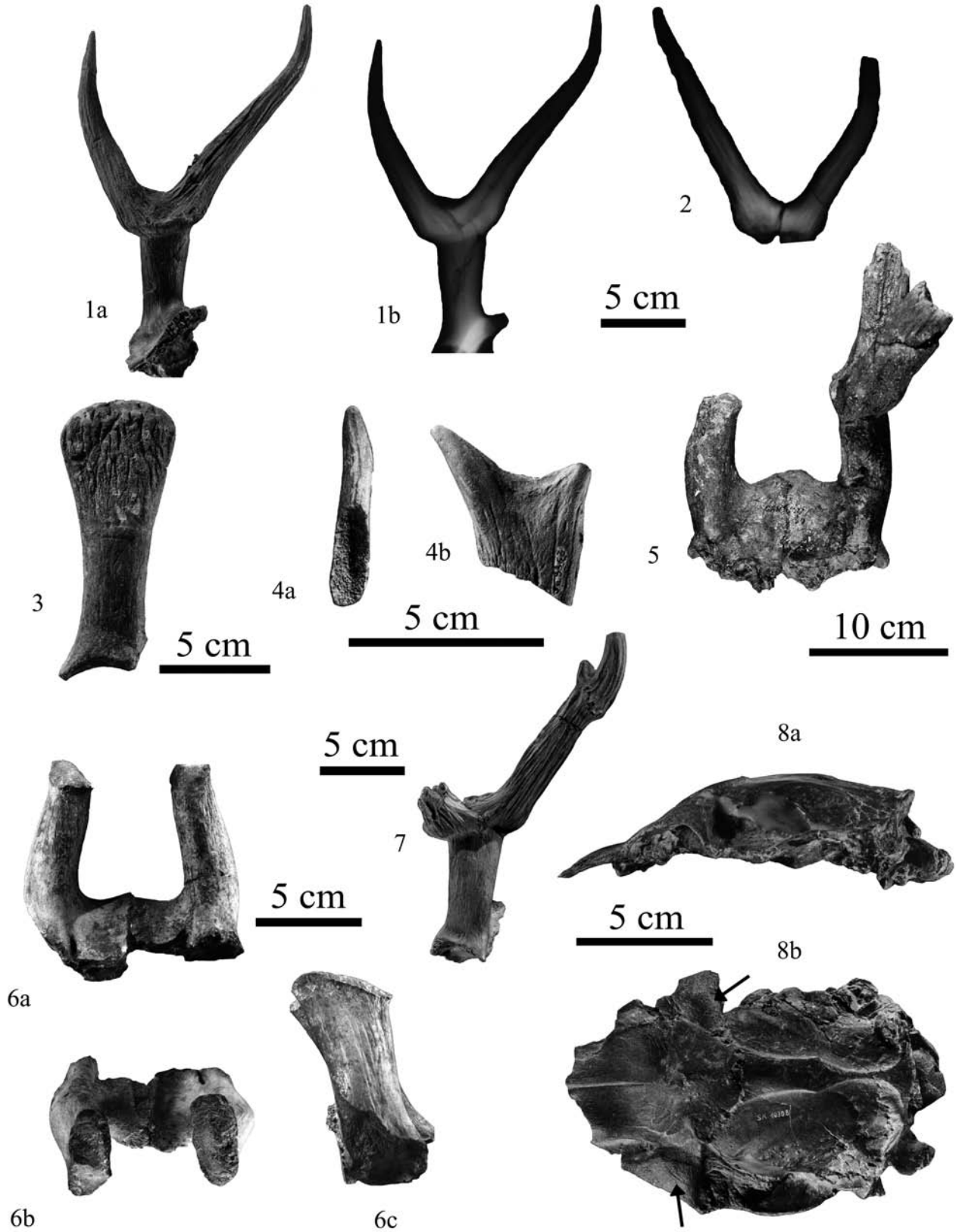
1a
1b
2
5 cm
3
4a
4b
5
5 cm
5 cm
10 cm
5 cm
7
8a
5 cm
5 cm
6a
8b
6b
6c

Fig. 5.—1 to 6: Casting process of the cranial appendages of *Dicrocerus elegans* from the Middle Miocene deposits of Sansan (France).
1: Sa9995. Right frontal bone bearing the complete cranial appendage. Adult specimen; third stage. The protoantler were probably at the end of the velveted phase. a: Medial view of the specimen. Note that the apices are completely formed and do not show evidence to be polished. b: Radiograph of this specimen confirming that the protoantler tissues are still alive. Note that the channels for the nourishing blood vessels (black lines) are visible; 2: Radiograph of a protoantler cast confirming that its tissues are dead. Note that the protoantler is completely mineralized and that there is no evidence of channels for the nourishing blood vessel; 3: Sa3352. Left frontal bone fragment bearing the pedicle. Juvenile specimen; growing after first stage. Note that, although the pedicle top is convex indicating that the protoantler was cast, the surface is very porous and furrowed suggesting that the subsequent growing cycle was started; 4: Sa3363. Protoantler cast. Juvenile specimen; first stage. Note that the base is concave and shows the spicules of the bone remaining after the osteoclastic separation from the pedicle; 5: SAN-50. Left and right frontal bones bearing the appendages. Adult specimen; fourth stage during the casting process. Note that the right pedicle top is convex indicating that the protoantler was cast, while the left protoantler remains attached to the pedicle. 6: Sa3318. Left and right frontal bones bearing the pedicles. Adult specimen; third stage after the casting. Note that the pedicle top is convex indicating that both protoantlers were cast; 7: Sa3408. Left frontal bone bearing the appendage. Adult specimen; fourth stage (the anterior branch is broken). Note that the posterior branch shows an anomalous re-growth giving the appearance of being a protoantler. This fact could be due either to the regeneration of the subsequent apex as a consequence of an injury that was produced when the branch was still growing, or to the apex sequestration and new growing during the next cycle; 8: Sa10308. Fragment of a skull that has been attributed to a protoantlerless female (Ginsburg and Azanza, 2001). This skull shows the wide and protruding sagital crest that typifies *Dicrocerus elegans*. Note the presence of buttons or knobs (arrows) on the supraorbital processes where the appendages grow.

with the successive cycles of cast and re-growth (see later).

There are several facts indicating that *Dicrocerus* protoantler could be spontaneously rejected. Several protoantler specimens have been found with a concave ventral surface which shows the bony spicules (see Fig.5:4a) remaining after the osteoclastic separation from the pedicle, as occurs with cast antlers (Goss, 1983). In turn, there are pedicle specimens in which the top is convex, indicating that the corresponding protoantler was cast. It is not feasible that taphonomical processes could have produced these surfaces.

The juvenile cast pedicle Sa3352 (Fig. 5:3) shows a very porous and furrowed distal surface, even on the convex top, thus suggesting that the subsequent growing cycle was started. In another specimen that preserved the left and right frontal bones bearing the appendages (SAN-50, Fig. 5:5), the left protoantler remains attached to the pedicle while the right pedicle shows the convex top indicating that the protoantler was already cast. This fact is often observed in present day deer, as there can be a delay of several hours, or even days, between the antler casting of one side and the other. We thus conclude that the animal died during the casting process. In the MHNT collection is common to find isolated protoantlers and pedicles belonging to the same appendage. The contact surface is broken but the ventral protoantler surface is somewhat concave and the top pedicle convex. This fact could suggest that the animals died when the osteoclastic separation was in process, and the detachment could have been produced as a consequence of the taphonomical processes because the junction between pedicle and protoantler became very slight. Before the beginning of the casting process, this junction is very strong because of the compact bone connection between the dead antler and the living pedicle (Goss, 1983; A.B. Bubenik, 1990). This also seems to occur in protoantlers given that both the pedicle and the protoantler remain attached in most of the Sansan specimens.

All cast specimens indicate that protoantlers are cast in their entirety. Occasionally antlers remain alive and covered by velvet all the time, e.g. in castrated deer. In such cases, they frequently freeze during winter. The sequestration of the dead frozen part followed by some regeneration is possible (Goss 1983; A.B. Bubenik, 1990). In the hypothesis that a permanently skin-covered appendage, as A.B. Bubenik (1990) proposed for protoantlers, it may be expected that partial sequestration could have been a common phenomenon. However, there are three specimens in which sequestration followed by regeneration of the branch apex could be supposed, although other explanations are also possible. The most impressive specimen is Sa3408 (Fig. 5:7) whose posterior branch shows an anomalous regrowth that mimics a protoantler. This structure could be the new antler growing during the cycle subsequent to the apex sequestration. However, apex regeneration during the same cycle is also possible. This fact can occur if the branch has been partly amputated due to injury while the antler is still growing (Goss, 1983; p. 205, Fig. 116). If the antler is only cracked and the distal portion keeps its original orientation, it is typically followed by fracture healing, accompanied by a conspicuous swelling around the region of the break. More

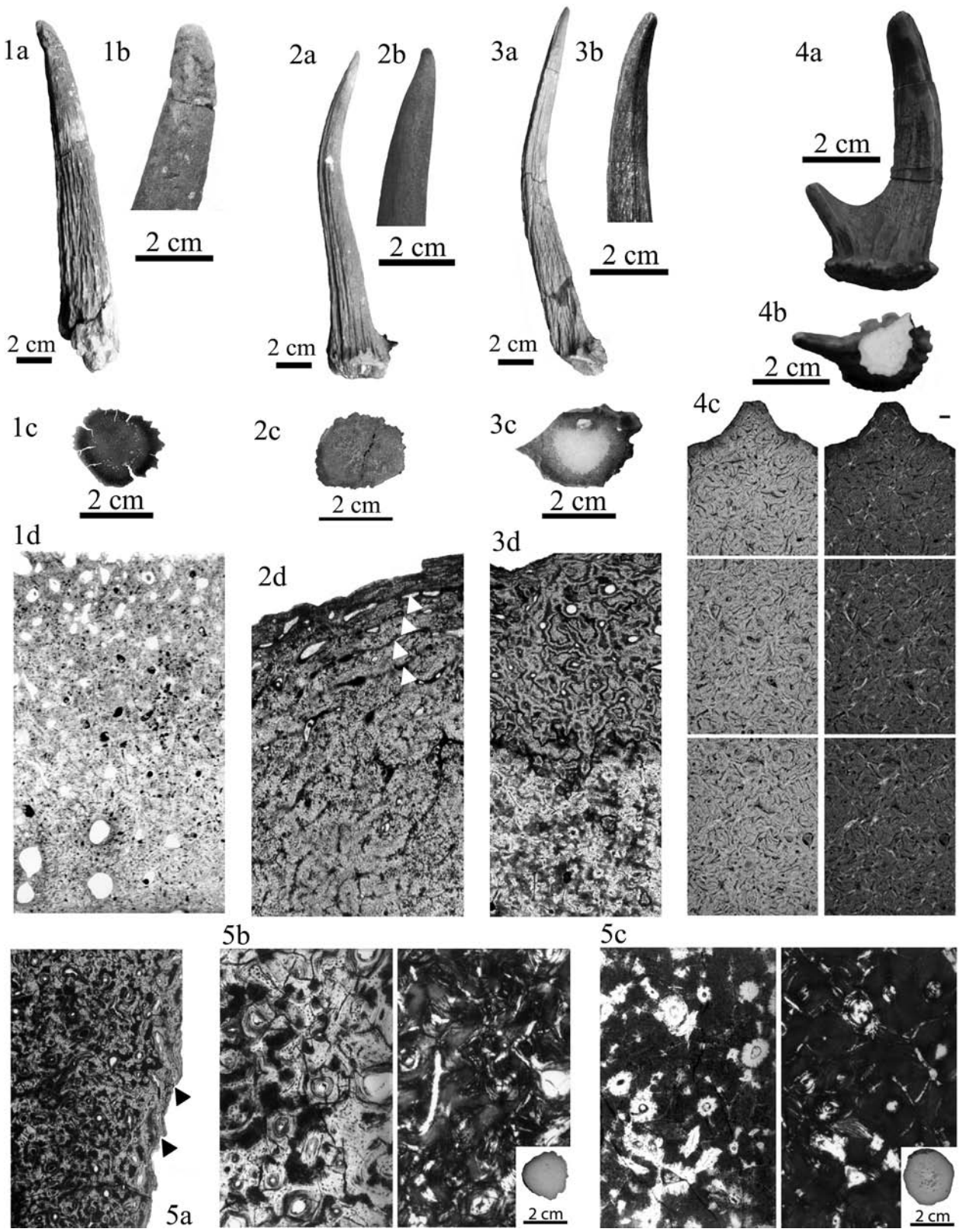
1a
1b
2 cm
2 cm
2a
2b
2 cm
2 cm
3a
3b
2 cm
2 cm
4a
2 cm
4b
2 cm
1c
2 cm
2c
2 cm
3c
2 cm
4c
1d
2d
3d
5a
5b
2 cm
5c
2 cm

