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The Petrosal Bone and Bony Labyrinth of Early to Middle Miocene European Deer (Mammalia, Cervidae) Reveal their Phylogeny

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ABSTRACT Deer (Cervidae) have a long evolutionary history dating back to the Early Miocene, around 19 million years ago. The best known fossils to document this history belong to European taxa, which all bear cranial appendages more or less similar to today's deer antlers. Despite the good fossil record, relationships of the earliest stem deer and earliest crown deer are much debated. This hampers precise calibration against the independent evidence of the fossil record in molecular clock analyses. While much has been written on the Early and Middle Miocene deer, only two phylogenetic analyses have been performed on these taxa to date mostly based on cranial appendage characters. Because the petrosal bone and bony labyrinth have been shown to be relevant for phylogeny in ruminants, we describe for the first time these elements for four iconic early cervids from Europe (*Procervulus dichotomus*, *Heteroprox larteti*, *Dicrocerus elegans* and *Euprox furcatus*) and include them in a phylogenetic analysis based on the ear region exclusively. The analysis recovered *E. furcatus* in a sister position to the living red deer (*Cervus elaphus*). Further, it placed *D. elegans* in a sister position to *Euprox* + *Cervus* and a clade Procervulinae that includes *P. dichotomus* and *H. larteti*, in sister position to all other deer. The inclusion of *E. furcatus* in crown Cervidae, which was previously suggested based on antler morphology, cannot be ruled out here but needs a more comprehensive comparison to other crown deer to be confirmed. J. Morphol. 000:000–000, 2016. © 2016 Wiley Periodicals, Inc.

KEY WORDS: phylogenetics; ear region; Ruminantia; Procervulinae; Dicrocerinae

INTRODUCTION

The early evolutionary history of deer (Cervidae) is not yet fully understood. With several taxa attributed to stem Cervidae from Early to Middle Miocene European localities (Janis and Scott, 1987; Azanza, 1993; Rössner, 1995; Gentry et al., 1999; Böhme et al., 2012), this group has a solid fossil record on which evolutionary hypotheses focusing on the origin of crown deer can be based. So far, three subgroups were proposed to represent stem Cervidae: Lagomerycinae (sometimes referred to as Lagomerycidae, sister clade to Cervidae), Procervulinae (sometimes referred to Procervulidae, sister clade to Cervidae) and Dicrocerinae (also referred to Dicrocerini, sister clade to crown Cervidae; Simpson, 1945; Bubenik, 1962; Ginsburg, 1985; Bubenik and Bubenik,

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1990; Azanza and Ginsburg, 1997; Gentry et al., 1999; Azanza et al., 2011; Suraprasit et al., 2014). Traditional views have also gathered *Procervulus* and the lagomerycines together (Teilhard de Chardin, 1939; Pilgrim, 1941). Others have even linked them to Giraffoids or Palaeomerycids and the tribe named Dicrocerini, as including *Dicrocerus*, *Heteroprox* and *Eurpox*, has also been related to subfamily Muntiacinae (see Janis and Scott, 1987 for a review). This short overview, detailed in Janis and Scott (1987), shows the large variability in opinions on the earliest deer. Their status as stem Cervidae mostly relies on the presence of cranial appendages resembling today's deer antlers in principle traits. Antlers (deciduous branched outgrowth of the frontal bone capable of regular regeneration) represent the autapomorphy characterizing deer among Vertebrata in general and extant and extinct ruminants in particular (Janis and Scott, 1987). Differences in stem cervid antlers are that they grew from more or less long pedicles of the frontal bone (Bubenik and Bubenik, 1990; Gentry, 1994; Gentry et al., 1999; Groves, 2007), that they lack the beam structure and a proximal circular protuberance, the burr. Lagomerycines have tricho- to multitomous branched antlers (e.g., Azanza and Ginsburg, 1997; Suraprasit et al., 2014), while procervulines and dicrocerines possess dichotomous branched ones with mostly two tines (Azanza, 1993). The lagomerycine *Heterocemas* has dichotomous branched appendages with several sprouts. The main mechanism of ramification in lagomerycine appendages is by sprouting (that forms cortical structures not necessarily growing from the apex), but also beam splitting (by division from the apex) exists. Deciduousness was observed in all stem cervid antlers (Ginsburg, 1985; Azanza and Ginsburg, 1997; Rössner, 1995).

Apart from their differences in antler shape, the Early and Middle Miocene deer share a similar dental and postcranial morphology. The Palaeomeryx fold on lower teeth and a closed gully on metatarsals are not exclusive features of deer. Hence, when fossil sites do not yield antlers or only antlerless female skulls, specimens are challenging to assess taxonomically. This is a crucial aspect in studies on stem cervid relationships and the origin of crown cervids, where accurate data on the stratigraphical occurrence of species is needed.

