COMPARATIVE ANATOMY, PHYLOGENY, AND SYSTEMATICS OF THE MIocene GIRAFFID DECCNATHERIUM PACHECOI CRUSAFONT, 1952 (MAMMALIA, RUMINANTIA, PECORA): STATE OF THE ART

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ABSTRACT — Decennatherium pachecoi Crusafont, 1952, is one of two giraffid species described from the Miocene of the Iberian Peninsula. This species is recovered exclusively from Vallesian faunas (MN9–10, late Miocene, 10–11 Ma). Despite being relatively well represented in the fossil record, except for the skull and ossicones, the complete vertebral column, and part of the dentition, its systematics and phylogenetic position among giraffids are the subject of debate. We update our knowledge of D. pachecoi, revising all Spanish material assigned to this species, as well as previously undescribed fossils. We reassess the systematics of Decennatherium, including its potential relationship with the second Iberian giraffid, the early Turolian Birgerbohlinia Crusafont, 1952, by means of the first cladistic analysis of the Giraffidae that includes Decennatherium together with the most relevant African and Eurasian taxa, both fossil and extant. Our results link Decennatherium with a ‘samothere’ clade, whereas Birgerbohlinia is nested within a ‘sivathere’ clade, thus refuting a previously assumed direct relationship between the two Spanish forms. Finally, we discuss some other possible finds of the genus Decennatherium in Greece, Turkey, and Iran.

SUPPLEMENTAL DATA — Supplemental materials are available for this article at free www.tandfonline.com/UJVP

INTRODUCTION

Giraffidae is a clade of pecoran ruminants united by the presence of a bilobed lower canine (Hamilton, 1978; Solounias, 2007). Giraffids bear ossicones, a type of epiphyseal, permanent, cranial appendage (Solounias, 2007; Grossman and Solounias, 2014), although this has been subject to controversy because it was stated that there is no evidence to apply this term to the horns of fossil giraffids (Geraads, 1986, 1991). Giraffids are represented by only two living genera, the African Okapia and Giraffa (Groves and Grubb, 2011), but they were very diverse during the Miocene, when the family was widespread throughout the Old World. The late Miocene was a period of giraffid diversification (Gentry, 1994; Solounias, 2007; Claus and Rössner, 2014). Two Miocene species are described from the Iberian Peninsula, Decennatherium pachecoi (Vallesian, MN9–10), present in the Calatayud-Teruel, Duero, and Tagus basins (Table 1, Fig. 1) and Birgerbohlinia schaubi (early Turolian, MN11; Crusafont, 1952). Since the first publication (Crusafont, 1952), very few works followed on the subject, and none in the past two decades (see Crusafont, 1961; Morales and Soria, 1981; Morales, 1985; Alcalá and Montoya, 1994; Montoya and Morales, 1991).

Several non-cladistic phylogenetic hypotheses have been proposed for Decennatherium pachecoi and Birgerbohlinia schaubi. Decennatherium pachecoi has been aligned with giraffines (Crusafont, 1952), samotheres (Morales and Soria, 1981), sivathere (Morales, 1985; Montoya and Morales, 1991), and bohlinines (Solounias, 2007), whereas B. schaubi has been aligned with either sivathere (Crusafont, 1952) or bohlinines (Solounias, 2007). Decennatherium pachecoi and B. schaubi were either considered directly related (Morales and Soria, 1981; Montoya and Morales, 1991) or, alternatively, to belong to two different lineages (Crusafont, 1952). Neither of these hypotheses was tested through cladistic analysis, and the relationships of these genera to each other and to other members of Giraffidae remain unresolved. The difficulties of clarifying these relationships derive from the plesiomorphic dentition and postcranial skeleton of giraffids and their morphological stability (Hamilton, 1978; Geraads, 1986). In addition, the few cranial remains assigned to D. pachecoi from Matillas, also known as Cendejas de la Torre (Crusafont, 1961; Morales, 1985), are problematic because they are poorly preserved and were not found in situ (Crusafont, 1952). We prefer to be cautious and not include them in this study until a more exhaustive examination of the site and the remains is carried out.

In this work, we revise all the Spanish material previously assigned to Decennatherium pachecoi, including previously undescribed fossils, with the aim of reassessing the systematic and phylogenetic position of this poorly understood giraffid. We particularly focus on the following questions: (1) What is the phylogenetic position of D. pachecoi within the Giraffidae based on our data? (2) What is the relationship of D. pachecoi to Birgerbohlinia schaubi, the only other late Miocene giraffid known from Spain? (3) How does D. pachecoi from Spain compare with other purported Decennatherium finds from Greece, Turkey, and Iran (Bosscha Erdbrink, 1976; Geraads, 1979, 1989; Geraads et al., 2005)?

Institutional Abbreviations — AMNH, American Museum of Natural History, New York, U.S.A.; CR, Crevillente-2, Museo de Geología de la Universidad de Valencia, Burjassot, Spain; ICP,
TABLE 1. Sites with *Decennatherium pachecoi* in the Iberian Peninsula.

| Site                              | Province              | Basin                  | Stage       | MN*   | References                                                                 |
|-----------------------------------|-----------------------|------------------------|-------------|-------|---------------------------------------------------------------------------|
| Nombrevilla (reference site)      | Nombrevilla, Zaragoza | Calatayud-Teruel (Ebro) | Early Vallesian | MN9   | Villalta and Crusafont, 1944; Crusafont, 1952; Montoya and Morales, 1991 |
| Los Valles de Fuentidueña         | Segovia               | Duero                  | Early Vallesian | MN9   | Crusafont, 1952; Montoya and Morales, 1991                               |
| Pedrajas de San Esteban           | Pedrajas de San Esteban, Valladolid | Duero                  | Early Vallesian | MN9   | Crusafont, 1952; Montoya and Morales, 1991                               |
| Relea                             | Relea, Palencia       | Duero                  | Early Vallesian | MN9   | Crusafont, 1952; Montoya and Morales, 1991                               |
| Masia de la Roma (La Roma 1)      | Between Peralejos and Alfambr, Teruel | Calatayud-Teruel (Ebro) | Early Vallesian | MN9   | Alcalá, 1994; Alcalá and Montoya, 1994                                   |
| Masía del Barbo                   | Alfambr, Teruel       | Calatayud-Teruel (Ebro) | Late Vallesian | MN10  | Alcalá, 1994                                                              |

*European land mammal unit.

Materials

The material of *Decennatherium pachecoi* Crusafont, 1952, described in this work represents the entire sample of fossils from Los Valles de Fuentidueña and reposited in the MNCN-CSIC. This sample represents the most complete and abundant set of *D. pachecoi* fossils, including described and undescribed material. Teeth and remains of the appendicular skeleton are relatively abundant. Other *D. pachecoi* material studied here comes from Nombrevilla, Relea, Pedrajas de San Esteban, Saldaña (Crusafont, 1952), Campisalabos (Crusafont 1966), La Roma, and Masia del Barbo (Alcalá, 1994; Alcalá and Montoya, 1994) (Table 1, Fig. 1).

Crania and postcrania of *Birgerbohlinia schaubi* Crusafont, 1952, considered in this study, come from its type locality, Piera (Torrent dels Traginers, Piera, MN11). The specimens are curated by the Institut Català de Paleontologia (Sabadell, Spain). The data from Crevillente-2 (Alicante) come from the...
descriptions and figures provided by Montoya and Morales (1991) and Montoya (1994).