Fig. 6.—Paleohistology of the cranial appendages.
1 to 4: *Dicrocerus elegans* from the Middle Miocene deposits of Sansan (France). a: specimen in lateral view, b: detailed of its apex, c: basal cross-section, d: microphotograph of the basal cross-section.
1: Sa-10324, complete branch of an appendage during the growing phase. Note that the apex is not completely formed, that its surface is rough and that the core is more porous than the cortex. Microcopically, the core has bigger porous but scarcer than the cortex; 2: Sa-ws1, complete branch of an appendage probably corresponding to the end of the growing phase. Note that the apex is completely formed although the surface remains rough. The outer part of the cortex is actively growing and four layers can be recognised (arrows); 3: Sa-ws2, complete branch of an appendage probably corresponding to the phase of velvet shedding. Note that the apex is completely formed, that its surface exhibits an incipient polished, and that the core is more mineralized than the cortex. Note also that there are two eccentric channels for the nourishing vessels; 4: Cast antler of *Muntiacus* sp. Specimen recovered by Léonard Ginsburg in Thailand. a: specimen in lateral view, b: detailed of the basal cross-section of its posterior branch and c: microphotographs (normal and polarised light) of the basal cross-section (Scale bar 200 μm). Note that there is not a cancellous core, contrary to other present-day deer antlers, and that the bone is inmature and no cortical layers are observed; 5: Sa-sw3, microphotographs (normal and polarised light) of a branch (5a and 5b) and the pedicle (5c) of a cranial appendage corresponding to an adult-senile male. Note the histological differences between the protoantler and the pedicle. The branch has the core completely mineralized, contrary to the pedicle, however the bone is less matured than the pedicle cortex bone. Some ridges are related to cortical bone deposition (arrows).

specifically, Sa11442 and Sa11443 specimens show a swelling or bony ring very near the apex and could correspond to this type of injury.

## Cycle and growth

The appendage growth was studied in detail using thin transversal sections of specimens in three distinct phases of the appendage growth (Fig. 6). All these specimens are isolated branches broken at their bases, and two of them (Fig. 6:2 and 6:3) clearly correspond to male protoantlers. Specimen Sa-10324 (Fig. 6:1) shows a not completely formed apex with a rough surface, and corresponds to an appendage of the growing phase. Macroscopically (Fig. 6:1c), it is observed that the appendage is made up of a cortex of solid bone and a more porous core, although this central region is not spongy bone as found in deer antlers or long bones. Microscopically, the cortex has abundant (although much smaller) pores than the core. The outer part of the cortex is more finely porous than the inner part, but layers are not recognised (Fig. 6:1d). Superficial blood vessels become buried by the bone laid down, thus resulting in grooves on the surface. Specimen Sa-ws1 (Fig. 6:2) shows a more completely formed apex, but the surface remains rough, and probably corresponds to an appendage at the end of the growing phase. Macroscopically (Fig. 6:2c), it is similar to Sa-10324 but the differences between the cortex and the core are less clear. The outer part of the cortex is actively growing and up to four peripherical layers can be recognised but only on the medial side of the branch (Fig. 6:2d). This microstructure resembles that of the merycodontine appendage (A.B. Bubenik, 1990) and the lagomerycid protoantler (Azanza & Ginsburg, 1997). Finally, specimen Sa-ws2 (Fig. 6:3) shows the completely formed apex with a polished surface, and probably corresponds to an appendage in the phase of velvet shedding. Macroscopically, it is very different (Fig. 6:3c) since the core is constituted by dense bone despite to still have a porous cortex. There are two eccentric channels for nourishing vessels, one significantly bigger than the other. However, the appendage is constructed of rather immature compact bone (Fig. 6:3d). It confirms the suggestion proposed by A.B. Bubenik (1990) that mineralization in *Dicrocerus* protoantlers progresses centrifugally from the core to the periphery. In contrast, the antler bone is composed of an outermost layer of compact bone containing Haversian systems and a central region of spongy bone formed by fewer, coarser lamellae with wider marrow spaces (Chapman, 1975). The mineralization in antlers progresses from the periphery to the inner part of the cortex and also from the base (A.B. Bubenik, 1990).

Sa-ws3 specimen (Fig. 6:5) corresponds to an adult male appendage, and is also here discussed. The junction between the pedicle and the protoantler has been glued, but sediment between them can be recognized. This specimen could be a similar case to that described above. The detachment could have been produced because the junction became very slight as a result of the osteoclastic separation being in process. If it is the case, this specimen correspond to an appendage at the end of the hard, bare, dead protoantler phase. There are some important histological differences between the branch (Fig. 6:5a and 6:5b) and the pedicle (Fig. 6:5c). Macroscopically, the branch is composed completely of dense bone but the pedicle consists of a thick cortex of solid bone and a core of spongy bone. However, the branch bone is less matured than the pedicle cortex bone. Haversian

osteons of secondary bone lamellae are observed mainly in the core region (Fig. 6:5a and 6:5b), but a dense Haversian tissue with successive generations of superimposed Haversian systems, as in lifelong bones, is only observed in the pedicle cortex (Fig. 6:5c). This fact confirms that the protoantler bone is younger than the pedicle bone, i.e. it evidences that protoantlers cast and re-grow. In true antlers, secondary and tertiary Haversian systems and interstitial lamellae are not observed (presumably because the life of the antler bone is limited and the antler is laid down annually in its entire width from the beginning; Chapman, 1975). It can be inferred that protoantlers have been borne by the animal for longer than true antlers, and if so, the query exists whether this could be for more than one annual cycle. On the medial side, the osteons of the cortex seem to be partially oriented suggesting appositional lamellae, sometimes in an oblique direction and in relation to some superficial thinnest ridges (Fig. 6:5a). This could confirm the suggestion proposed by A.B. Bubenik (1990) that the cortex can remain active, even if the appendage construction is completed. However, the antler is so mineralized that supposedly, the tissues were already dead.

Many specimens of protoantlers which are still attached to the pedicle show worn and polished apices (Fig.1 and 2). In some of them, an important loss of bony material is apparent (Fig. 2:6 and 2:7). Moreover, specimen Sa3324 shows one of the apices broken in where the scar also appears polished (Fig. 1:4). This fracture must have occurred once the bone was dead and free from the velvet-like skin, and when the animal used the appendages. All these facts evidence the hard, bare, dead protoantler phase before casting.

The radiograph of a cast male protoantler (Fig. 5:2) shows a completely mineralized protoantler bone with no evidence of channels for the nourishing blood vessel, thus corroborating that its tissues died before casting. A contrary case is that found in the complete male appendage Sa9995. The protoantler was probably at the end of the growing phase and is still covered by a velvet-like skin, because the apices are completely formed and show no evidence of polishing (Fig. 5:1a) A radiograph of this specimen confirms that the protoantler tissues were still alive. The bone is not completely mineralized and the channels for the nourishing blood vessels are visible (Fig. 5:1b), indicating that blood flow was still possible throughout the entire appendage at the time of death.

As described above, the *Dicrocerus* protoantler frequently shows small protuberances or knobs that could be cortical structures. One of them (Fig. 2:3) could have a genetic basis since it has often been found in the same position, while others have not. It could be related to the more unusual mechanism of sprouting which proceeds through exostosis (A.B. Bubenik, 1990). This mechanism indicates a highly active cortex and could be linked to appendage mineralization progressing centrifugally (A.B. Bubenik, 1990).

## Ontogenetical sequence

Appendages are found to change in size and morphology with successive castings, and we can therefore design a lineal ontogenetic sequence. Specimens corresponding to both male and female morphotypes are respectively ordered in figures 1 and 2, according to a hypothetical ontogenetic sequence. The following five stages can be easily recognised.

*First stage, juvenile-subadult*. Juvenile appendages are not a spike, as in modern deer. Stehlin (1939) attributed the youngest state to unbranched specimens whose morphology resembles to that of the youngest specimens in *Heteroprox* and *Euprox*. However, they consist of a long, laterally flattened shaft whose apex is usually forked with no appreciable limit between the pedicle and the protoantler. The very small protoantler has still not been rejected.

*Second stage, subadult*. Long pedicle. After the first casting, the small protoantler was regenerated (its base is larger than the pedicle top, a ring or swollen bone appears around the base) but branches are short, similar in size, and closer together.

*Third stage, adult*. Moderately long pedicle with less flattened section. The protoantler base is clearly larger than the pedicle top, and a coronet-like structure appears only developed on the medial side. The branches are very long, the biggest being the posterior one.

*Four stage, adult*. Short pedicle and more rounded in section. The protoantler base is much larger than the pedicle top, and the branches are set well apart.

*Five stage, adult-senile*. Very short pedicle. The protoantler base is much larger than the pedicle top, and the branches are greatly separated from each other as observed in four stage. Branches are short-

er and have similar size. Accessory branches or anomalous morphologies are common.

It is not easy to know the age at which the animal could bear appendages at each of these development stages. There is a fragment of skull in Sansan belonging to a certainly very young animal, as its size, thin frontal bones, and open sutures indicate. This skull bears appendages that are similar in morphology but very small and thinner than the usual female first stage ones. According to Ginsburg & Azanza (1991), this specimen could suggest that appendages are developed very early in the development of *Dicrocerus*, similar to those that occur in *Rangifer* in which antlers develop in prepubertal individuals (Lincoln & Tyler 1992). However, specimen Sa3567 (Fig. 2:5), a complete female skull bearing appendages whose protoantlers were not still rejected, shows that all upper check teeth were already erupted at the time of the first stage appendages. If compared with the development in modern deer, this fact indicates that the individual was at least subadult. It could be that the first appendages were borne for over a year. This could explain the observation of A.B. Bubenik (1990) that specimens Sa3322, Sa3364, and Sa3320 (that he attributed to *Heteroprox*) had been growing for more than one cycle. Also, the histological features of hard protoantlers suggest that the bone is more mature than in antlers and, consequently, that protoantlers had been growing over a longer period of time, but more than an annual cycle?