As *Euprox* is the only genus among Early and Middle Miocene deer, having antlers with a burr and a backwards inclination like crown cervids some palaeontologists consider this genus as the earliest known crown deer at 13.8 Ma and that it even could be nested within Muntiacini (Azanza, 1993; Dong, 2007; Wang and Zhang, 2011; Azanza et al., 2013; Hou, 2015). This estimated age is a conservative estimate because *Euprox minimus* was found in the Middle Miocene site of Göriach (Austria), dated to zone MN5 and older than Mühlbach and Grund sites dated approximately 15 Ma (Daxner-Höck, 2003). However, molecular biologists neglect the assessment of *Euprox* and consider the first crown cervids to be the oldest known fossil representatives of crown genera, that is, *Muntiacus*, and use them to calibrate their phylogenetic trees (*Muntiacus noringenensis* from the E. Qaidam Basin in China at ca. 11 to 9 Ma, Late Miocene, Dong et al., 2004; *Muntiacus leilaoensis* from Yuanmou Lufeng in China at ca. 9 to 7 Ma, Late Miocene, Han, 1985; or even a younger dating; Pitra, 2004; Gilbert et al., 2006; Hassanin et al., 2012). Consequently, the lack of consensus on the origin of crown cervids partly arises from the lack of knowledge of extinct genera and the noninformative characters of morphological features (teeth, antlers) that are usually used for the systematics of ruminants (Janis and Scott, 1987; Janis and Theodor, 2014).

The petrosal bone has been largely used for the reconstruction of artiodactyl phylogeny (Sigogneau, 1968; Webb and Taylor, 1980; Luo and Gingerich, 1999; O'Leary, 2010; Orliac, 2013; Ravel and Orliac, 2014) to provide valuable characters that help to differentiate ruminant groups (O'Leary, 2010; Mennecart and Costeur, in press a). The bony labyrinth, which is embedded in the petrosal bone has also shown a great potential to be used in several groups of mammals and a plethora of palaeocological (Grohe et al., 2015; Pfaff et al., 2015), phylogenetic (Ekdale, 2013; Macrini et al., 2013; Mennecart and Costeur, in press a), ontogenetic (Sánchez-Villagra and Schmelzle, 2007) and evolutionary (Spoor et al., 2002) analyses. Yet, it is rarely studied in ruminants, but recently, Costeur (2014), Costeur et al. (2014) and Mennecart and Costeur (in press a,b) have shown that it is a significant structure to build hypotheses on ruminant phylogenetics. In addition, they have shown that its morphological variability is not a limiting factor.

In this study, we provide an alternative for the reconstruction of phylogenetic relationships among Early and Middle Miocene deer based on the ear region.

MATERIAL AND METHODS

Material

Four specimens housed at various collections were investigated and CT-scanned. They were previously attributed to the Procervulinae (*Procervulus dichotomus* (Gervais, 1859) and *Heteroprox larteti* (Filhol, 1891)), to the Dicrocerinae (*Dicrocerus elegans* Lartet, 1837), and to the debated Cervidae *Euprox furcatus* (Hensel, 1859). Except for *P. dichotomus*, which is a complete skull (Rössner, 1995), all the specimens are isolated petrosal bones that have been attributed thanks to comparison with scanned skull material. We preferred here the isolated petrosal bones for a direct observation. The morphology of the bony labyrinth is straightforward and allows us to identify a

TABLE 1. Information of the four studied fossil specimens (Fr: France; Ge: Germany)

Species	Inventory number	Locality	Mammalian age	Numerical age	Institution scanner	Voxel size (µm)
Procervulus dichotomus	SNMB-BSPG 1979XV555	Rauscheröd (Ge)	MN4	17 Ma	SNMB	35.1
Heteroprox laterti	NMB Sth.2394a	Steinheim (Ge)	MN7/8	13.5 Ma	NMB	40.0
Dicrocerus elegans	MNHN.F.SA9952	Sansan (Fr)	MN6	15 Ma	MNHN	23.7
	MNHN.F.SA9954	Sansan (Fr)	MN6	15 Ma	MNHN	23.7
Euprox furcatus	NMB Sth.2394c	Steinheim (Ge)	MN7/8	13.5 Ma	NMB	40.0

specimen to the species level based on available comparative material (see Mennecart and Costeur, in press a). When available, we have chosen isolated material to provide direct comparative illustrations of the fossils. Appendix A is a 3D-file containing the petrosal bone reconstruction of *P. dichotomus* can be found in Supporting Information (data 1). Table 1 synthesizes specimen information as well as the settings used for CT-scanning. Data on comparative material for the phylogenetic analysis comes from O'Leary (2010), Orliac et al. (2012), Costeur (2014), Orliac and O'Leary (2014) and Mennecart and Costeur (in press a; see the phylogenetic section for a detailed list of comparative material). The bony labyrinth of *Cervus elaphus* used here was reconstructed from the specimen NMB 11147 and is given in Supporting Information Data 2.

The petrosal bone of *H. larteti* and *E. furcatus* were scanned using X-ray microtomography at the Biomaterials Science Center of the University of Basel using a nanotom R m (phoenix_x-ray, GE Sensing & Inspection Technologies GmbH, Wunstorf, Germany). *P. dichotomus* was scanned on the same GE Phoenix nanotom CT-scanner at the Staatliche Naturwissenschaftliche Sammlungen Bayerns (SNSB) in Munich (Gemany). Finally, the petrosal bone of *D. elegans* was scanned on the Ast-RX platform of the Muséum National d'Histoire Naturelle (MNHN) in Paris.