Data regarding the middle Miocene basal giraffids *Injannahtherium arabicum* Morales, Soria, and Thomas, 1987, from Al Jadidah (Saudi Arabia), come from casts housed at the MNHN-CSIC (Madrid, Spain) and those regarding *Giraffokeryx pachecoi* Pilgrim, 1911, from Chihi and Hasnot (Pakistan), come from specimens housed in the AMNH.

Other cranial and postcranial data from material in the AMNH includes the giraffids *Samotherium major* Bohlin, 1926, *Samotherium boissieri* Forsyth Major, 1888, *Palaeanotherus rouenii* Gaudry, 1861, and *Bohlina attica* Gaudry and Lartet, 1856, all from the late Miocene of Samos, Greece; *Schansitherium tafeli* Killgus, 1922, *Samotherium sinense* Schlosser, 1903, and *Honanotherium schlosseri* Pilgrim, 1911, all from the late Miocene and early Pliocene of Shansi, China; *Bramatherium perimense* Falconer, 1845, from the late Miocene of Perim Island, India; and *Bramatherium megacephalum* Lydekker, 1876, from the late Miocene of Dhoikh Pathan, Pakistan; and *Sivatherium giganteum* Falconer and Cautley, 1836, from the early Pleistocene of the upper Siwaliks near Siwan, Kalka, and Chandigarh, India. Additional anatomical data were collected from osteological material of the extant giraffids *Giraffa camelopardalis* of the extant giraffids we included data on *Giraffa stillei* Gaudry, 1861, and *Giraffa giraffids we included data on *Giraffa*. Among more recent forms such as *D. pachecoi* from Spain.

**Methods**

**Measurements**—All measurements were taken with digital calipers. The raw measurements and their main statistics are detailed in Supplementary Data 1 and 2. We follow the set of measurements proposed by Sánchez and Morales (2008) and Quiralte (2011). For comparison measurements and their main statistics, see Supplementary Data 3.

**Nomenclature**—We use the anatomical terminology of Barone (1999) for the cranial and postcranial skeleton, and that of Azanza (2000) (in Sánchez and Morales, 2008) for dental nomenclature.

**Phylogenetic Analysis**—The data matrices were compiled in Excel and run in TNT (Goloboff et al., 2008) using maximum parsimony (see Phylogenetic analysis below). We focused on several taxa that are historically used in the interpretation of the phylogenetic relationships of *Decennatherium* and so are useful to our study.

As the outgroup, we chose *Canthumarhyx sirtensis* Hamilton, 1973 (=Zaraiz zelteni) from the early Miocene of Gebel Zelten, Libya, and Moruorot and Rusinga Island, Kenya (Hamilton, 1973, 1978; Grossman and Solounias, 2014). *Canthumarhyx sirtensis* was recognized as a giraffoid by Hamilton (1978) on the basis of its bilobed canines that separate the giraffes from the rest of the Pecora. Furthermore, some researchers have assigned *C. sirtensis* to the Giraffidae (e.g., Harris et al., 2010; Grossman and Solounias, 2014) and recognize it as the most basal member of the family. In *C. sirtensis*, the accessory lobe is very small relative to the anterior lobe, whereas in other giraffids the accessory lobe is large, indicating that the accessory lobe developed gradually with the initial development of a small accessory lobe (Hamilton, 1978). The small accessory lobe in *C. sirtensis* is thus apomorphic relative to other non-giraffid giraffomorphs (Sánchez et al., 2015), but plesiomorphic relative to giraffes with large accessory lobes (Hamilton, 1978). The same applies to other features such as overall size, metacarpal morphology, or the occlusal pattern of the lower premolars of *C. sirtensis*, which differ from those of boids, cervids, and antilopids but are plesiomorphic relative to other giraffids such as *Giraffokeryx primaevus* from the middle Miocene of Gebel Zelten (Kenya) (Churcher, 1970; Hamilton, 1978). All these features combine to make *C. sirtensis* the outgroup for our analysis.

Apart from *D. pachecoi*, the ingroup is composed of several taxa used in the classical phylogenetic hypotheses for *D. pachecoi*. This group includes basal giraffids such as *Georgiomeryx georgalasi* Paraskevaidis, 1940, and *Giraffokeryx pachecoi* Pilgrim, 1911, several representatives of late Miocene genera such as *Palaeanotherus rouenii*, *Samotherium major*, S. boissieri, *Bramatherium megacephalum*, and *Helladotherium diuvernii*, and more recent forms such as *Okapia johnstoni*, *Giraffa camelopardalis*, and *Sivatherium giganteum*. Finally, we have also included the European and Middle Eastern *Palaeanotherus major*, *P. macedoninae*, and *D. crassifonti* (Bosscha Erdbrink, 1976; Geraads, 1979, 1989; Bonis and Bouvrain, 2003). This allows us for the first time to test the cladistic relationships of these specimens with *D. pachecoi* from Spain.

The characters used (Appendices 1 and 2; Supplementary Data 4) in our analysis were mostly derived from the literature (Hamilton, 1978; Solounias, 2007), with the exception of a few characters (22–29, 31, 35, and 37–43). In some cases, there was not enough material, or we have not yet revised enough material, to include some characters without reducing robustness of the analysis, and this was the case of the cervical vertebrae. We used outgroup comparison (Watrous and Wheeler, 1981) to establish
the polarity of the character states. All characters are unordered and unweighted.

**SYSTEMATIC PALAEONTOLOGY**

**MAMMalia Linnaeus, 1758**

**Cetartiodactyla** Montgelard, Catzeflis, and Douzery, 1997

**Ruminantia Scopoli, 1777**

**Giraffidae** Gray, 1821

**Decennatherium** Crusafont, 1952

**Decennatherium Pacheco** Crusafont, 1952

(Figs. 2–10)

Giraffinae (nov. gen.?) pacheco, nov. sp. (Villalta and Crusafont, 1944).

Achtiaria sp. (Meléndez, Villalta, and Crusafont, 1944).

**Holotype**—An m1 from Nombrevilla, Crusafont, 1952: Lam. XXV 3, 3a.

**Paratypes**—The remaining material from Nombrevilla and Los Valles de Fuentidueña listed in Crusafont, 1952.

**Type Locality and Horizon**—Nombrevilla, Calatayud-Teruel Basin, late Miocene, Spain.

**Referred Material**—Los Valles de Fuentidueña (LVF): MNCN-32714, petrosal; MNCN-32367, petrosal; MNCN-32368, petrosal; MNCN-32369, petrosal; MNCN-32372, petrosal; MNCN-43490, maxilla fragment with left M1 and M2; MNCN-43489, left P4; MNCN-43496, right M3; MNCN-43450, left m2; MNCN-43451, left mandible fragment with dp3 and dp4; MNCN-43448, right mandible fragment with p4 and m1; MNCN-43449, left mandible fragment with p4, m1, m2, and part of m3; MNCN-32052, right dp4; MNCN-43452, right dp2; MNCN-43453, left p2; MNCN-43454, right p2; MNCN-43455, left p2; MNCN-43456, right p2; MNCN-43457, right p2; MNCN-43458, left p2; MNCN-43459, right p2; MNCN-43460, left p2; MNCN-32288, left p2; MNCN-43461, right p3; MNCN-43462, left p3; MNCN-43463, left p3; MNCN-43464, left p3; MNCN-43465, right p3; MNCN-43466, left p3; MNCN-43467, left p3; MNCN-43468, left p3; MNCN-43469, left p4; MNCN-43470, right p4; MNCN-43471, right p4; MNCN-43472, right p4; MNCN-43473, right p4; MNCN-43476, left m1; MNCN-43477, right m1; MNCN-43478, right m1; MNCN-43479, left m1; MNCN-43480, right m1; MNCN-43481, left m2; MNCN-43482, right m2; MNCN-43483, right m3; MNCN-43484, right m3; MNCN-43485, left m3; MNCN-43486, left m3; MNCN-43487, left m3. Abundant postcranial material is listed in Supplementary Data 1, Tables S6–S16.