## Discussion and conclusions

As mentioned above, the nature of the *Dicrocerus* appendages has been variously interpreted by different authors, either as lifelong protuberances, facultative perennial appendages or deciduous antler-like appendages. Establishing the homology between dicrocerine protoantlers and true antlers is no easy task because it should be based on comparisons between the details of the developmental processes and the inducing and contributing tissues, all of which are very speculative in fossil organisms.

As occur in deer antlers, dicrocerine appendages are probably of an apophyseal nature, i.e. they are originated as an upgrowth from the frontal periosteum with the overlying skin playing a passive role (Goss, 1990). The occurrence of apophyseal appendages seems to be more common in mammals than epiphyseal ones (Solounias, 1988a, 1988b). A.B. Bubenik (1983) and Geraads (1986) state that such apophyseal nature can be recognised through the microstructure of the bone composed of a cortex of compact bone and a typical bone marrow, as occurs in the pedicle and the antler. In dicrocerine appendages, this microstructure is only observed in the pedicle, while the final 'velvet' protoantlers have a reversed microstruture where mineralization progressed centrifugally from the core until the hard protoantler is completely constructed by compact bone. There is, however, no dense Haversian tissue with successive generations of Haversian systems superimposed typically of epiphyseal lifelong appendages. Janis & Scott (1987), however, questioned the reliability of this criteria since the apophyseal growth is only experimentally demonstrated in deer antlers (Goss, 1983), and it is difficult to state whether their unique histological appearance relates to their mode of development or to their deciduous nature.

The rise and fall of different hormonal segregations, among which testosterone plays a dominant role (G.A. Bubenik, 1990), control the cycle and growth of the antler proper. Once the growth is complete, a sudden rise of testosterone secretion triggers a profound mineralization of the antler. The tissues above the pedicle die because the blood supply to the surface is cut off, and a compact bridge between antler and pedicle is built up (A.B. Bubenik, 1983, 1990). As soon as the testosterone levels drop drastically, numerous osteoclasts destroy simultaneously a narrow zone of bone at the junction of the living bone of the pedicle and the dead bone of the antler (Goss, 1983). The weight of the antler itself effects the detachment when the points of attachment between the antler and the pedicle became extremely attenuated. The regenerated antler is marked by the burr or coronet, a bony rim at the base of the antler which seals the pedicle skin.

Because we have found cast specimens showing the spicule remnants of the osteoclastic erosion, the protoantler in *Dicrocerus*, as well as in lagomerycids and procervulines (Ginsburg, 1985; Azanza, 1993; Azanza & Ginsburg, 1997), was capable of spontaneous autonomy in its entirety. However, there are important differences between these cast specimens. Radiographs and longitudinal sections of these specimens show that in lagomerycids and procervulines their rejection was produced without the protective bridge at the joint with the pedicle (A.B.

Bubenik, 1990; Azanza & Ginsburg, 1997). Indeed, the mineralisation was not enough to cut off the blood supply from the pedicle and consequently the protoantler tissues were still alive when their rejection occurred. A similar sequestration process of tines or distal parts has been studied in the antlers of castrate deer (A.B. Bubenik *et al*., 1990). In contrast, the entire proantler in *Dicrocerus* is constructed of compact bone (not only at the protective bridge and cortex as in true antlers) and the blood supply was cut off. Consequently, the tissues were dead long before their casting occurred. This is also evidenced by the wear and the polish of the apices, which can only be produced if the protoantlers are hard, bare and dead, and used by the animal. This, however, has not been observed in lagomerycid or procervuline protoantlers.

In our opinion, the protoantlers of *Dicrocerus* could be deciduous. The cycle seems to be very similar to that of true antlers, since it includes the phases of the velvet-like skin shedding and of the hard, bare, dead antler before casting. Despite to be developed only around the medial side, the coronet-like structure suggests a more similar regeneration process, perhaps in relation to a velvet-like skin. Due to these both features, dicrocerines seem to be closely related to true antlered deer (Azanza, 1993). However, the histological differences between both appendages should not be neglected. For this reason, we maintain the denomination of protoantlers for the appendages of *Dicrocerus*.

These histological features resemble some peculiarities of particular cases of velvet antlers in castrated deer, as was noted by A.B. Bubenik (1990) and A.B. Bubenik *et al*. (1990). In these cases, the adrenals seem to produce enough corticoids to keep the shape under control (G.A. Bubenik 1990). For instance, the reverse microstructure with dense bone in the centre and more porous bone at the periphery is observed in these velvet antlers, and if they were partially or totally sequestered, the base is concave (A.B. Bubenik *et al*., 1990). If there is no such hormonal compensation, an uncontrolled proliferation of unmineralized tissues (perukes) succeeds castration, as is common in muntiacines and *Capreolus* (Groves & Grubb, 1990). This fact has a malignant impact on the calcium/phosphorous metabolism, forcing the body to utilize these elements from the skeleton.

There are also similarities with the antlers of tropical deer. The bases of cast antlers show a different degree of concavity depending on individual age. The cycle is similar to that of temperate deer but aseasonal, and the antlers may even be borne for longer than one cycle. All these facts seem to be related to hormonal levels. The plasma testosterone never drops so low that spermatogenesis is discontinued (e.g. in the chital *Axis axis*, Loudon & Curlewis, 1988). Tropical deer, such as chital and hog deer (*Axis porcinus*), tend to have low proportions of cancellous bone in their antlers (Kitchener, 1991). This antler structure could convey antler biomechanical properties (greater stiffness and strength to the antlers of tropical deer relative to temperate deer) that correlate with the functional need for the antlers of tropical deer to resist damage accumulation and have a longer working life than those of temperate species that fail to span a year round (Kitchener, 1991). According to Blob & Labarbera (2001), the high antler stiffnesses of tropical deer may reflect the retention of an ancestral condition, rather than the adaptation to year-round antler use. The antler structure of muntjacs is not sufficiently known. We studied the thin section of a cast antler of *Muntiacus* sp. from Thailand (Fig. 6:4) in which a high proportion of compact bone is also observed. The core is more porous than the cortex, but a central region of cancellous bone is not developed. Histologically, it is more similar to the growing protoantler Sa-ws2 than to the cast protoantlers. However, peripheral layers are not observed. In Muntiacines, the antler cycle is also aseasonal and antlers may be frequently borne for more than one cycle. The bornean endemic *Muntiacus atherodes* even possesses antlers of normally non deciduous nature (Groves, 2007).

Main similarities observed with the appendages of *Rangifer tarandus* are sexual dimorphism and the developmental times of the antlers, as above described. Also, the formation of sprouts (implying a highly active cortex) seems to be present in *Rangifer* antlers more frequently than in other deer (A.B. Bubenik, 1975). In *Rangifer,* these peculiarities are in relation to a lower regulation of the antler cycle by the seasonal variation of circulating levels of sexual hormones. It could be speculated that is also the case of *Dicrocerus* (Ginsburg & Azanza 1991). Lincoln & Tyler (1994) concluded that ovarian estradiol ($E_2$) is the main regulator of the antler cycle in the female reindeer and adrenal androgen androstenedione may be the secondary steroid involved in antlerogenesis. In the male reindeer, the correlation between testosterone (T) levels and the antler cycle is less pronounced than in other deer (G.A. Bubenik

*et al*., 1997). A significant correlation has been found between T and $E_2$ levels in males which may indicate that reindeer testes aromatize a considerable amount of T into $E_2$, and it could be speculated that in addition to T, $E_2$ could play the role of a secondary steroid involved in the male reindeer antlerogenesis (G.A. Bubenik *et al*., 1997).

Importantly, some ecological resemblances existing between *Dicrocerus* and *Rangifer* could explain the evolution of antlers on female *Dicrocerus*. The functional advantages of horn possession in females remain unresolved, but could included defence against predators (Packer 1983), mimicry of male offspring (Estes 1991), and competition for resources (Geist 1977, Clutton-Brock 1982, Roberts 1996). Evidence from *Rangifer tarandus* discards the two first hypotheses (Schaefer & Mahoney, 2001). Observations of active defence are rare (Estes 1991) and antlers as a means to mimic juvenile male offspring and to guard against aggression by dominant males (Estes, 1991) cannot account for the somewhat different chronology of antler casting between sexes (Bergerud, 1976). Female antlers serve as weapons to be used in intraspecific, often intrasexual, contest for limited feeding resources (Roberts, 1996). Data from Schaefer & Mahoney (2001) support that antlers on female caribou provide functional advantages in interference competition for winter food, but that antler possession may decline in instances of higher animal densities and diminished nutritional state. *Dicrocerus elegans* is the biggest deer found during the Early-Middle Miocene, and since its morphology is similar to that of the muntjaks, it would seem more likely to have been a browser. Microwear data, however, support that, at least in Sansan, this species was a seasonal mixed-feeder (Solounias & Moelleken, 1994), thus suggesting that *Dicrocerus* inhabited a more open habitat than that observed for contemporaneous deer in which the availability of resources fluctuated seasonally. The extraordinary abundance of antlers recovered in Sansan (more than four hundred; an exclusive case in the Miocene ruminant fauna), supports the hypothesis that *D. elegans* was gregarious (DeMiguel *et al*., 2008) and that herds were very large numbered. With these ecological features, one would expect an opportunist behaviour for *D. elegans* and, therefore, a very high intraespecific competition for feeding resources.

We conclude that *Dicrocerus* protoantlers and antlers could be homologous appendages. Histological differences could be related to differences in hormonal regulation which can be caused by the fact that:

1) *Dicrocerus* inhabited a tropical environment, and therefore the animal hormonal levels could have not varied sufficiently throughout the year and the mineralization could have not been blocked at every cycle.

2) Females also developed protoantlers. Thus, the hormones regulating the protoantler cycle are not testicular androgens and the sensitivity of hormone receptors in the velvet-like and bony tissues could be different.

It should not be overlooked that the dicrocerine protoantler appears at the end of the Early Miocene (MN3, 20-17Ma; Larrasoaña *et al*., 2006), at the same time that other cranial appendages in ruminants (Janis, 1982, 1990; Morales *et al*., 1992), and were evolved throughout the Middle Miocene when a process of global warming known as Miocene Climatic Optimun (MCO 17 - 15 Ma, Zachos *et al*., 2001; with a maximum peak around 16,8 - 16,2 Ma, Shevenell & Kennett, 2004) took place. The locality of Sansan was deposited at the end of the MCO (Chrons C5ADr - C5Br, age estimated between 15,0 - 15,2 Ma, Sen & Ginsburg, 2000; however, this age is too older according to Daams *et al*., 1999, who proposed an age of 13,6 Ma based on biochronological and magnetostratigraphical record of Spanish Neogene basins). In contrast, true antlers appear several million years later and evolved in relation with the following and drastic cooling process known as Middle Miocene Climatic Transition (MMCT 14,2 - 13,8 Ma, Shevenell *et al*., 2004; with minimum temperatures estimated at around 13,9 Ma; Holbourn *et al*., 2005). The first true antlered deer seems to be *'Euprox' minimus*, whose oldest record is the Austrian locality of Göriach (MN6) in where *D. elegans* is also present. Dicrocerines disappear just at the end of this climatic event. Given the importance of these climatic changes, and their coincidence with the evolutionary pattern here described, it is highly probable that both phenomena are strongly related as Azanza (1993) already suggested.