Image segmentation and reconstructions of the bony labyrinths were performed using AVIZO 7.0. Measurements (Table 2) and nomenclature (Fig. 1) follow O'Leary (2010) for the petrosal bone and Orliac et al. (2012), Ekdale (2013) and Macrini et al. (2013) for the bony labyrinth.

Cladistic Analysis

We performed a cladistic analysis based on a matrix of 23 characters: 11 characters on the petrosal bone and 12 characters on the bony labyrinth (expanded from Mennecart and Costeur (in press a); see Appendix A and Supporting Information data 3) in order to understand the specificities of the cervid petrosal bone and of the bony labyrinth within the Ruminantia. We have excluded the characters of the cranial appendages which usually serve to structure the basal nodes of the phylogenetic tree of Pecora (e.g., Sánchez et al., 2015). Our aim was to test the phylogenetic relationships of fossil deer described above with the extant red deer *C. elaphus* (see O'Leary, 2010 for the morphology of the petrosal bone and this study for the bony labyrinth, illustrated in Supporting Information data 2). For comparative purposes with other pecoran ruminants, we added the Moschidae lineage with an extant musk deer (*Moschus moschiferus*) and the Mid-Miocene *Micromeryx flourensianus* (Costeur, 2014; Mennecart and Costeur, in press a). In addition, we also included the non-pecoran tragulids with the Mid-Miocene *Dorcatherium crassum* and the extant *Tragulus javanicus* (Mennecart and Costeur, in press a). The earliest artiodactyls *Diacodexis ilicis* and *Homacodon vagans* from the Eocene of North America were chosen as outgroups (Orliac et al., 2012; Orliac and O'Leary, 2014).

The analysis was performed using WinClada (Nixon, 2002). All characters were equally weighted without any ordering. All multistate characters were treated as unordered. We run an exhaustive search which resulted in only one tree with 35 steps. For each node, the list of non-ambiguous synapomorphies is given in Figure 2. Appendix A and Supporting Information data 3 give the list of characters and their states.

Institutional Abbreviations

SNSB-BSPG—Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany.

MNHN—Muséum National d'Histoire Naturelle, Paris, France.

NMB—Natuhistorisches Museum Basel, Switzerland.

TABLE 2. Measurements of the bony labyrinths of the four fossil specimens and Cervus elaphus

	Procervulus dichotomus	*Hetroprox larteti*	*Dicrocerus elegans*	*Euprox furcatus*	*Cervus elaphus*
Accession number	SNMB-BSPG1979XV555	NMB Sth.2394a	MNHN.F.SA9954	NMB Sth.2394c	NMB 11147
Number of turns	2.5	2.25	2.5	2.5	2.25
Cochlear aspect ratio	0.52	0.56	0.57	0.55	0.53
Volume labyrinth (mm^3)	74	78	84	66	157
asch	5.42	5.14	4.73	5.14	5.91
ascw	4.73	4.81	4.92	5.37	5.89
psch	4.71	4.5	4.49	4.44	5.53
pscw	4.64	4.5	4.53	4.84	5.68
lscl	4.53	4.19	4.32	4.33	4.3
lscw	4.03	4.02	4.42	3.98	5.1
Stapedial ratio	1.37	1.47	1.6	1.62	1.56
Angle asc-psc	83	88	72.5	83	82
Angle asc-lsc	69	82	75	68	72
Angle psc-lsc	87	90	93	84	81

asc, anterior semicircular canal; **psc**, posterior semicircular canal; **lsc**, lateral semicircular canal. **asch**, height of the anterior semicircular canal; **ascw**, width of the anterior semicircular canal; **psch**, height of the posterior semicircular canal; **pscw**, width of the posterior semicircular canal; **pscl**, Length of the lateral semicircular canal; **pscw**, width of the lateral semicircular canal.