**Diagnosis**—Large giraffid with elongated dp3 and dp4. The dp3 with posterolingual conid lingually attached to the posterior stylid, mesolingual conid absent, anterior conid and anterior stylid separated. Elongated DP3 with the anterior lobe almost twice as long as the posterior one; a strong anterior style, rounded, and very wide; strong buccal cone and unfolded lingual cone. p2 very simple, without mesolingual conid and with a coniform mesobuccal conid. p3 with posterobuccal conid always attached to the mesobuccal conid; a variably sized conid probably homologous to the mesolingual conid may or may not exist. Complex p4 of variable morphology, continuous lingual wall, posterobuccal conid always attached to the mesobuccal conid. Lower molars with weak metastylid that fades with wear, no buccal or lingual cingulids. The m3 with a well-developed third lobe, semicircular hypocuneid and strong entoconulid, weak basal columns. The P4 with a posterolingual spur. Upper molars longer than wide, styles parallel and weak, buccal cingulum poorly developed, lingual cone and metacone separated, occlusally exposed dentine area fuses late in wear, no basal pillars. Postcranial skeleton with limbs of medium relative length and robustness and shallow to medium metacarpal III–IV posterior trough.

**Occurrence**—The type locality of *Decennatherium pacheco* is Nombrevilla (Calatayud-Teruel Basin, MN9, early Vallesian, located near the village of Daroca, Zaragoza Province, Spain; Fig. 1). This species was also described from the Duero Basin in the fossil sites of Los Valles de Fuentidueña (Segovia, MN9), Pedrajas de San Esteban (Valladolid, MN9), Relea (Palencia, MN9), and Saldaña (Palencia, MN9) (Villalta and Crusafont, 1944; Crusafont and Pairó, 1952). Other findings from the Calatayud-Teruel Basin include Masaia de la Roma (La Roma 1, Teruel, MN9) (Alcalá, 1994; Alcalá and Montoya, 1994) and Masaia de Barbo (Teruel, MN10) (Alcalá, 1994).

**Stratigraphic Range**—Late Miocene: early Vallesian (MN9) to late Vallesian (MN10) (11.2–8.9 Ma).

**ANATOMICAL DESCRIPTION AND COMPARISONS**

**Cranial Skeleton**

**Petrosal**—In cerebellar view, the petrosal bone (Fig. 3A) preserves the internal acoustic meatus, with the foramen acusticum superius and the foramen acusticum inferius separated by the crista transversa. The surface around the acoustic meatus is smooth as in *Giraffa camelopardalis*, and the prefrontal commissure fossa is absent as in *G. camelopardalis*. The bone surrounding the internal acoustic meatus where cranial nerves VII and VIII enter the petrosal is smooth and featureless as in the rest of Cetartiodactyla (OLeary, 2010). The suprameatal area consists of a relatively simple flat or convex bar of bone that meets the dorsolateral surface of the petrosal at a right angle.

**Upper Dentition**—The only P3 known from Nombrevilla (Crusafont, 1952: Lam. XX, fig. 1) does not have a strong buccal cone. The P4 (Fig. 3C1–C2) is clearly longer than wide. The anterior style is moderate, thicker than the posterior style. The buccal cone is closer to the anterior style. The lingual face is simple, with a half-moon shape and a weak posterolingual spur as in the P4 from Relea (Crusafont, 1952: Lam XX, fig. 5, 5a). The P4 from Nombrevilla show intraspecific variability, with some specimens having a indentation on the posterolingual crista (Crusafont, 1952: Lam XX, fig. 4), and others lacking it (Crusafont, 1952: Lam XX, figs. 2, 3, 5a). In *Bohlinia attica*, the indentation is present (Bohlin, 1926:pl. X, fig. 7; Geraads, 2009). In *Homoana-therium schlosseri*, the indentation on the posterolingual crista is also polymorphic, showing different shapes and degrees of

![FIGURE 2. Skeletal and dental representation of Decennatherium pacheco (black).](image-url)
development, ranging from no more than a small bump in some specimens (Bohlin, 1926:pl. X, fig. 3) to filiform and well developed in others (Bohlin, 1926:pl. XI, fig. 2). Intraspecific variation is also found in Birgerbohlinia schaubi from Crevillente-2, where some specimens are characterized by the division of the internal valley (CR2-652), whereas others have only a slight posterolingual projection (CR2-536). This phenomenon even affects the buccal root of the tooth, which also shows a tendency to divide.
(Montoya and Morales, 1991), as can be observed in other giraffid species such as *Bramatherium megacephalum* or *Giraffokeryx punjabiensis* (Colbert, 1935b).

The M1 (Fig. 4A, B) has a buccal wall with stronger para-style and mesostyle and weaker metastyle. The protocone and metaconule are simple and well separated, with the anterior lobe wider than the posterior one. The occlusally exposed dentine area fuses in late stages of wear, and the enamel is very rugose. The M2 (Fig. 4A, B) is similar to the M1. The M3 (Fig. 3D1, D2) has a hypsodonty index (height/length in an unworn specimen) of 0.75. The buccal wall has stronger para-style and mesostyle and a weaker metastyle. The protocone and metaconule are simple and well separated. The occlusally exposed dentine area also fuses in late stages of wear, and the enamel is very rugose. The anterior lobe is wider than the posterior lobe. The main features to compare in the M3 are a small notch on the anterior part of the anterior lobe and another notch on the posterior part of the posterior lobe. In this respect, *D. pachecoi* differs from *B. schaubi*, which lacks this feature, as do *G. camelopardalis* and *H. schlosseri*. In *Bramatherium perimense*, there is a small notch on the posterior part of the posterior lobe, and in *Bramatherium megacephalum* there is one on the anterior lobe. The anterior lobe has a more 'V'-shaped lingual wall in these species, whereas in *D. pachecoi* it is more rounded. *Decennatherium pachecoi* also has a weaker para-style than *H. schlosseri*.

The length/width (L/W) index mean values of the upper molars are 1.067 (N = 11), similar to those of most of giraffids (~1.024; N = 810).

**Lower Dentition**—The bilobed lower canine has a large, rounded anterior lobe that is larger than the posterior one. Its corners are not sharp as in *G. camelopardalis* (Crusafont, 1952: pl. XXII, fig. 4). The p2 (Fig. 3E1–E3) is a simple tooth with no morphological variability (N = 17). The anterior conid is strong, and there is no anterior stylid. The mesolingual and posterolingual conids are always separate. The p2 has a stable morphology.
and only varies in size. It is similar in proportions and shape to p2s of *Samotherium major*, *S. boissieri*, *S. neumayri*, and *Schansitherium tafeli* that also have separate mesolingual and posterolingual conids (Hamilton, 1978). In contrast, *B. schaubi* has a wider p2, with a much more robust protoconid and more marked and separated mesolingual and posterolingual conids (Montoya and Morales, 1991).