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## Appendix

Appendix 1.—Appendage measurements (mm) of *Dicrocerus elegans* from the Middle Miocene locality of Sansan (France). (See abreviations on the text).

| sigle | morphotype | L_ped | DAPb _ped | DTb _ped | DAPd _ped | DTd _ped | DAPb _pa | DTb _pa | Hbif _pa | DAPb _br_a | DT _ br_a | Lp _b_ a | La_br _a | DAPb _br_ p | DTb _br_p | La_br _ p | Lp _br_p |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Sa 3564 | M | 42,95 | | | 35,04 | 21,79 | 59,27 | 38,29 | 22,05 | 23,06 | 23,22 | 134,35 | 159 | 23,93 | 23,43 | | |
| Sa 3563 | M | 47,94 | 28,23 | 24,36 | 34,44 | 25,13 | 64,34 | 38,39 | 27,52 | 23,14 | 21,47 | 135,36 | 162 | 24,08 | 21,85 | 172 | 186 |
| Sa 3538 | M | | | | 31,28 | 25,19 | 58,87 | 48,23 | 33,4 | 24,4 | 26,06 | | | 25,63 | 26,1 | | |
| Sa 3491 | M | | | | | | 51,75 | 40 | 33,15 | 19,62 | 20,89 | | | 24,46 | 22,73 | | |
| Sa 3488 | M | 50,55 | 26,72 | 21 | 31,64 | 18,6 | 57,11 | 35,95 | 25,49 | 19,46 | 22,29 | 138,08 | 165,5 | 25,67 | 24,66 | | |
| Sa 3398 | M | 57,41 | 27,56 | 21,75 | 33,97 | 20,33 | 60,61 | 33,7 | 22,95 | 20,58 | 19,78 | | | 23,73 | 22,48 | | |
| Sa 3559 | M | 45,95 | 28,64 | 26,06 | 32,54 | 22,39 | 62,93 | 39,29 | 28,68 | 23,45 | 19,51 | | | 25,32 | 26,63 | | |
| Sa 3422 | M | 44,33 | 28,29 | 25,83 | 30,68 | 22,04 | 59,06 | 44,26 | 30,93 | 21,35 | 22,05 | 125,26 | 141,87 | 25,61 | 24,45 | 165,7 | 184,6 |
| Sa 3424 | M | 44,13 | 28,72 | 26,58 | 30,66 | 21,85 | 57,85 | | 22,16 | 24,07 | 18,79 | 137,15 | | 25,04 | 22,22 | 174 | 192,6 |
| Sa 9994 | M | 52,33 | 26,94 | 22,85 | 35,87 | 21,8 | 57,28 | 37,39 | 29,24 | 25,58 | 20,63 | 124,78 | 155 | 26,27 | 22,96 | 146 | 166 |
| Sa 3386 | M | 47,17 | 23,89 | 20,76 | 28,2 | 18,09 | 51,27 | 33,79 | 27,99 | 18,16 | 18,85 | | | 20,88 | 17,57 | | |
| Sa 3531 | M | 54,32 | 26,53 | 26,68 | 35,14 | 21,78 | 62,25 | 37,55 | 25,85 | 23,04 | 19,28 | 98,53 | 123,87 | 22,38 | 16,69 | | |
| Sa 3475 | M | 47,5 | 27,12 | 21,88 | | 17,59 | 61,59 | 34,22 | 27,29 | 21,59 | 19,35 | 124,2 | 150 | 20,01 | 19,45 | 143,45 | 176,8 |
| Sa 3519 | M | 52,38 | 27,07 | 24,65 | 29,81 | 24 | 58,75 | 38,31 | 31,2 | 21,51 | 21,72 | 157 | 189 | 27,46 | 18,12 | | |
| Sa 3393 | M | 53,5 | 23,69 | 20,4 | 33,47 | 20,54 | 54,44 | 32,91 | 23,16 | 21,69 | 21,54 | | | 21,79 | 23,38 | | |
| Sa 3389 | M | 57,89 | 25,35 | 21,87 | 33,9 | 18,57 | 57,33 | 31,65 | 26,22 | 22,02 | 21,27 | | | 21,39 | 24,31 | | |
| Sa 3566 | M | 57,83 | 27,97 | 27,91 | 42,47 | 24,12 | 74,48 | 42,6 | 31,32 | 24,31 | 24,36 | | | 28,34 | 27,23 | | |
| Sa 3402 | M | 58,27 | 22,25 | 18 | 29,47 | 15,52 | 49,39 | 25,38 | 22,36 | 14,36 | 14,75 | | | 19,61 | 17,06 | | |
| Sa 3392 | M | 68,25 | 25,13 | 20,41 | 36 | 13,75 | 51,5 | 20,57 | 13,84 | 15,95 | 16,34 | | | 15,1 | 14,24 | | |
| Sa 3518 | M | 54,14 | 31,06 | 27,63 | 38,62 | 25,33 | 72,23 | 45,38 | 29,74 | 25,42 | 21,8 | | | 27,31 | 23,9 | | |
| Sa 9992b | M | 50,01 | 29,3 | 21,28 | 37,7 | 20,99 | 68,01 | 39,19 | 27,54 | 30,69 | 21,64 | 146 | 169 | 27,25 | 25,91 | | |
| Sa 3436 | M | | | | 34,9 | 22,15 | 56,99 | 38,44 | 21,79 | 22,15 | 20,25 | 142,84 | 166,2 | | 24,54 | 175 | 193 |
| Sa 3529 | M | 50,17 | 22,85 | 17,44 | 33,43 | 14,66 | 48,7 | 30,82 | 23,27 | 19,25 | 16,41 | | | 19,43 | 19,81 | | |
| Sa 9995 | M | 48,08 | 25,31 | 23,45 | 32,98 | 19,38 | 56,3 | 34,45 | 24,59 | 21,27 | 20,52 | 115,72 | 141,58 | 24,47 | 24,5 | 157 | 175 |
| Sa 3560 | M | 49,66 | | | 34,76 | 22,37 | 71,46 | 40,68 | 26,11 | 22,71 | 21,27 | 175 | 204 | 22,98 | 21,87 | 195,5 | 223,5 |
| Sa 3435 | M | 45,21 | 26,02 | 23,24 | 28,97 | 20,96 | 56,39 | 33,75 | 30,49 | 21,89 | 22,76 | 139,72 | 166,5 | 23,43 | 21,66 | | |
| Sa 3413 | M | 43,06 | 27,96 | 26,03 | 30,45 | 21,81 | 59,88 | 47,14 | 26,73 | 22,78 | 21,66 | 115,78 | 143,7 | 28,76 | 23,31 | | |
| Sa 3495 | M | 41,85 | 26,3 | 22,99 | 32,77 | 18,1 | 55,09 | 32,04 | 19,91 | 20,2 | 19,94 | | | 22,8 | 20,15 | | |
| Sa 3423 | M | 48,61 | 25,3 | 24,94 | 29,57 | 22,7 | 51,01 | 40,51 | 26,92 | 21,75 | 20,41 | | | 24,87 | 24,51 | | |
| Sa 3409 | M | 49,53 | 26,09 | 21,84 | 34,11 | 21,08 | | 36,51 | 25,56 | | | | | 23,32 | 19,77 | | |
| Sa 3408 | M | 48,55 | 26,78 | 21,42 | 33,53 | 17,56 | 61,28 | 38,03 | 26,67 | | | | | 23,69 | 22,16 | | |
| Sa 3528 | M | 43,81 | 29,54 | 23,86 | 34,04 | 21,6 | 64,28 | 45,13 | 27,37 | 20,78 | 20,57 | | | 26,15 | 23,57 | | |
| Sa 3360 | M | 40,29 | 25,72 | 21,68 | 30,68 | 20,22 | 52,89 | 32,69 | 25,61 | 20,66 | 17,36 | | | 20,74 | 19,26 | | |
| Sa 3406 | M | 37,82 | 27,17 | 22,83 | 32,67 | 21,91 | 54,28 | 35,12 | 25,31 | 22,64 | 23,87 | | | 19,57 | 19,32 | | |
| Sa 3561 | M | 27,44 | 28,88 | 27,07 | 31,55 | 25,62 | 57,45 | | 29,65 | 21,84 | 20,59 | | | 27,42 | 24,33 | | |
| Sa 3506 | M | 30,43 | 26,92 | 22,19 | 28,85 | 19,95 | | | | 18,41 | 19,23 | | | | | | |
| Sa 3426 | M | 37,55 | 28,55 | 24,43 | 29,85 | 23,58 | 56,97 | | 30,21 | 23,77 | 21,35 | 114,95 | 137,07 | 24,75 | 23,69 | 176 | 195,5 |
| Sa 3520 | M | 38,63 | 27,26 | 23,83 | 33,31 | 22,01 | 64,51 | 38,32 | 27,82 | 22,96 | 22,04 | | | 41,4 | 23,1 | | |
| Sa 3534 | M | 29,58 | | | | | 63,23 | 46,17 | 25,6 | 25,37 | 26,5 | 131,59 | 160,2 | 27,7 | 15,17 | 186,5 | 209 |
| Sa 3482 | M | 40,07 | 28,14 | 24,7 | 34,75 | 20,68 | 61,01 | 37,52 | 24,57 | 20,52 | 20,27 | | | 23,37 | 20,37 | | |
| Sa 3532 | M | 42,27 | 21,91 | 25,85 | 29,44 | 22,91 | 62,01 | 45,86 | 22,1 | 23,81 | 27,12 | | | 29,85 | 27,12 | 196 | 212 |
| Sa 3505 | M | 41,5 | 23,96 | 19,88 | 27,02 | 19,84 | 56,77 | 33,56 | 21,48 | 20,37 | 20,78 | | | 24,91 | 21,42 | | |
| Sa 11460d | M | 43,4 | 25,71 | 22 | 31,53 | 25,37 | | | 28,36 | | | | | 27,46 | 25,77 | | |
| Sa 11460g | M | 35,53 | 26,02 | 25,34 | 31,29 | 21,72 | | | 28,32 | 22,58 | 20,4 | | | | | | |
| Sa 3418 | M | 43,49 | 24,62 | 23,52 | 25,98 | 22,4 | | | 23,34 | | | | | 22,44 | 22,73 | | |
| Sa 3425 | M | 29,26 | 26,98 | 25,56 | 30,69 | 24,04 | 59,71 | 38,81 | 30,43 | 24,28 | 23,04 | | | 26,82 | 21,29 | 190,5 | 210,5 |
| Sa 11436g | M | 55,57 | 27,21 | 21,62 | 33,52 | 19,62 | 52,63 | 37,15 | 23,24 | 23,21 | 16,55 | | | 24,66 | 19,89 | | |
| Sa 11436d | M | 56,47 | 26,15 | 22,7 | 33,05 | 19,44 | 55,07 | 36,24 | 24,89 | 20,64 | 21,07 | | | 22,16 | 24,52 | | |
| Sa 3486 | M | 62,4 | 22,93 | 21,31 | 30 | 17,93 | | 29,99 | 21,1 | 19,19 | 18,73 | 115,72 | 129,45 | 20,54 | 21,61 | | 144,32 |
| Sa 3355 | M | 60,43 | 23,13 | 20,26 | 33,6 | 17,56 | 55,82 | 35,87 | 24,09 | 21,27 | 19,89 | | | 20,62 | 26,51 | | |
| Sa 3558 | M | 60 | 24,28 | 21,05 | 29,49 | 17,3 | 46,17 | 32,89 | 24,26 | 18,68 | 16,41 | | | 17,15 | 17,95 | 135,45 | 146,26 |
| Sa 3562 | M | 55,56 | | | 31,22 | 18,32 | 59,26 | 37,23 | 26,04 | 25,53 | 19,2 | | | 20,89 | 21,34 | | |
| Sa 3494 | M | 56 | 25,06 | 21,59 | 35,58 | 19,65 | 58,66 | 33,82 | 25,7 | 20,97 | 21,33 | 136,31 | 153,01 | 21,73 | 24,53 | | |
| Sa 3483 | M | 56,02 | 26,34 | 18,15 | 33,93 | 20,34 | 71,15 | 39,91 | 29,73 | 24,13 | 26,3 | | | 28,18 | 24,92 | | |
| Sa 3526 | M | 56,39 | 24,85 | 24,07 | | 23,41 | | | 26,4 | 23,54 | 23,13 | 120,4 | 140,39 | 29,4 | 25,72 | 153 | 154,5 |
| Sa 3496 | M | 62,91 | 24,03 | 21,75 | 28,16 | 16,76 | 45,9 | 31,96 | | 16,71 | 14,9 | | | 17,23 | 16,77 | | |
| Sa 3492 | M | 42,01 | 33,98 | 28,78 | 37,53 | 26,29 | 75,77 | 43,46 | 35,78 | 30,42 | 22,66 | | | 35,22 | 25,44 | | |
| Sa 3388 | M | 29,65 | 26,39 | 26 | 30,91 | 22,57 | 74,24 | 45,1 | 28,44 | 25,44 | 23,45 | | | 28,37 | 30 | | |
| Sa 3535 | M | 34,49 | 28,98 | 24,68 | | | 67,47 | 38,89 | 30,8 | 27,61 | 25,96 | | | 28,49 | 22,54 | | |
| Sa 3514 | M | 44,39 | 28,58 | 25,06 | 30,27 | 21,68 | 54,9 | | 26,13 | 24,43 | 21,93 | | | 22,82 | 23,05 | | |