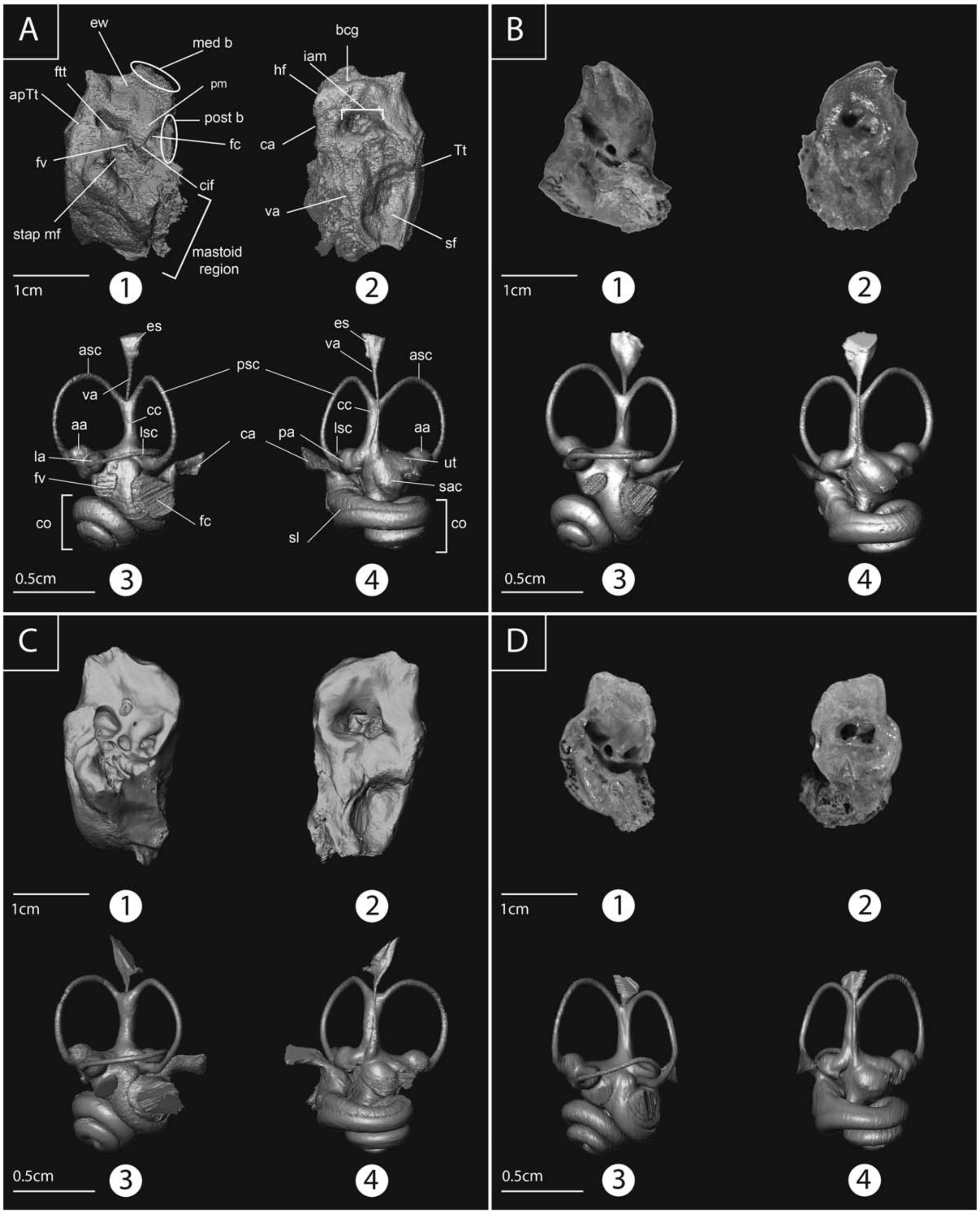

Fig. 1. Petrosal bone in ventrolateral (**1**) and dorsolateral (**2**) views and bony labyrinth in posterolateral (**3**) and anteromedial (**4**) views of *Procervulus dichotomus* (SNSB-BSPG 1979XV555, **A**) compared to those of *Hetroprox larteti* (NMB Sth.2394a, **B**), *Dicrocerus elegans* (MNHN.F.SA9952, **C1–2**; MNHN.F.SA9954, **C3–4**) and *Euprox furcatus* (NMB Sth.2394c, **D**). **aa**, asc ampulla; **apTt**, anterior process of the tegmen tympani; **asc**, anterior semicircular canal; **bcg**, possible basicapsular groove; **ca**, cochlear aqueduct; **cc**, common crus; **cif**, crista interfenestralis; **co**, cochlea; **es**, endolymphatic sac; **ew**, epitympanic wing; **fc**, fenestra cochleae; **ftt**, fossa for tensor tympani muscle; **fv**, fenestra vestibuli; **hf**, hiatus Fallopii; **iam**, internal acoustic meatus; **la**, lsc ampulla; **lsc**, lateral semicircular canal; **med b**, contact zone for medial bulla; **pa**, psc ampulla; **pm**, promontorium; **post b**, contact zone for posterior bulla; **psc**, posterior semicircular canal; **sac**, saccule; **sf**, subarcuate fossa; **sl**, secondary lamina; **stap mf**, fossa for stapedial muscle; **Tt**, tegmen tympani; **ut**, utricule; **va**, vestibular aqueduct.