The p3 has four morphotypes, similarly to *B. schaubi* (Montoya and Morales, 1991). Two have an isolated conid, probably homologous to the mesolingual conid between the anterior and medial valleys (Table 2: morphotypes 3 and 4), and two do not have it (Table 2: morphotypes 1 and 2) (Figs. 3F1–F3, G–I, 5A–D). The conid attached to the base of the posterolingual conid is variable in size. The posterolingual and posterobuccal conids can be united lingually (Table 2: morphotypes 1, 2, and 3) (e.g., MNCN-43462) or separated (Table 2: morphotypes 3 and 4) (e.g., MNCN-43467). The anterior stylid may be absent (morphotypes 1 and 4) (e.g., MNCN-43462) or present (Table 2: morphotypes 2 and 3) (e.g., MNCN-43461). In every case, the protoconid is strong and more coniform than in the p4. The sample from Nombrevilla corresponds to morphotype 3 (Crusafont, 1952:pl. XXIII, figs. 8a, 9a, 10a, 11; pl. XXIV, fig. 3a). The most represented morphotype in the sample from Nombrevilla and Los Valles de Fuentidueña (N = 12) is morphotype 3, at 50%, followed by morphotypes 4, 2, and 1 (Table 2).

Despite its high intraspecific variability, the p3 could be a very useful tooth for comparing different giraffid species (Fig. 5). When looking for the isolated mesolingual conid attached to the base of the posterolingual conid (Table 2: morphotypes 3 and 4, which represent the 74.97% of the total sample from Nombrevilla and Los Valles de Fuentidueña), we found that feature in two other giraffid species only, *Schansitherium tafeli* (including *Palaeotragus decipiens*) (Solounias, 2007) has almost an identical p3 (Fig. 5E), although the p3 of *Sh. tafeli* shows a slightly different anterior morphology (Bohlin, 1926). *Samotherium neumayri* also has this morphology (Fig. 5F) (McQuenem, 1924). However, the *S. neumayri* specimen described by Rodler and Weithofer (1890) has an isolated mesolingual conid that is more like a mesolingual crest rather than a conid (Hamilton, 1978:fig. 5).

The p3 of *D. pachecoi* is similar in size to those of *Br. megacephalum* (Fig. 5O) (Colbert, 1935b) and falls within the low values of *B. schaubi*. *Samotherium sinense*, *H. schlosseri*, *Sh. tafeli*, and the different species of *Giraffa* and *Giraffokeryx* are a little bit smaller (Böhlin, 1926), but closer in size to *D. pachecoi* than to the smaller species of *Palaeotragus*. The species of *Stavatherium* have generally a much larger p3 (Harris, 1976a, 1976b, 1987, 1991).

The p3 of *D. pachecoi* has similar proportions to those of the rest of giraffids, being only slightly longer than wide (L/W = 1.14–1.60), whereas some specimens of the giraffids *Cantuhermeryx sirtensis* (Hamilton, 1973, 1978), *Palaeotragus tungurien- sis*, and *P. microdon* have L/W values ~2.

The p4 is molarized and also has high morphological variability. This affects not only the size of the teeth but also the position of the posterolingual conid. This conid can be aligned with the mesolingual conid, diagonal to it, or perpendicular to it and attached to the posterobuccal conid. This gives rise to three morphotypes (Table 2). The rest of the morphology is stable, with a strong incision on the buccomedical wall between the posterobuccal and mesobuccal conids (Fig. 3I–J, K, L) (Morales and Soria, 1981). All the morphotypes are represented in the sample from Nombrevilla (Crusafont, 1952). The p4 from Másia del Barbo (MLSP-676c) falls within *D. pachecoi* morphotype 3 (Alcalá and Montoya, 1994). The most represented morphotype in the complete sample (N = 10) is morphotype 3 (50%), followed by morphotypes 2 (30%) and 1 (20%). Morphotype 2 of the p4 of *D. pachecoi* is morphologically similar to that of *Sh. tafeli*, *S. boissieri*, and *S. neumayri* (Hamilton, 1978). The p4 of *B. schaubi* from Crevillente (CR2-215) and Piera (IPS-936, IPS-35238) are more complex in occlusal topology and have the protoconid and the hypoconid completely separated, with a very deep groove on the buccal wall. The p4 of *B. schaubi* have an individualized entoconid, not attached to the hypoconid, which together with the metaconid forms a complete lingual wall that is very rare in *D. pachecoi*, with only some specimens from Los Valles de Fuentidueña having a faint version of this structure (Montoya and Morales, 1991). Also, in *B. schaubi*, the anterior lobe is almost the same size as the posterior lobe, whereas in *D. pachecoi* the posterior part is almost one-third of the total length of the tooth.

The lower molars have a lingual wall with a weak metastylid. The metaconid and entoconid are aligned and similar in size. The buccal wall has an elongated protoconid and hypoconid. The m3 has a big third lobe, formed by a strong entocolumid in a lingual position. The semicircular hypohilid is attached to the entocolumid and to the posterior side of the hypoconid (Fig. 3M1–M3, N1–N3, O1–O3). In the m1 of *D. pachecoi*, the occlusally exposed dentine area fuses late in wear, even later than in *G. camelopardalis*. The medial notch is open anteriorly as in *G. camelopardalis*, and the external ribs are more prominent than in *G. camelopardalis*. The m2 has a canal on the posterior side of the first lobe lingually as in *H. schlosseri*. The m3 proportions (L/W) are similar to those of most of the Giraffidae, around twice as long as wide (1.75–2.25), and their morphology also conforms to that of most Giraffidae. *Birgerbohlinia schaubi* has stronger ribs and stylids than *D. pachecoi*, especially the metastylid. The anterior and posterior lobes are sharper, whereas in *D. pachecoi* they are more rounded. In *B. schaubi*, the third lobe of the m3 is longer than the second lobe, whereas in *D. pachecoi* it is smaller, even when taking size variation into account.

**Deciduous Dentition**—The DP3 (Morales and Soria, 1981: fig. 8a, b) has a well-developed anterior lobe, elongated relative to the posterior lobe. The buccal wall has a strong mesostyle, prominent relative to the paracone, and the parastyle is also strong. The protocone is slightly unfolded, not reaching the postparacrista (Morales and Soria, 1981). The dp3 (Fig. 4E, F) is similar to p3 in morphotypes 1 and 2, as is the case in other giraffids such as *B. schaubi* where the dp3 is very similar to the p3. It has a bifurcate anterior part, and the posteroconid conid expands backwards and is lingually united to the posteroconid conid. It also has an isolated mesolingual conid attached to the posteroconid conid, although overall the dp3 is narrower and more elongated than the p3. The dp4 (Fig. 4E–F) lingual wall has a posteroconid conid that is wider than the mesolingual and anterior conids. The latter differs from the mesolingual and posteroconid conids in having a lingual wall that is more ‘V’-shaped than the other two. The buccal wall has well-marked anterior stylid and metastylid. There is a basal pillar between the first and the second lobe and between the second and the third lobe buccally in MNCN-32052. There are no pillars present in MNCN-43450. *Birgerbohlinia schaubi* also shows variability in these characters, because most of the specimens present the pillar between the second and the third lobe (IPS-962, IPS-35233, and IPS-5107), but there is another specimen (IPS-5148) where the pillar is between the first and the second lobe.