Appendix 1 *(continuation)*.—Appendage measurements of *Dicrocerus elegans* from the Middle Miocene locality of Sansan (France). (See abreviations on the text).

| sigle | morphotype | L_ped | DAPb _ped | DTb _ped | DAPd _ped | DTd _ped | DAPb _pa | DTb _pa | Hbif _pa | DAPb _br_a | DT _ br_a | Lp _b_ a | La_br _a | DAPb _br_ p | DTb _br_p | La_br _ p | Lp _br_p |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Sa 3396 | M | 40,23 | 27,73 | 26,22 | 34,42 | 26,39 | 62,11 | | 35,06 | 25,87 | 24,33 | | | 24,73 | 21,13 | | |
| Sa 3557 | M | 47,02 | 27,57 | 26,98 | 33,95 | 23,5 | 69,41 | 39,61 | 24,32 | 22,45 | 20,6 | | | 22,75 | 20,71 | | |
| Sa 3397 | M | 26,95 | 26,39 | 23,15 | 29,23 | 21,68 | 52,04 | 41,84 | 25,34 | 22,38 | 20,99 | | | 24,96 | 24,63 | 158 | 185 |
| Sa 3411 | M | 32,15 | 27,94 | 26 | 32,18 | 26,6 | 61,79 | 41,77 | 23,5 | | | | | 25,24 | 21,52 | | |
| Sa 3527 | M | 36,71 | 27,1 | 26,59 | 32,33 | 23,34 | 56,38 | 37,67 | 23,76 | 21,92 | 19,4 | | | 22,47 | 24,83 | | |
| Sa 3385 | M | 25,71 | 28,03 | 24,95 | 31 | 24,21 | 59,15 | 47,62 | 31,98 | 24,35 | 25,36 | | | 23,2 | 22,91 | | |
| Sa 3521 | M | 69,25 | 25,02 | 22,57 | 29,27 | 20,26 | 46,59 | 36,05 | 30,24 | 20,96 | 18,28 | | | 22,85 | 19,84 | | |
| Sa 3366 | M | 66,01 | 24,45 | 21,78 | 29,18 | 19,42 | 49,53 | 34,56 | 28,62 | 21,37 | 18,05 | | | 24,27 | 21,15 | | |
| Sa 11434g | M | 60,16 | 27,61 | 26,39 | 34,08 | 21,93 | 67,55 | 44,74 | 30,6 | 26,21 | 23,21 | 142,14 | 173,5 | 27,41 | 25,44 | 175 | 200 |
| Sa 11434d | M | 61,42 | 28,18 | 26,94 | 37,01 | 24,06 | 67,14 | 23,34 | 31,76 | 23,62 | 23,48 | | | 27,7 | 27,64 | 167 | 195,5 |
| Sa 3507g | M | 43,64 | 23,68 | 25,88 | 31,73 | 23,34 | | | 27,65 | 20,37 | 19,78 | | | | | | |
| Sa 3507d | M | 44,07 | 26,66 | 22,86 | 30,83 | 21,81 | 56,64 | 35,08 | 27,04 | 19,76 | 22,22 | | | 23,86 | 21,24 | | |
| Sa 3490g | M | 48,55 | 29,33 | 23,14 | 35,61 | 22,94 | 66,11 | 46,81 | 30,82 | 29,55 | 22,66 | | | 31,01 | 29,03 | | |
| Sa 3490d | M | 46,17 | | | | | 70,06 | 48,84 | 30,86 | 26,32 | 20,85 | | | 30,72 | 26,02 | | |
| Sa 3318g | M | 65,4 | 31,35 | 25,64 | 39,99 | 19,8 | | | | | | | | | | | |
| Sa 3318d | M | 60,27 | 30,8 | 24,84 | 41,2 | 20,65 | | | | | | | | | | | |
| Sa 3429g | M | 35,47 | 26,84 | 27,73 | | 22,95 | | | | | | | | | | | |
| Sa 3429d | M | 36,41 | 28,98 | 27,62 | 31,29 | 23,77 | | | | | | | | | | | |
| Sa 3419g | M | 38,8 | 27,75 | 26,3 | 34,87 | 24,9 | | | | | | | | | | | |
| Sa 3419d | M | 37,33 | 27,9 | 27,08 | 34,9 | 26,58 | | | | | | | | | | | |
| Sa 3421 | M | 43,59 | 26,49 | 24,42 | 32,29 | 20,47 | | | | | | | | | | | |
| Sa 10961 | M | 34,3 | 27,19 | 23,23 | 21,6 | | | | | | | | | | | | |
| Sa 10334 | M | 40,9 | 26,21 | 20,24 | 35,98 | 25,52 | | | | | | | | | | | |
| Sa 10937 | M | 44,91 | 24,56 | 23,07 | 30,7 | 20,6 | | | | | | | | | | | |
| Sa 10679 | M | 56,49 | 23,18 | 20,67 | 29,07 | 18,57 | | | | | | | | | | | |
| Sa 10332 | M | 36,07 | 26,8 | 25,88 | 30,47 | 21,13 | | | | | | | | | | | |
| Sa 10938 | M | 49,14 | 22,64 | 20,56 | 25,14 | 18,71 | | | | | | | | | | | |
| Sa 3420 | M | 46,14 | 28,88 | 24,95 | 35,46 | 21,33 | | | | | | | | | | | |
| Sa 3525 | M | 48,97 | 26,4 | 26,41 | 31,1 | 23,35 | | | | | | | | | | | |
| Sa 3547 | M | 48,8 | 26,89 | 22,06 | 35,29 | 23,35 | | | | | | | | | | | |
| Sa 3416 | M | | | | | | 56,11 | 34,66 | 23,8 | 18,56 | 16,9 | | | 21,84 | 19,12 | | |
| Sa 3517 | M | | | | | | 48,68 | 49,14 | 18,23 | 22,72 | 20,07 | 113,61 | 137,58 | 19,45 | 20,59 | | |
| Sa 3479 | M | | | | 30,1 | 14,83 | 48,55 | 29,48 | 24,65 | | | | | 19,79 | 19,82 | | |
| Sa 3433 | M | 50,77 | | | 41,75 | 16,34 | 59,14 | 33,95 | 24,25 | 22,68 | 20,86 | 114,64 | 135,85 | 23,25 | 19,63 | 146,83 | 165 |
| Sa 3407 | M | | | | 29,08 | 20,44 | 54,01 | 37,66 | 29,22 | 20,46 | 18,75 | | | 24,44 | 19,74 | | |
| Sa 3359 | M | | | | 31,37 | 17,51 | 56,3 | 37,73 | 31,12 | 18,85 | 19,21 | | | 23,94 | 21,76 | | |
| Sa 3516 | M | | | | | | 65,11 | 41,9 | 28,41 | 22,73 | 23,18 | | | 27,79 | 25,78 | | |
| Sa 3515 | M | | | | 35,69 | 23,49 | 61,53 | 39,63 | 28,72 | 24,92 | 22,16 | | | 26,71 | 26,7 | | |
| Sa 3510 | M | | | | 34,33 | 28,32 | 68,72 | 44,98 | 26,63 | 22,47 | 24,98 | | | 29,59 | 32,92 | | |
| Sa 3403 | M | | | | 32,44 | 20,43 | 61,27 | 35,9 | 25,97 | 19,17 | 21,96 | | | 20,84 | 17,77 | 135,57 | 156,8 |
| Sa 3493 | M | | | | 39,45 | 24,28 | 66,59 | 43,45 | 30,79 | 30,58 | 25,56 | | | 31,15 | 28,83 | | |
| Sa 13530 | M | | | | 29,54 | 19,38 | 52 | 36,53 | 30,48 | 21,03 | 24,48 | | | | 21,31 | | |
| Sa 3391 | M | | | | | 16,88 | 63,38 | 41,13 | 14,49 | 26,94 | 23,13 | | | 23,47 | 22,67 | | |
| Sa 3523 | M | 47,06 | 29,97 | 24,41 | 36,88 | 22,62 | 62,76 | 37,97 | 20,48 | 25,91 | 20,49 | | | 27,34 | 21,74 | | |
| Sa 3508 | M | | | | 30,19 | 21,35 | 54,13 | 39,34 | 29,75 | 21,73 | 19,2 | | | 21,74 | 22,21 | | |
| Sa 10639 | M | | | | | | 65,11 | 37,67 | 24,8 | 23,01 | 23,78 | | | 26,26 | 23,45 | | |
| Sa 3511 | M | | | | 32,19 | 24,27 | | | 18,47 | 25,19 | 34,01 | | | | | | |
| Sa 3431 | M | | | | | | 65,33 | 43,05 | 33,71 | 26,85 | 22,19 | | | 28,1 | 25,23 | | |
| Sa 3524 | M | 29,46 | 26,78 | 24,93 | 29,92 | 22,04 | 65,63 | 45,05 | 23,47 | 23,53 | 22,99 | | | 28,74 | 29,33 | | |
| Sa 3404 | M | | | | | | 57,43 | 45,16 | 27,96 | 24,67 | 20,25 | | | 25,15 | 24,76 | | |
| Sa 3361 | M | | | | | | | | 26,31 | | | | | 25,16 | 24,95 | | |
| Sa 10820 | M | | | | | | | | 14,46 | 17,87 | 16,45 | | | | | | |
| Bâle | M | | | | | | 40,18 | 27,64 | 23,06 | 14,68 | 12,44 | | | 19,93 | 13,9 | | |
| Sa 10563 | M | | | | | | 55,57 | 42,35 | 26,79 | 24,13 | 20,47 | | | 27,27 | 23,7 | | |
| Sa 3433 | M | 54,33 | | | 39,43 | 17,46 | 58,7 | 33,06 | 24,05 | 21,98 | 21,13 | | | 22,88 | 19,88 | | |
| Sa 3513 | M | 52,03 | 26,8 | 23,14 | 33,62 | 20,27 | 61,74 | 36,49 | 20,84 | 20,79 | 20,25 | | | 29,57 | 23,13 | | |
| Sa 3387 | M | 63,5 | 25,29 | 18,37 | 36,11 | 15,91 | 53,82 | 29,6 | 24,51 | 20,3 | 17,96 | | | 21,69 | 19,82 | 157,9 | 150,9 |
| Sa 3499 | M | 54,02 | 23,32 | 21,13 | 28,15 | 13,37 | 61,2 | 39,23 | 30,97 | 25,59 | 22 | 145,49 | 162,7 | 27,04 | 20,58 | | |
| Sa 10562 | M | 53,62 | 23,05 | 21,94 | 32,83 | 19,8 | 63 | 40,65 | 27,33 | 23,48 | 21,55 | | | 28,31 | 22,45 | | |
| Sa 3530 | M | 51,24 | 22,69 | 20,38 | 29,64 | 18,93 | 56,09 | 39,65 | 23,81 | 20 | 23,48 | | | 21,06 | 21,45 | | |
| Sa 3401 | M | | | | 32,45 | 31,84 | 54,09 | 39,05 | 23,92 | 22,5 | 21,19 | | | 24,82 | 22,56 | | |
| Sa 3498 | M | 49,57 | 23,97 | 21,66 | 26,83 | 18,59 | 47,48 | 32,42 | 31,33 | 19,65 | 17,97 | 114,49 | 141,06 | 23,86 | 19,62 | | |
| Sa 3501 | M | 41,34 | 25,35 | 22,93 | 27,3 | 20,49 | 51,57 | 32,83 | 26,2 | 22,46 | 19,72 | | | 25,54 | 21,56 | 178,5 | 196 |