RESULTS

Petrosal Bones

Figure 1 illustrates all four fossil petrosal bones of all four fossil stem cervidae *P. dichotomus*, *H. larteti*, *D. elegans* and *E. furcatus*. They all look similar to that of the living red deer, *Cervus elaphus*, which was added to the comparative analysis (data from O'Leary, 2010). All four petrosal bones share a large fossa for the Tensor Tympani slightly excavating into the tegmen tympani; a similar sized and hemiellipsoid promontorium; and a shallow subarcuate fossa or a wedge-shaped mastoid region. The basicapsular groove is ventral in *P. dichotomus* and *H. larteti* (Fig. 1A,B) as observed in *C. elaphus*; it is ventromedial to dorsal in *D. elegans* and *E. furcatus* (Fig. 1C,D), slightly less dorsal than in *M. moschiferus* and *M. flourensianus* but still on this side of the petrosal bone. They all share the same condition of the hiatus Fallopii medially positioned on the tegmen tympani. Contrary to *C. elaphus*, all four early Cervidae have no clearly visible transpromontorial sulcus. *H. larteti* and *D. elegans* show a bifid apex (Fig. 1B,C), the condition in *E. furcatus* is difficult to identify because of the poor preservation state of the specimen. The crista interfenestralis is broad in all four stem taxa, as in *C. elaphus*. The facial sulcus is broad as in *C. elaphus*. Poor preservation in this area prevents to identify a fossa for the head of the malleus, which is absent in *C. elaphus* (O'Leary, 2010). *P. dichotomus*, *D. elegans*, *E. furcatus* and to a lesser extent *H. larteti* have a broad posteromedial flange as in *C. elaphus*.

Bony Labyrinth

Figure 1 illustrates the four fossil bony labyrinths. The bony labyrinth of *C. elaphus* is given in Supporting Information data 2. The bony labyrinth of *P. dichotomus* and *H. larteti* shares striking similarities. Their cochlea is grouped under the vestibule and has 2.5 turns in *P. dichotomus* and 2.25 in *H. larteti* turns (Table 2). The cochlear aspect ratio measures 0.52 in *P. dichotomus* and 0.56 in *H. larteti*; they both have rather low cochleas. The basal turn is thick and much more developed as the second turn; it is more elongate medially in *P. dichotomus* than in *H. larteti*. The secondary bony lamina is well visible over about a third of the basal turn. The cochlear aqueduct is large, long and flat in section. It bends posterolaterally at mid-course, markedly in *P. dichotomus* and to a lesser extent in *H. larteti*. Their stapedial ratio describing the moderately ellipsoid shape of their fenestra vestibuli measures 1.37 in *P. dichotomus* and 1.47 in *H. larteti* (Table 2). The respective semicircular canals have overall a similar shape, the posterior semicircular canal being slightly curved and less round in *H. larteti*. Both the anterior and posterior semicircular canals extend high above the common crus giving an acute V-shaped indentation to the space between them at the level of the common crus (Fig. 1A,B). The anterior semicircular canal is the highest. The lateral semicircular canal is straight. Its posterior limb enters high (dorsally) in the posterior ampulla and thus shows no fusion, even partial with the posterior ampulla. They both have a long and straight vestibular aqueduct (slightly curved in *P. dichotomus*), which is longer than the common crus and originates slightly anteriorly with regards to the mid-line of the common crus. The overlying endolymphatic sac is elongated, funnel-like in shape and rather large. It extends largely above the level of the semicircular canals (Fig. 1A,B).

D. elegans has a different bony labyrinth (Fig. 1C). The cochlea is longer with 2.5 turns, the basal turn is still massive but less than in the Procervulinae, the secondary bony lamina is visible over half of the basal turn. The cochlear aspect ratio measures 0.57 in the range of both Procervulinae (Table 2). The cochlear aqueduct is massive and long, not as flat as in the Procervulinae but it bends at mid-course, much like in *P. dichotomus*. The stapedial ratio measures 1.6. The semicircular canals are all straight. The anterior and posterior semicircular canals extend above the level of the common crus, but less than in the Procervulinae so that no acute V-shaped indentation can be observed; the anterior semicircular canal is slightly more extended dorsally than the posterior one. The lateral semicircular canal is long and its posterior limb enters the posterior ampulla at mid-height, so a little lower than it does in the Procervulinae, partly merging with the posterior ampulla. The vestibular aqueduct is straight and originates anteriorly with regards to the midline of the common crus. It extends just slightly above the level of the common crus, less than in the Procervulinae. The endolymphatic sac is elongate and a little less funnel-shaped as in the Procervulinae, its extent is ventro-dorsally truncated as it opens in a slit like manner on the petrosal bone. It extends largely above the level of the semicircular canals.

The bony labyrinth of *E. furcatus* has a cochlea with 2.5 turns (Fig. 1D and Table 2). The basal turn is thinner than in the bony labyrinth of fossil deer studied so far. The secondary bony lamina is visible over about a third of the basal turn. The cochlear aspect ratio measures 0.55 in the range of *C. elaphus* and of the other studied fossil taxa. The cochlear aqueduct is large, but less massive than in the other studied fossil taxa, it also bends medially at mid-course but less than in *D. elegans* or *P. dichotomus*. The stapedial ratio measures 1.62. The anterior and posterior semicircular canals extend dorsally over the common crus, the anterior one being higher than the posterior one. The lateral semicircular canal is strongly curved and its posterior limb enters the posterior ampulla at mid-height, being partly fused with it as in *D.*