**Postcranial Skeleton**

**Scapula**—There is only one partially preserved scapula, with the lateral side of the glenoid cavity partially broken and showing porous bone tissue. The scapular spine is noticeable, but broken. The acromion and the coracoid process are missing. The supraglenoid tuberosity is robust and almost symmetrical. The supraspinatous fossa has a medium depth, and is proportionally bigger than the infraspinous fossa. The neck is robust (Fig. 6A). In medial view, the fossa subscapularis is concave and has a smooth surface. In distal view, the glenoid cavity is broken on its
lateral border and has a rounded medial border. The proportions are similar to *S. sinense* (Bohlin, 1926; Lam VIII, fig. 7). *Birgerbohlinia schaubi* has a noticeable scapular spine, and the acromion is broken.

**Humerus**—Unfortunately, the only preserved proximal humerus specimen is in poor condition (Fig. 6B, C). The tuberculum majus is small, but this may be due to damage to the proximal part. The specimen is more similar to *Bo. attica* (Geraads, 1979) than to *H. schlosseri, S. sinense, or P. microdon*, where the tuberculum majus is large (Bohlin, 1926). The deltoid tuberosity is large and extends obliquely until the middle of the diaphysis on its cranial side as in *S. sinense* and *H. schlosseri* (Bohlin, 1926), being more marked and robust and occupying a larger portion of the diaphysis than in *B. schaubi*. In cranial view, the distal articulation has a deep rugose surface on the radial fossa, a quadrangular trochlea (occupying about 2/3 of the surface), and a triangular, narrower capitulum (1/3), so the trochlea is about twice as wide as the capitulum. There is no transversely oriented oval compression facet proximal to the medial condyle and lateral to the coronoid fossa as in *Giraffokeryx primaevus* (Churcher, 1970). Caudally, the olecranon fossa is oval and very deep and long, whereas in *G. camelopardalis* it is shorter but deep (Churcher, 1970), and in *B. schaubi* more triangular-rounded and deep. The lateral epicondyle has a prominent rugose surface with grooves for the ulnar lateralis muscle. Distally, there is no transversely oriented oval compression facet proximal to the medial condyle and lateral to the coronoid fossa as in *G. camelopardalis, H. schlosseri, S. sinense* (Bohlin, 1926), and *B. schaubi* (this facet is present in *O. johnstoni* and *Gi. primaevus*, Churcher, 1970).

**Radioulna**—The specimens have a dorsocaudally compressed diaphysis (Fig. 6D, E). In cranial view, there is a very weak medial tuberosity, and in specimen MNCN-30784, 83 mm from the medial border, there is a strong crest that extends obliquely towards the caudal side of the bone. There is no stop facet for the humerus at the medial angle of the anterior surface as in *Gi. primaevus* (Churcher, 1970). In proximal view, the articular surface shows an almost straight cranial border and a rounded caudal border. The ulnar facet is triangular. There is a subquadrangular capitular medial fossa and a more triangular lateral fossa with a more acute concavity. Overall, the radius is slightly more bent and twisted medially than in *G. camelopardalis* The radial shaft is rounded on the cranial surface and slightly concave on the caudal surface as in *H. schlosseri* (Bohlin, 1926) or *Gi. primaevus* (Churcher, 1970) (although *Gi. primaevus* is more slender in relation to its length), whereas in *G. camelopardalis* there is less cranial convexity and the caudal surface is flat or slightly convex. In *S. sinense*, the convexity is more acute (Bohlin, 1926). When comparing the robustness, *D. pachecoi* is closest to *H. schlosseri* or even *S. sinense, B. schaubi*, or *H. duvernayi*, whereas *G. camelopardalis* and *Pa. microdon* radii are much more slender. The radius of *O. johnstoni* is much shorter and that of *Bo. attica* is longer (Bohlin, 1926). The ulna has a strong rectangular olecranon, and the anconal process is well developed.

**Scaphoid**—The specimens show approximately parallel medial and lateral sides (Fig. 7A1–A4). Laterally, there is a facet that is parallel to the proximal border. This facet has a poorly defined contact limit with the radial facet. There is also a triangular facet located on the dorsal distal angle that in a large specimen extends towards the dorsal and palmar borders. In medial view, the dorsal border is straight. The proximalpalmar process is wide and blunt and placed almost at the same level as the dorsal process. The proximal and distal facets are separate. The proximal side is wide, with a sinuous surface, dorsally convex and palmarly concave. The distal facet for the magnotrapezoid is wide, with a flat and oblique dorsal part placed at a different level from the rest of the facet. In lateral view, there is one continuous facet parallel to the proximal border and a rectangular facet that is located on the dorsal end and extends one-third of the specimen parallel to the distal border. *Decennatherium pachecoi* is almost identical in this regard to *S. sinense* (Bohlin, 1926). In *G. camelopardalis*, there is one continuous facet parallel to the proximal border, a rectangular facet that extends to two-thirds of the specimen, and sometimes there is a small posterior facet. In *O.

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**TABLE 2. Decennatherium pachecoi p3 and p4 morphotypes.**

| p3 Morphotype 1 | Morphotype 2 | Morphotype 3 | Morphotype 4 |
|----------------|-------------|-------------|-------------|
| No isolated mesolingual conid | No isolated mesolingual conid | Isolated mesolingual conid | Isolated mesolingual conid |
| Posterolingual conid lingually united to the postero labial conid | Posterolingual conid lingually united to the postero labial conid | Posterolingual conid lingually united to the postero labial conid or not | Posterolingual conid not lingually united to the postero labial conid |
| Parastylid absent | Parastylid present | Parastylid present | Parastylid absent |

| Percentage (%) from all the Spanish sites. |
|-------------------------------------------|
| p3                                        |
| 8.33% (n = 1)                             |
| 16.66% (n = 2)                            |
| 50% (n = 6)                               |
| 25% (n = 3)                               |
| p4                                        |
| 20% (n = 2)                               |
| 30% (n = 3)                               |
| 50% (n = 5)                               |
FIGURE 5. *Decennatherium pachecoi* from Los Valles de Fuentidueña, p3 morphotypes, A, MNCN-43462, B, MNCN-43463, C, MNCN-43461, and D, MNCN-43465. E, *Schantherium tafeli* (Bohlin, 1926: fig. 47). F, *Samotherium neumayri* (Hamilton, 1978: fig. 5). G, n.88, *Palaeogiraffa major* (=*Decennatherium* cf. *pachecoi*) from Ravin de la Pluie (Geraads, 1979). *Palaeogiraffa mac- edonae* (=*Decennatherium*? *macedonae*) from Pentalophos (Geraads, 1989). H, PNT-138, I, PNT-111, J, and PNT-137. K, *Giraffokeryx primaevus* (Hamilton, 1978: fig. 4). L-M, *Birgerbohlinia schaubi* from Crevillente-2: L, CR2-215 and M, CR2-879. N, VP-868, *Birgerbohlinia schaubi* from Piera (Montoya and Morales, 1991). O, AM 19670, *Bramatherium megacephalum* (Colbert, 1935b). P, SAM-PQ-1-L31137, *Sivatherium hendeyi* (Harris, 1976b). Q, KNM-ER 777, *Sivatherium mauressium* (Harris, 1991). R, *Samotherium boissieri* (Hamilton, 1978: fig. 5).