Appendix 1 *(continuation)*.—Appendage measurements of *Dicrocerus elegans* from the Middle Miocene locality of Sansan (France). (See abreviations on the text).

| sigle | morphotype | L_ped | DAPb _ped | DTb _ped | DAPd _ped | DTd _ped | DAPb _pa | DTb _pa | Hbif _pa | DAPb _br_a | DT _ br_a | Lp _b_ a | La_br _a | DAPb _br_ p | DTb _br_p | La_br _ p | Lp _br_p |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Sa 9990d | M | 51,16 | 25,06 | 23,22 | 31,14 | 19,57 | | | | 23,35 | 19,82 | 134,1 | | | | | |
| Sa 3160g | M | 44,99 | 37,63 | 24,08 | | | | | 27,58 | | | | | | | | |
| Sa 3160d | M | 35,78 | 26,99 | | | | 63,12 | 38,57 | 28,02 | 24,14 | 26,99 | | | | | | |
| Sa 11433g | M | 52,18 | 21,21 | 17,61 | 23,78 | 15,31 | | | | 18,01 | 19,3 | 107,34 | 142,4 | 19,2 | 23,64 | 150,01 | 173,5 |
| Sa 11433d | M | 51,23 | 20,77 | 18,41 | 34,31 | 16,61 | | | | | | 106,21 | 143,93 | | | 169,5 | 187,5 |
| Sa 3325 | M | 57,47 | 22,32 | 18,88 | 25,75 | | 46,61 | 31,19 | 23,68 | 20 | 19,09 | 102,69 | 123,71 | 23,13 | 24,4 | 169,5 | 185,5 |
| Sa 3328 | M | 47,51 | 27,9 | 24,88 | | | | | | | | | | | | | |
| Sa 13970 | M | | | | 32,3 | 22,16 | 62,73 | 45,38 | 31,4 | 26,06 | 25,94 | 153,02 | 187,5 | 30,24 | 24,36 | 161,5 | 188 |
| Sa 3554 | M | 57,18 | 30,69 | 27,3 | 38,39 | 24,61 | 73,63 | 42,44 | 34,53 | 35,15 | 25,65 | | | 33,15 | 28,53 | | |
| Sa 3324g | M | | 27,84 | 28,2 | 44,37 | 20,26 | 79,42 | 46,85 | 26,68 | 26,22 | 26,15 | | | 28,99 | 25,22 | 201 | 227,5 |
| Sa 3324d | M | 56,86 | 28,99 | 26,29 | 45,18 | 22,94 | 79,68 | 41,7 | 22,78 | 26,1 | 27,95 | 146,02 | 171 | 28,79 | 26,3 | 215 | 229 |
| Sa 3319g | M | 48,25 | 24,61 | 22,45 | 27,94 | 19,81 | 48,59 | 34,66 | 24,67 | 21,2 | 20,83 | | | 23,1 | 21,58 | | |
| Sa 3319d | M | 48,37 | 24,73 | 22,33 | 29,53 | 18,69 | 53,53 | 31,26 | 23,57 | 20,18 | 19,09 | | | 25,88 | 21,7 | | |
| Sa 3556g | M | 47,02 | 30,36 | 27,67 | 34,67 | 23,68 | 64,24 | 40,59 | | | | | 186 | | | | |
| Sa 3556d | M | | | | | | | | | | | | 165 | | | | |
| Sa 3323 | M | 68,03 | 25,4 | 18,68 | 38,78 | 13,33 | 49,2 | 22,82 | 15,51 | 14,92 | 13,98 | 72,39 | 83,02 | 19,43 | 15,86 | 70,07 | 73,78 |
| Sa 3564 | M | 42,95 | | | 35,04 | 21,79 | 59,27 | 38,29 | 22,05 | 23,06 | 23,22 | 134,35 | 159 | 23,93 | 23,43 | | |
| Sa 3563 | M | 47,94 | 28,23 | 24,36 | 34,44 | 25,13 | 64,34 | 38,39 | 27,52 | 23,14 | 21,47 | 135,36 | 162 | 24,08 | 21,85 | 172 | 186 |
| Sa 3538 | M | | | | 31,28 | 25,19 | 58,87 | 48,23 | 33,4 | 24,4 | 26,06 | | | 25,63 | 26,1 | | |
| Sa 3491 | M | | | | | | 51,75 | 40 | 33,15 | 19,62 | 20,89 | | | 24,46 | 22,73 | | |
| Sa 3488 | M | 50,55 | 26,72 | 21 | 31,64 | 18,6 | 57,11 | 35,95 | 25,49 | 19,46 | 22,29 | 138,08 | 165,5 | 25,67 | 24,66 | | |
| Sa 3398 | M | 57,41 | 27,56 | 21,75 | 33,97 | 20,33 | 60,61 | 33,7 | 22,95 | 20,58 | 19,78 | | | 23,73 | 22,48 | | |
| Sa 3548 | M | | | | | 16,43 | 52,49 | 34,77 | 23,97 | 19 | 17,4 | | | 24,32 | 21,55 | | |
| Sa 3549 | M | | | | 26,65 | 16,98 | | | 28,99 | | | | | | | | |
| Sa 3543 | M | | | | 25,81 | 19,2 | 47,86 | 31,92 | 29,91 | | | | | 22,6 | 18,93 | | |
| Sa 3540 | M | | | | 28,23 | 27,22 | | | | | | | | | | | |
| Sa 3395 | M | | 27,44 | 21,4 | 32,01 | 20,12 | 51,89 | 32,68 | 21,18 | 16,99 | 18,61 | | | 20,46 | 20,52 | | |
| Sa 3536 | M | 38,56 | 21,76 | 19,14 | 25,07 | 19,46 | 57,99 | 40,86 | 21,5 | 16,25 | 16,86 | 85,2 | 109,37 | 23,61 | 21,84 | 150 | 166 |
| Sa 3478 | M | 35,68 | 21,76 | 20,97 | 25,91 | | 57,4 | 41,51 | 29,94 | 23,74 | 21,5 | | | 26,99 | 22,25 | | |
| Sa 3405 | M | 33,86 | 23,64 | 13,47 | 25,83 | 20,52 | 53,81 | 41,76 | 21,83 | 22,68 | 20,4 | 148,47 | 171,5 | | 22,6 | 178 | 197 |
| Sa 3545 | M | | | | 4124 | | 11,67 | 4124 | | 11,67 | | 15,51 | 8,3 | | 14,48 | 11,58 | | 40,3 |
| Sa 3364 | M | 69,61 | 69,61 | 19,36 | 50,22 | 18,43 | 50,22 | 18,43 | | 15,7 | 24,2 | | 40,62 | 21,29 | 15,8 | | 68,71 |
| Sa 3394 | M | | | | 56,8 | 19,62 | 56,8 | 19,62 | | 21,01 | | | | 21,61 | 14,86 | | 59,39 |
| Sa 3346 | M | 78,58 | 78,58 | 18,64 | 45,78 | 13,76 | 45,78 | 13,76 | | | | | 16,03 | 15,25 | 13,56 | | 27,64 |
| Sa 3352 | M | 88 | 88 | 19,42 | | | | | | | | | | | | | |
| Sa 3345 | M | 91,2 | 91,2 | 19,18 | 49,12 | 16,95 | 49,12 | 16,95 | | | | | | | | | |
| Sa 3353 | M | 80 | 80 | 16,15 | 35,95 | 11,41 | 35,95 | 11,41 | | | | | | | | | |
| Sa 3322 | M | 113,14 | 113,14 | 20,51 | 50,4 | 13,88 | 50,4 | 13,88 | | 15,31 | 17,52 | | 28,65 | 18,3 | 15,37 | | 38,19 |
| Sa 3321 | M | 76,65 | 76,65 | 17,58 | 42,96 | 12,55 | 42,96 | 12,55 | | | | | 15,33 | 15,92 | 12,33 | | 28,14 |
| Sa 3567 | M | 90,84 | 90,84 | 15,97 | 21,92 | 6,84 | 21,92 | 6,84 | | | | | | | | | |
| Sa 3567 | M | | | 17,19 | 22,16 | 7,51 | 22,16 | 7,51 | | | | | | | | | |
| Sa 10335 | M | 80,58 | 20,79 | 13,47 | 32,52 | 9,92 | 32,52 | 9,92 | | | | | | | | | |
| Sa 10339a | M | 68,3 | 19,33 | 14,76 | 35,71 | 15,58 | 35,71 | 15,58 | | | | | | | | | |
| Sa 10339b | M | | | | 33,52 | 14,71 | 33,52 | 14,71 | | | | | | | | | |
| Sa 3363 | M | | | | 26,93 | 9,64 | 26,93 | 9,64 | 28,88 | | | | | 14,7 | 8,1 | | 30,4 |
| Sa 3412 | M | 52,31 | 16,41 | 13,82 | 22,65 | 12,08 | 22,65 | 12,08 | | | | | | | | | |
| Sa 10319 | M | | 13,36 | 12,45 | | | | | | | | | | | | | |
| Sa 3358 | F | 60,61 | 18,78 | 17,46 | 27,63 | 13,09 | 40,88 | 28,7 | 28,86 | 18,25 | 14,49 | | | 18,17 | 16,74 | 107,36 | 115,28 |
| Sa 3466 | F | 52,31 | 18,97 | 15,19 | 26,93 | 11,97 | 40,41 | 28,48 | 17,77 | 13,19 | 11,7 | 46,03 | 61,78 | 20,01 | 18,05 | | |
| Sa 3454 | F | 46,27 | 16,61 | 14,01 | 23,72 | 12,8 | 34,47 | 24,39 | 16,65 | 14,3 | 14,85 | 50,22 | 62,79 | 15,48 | 21,83 | | |
| Sa 3464 | F | 37,42 | 20,61 | 16,72 | 24,22 | 13,95 | 45,39 | 28,38 | 15,76 | 17,19 | 15,6 | | | 20,08 | 16,65 | | |
| Sa 10318a | F | | 18,98 | | 21,76 | 15,39 | 37,23 | 25,31 | 15,36 | 16,42 | 13,77 | 48 | 68 | 18,66 | 16,31 | | |
| Sa 10318b | F | 40,37 | 19 | 16,42 | 20,92 | 13,84 | 32,17 | 25,59 | 18,75 | 11,29 | 10,05 | 29,93 | 50,52 | 19,87 | 15,54 | | |
| Sa 3447 | F | 48,68 | 19,51 | 16,71 | 23,07 | 15,68 | 36,52 | 20,38 | | | | | | | | | |
| Sa 11470 | F | 52,02 | 17,54 | | 24,6 | 12,73 | 34,67 | 11,4 | 16,28 | 11,68 | 9,78 | 32,85 | 41,55 | 19,29 | 17,11 | | |
| Sa 3362 | F | 45,87 | 20,33 | 16,37 | 28,94 | 14,7 | 40,37 | 26,56 | 19,86 | | | | | 17,64 | 18,85 | | |
| Sa 3451g | F | 42,41 | 20,53 | 18,69 | 25,52 | 13,56 | | | 21,99 | 15,92 | 11,91 | 40,18 | 18,19 | | | | |
| Sa 3451d | F | | 19,44 | 15,13 | 21,04 | 14,93 | 36,66 | | 17,93 | 15,13 | 12,27 | | | 17,39 | 16,8 | | |
| Sa 3439 | F | 42,92 | 18 | 14,78 | 21 | 13,86 | 37,5 | 24,3 | 17,2 | 14,72 | 14,09 | | | 18,08 | 19,8 | | |
| Sa 3500 | F | 48,56 | 19,24 | 14,9 | | 12,71 | | | | | | | | 17 | 17,28 | 117,43 | 126,85 |
| Sa 10325 | F | 43,7 | 18,31 | 15,49 | 24,95 | 13,84 | 31,18 | 21,56 | 18,66 | 12,71 | 10,86 | | | 18,76 | 14,67 | 98,09 | 111,88 |
| Sa 11435g | F | 34,63 | 17,07 | 16,85 | 18,81 | 14,55 | 35,48 | 26,72 | 20,57 | | | | | 21,54 | 15,74 | 114,68 | 133,56 |
| Sa 11435d | F | 33,66 | 18,87 | 15,85 | 18,85 | 13,94 | 39,46 | 26,03 | 21,04 | 12,48 | 10,55 | | | 19,5 | 17,12 | | |