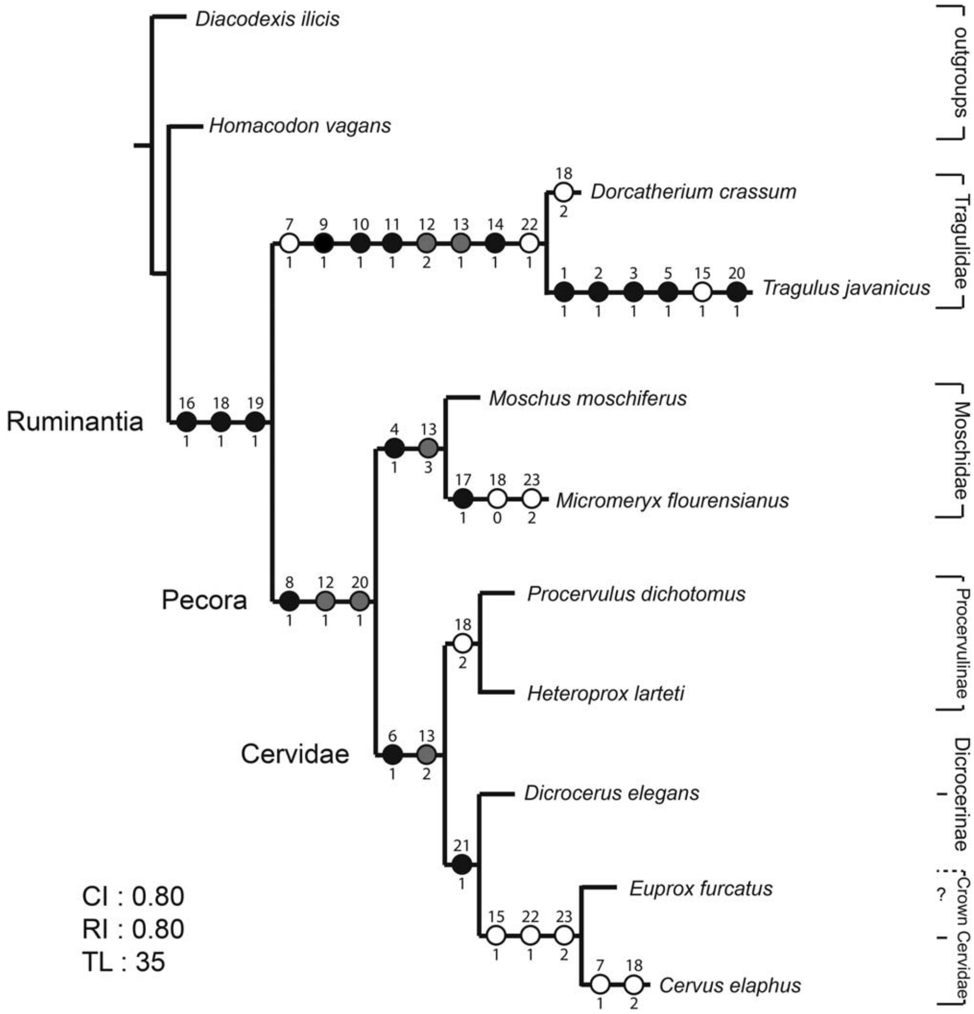

Fig. 2. Phylogenetic tree of selected ruminants based on 23 characters of the petrosal bone and bony labyrinth (see Appendix A and Supporting Information data 3 for the description of characters and character states). For each node the list of the non-ambiguous synapomorphies is given and each synapomorphy is represented by a black circle (strict synapomorphy) or an open white circle (homoplasic synapomorphy). Ambiguous characters are represented by grey circles. The upper numbers indicate the character number and the lower numbers the states for these characters. CI: consistency index; RI: retention index; TL: tree length.

elegans. The vestibular aqueduct of *E. furcatus* has the same length as the common crus, so shorter than in the other stem deer. It is straight and originates anteriorly as in the other taxa. The overlying endolymphatic sac is thin and more triangular in shape; it does not extend above the level of the semicircular canals.

PHYLOGENETIC ANALYSIS AND DISCUSSION

The phylogeny of the early Cervidae has been discussed frequently, but no consensus has been reached yet arisen. Only Azanza (1993, 2000) and Vislobokova (1983, 1990) analysed the four emblematic Early-Mid Miocene cervid genera that are *Procervulus*, *Heteroprox*, *Dicrocerus* and *Euprox* together. Their works, based on antlers, dental and postcranial morphology has resulted in identifying the Lagomerycidae as sister clade to Cervidae and the Procervulinae and Dicrocerinae as two stem clades. *Euprox* was included in the crown clade Muntiacini. To what extent antler morphology reflects phylogenetic relationships is not yet fully understood because some characters such as the parallel disposition of the pedicles in Procervulinae have been acquired independently in other genera including *Dicrocerus* and *Euprox* (Azanza, 1993).

The single obtained tree (Fig. 2) confirms Tragulidae as sister group of Pecora, both forming the clade Ruminantia (e.g., Hassanin et al., 2012). Numerous petrosal and bony labyrinth apomorphies allow for a clear distinction between Tragulidae and Pecora (characters 8, 9, 10 and 11 of the petrosal bone; and character 14 of the bony labyrinth), as already evidenced by Mennecart and Costeur (in press a). The Cervidae, including the earliest fossil taxa, forms a monophyletic group

(Fig. 2) that can be distinguished from the Moschidae by the shape and extent of the fossa for the tensor tympani muscle (character 4 and 6, respectively), and the insertion of the lateral semicircular canal in the vestibule towards the posterior ampulla (character 13). The latter seems to be a very reliable character for the phylogeny of ruminants (Mennecart and Costeur, in press a).