FIGURE 6. *Decennatherium pachecoi* from Los Valles de Fuentidueña, forelimb elements. A, MNCN-30783, right scapula fragment, in lateral view. B-C, MNCN-30774, right humerus, in B, cranial and C, caudal views. D, MNCN-30784, right radius proximal fragment, in cranial view. E, MNCN-43419, proximal fragment of left ulna, in medial view. Scale bar equals 5 cm.
FIGURE 7. *Decennatherium pachecoi* from Los Valles de Fuentidueña, carpals, phalanges, and sesamoids. A, MNCN-42623, left scaphoid in A1, medial, A2, proximal, A3, lateral, and A4, distal views. B, MNCN-42607, right semilunar in B1, medial, B2, proximal, B3, lateral, and B4, distal views. C, MNCN-32077, right pyramidal, in C1, medial, C2, lateral, and C3, dorsal view. D, MNCN-54851, right pisiform, in D1, medial and D2, lateral views. E, MNCN-42588, left unciform, in E1, proximal and E2, medial views. F, MNCN-43586, right magnotrapezoid, in F1, proximal and F2, lateral views. G, MNCN-32070, exterior proximal right sesamoid, in lateral view. H, MNCN-43582, right distal sesamoid, in proximal view. I, MNCN-32073, interdigital proximal right sesamoid, in distal view. J, MNCN-42728, third phalanx of right digit, in J1, proximal, J2, interdigital, and J3, exterior views. K, MNCN-42724, second phalanx of left digit, in K1, proximal, K2, dorsal, and K3, exterior views. L, MNCN-42667 first phalanx of right digit, in L1, proximal, L2, dorsal, and L3, interdigital views. Scale bar equals 5 cm.
Johnstoni, there is dorsoproximally a rectangular facet, distally another facet that only occupies the first third of the total length, and there is a small facet posteriorly.

**Semilunar**—In dorsal view, the proximolateral section projects laterally, the medial border is straight, and the lateral one is inclined (Fig. 7B1–B4). In proximal view, the dorsal profile bulges and is shaped as an elongated ellipse in all the specimens. The proximal articular surface is concave and narrows centrally. The dorsal half is wider than the palmar half. On the medial surfaces, the proximal facets for the scaphoid form a continuous, more or less straight border. The dorsodistal facet is subrectangular and narrower than in *G. camelopardalis*. In lateral view, the dorsoproximal facet for the pyramidal is triangular-semicircular-shaped and wide. The central facet for the pyramidal is large and semicircular in outline and is placed on a protuberance that projects slightly distally. The dorsoproximal facet for the pyramidal is more rounded in *S. sinense*, whereas in *G. camelopardalis* this facet extends palmarly and is continuous with the distal facet for the pyramidal. In *D. pachecoi*, this facet is more hexagonal than in *O. johnstoni*. In the distal articulation, the dorsal facet for the unciform is narrower than the magnotrapezoid facet, which is quadrangular and flat. The keel between these two facets is rather dull. The concavity in the central area is strong.

**Pyramidal**—The specimens have a slightly concave dorsal profile in lateral view (Fig. 7C1–C3). The distopalmar process is thick and well developed, whereas in *G. camelopardalis* it is less developed. The profile of the distal facet is concave as well. The morphology of the facet for the pisiform is slightly sigmoidal (almost oval). In dorsal view, the proximal facet for the semilunar is developed and rounded in all the specimens. On the medial surface, the central facet is relatively big and subtriangular. The central knob is located behind this facet and is slightly connected to it. This knob is well developed. The internal facet of the distal process is semicircular in shape.

**Pisiform**—In lateral/medial view, the pisiform has an asymmetric contour (Fig. 7D1–D2). The dorsal border is rounded and convex, and the palmar area is thickened. The dorsal facet for the pyramidal is convex and shows a pear-like/oval contour, like in *S. sinense*, whereas in *G. camelopardalis* it is more rounded. The overall shape varies, similar to the boxing glove shape of *O. johnstoni* or more narrow but also thick. These two morphologies can also be seen in *G. camelopardalis*, and they may represent sexual dimorphism or intraspecific variability (Singer and Bones, 1960). In *O. johnstoni*, this bone is slightly pointed on its proximal edge, and it is also mediolaterally narrower instead of wide as in specimens of *D. pachecoi*. The main difference between specimens of *D. pachecoi* and *O. johnstoni* is the dorsal facet for the pyramidal. In *D. pachecoi*, it has a pear-like contour and extends towards the distal face of the bone, whereas in *O. johnstoni* it does not reach the distal part and instead of presenting a pear-like shape, it resembles a bullet.

**Magnotrapezoid**—In proximal view, the dorsal side is wide, with a rounded outline (Fig. 7F1–F2). The edge between the proximal facets for the scaphoid and the semilunar has an inflection of ~130° or ~230° depending on the view. The lateral facet for the semilunar is narrower than the one for the scaphoid. The palmar border outline is slightly winding or nearly straight. In lateral view, it shows a facet for the unciform, which is parallel to the proximal border, almost reaches the distal surface, and extends proximally towards the palmar side of the bone, recalling a scythe-like shape as in *H. schlosseri*, *O. johnstoni*, and *G. camelopardalis*, although in the latter three taxa it does not extend as far distally. In *B. schaubi* also, this facet does not extend as far. The palmar-distal end of the medial surface has a small groove for ligament insertion. In palmar view, the border for the scaphoid facet has a medial elongation towards the distal face, very similar to *H. schlosseri*.

**Unciform**—The surface of the proximal articular surface is wide, with a rounded dorsal border (Fig. 7E1–E2). The proximal facet for the pyramidal is wide and lateromedially concave; it is also wider than the facet for the semilunar. There are two facets for the magnotrapezoid on the medial surface. The dorsoproximal facet is big, with a squarer dorsal part that extends palmarly parallel to the proximal border and is scythe-like in shape. There

![FIGURE 8. Decennatherium pachecoi from Los Valles de Fuentidueña, metacarpal. MNCN-42769, left metacarpals III–IV, in A, dorsal, B, palmar, and C, proximal views.](image1)

![FIGURE 9. Metacarpal and cross-section outlines. All are schematic. A, MNCN-42769, Decennatherium pachecoi from Los Valles de Fuentidueña. B, IPS-935, Birgerbohlinia schaubi from Piera. Scale bar equals 10 cm.](image2)
is a smaller distopalmar facet that is almost square. The two facets for the magnotrapezoid are separated only by an edge that is parallel to the medial border of the semilunar facet. In *G. camelopardalis*, *S. sinense*, and *H. schlosseri*, there is no second facet, and in *G. camelopardalis* and *S. sinense*, the square dorsoproximal facet slightly extends palmarly (Bohlin, 1926). In *Okapia*, it is not scythe-shaped, but is more rounded, as in *S. sinense*. In palmar view, the proximal facets are almost level, but the facet for the semilunar is slightly higher and separated from the pyramidal facet by a low edge. The palmar-lateral process is developed and slightly exceeds the limits of the distal surface.