Appendix 1 *(continuation)*.—Appendage measurements of *Dicrocerus elegans* from the Middle Miocene locality of Sansan (France). (See abreviations on the text).

| sigle | morphotype | L_ped | DAPb _ped | DTb _ped | DAPd _ped | DTd _ped | DAPb _pa | DTb _pa | Hbif _pa | DAPb _br_a | DT _ br_a | Lp _b_ a | La_br _a | DAPb _br_ p | DTb _br_p | La_br _ p | Lp _br_p |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Sa 11461g | F | 43,27 | 21,31 | 15,89 | 20,79 | 15,21 | 44,38 | 29,55 | 26,14 | 13,13 | 10,56 | | | 17,71 | 13,47 | | |
| Sa 11461d | F | 39,17 | 19,87 | 15,21 | 22,19 | 14,05 | 49,17 | 33,29 | 21,09 | 14,26 | 11,17 | | | 15,96 | 14,78 | 93,12 | 112,07 |
| Sa 3414 | F | 41,23 | | | 23,32 | 15,99 | 44,03 | 30,22 | 19,16 | 18,14 | 14,61 | 65,85 | 90,08 | 22,12 | 17,24 | 112,78 | 128,95 |
| Sa 3442 | F | | | | | | 46,33 | | | | | | | | | | |
| Sa 3456 | F | 37,3 | 20 | 17,05 | 21,83 | 16,6 | 42,02 | 34,49 | 23,21 | 16,86 | 12,9 | 57,85 | 78,75 | 20,4 | 18,02 | 105,11 | 126,44 |
| Sa 10326 | F | 38,57 | 19,98 | 17,62 | 23,98 | 16,67 | 44,19 | 29,84 | 21,28 | 14,28 | 12,87 | | | 19,53 | 14,24 | | |
| Sa 10676 | F | 42,74 | 21,54 | 16,75 | 25,05 | 16,21 | 46,73 | 31,32 | 20,83 | 16,48 | | | | 22,29 | 17,81 | | |
| Sa 11464 | F | 42,06 | 21,54 | 15,67 | 23,29 | 17,29 | 46,87 | 28,29 | 22,42 | 17,65 | 17 | 84 | 102,66 | 23,95 | 19,28 | | |
| Sa 3462 | F | 40,21 | 21,02 | 17,04 | 23,4 | 16,84 | 45,1 | 31,21 | 20,62 | 16,05 | 15,38 | | | 19,69 | 17,92 | | |
| Sa 3390 | F | 40 | 22,16 | 18,42 | 29,32 | 15,71 | | | | 22,9 | 20,6 | 147 | 170 | 20,89 | 19,89 | | |
| Sa 3473 | F | | | | 20,92 | 15,09 | 43,87 | 31,51 | 23,54 | 19,24 | 17,64 | 91,98 | 113,91 | 23,4 | 18,07 | 122,43 | 137 |
| Sa 3461 | F | | | | | | 47,13 | 32,74 | 24,63 | 14,71 | 11,39 | 69,97 | 86,25 | 24,12 | 15,97 | | |
| Sa 3450 | F | | | | 22,61 | 14,08 | 42,64 | 28,79 | 18,69 | 16,05 | 14,61 | | | 16,74 | 15,81 | | |
| Sa 3487 | F | | | | 24,79 | 13,5 | | 22,12 | | | | | | | | | |
| Sa 3512 | F | | | | 29,91 | 16,07 | 51,4 | 27,48 | 21,92 | | | | | 26 | 19,78 | 130,64 | 142,07 |
| Sa 10330 | F | | | | | | 46,75 | 34,64 | 23,75 | 15,98 | 15,94 | 78,12 | 101 | 23,31 | 21,98 | | |
| Sa 3458 | F | | | | 28,37 | 12,77 | 39,54 | 20,32 | 21,99 | 19,9 | 12,82 | | | 16,67 | 15,9 | | |
| Sa 3489 | F | | | | 25,52 | 16,24 | 46,89 | 25,82 | 39,32 | | | | | | | | |
| Sa 10825 | F | | | | | | 39,64 | 26,91 | 16,92 | 14,46 | 11,6 | | | | | | |
| Sa 13532 | F | | | | 25,05 | | 47,35 | 25,89 | 25,86 | 19,96 | 14,93 | | | 19,42 | 18,82 | | |
| Sa 13531 | F | | | | 26,33 | 12,97 | 43,37 | 20,42 | 17,86 | 16 | 12,26 | | | 19,06 | 17,32 | | |
| Sa 3445 | F | 41,27 | | | 21,95 | 15,68 | 41,31 | 28,94 | 17,03 | 19,46 | 16,88 | | | 22,5 | 22,07 | | |
| Sa 3460 | F | | | | | | 45,22 | 31,05 | 20,53 | 15,35 | 14,74 | 54,45 | 77,5 | 18,4 | 16,41 | 91,52 | 113,61 |
| Sa 3449 | F | 31,5 | 20,51 | 16,26 | 25,31 | 15,47 | 35,6 | 23,61 | 18,91 | 13,01 | 12,92 | | | | | | |
| Sa 3443 | F | 24,59 | 19,66 | 18,76 | 22 | 16,2 | 44,63 | 27,52 | 19,72 | 17,2 | 14,57 | | | 16,08 | 19,38 | | |
| Sa 3444 | F | 20,81 | 19,57 | 17,99 | 21,09 | 16,28 | 45,07 | 32,32 | 19,62 | 16,95 | 17,5 | | | 24,98 | 19,46 | | |
| Sa 3455 | F | 29,08 | 20,67 | 17,35 | 24,59 | 16,22 | 36,97 | 26,87 | 18,11 | 13,55 | 14,65 | | | | | | |
| Sa 3452 | F | 17,34 | 20,64 | 17,79 | 21,02 | 17,34 | 41,06 | 29,84 | 19,72 | 14,54 | 15,31 | | | 20,97 | 18,16 | | |
| Sa 3448 | F | 18,18 | 23,2 | 19,62 | 22,77 | 19,34 | | | | | | | | | | | |
| Sa 3326 | F | 24,96 | 14,82 | 18,69 | 19,33 | 15,42 | 38,94 | 29,19 | | 10,75 | 11,64 | | 61,68 | 10,18 | 11,28 | | 54,39 |
| Sa 3357 | F | 25,78 | 19,41 | 15,82 | 21,73 | 14,83 | 44,13 | 29,25 | 16,87 | 14,19 | 12,33 | 47,42 | 65,44 | 21,77 | 13,19 | | |
| Sa 3502 | F | | 20,3 | | 23,12 | 15,62 | 42,11 | 29,93 | 11,11 | 14,85 | 13,23 | 67,67 | 87,7 | 19,62 | 20,79 | | |
| Sa 11438 | F | 22,81 | 22,08 | 21,41 | 26,73 | 19,53 | 58,28 | | 21,29 | | 17,6 | 94,73 | 105,19 | 24,6 | 21,77 | | |
| Sa 9996 | F | 27 | 22,56 | 17,41 | 25,88 | 18,3 | 45,89 | 33,1 | 21,11 | 16,75 | 15,86 | | | 22,41 | 17,65 | 125,86 | 136,11 |
| Sa 3468 | F | | 20,96 | 16,2 | 22,22 | 14,58 | 40,18 | 26,58 | 21,22 | 14,29 | 13,33 | 64,65 | 89,04 | 19,09 | 18,37 | | |
| Sa 3441 | F | 34,02 | 15,61 | 18,7 | 20,3 | 14,95 | 41,2 | 26,31 | 20,24 | 12,97 | 10,23 | | | 16,78 | 14,8 | | |
| Sa 3467 | F | 27,43 | 20,02 | 17,88 | 20,88 | 16,3 | 44,09 | 28,88 | 17,67 | 17,72 | 13,63 | | | 19,21 | 15,46 | | |
| Sa 9997 | F | 33,56 | 21,48 | 16,33 | 23,95 | 16,64 | 52,92 | 27,5 | 17,9 | 17,08 | 18,63 | | | 24,6 | 21,61 | | |
| Sa 3497 | F | 29,05 | 19,13 | 16,71 | 21,14 | 15,98 | 43,86 | 31,43 | 23,09 | 19,27 | 12,88 | | | 20,03 | 15,59 | | |
| Sa 3437 | F | 45,25 | 21,9 | 18,29 | 23,81 | 16,53 | 49,03 | 31,29 | 18,31 | 15 | 14,25 | | | 20,85 | 16,51 | | |
| Sa 3470 | F | 23,26 | 17,69 | 21,45 | 25,19 | 18,77 | 44,82 | 34,46 | 26,53 | 17,61 | 16,21 | 70,68 | 102,56 | 22,75 | 16,84 | | |
| Sa 3438 | F | 44,43 | 24,74 | 17,42 | 27 | 16,68 | 59,13 | 29,64 | 22,41 | 18,08 | 15,38 | 62,01 | 88,4 | 20,18 | 19,09 | 116,48 | 133,62 |
| Sa 10321 | F | 27,2 | 20,72 | 19,43 | 22,81 | 19,03 | 51,41 | 39,75 | 25,92 | 18,99 | 17,37 | 88 | 118,97 | 24,54 | 19,28 | | |
| Sa 3428 | F | 31,14 | 21,67 | 17,39 | 23,55 | 15,39 | | | | | | | | | | | |
| Sa 3423 | F | 40,4 | 21,48 | 15,47 | 28,46 | 15,75 | 50,76 | 32,63 | | 17,64 | 15,85 | 65,91 | 86,99 | 29,15 | 21,04 | | |
| Sa 10640 | F | | | | | 16,53 | 41,72 | 33,2 | 22,86 | 15,09 | 13,08 | | | 15,57 | 14,79 | | |
| Sa 3356 | F | | | | 26,55 | 12,94 | 49,96 | | 24,19 | 13,28 | 23,56 | 89,05 | 114,43 | | | | |
| Sa 3522 | F | | | | | | 40,28 | 28,54 | 20,75 | | | | | 20,68 | 18,17 | | |
| Sa 3503 | F | | | | | 17,24 | 31,8 | 23,05 | | | | | | 23,11 | 17,49 | | |
| Sa 3571 | F | | 23,92 | 17,52 | | | | | | | | | | | | | |
| Sa 10327 | F | | | | 21,05 | 16,9 | 38,73 | 28,93 | 21,67 | | | | | 19,16 | 15,69 | 96,57 | 124,76 |
| Sa 3546 | F | | | | | | 45,14 | 30,61 | 20,19 | | | | | 22,04 | 18,18 | | |
| Sa 11437 | F | 33,78 | 22,21 | 19,61 | 25,88 | 18,72 | 54,43 | 37 | 20,55 | 20,47 | 19,12 | 83,66 | 113,19 | 31,63 | 21,79 | | |
| Sa 10340g | F | | 18,58 | 15,55 | 19,01 | 13,85 | 35,47 | 28,05 | 14,07 | 10,47 | 9,62 | 37 | 50,46 | 19,21 | 14,94 | 97,62 | 106,79 |
| Sa 10340d | F | 39,07 | 18,46 | 14,36 | 20,58 | 14,97 | 43,77 | 23,9 | 17,09 | 13,82 | 11,49 | | | 19,54 | 13,55 | 100,59 | 113,75 |
| Sa 3469 | F | | | | 24,71 | 12,34 | 37,11 | 22,59 | 18,9 | 14,68 | 12,48 | | | 17,57 | 21,84 | | |
| Sa 3457 | F | 36,46 | | | 21 | | 38,98 | 29,11 | 20 | 15,39 | 13,05 | 64,29 | 82,65 | 18,31 | 14,63 | 98,86 | 115,4 |
| Sa 10331 | F | | 20,24 | 15,75 | 20,67 | 16,1 | | 25,37 | 15,76 | 15,42 | 12,8 | | | | | | |
| Sa 3446 | F | 35,63 | 20,31 | 17,62 | 21,94 | 17,23 | 41,5 | 31,05 | 21,9 | 16,82 | 14,05 | 74,09 | 97,48 | 18,89 | 16,03 | 108,34 | 125,25 |
| Sa 3459 | F | 40,92 | 19,21 | 16,71 | 22,43 | 15,78 | 49,94 | 32,95 | 23,29 | 19,63 | 16,31 | | | 19,06 | 19,01 | | |
| SAN665 | F | | | | 23,41 | 12,79 | 35,96 | 22,71 | 13,83 | 12,3 | 12,07 | 50,28 | 61,4 | | | | |
| Sa 3330g | F | 32,17 | 21,74 | 20,71 | 22,28 | 19,1 | 44,58 | 31,1 | 28,25 | 16,59 | 15,38 | | | 23,78 | 19,98 | | |
| Sa 3330d | F | 29,97 | 25,39 | 20,37 | | | | | | | | | | | | 112,76 | |