Procervulus is often considered as the most basal stem cervid (e.g., Janis and Scott, 1987; Groves, 2007) or even sister taxon to the family Cervidae. After Bubenik (1962) proposed the family name Procervulidae for a range of Early Miocene taxa, Ginsburg (1985) restricted it to *Procervulus* as the sister clade of the Cervidae. Bubenik and Bubenik (1990) considered Procervulidae to be not closely related to Cervidae but to Lagomerycidae based on the description of *Procervulus aurelianensis* (= *P. dichotomus* after Gentry et al., 1999). Azanza (1993) preferred to define the subfamily Procervulinae based on the single synapomorphy of a parallel disposition of the cranial pedicles. Our analysis placed *P. dichotomus* indeed as a member of stem Cervidae (Fig. 2). Morphological differences in the ear region when compared to later Cervidae are not sufficient to exclude *P. dichotomus* from Cervidae, in line with Azanza (1993, 2000). Thus we consider *Procervulus* a member of the stem Cervidae. The phylogenetic position of *Heteroprox* with regards to *Procervulus* has been largely discussed on the basis of antlers shape (Azanza, 1993). Rössner (1995), Gentry et al. (1999) and Groves (2007) proposed a direct filiation between *Procervulus* and *Heteroprox*, while Gentry (1994) considered *Procervulus* as the ancestor of a clade formed by *Heteroprox* and the lineage *Euprox*-crown Cervidae. Simpson (1945) and Bubenik and Bubenik (1990) included *Heteroprox* within the Dicrocerini/inae, and considered it as more or less related to *Dicrocerus*. Our phylogenetic analysis places *P. dichotomus* and *H. laterti* in a distinct clade, which is the sister group to *D. elegans*, *E. furcatus* and *C. elaphus* (Fig. 2). They are clearly different from the other Middle Miocene Cervidae by possessing a more elongate vestibular aqueduct (character 18) and a lack of fusion of the lateral semicircular canal with the posterior ampulla (character 21). Their cochlea is also less derived in being more massive, especially the basal turn, a plesiomorphic condition seen in the earlier artiodactlyls *Diacodexis* and *Homacodon* (Orliac et al., 2012; Orliac and O'Leary, 2014). Independently to the shape of the cranial appendages, the dentition and the postcranial skeleton, our results support the hypothesis of a monophyly of *Procervulus* and *Heteroprox* at the base of Cervidae (Vislobokova, 1983, 1990; Azanza, 1993, 2000). Consequently, the subfamily Procervulinae is redefined as basal deer showing the combination of the following characters: up-right antlers without a coronet structure (Azanza, 1993, 2000), posterior limb of the lateral semicircular canal entering the posterior ampulla high preventing any fusion of the canal with ampulla, short cochlea with a massive basal turn, long vestibular aqueduct extending above the level of the common crus and up to the maximal height of the anterior semicircular canal, elongated and funnel-shaped endolymphatic sac, anterior and posterior semicircular canals extending largely above the level of the common crus.

Based on the sole antler morphology, *Dicrocerus* was long considered as part of the *Lagomeryx* lineage (Gentry, 1994), of the stem Cervidae, or as being the "world's earliest deer known" (Goss, 1983; Bubenik and Bubenik, 1990; Geist, 1998). It was also considered as a transitional from towards Cervinae or an early member of Muntiacinae (Vislobokova, 1990). However, Azanza (1993, 2000) and Azanza et al. (2011) noticed that the coronet-like structure and the live shedding of the "protoantlers" of *Dicrocerus* are more derived than those observed in the Procervulinae and Lagomerycidae. They also hypothesized that the Dicrocerinae (*Dicrocerus*, *Stehlinoceros* and *Acteocemas*) are transitional forms between the Procervulinae and the crown Cervidae, such as previously proposed by Vislobokova (1990). Our phylogenetic analysis is consistent with this hypothesis. *D. elegans*, *E. furcatus* and *C. elaphus* differ from the Procervulinae by the above-mentioned characters 18 and 21 (Fig. 2). Nevertheless, *D. elegans* appears to be the sister taxon to *E. furcatus* and *C. elaphus*. *E. furcatus* shows the most derived characters among the fossil cervids considered in this analysis (Fig. 2). However, its phylogenetic position remains uncertain although crucial in the definition and the origin of the crown Cervidae (Gentry et al., 1999). Bubenik and Bubenik (1990), Gentry (2000), Dong et al. (2004) and Groves (2007) hypothesized that *Euprox* is the direct precursor of the crown Cervidae. However, recent analyses show that *Euprox* could be nested within the Muntiacini tribe (Vislobokova, 1983, 1990; Azanza, 1993; Dong, 2007; Wang and Zhang, 2011; Azanza et al., 2013; Hou, 2015). *E. furcatus* shares with *C. elaphus* a curved lateral semicircular canal (character 15), a relatively thin basal cochlear turn (character 22), and an ovoid to circular section of the cochlear aqueduct (character 23). These characters are found in all Cervidae, but they are homoplasic within Ruminantia (Fig. 2). Without further members of crown Cervidae in this analysis, we are unable to include or exclude *E. furcatus* in/from the crown Cervidae. Future analyses including additional extant deer may confirm the origin of crown Cervidae by 9 Ma (*Muntiacus noringenensis*, Dong et al., 2004) or recalibrate it to at least 13.8 Ma, if *Euprox* is confirmed to be part of the modern Cervidae.