**Metacarpal III–IV**—The only specimen is slender, and of medium length (Figs. 8A–C, 9). The proximal articular surface is semicircular as in *S. sinense* (Bohlin, 1926), with a circular sector-shaped facet for the magnotrapezoid occupying more than two-thirds of the area. The unciform facet is triangular in outline. The keel that separates the two facets is thin and fades palmarly. The synovial fossa is well developed and oval. The diaphysis smoothly widens proximally and distally. The distal trochleae are proportionally short and wide, and the keels extend dorsally, becoming slightly sharper palmarly. The intertrocchlear incision is wide and digit-shaped. In lateral view, the more dorsal part of the distal articular surface is rounded (not flattened). The internal articular surfaces of the trochleae are wider and more rectangular than the external ones. The central groove on the dorsal surface of the diaphysis is very shallow, almost imperceptible. The dorsoproximal tuberosity is well developed. In lateral position, the sulcus for the lateral extensor tendon is short. On the proximal end of the palmar surface, there is a rugose area where the interosseous muscles and the flexor carpi radialis muscle insert. The posterior trough is a central palmar concavity on the diaphysis (Solounias, 2007). This trough is moderately deep to shallow (Fig. 9) and extends approximately two-thirds down the shaft. The posterior trough in *D. pachecoi* specimens is shallower than in *B. schaubi*, *Bohlinia*, *H. schlosseri* (Bohlin, 1926), and *I. arabicum* (very deep) (Moraes et al., 1987), and it is also shallower than in *O. johnstoni*, *B. megacephalum* (Colbert, 1935a; Singer and Boné, 1960), and *He. duvernoyi* (Simionescu and Barbu, 1939). In fact, it is of similar depth to *Samotherium* species, where the trough is medium to shallow and a little bit deeper than in *G. camelopardalis*. Figure 9 shows the differences in proportions and in the depth of the posterior trough between *D. pachecoi* and *B. schaubi*.

The proximal transverse diameter/total length $\times 100$ index value of 18.75 indicates a similar robustness to species of *Samotherium* or *Okapia*, whereas the species of *Sivatherium* (Singer and Boné, 1960; Harris, 1976b), *Helladotherium* (ca. 20–29) (Gaudry et al., 1873; Pilgrim, 1911; Bohlin, 1926; Kostopoulos et al., 1996), *Bramatherium* (ca. 22–26) (Colbert, 1935a), and Birgerbohlinia (ca. 21–24) are more robust, and the species of *Palaeotragus*
and narrow), than in very rugose. The insertion of this muscle is more pronounced epicondyle, where the semimembranosus muscle attaches, is wide (seler, H. duvernoyi, G. camelopardalis (small and shallow). The condyles are very massive as in B. schaubi, but shallower than in G. camelopardalis. There is a marked triangular extensor fossa like in other giraffids, and the fossa for the popliteal muscle shows a similar development to B. schaubi, but shallower than in G. camelopardalis. The medial epicondyle, where the semimembranosus muscle attaches, is very rugose. The insertion of this muscle is more pronounced than in Gi. primaevus and O. johnstoni. The intercondylar fossa is bigger, deeper, and broader than in G. camelopardalis (deep and narrow), B. schaubi (broad, small and shallow), O. johnstoni (small and deep, but less than in Giraffa), and Gi. primaevus (small and shallow). The condyles are very massive as in S. boisieri, H. duvernoyi, G. camelopardalis, and B. schaubi and have the characteristic mushroom-shaped cap typical of giraffids. They are set with the lateral condyle oriented dorsocaudally and the medial obliquely. Okapia johnstoni and Gi. primaevus have less massive condyles.

Patella—There are three specimens with a high degree of variability. In plantar view, the lateral articular surface is separated from the medial articular surface by a groove. The lateral surface is half the size of the medial surface (Fig. 11A, B). In cranial view, the medial angle is close to 90°, whereas the lateral border is straight or shows a small angle. The apex is acute in one of the three specimens (MNCN-42660); the other two are slightly broken or blunt. Okapia johnstoni and G. camelopardalis patellae are sharper in their angles, giving the appearance of an isosceles triangle caudally. Okapia johnstoni is smaller and more delicate, whereas G. camelopardalis is more robust, more similar to D. pachecoi specimen MNCN-42661, which is blunt with no apex, and which is also similar to S. sinense (Bohlin, 1926). The patella of B. schaubi is robust as in G. camelopardalis, but it is sharper not rounded.

Tibia—This is a very robust bone, in absolute value longer than the metatarsals and the femur (Fig. 10A–D; Supplementary Data 3, Table 3S). The corpus has a straight dorsal border and a convex plantar border. MNCN-42660, left patella, in A, cranial and B, caudal views. MNCN-42764, left metatarsals III–IV, in C, proximal, D, dorsal, and E, plantar views. Scale bar equals 5 cm.

FIGURE 11. Decennatherium pachecoi from Los Valles de Fuentidueña, hind limb. MNCN-42660, left patella, in A, cranial and B, caudal views. MNCN-42764, left metatarsals III–IV, in C, proximal, D, dorsal, and E, plantar views. Scale bar equals 5 cm.

Astragalus—This is one of the most abundant elements (Nsample = 24) and gives us the minimum number of individuals in the Los Valles de Fuentidueña sample (Nindividuals = 13). Overall, the astragalus is relatively slender, long, and tall as in S. boisieri (Fig. 12H–J). The sustentacular surface has parallel borders, so the internal border does not form a broken line. On the medial side, this surface continues with the navicular facet, but there is no fossa for the navicular posteroplantar process on the lateral border where there is a slight depression for the corresponding navicular facet. The prolongation of the deep notch for a medial outgrowth on the posterior edge for the navicular-cuboid (posteroplantar process), apparently typical of G. camelopardalis, He. duvernoyi (Simionescu and Barbu, 1939), and H. schlosseri, is almost entirely absent, as in S. sinense (Bohlin, 1926). The astragalus of G. camelopardalis is also much wider and thicker (see Supplementary Data 3, Table 4S).

Calcaneum—The corpus has a straight dorsal border and a convex plantar border (Fig. 12A–D). The outline of the calcaneal tuber is pentagonal and symmetrical as in H. schlosseri (Bohlin, 1926). The posterior fossa is very shallow with rounded margins. The malleolar facet has a flat or slightly concave distal part, narrower than the proximal part, which is convex. The distal facet for the astragalus is rectangular, and its upper border is continuous with the cuboid facet, which is semicircular and small. The broad, helicoidal facet for the navicular-cuboid distal side faces the medial side of the calcaneum completely, as in S. boisieri. The facet for the entocuneiform is subtriangular and concave and has a small oval fossa in its center. Birgerbohlinia
schaubi differs from D. pachecoi in that the tuber calcis is not as symmetrical.

Navicular-Cuboid—Tall and robust specimens (N = 12) (Fig. 12K, L) with a subrectangular proximal articular surface for the astragalus. There is a shallow plantar fossa between the two halves of the proximal articulation. The lateral facet for the calcaneum almost reaches the dorsal border of the specimen. The dorsal facet for the metatarsal is slightly kidney-shaped. The facet for the entocuneiform is convex and oval. In lateral view, there is a distoplantar tuberosity and an insertion groove for the peroneus longus muscle, which is relatively wide and well developed. This groove does not widen distally and is less projected posteriorly. In D. pachecoi, plantarly than in D. pachecoi, the ectomesocuneiform is fused to the entocuneiform, similar to B. schaubi, whereas in D. pachecoi, the tuberosity is thinner but highly developed, and in S. sinense and S. cf. neumayri, the tuberosities are not too strong. The last difference is related to the fusion to the cuneiform bones. In D. pachecoi, as in He. duvernoyi, the entocuneiform is separate from the ectomesocuneiform, and both are separate from the navicular-cuboid (Simionescu and Barbu, 1939), whereas in O. johnstoni the entocuneiform and also the entocuneiform are fused to the navicular-cuboid, and in G. camelopardalis the ectomesocuneiform is fused to the entocuneiform, but the fused cuneiforms are not fused to the navicular-cuboid. In B. attica, H. schlosseri, S. sinense, and G. primaevus (Bohlín, 1926; Churcher, 1970), the ectomesocuneiform and the entocuneiform are not fused to the navicular-cuboid, similar to D. pachecoi.