Appendix 1 *(continuation)*.—Appendage measurements of *Dicrocerus elegans* from the Middle Miocene locality of Sansan (France). (See abreviations on the text).

| sigle | morphotype | L_ped | DAPb _ped | DTb _ped | DAPd _ped | DTd _ped | DAPb _pa | DTb _pa | Hbif _pa | DAPb _br_a | DT _ br_a | Lp _b_ a | La_br _a | DAPb _br_ p | DTb _br_p | La_br _ p | Lp _br_p |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Sa 3477 | F | 34,17 | 17,95 | 16,1 | 24,31 | 16,72 | 49,23 | 36,81 | 30,04 | 14,98 | 15,27 | | | 22,67 | 21,09 | | 136,51 |
| Sa 3453 | F | | | | 22,91 | 12,84 | 34,36 | 24,95 | 14,19 | 15,72 | 14,28 | 62,93 | 76,84 | 16,17 | 19,45 | 93,27 | |
| Sa 10333 | F | | | | | | 45,86 | 32,43 | 21,02 | 13,97 | 14,49 | | | 17 | 19,46 | | 110,44 |
| Sa 3471 | F | | | | | | 45 | 31,25 | 23,98 | 15,23 | 13,17 | 63,29 | 82,93 | 18,26 | 12,51 | 127,38 | |
| Sa 3480 | F | 34,6 | 25,55 | 18,25 | 30,18 | 18,68 | 52,58 | 30,73 | 21,14 | 22,56 | 16,53 | | | | | | 136,7 |
| Sa 3440 | F | | 19,81 | 14,91 | 22,56 | 15,3 | 42,87 | 29,16 | 20,41 | 14,48 | 12,8 | | | 18,5 | 15,78 | 73,31 | |
| Sa 3329 | F | 28,54 | 19,76 | | 23,17 | 16,78 | 48,7 | 31,98 | 17,13 | 44,29 | 73,31 | 14,47 | 12,3 | 16,19 | | 53,17 | 91,74 |
| Sa 3327 | F | | | | | | | | 23,21 | | | | | 15,23 | 14,18 | | 80,27 |
| Sa 3553 | F | 17,68 | 20,76 | 21,24 | 20,67 | 19,35 | 51,03 | 39,17 | 30,41 | 19,25 | 14,77 | 58,96 | 87 | 21,63 | 17,58 | | |
| Sa 3552 | F | 42,22 | 17,62 | 15,08 | 21,95 | 11,61 | 30 | 22,04 | | | | | | 17,7 | 16,57 | | |
| Sa 3555g | F | | 24,71 | 22,35 | | | | | | | | | | | | 119,11 | |
| Sa 3555d | F | 11,91 | 25,23 | | | | 41,32 | 34,89 | | 23,91 | 22,19 | | | 24,92 | 32,23 | | |
| Sa 3548 | ? | | | | | 16,43 | 52,49 | 34,77 | 23,97 | 19 | 17,4 | | | 24,32 | 21,55 | | |
| Sa 3549 | ? | | | | 26,65 | 16,98 | | | 28,99 | | | | | | | | |
| Sa 3543 | ? | | | | 25,81 | 19,2 | 47,86 | 31,92 | 29,91 | | | | | 22,6 | 18,93 | | |
| Sa 3540 | ? | | | | 28,23 | 27,22 | | | | | | | | | | | |
| Sa 3395 | ? | | 27,44 | 21,4 | 32,01 | 20,12 | 51,89 | 32,68 | 21,18 | 16,99 | 18,61 | | | 20,46 | 20,52 | | |
| Sa 3536 | ? | 38,56 | 21,76 | 19,14 | 25,07 | 19,46 | 57,99 | 40,86 | 21,5 | 16,25 | 16,86 | 85,2 | 109,37 | 23,61 | 21,84 | 150 | 166 |
| Sa 3478 | ? | 35,68 | 21,76 | 20,97 | 25,91 | | 57,4 | 41,51 | 29,94 | 23,74 | 21,5 | | | 26,99 | 22,25 | | |
| Sa 3405 | ? | 33,86 | 23,64 | 13,47 | 25,83 | 20,52 | 53,81 | 41,76 | 21,83 | 22,68 | 20,4 | 148,47 | 171,5 | | 22,6 | 178 | 197 |
| Sa 10335 | ? | 80,58 | 20,79 | 14,76 | 32,52 | 9,92 | 32,52 | 9,92 | | | | | | | | | |
| Sa 10339a | ? | 68,3 | 19,33 | | 35,71 | 15,58 | 35,71 | 15,58 | | | | | | | | | |
| Sa 10339b | ? | | | | 33,52 | 14,71 | 33,52 | 14,71 | | | | | | | | | |
| Sa 3363 | ? | | | 13,82 | 26,93 | 9,64 | 26,93 | 9,64 | 28,88 | | | | | 14,7 | 8,1 | | 30,4 |
| Sa 3412 | ? | 52,31 | 16,41 | 12,45 | 22,65 | 12,08 | 22,65 | 12,08 | | | | | | | | | |
| Sa 10319 | ? | | 13,36 | 15,08 | | | | | | | | | | | | | |
| Sa 3348 | ? | 82,3 | 19,12 | | 31,27 | 8,4 | 31,27 | 8,4 | | | | | | | | | |
| Sa 3351 | ? | | | 12,98 | 30,54 | 10,39 | 30,54 | 10,59 | | | | | | | | | |
| Sa 3349 | ? | | 16,86 | 15,83 | | | | | | | | | | | | | |
| Sa 10337 | ? | 74,73 | 18,25 | 15,4 | | | | | | | | | | | | | |
| Sa 3320 | ? | 88,74 | 20,5 | | 24,1 | 4,9 | 24,1 | 4,9 | | | | | | | | | |