CONCLUSIONS

Our phylogenetic analysis of Early and Middle Miocene cervids, based on morphological traits of the ear region only, generated results in accordance with previous assumptions based on antler morphology. The petrosal bone and bony labyrinth of cervids appear to carry a strong phylogenetic signal in Cervidae and in particular in the four stem cervids studied. The results confirm the grouping of *Procervulus dichotomus* and *Heteroprox larteti* within the Procervulinae. We extend the definition of this subfamily with a number of characters of the bony labyrinth such as the high insertion of the posterior limb of the lateral semicircular canal in the posterior ampulla and the elongated vestibular aqueduct. Our results also confirm that Dicrocerinae (*Dicrocerus elegans*) is more closely related to the crown deer. The phylogenetic position of *Euprox furcatus* at the base of the crown Cervidae remains tentative. The derived condition of its bony labyrinth with respect to other stem taxa analysed here is interesting and could resuscitate earlier hypotheses considering *Euprox furcatus* as a crown deer, making it the earliest crown cervid known. However, additional data including further extant and extinct cervids are needed to clarify this hypothesis.

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CONFLICT OF INTEREST

The authors declare no conflict of interest

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APPENDIX A: DESCRIPTION OF THE PETROSAL AND BONY LABYRINTH CHARACTERS USED IN THE PHYLOGENETIC ANALYSIS. ALL CHARACTERS ARE TREATED AS UNORDERED

Petrosal Bone

1. Hiatus Fallopii: distinct hole in medial position on the tegmen tympani (0); distinct hole in ventral position on the tegmen tympani (1) (from Mennecart and Costeur, in press a).

2. Number of convexities of the promontorium: one convexity (0); two convexities (1) (from O'Leary, 2010).

3. Fossa for the tensor tympani muscle: shallow (0); deep (1) (from O'Leary, 2010).

4. Shape of the fossa for the tensor tympani muscle: round to square (0); elongated and bean-shaped (1) (from Mennecart and Costeur, in press a).

5. Size of the fossa for the tensor tympani muscle: large (0); small (1) (from Mennecart and Costeur, in press a).

6. Extent of the fossa for the tensor tympani muscle: not excavated into the tegmen tympani (0); excavated into the tegmen tympani (1) (from O'Leary, 2010).

7. Transpromontorial sulcus: present (0); absent (1) (from O'Leary, 2010).

8. Medial protrusion of the pars cochlearis: absent (0); present (1) (from O'Leary, 2010).

9. Knob anterior to the subarcuate fossa: absent (0); present (1) (from Mennecart and Costeur, in press a).

10. Subarcuate fossa: deep (0); shallow (1) (from O'Leary, 2010).

11. Shape of mastoid region: wedge (0); knob (1) (from O'Leary, 2010).

Bony Labyrinth

12. Number of cochlear turns: equal or less than two (0); between two and three (1); equal or more than three (2) (modified from Ekdale, 2013).

13. Insertion of the lateral semicircular canal in the vestibule towards the posterior ampulla: low in posterior ampula (0); high dorsally between posterior ampula and commun crus (1); high in

posterior ampula (2); anterior to posterior ampula in vestibule (3) (modified from

Ekdale, 2013).

14. Extension of the lateral semicircular canal with respect to the plane of the posterior semicircular canal in dorsal or lateral view: no extension beyond the plane (0); extension beyond the plane (1) (modified from Macrini et al., 2013; Ekdale, 2013).

15. Lateral semicircular canal: straight (0); curved (1) (modified from Macrini et al., 2013).

16. Secondary common crus: present (0); absent (1) (from Macrini et al., 2013).

17. Course of the vestibular aqueduct with respect to the common crus: parallel (0); diverging (1) (from Mennecart and Costeur, in press a).

18. Length of the vestibular aqueduct: less than the common crus (0); same as common crus (1); longer than common crus (2) (from Mennecart and Costeur, in press a).

19. Size of the endolymphatic sac: small (0); large (1) (from Mennecart and Costeur, in press a).

20. Endolymphatic sac position with regards to the distal end of the common crus: not covering the common crus (0); covering the common crus (1) (from Mennecart and Costeur, in press a).

21. Fusion of the lateral semicircular canal with posterior ampulla: absent (0); partial to complete fusion (1).

22. Relative thickness of the basal cochlear turn: thick (0); thin (1).

23. Section of the cochlear aqueduct: flat (0); ovoid to circular (1).