Ectomesocuneiform—In proximal view, the general contour is semicircular, rounded on its mediadorsal border, straighter medially, and pointed in the dorsolateral angle (Fig. 12G). The plantar profile is asymmetric due to the presence of an expansion of the medial angle of the proximal articular surface. The surface of the proximal articulation is concave. It presents a large development. In general, it is an elongated facet, semicircular in shape. The distal facet for the metatarsal is kidney-shaped, and its surface is dorsally slightly convex and plantarly flatter. In addition, on the proximal surface, there is a depression on the medial margin in G. camelopardalis. In the D. pachecoi specimen this depression is much smaller and shallower. When compared with B. schaubi, the main difference is that, whereas in D. pachecoi the ectomesocuneiform is slightly kidney-shaped with no expansions, in B. schaubi from Piera there is a posterior plantar lobe differentiated from the main one, which occupies about one-fourth of the specimen.

Metatarsals III–IV—The specimens are slender and of medium length (Fig. 11C–E). In dorsal view, there is a small step between the medial and lateral proximal facets, which are located at slightly different levels. The common digital artery extends superficially on the dorsal surface of the metatarsals III–IV within a canal (the metatarsal sulcus) that is distally open. This moschid-type condition (Sánchez et al., 2010) is superficial but not as superficial as in extant bovids. The metatarsal sulcus extends from the proximal end, where it is shallow, and becomes deeper in the middle part of the diaphysis. On the lateral surface, there is a proximal canal for the extensor digitorum lateralis, much shallower than that of O. johnstoni. The palmar trough is medium to shallow in depth and broad. It is similar to the metacarpal trough, of medium to shallow depth of samburuses, much shallower than that of B. schaubi or H. schlosseri and deeper than that of He. duvernoyi or G. camelopardalis. It
occupies approximately the proximal two-thirds of the diaphysis. In proximal view, the kidney-shaped articular facet for the ectomesocuneiform is similar in size to the navicular-cuboid facet, which is semicircular. The entocuneiform facet is relatively big and teardrop-shaped, and it stands out over the plantar profile. In *S. sinense*, there is another small medial facet near the entocuneiform facet connecting the ectocuneocuneiform facet and the entocuneiform facet in a small area. In *G. camelopardalis*, these facets are also connected but over the entire contact surface. In *H. schlosseri*, they are connected too, more than in *S. sinense* but less than in *G. camelopardalis*. In *P. microdon*, the facets are well separated. In *D. pachecoi, B. schaubi, and G. primaevus*, they are only barely separated (Fig. 13). The metatarsal broadens distally in the last fifth of the bone. The distal trochleae are well separated. In *O. johnstoni* and *H. duvernoyi*, there is another small medial facet near the entocuneiform facet connecting the ectomesocuneiform facet and the navicular-cuboid facet. The metatarsal broadens distally in the last fifth of the bone. The distal trochleae are well separated. In *O. johnstoni* and *H. duvernoyi*, there is another small medial facet near the entocuneiform facet connecting the ectomesocuneiform facet and the navicular-cuboid facet. The metatarsal broadens distally in the last fifth of the bone. The distal trochleae are well separated. In *O. johnstoni* and *H. duvernoyi*, there is another small medial facet near the entocuneiform facet connecting the ectomesocuneiform facet and the navicular-cuboid facet.

**Metatarsals II and V**—*Decennatherium pachecoi* has medio-proximally 50 mm long shallow depressions in the place of the second metatarsal in two of the specimens (Morales and Soria, 1981). This is similar to *G. primaevus* where lateral and medial depressions that extend about 50 mm on the lateral angle and 80–100 mm on the medial angle show that metapodials II and V were present (Churcher, 1970). *Decennatherium crusatofonti* has a rudimentary second metatarsal bone fused to the third metatarsal (Bosscha Erdbrink, 1976). Generally, in both *O. johnstoni* and *G. camelopardalis*, the split metapodials II and V were lost or the surviving centers of ossification incorporated in the formation of palmar/plantar ridges at the proximal ends.

**First Phalanx**—In dorsal view, this element resembles a cone-shape, wider in the proximal part and narrowing distally (Fig. 7L–L3). In proximal view, the contour for the proximal articular surface is asymmetric, with the interdigital half shorter with a rounded profile and the lateral half longer with a straight border. The central groove is medium-deep and relatively wide, entering slightly on the palmar/plantar border. On the palmar/plantar surface, the proximal areas for ligament insertion stand out, forming two long and rugose surfaces with a sulcus between them, more or less deep depending on the specimen. These prominent rugose areas are where the collateral and sesamoid ligaments, as well as the interosseus muscle tendon, attach, and have a similar development to those of *S. sinense*, whereas they are much less developed in *H. schlosseri*. The interdigital surface also presents some rugose areas for the interdigital ligament, although this surface is almost even, implying that it was not very strong. The distal articular surface is trapezoidal and asymmetric, with the lateral half almost twice as wide as the interdigital one. The general shape of *D. pachecoi* first phalanges is closest to that of *H. schlosseri*, whereas those of *O. johnstoni, P. microdon*, and *G. camelopardalis* are more slender and *He. duvernoyi* first phalanges are more robust and transversely wider.

There is no meaningful morphological difference between the 30 studied phalanges, and their size only varies within a small range. Two groups can be differentiated among the complete phalanges according to their general dimensions. Longer ones may be interpreted as phalanges of the manus and the shorter ones as phalanges of the pes (Bohlin, 1926; Crusafont, 1952), or the longer ones may represent lateral phalanges and shorter ones medial ones (Meequenem, 1924). But this difference in dimensions may also be interpreted as sexual dimorphism, and we would need to analyze the autopodium of a complete articulated specimen to be sure. Anyway, the overall morphology of the two groups is almost identical and in fact distinguishing anterior from posterior phalanges is not easy because there are no critical morphological or metrical thresholds between them. This homogeneity agrees with that observed in the related measurements of the distal epiphyses of both metapodials, in particular those of the pulleys.

**Second Phalanx**—In both lateral and dorsal views, the second phalanges are very robust and transversely wide, with strong proximal and distal ends (Fig. 7K1–K3). The proximal articular surface is wider transversally than the distal articular surface. In proximal view, the articular surface for the first phalanx is typically subquadrangular in shape. The concavity of the proximal articular surface is low, and the crest that divides the two articular halves is subtle. The postarticular platform is proximally elongated, and the dorsal extensor process is prominent and rugose as in *S. sinense* (Bohlin, 1926), whereas in *B. schaubi* the dorsal extensor process is not very developed, and in *G. camelopardalis* and *O. johnstoni*, it can barely be appreciated. On the proximal end of the middle phalanx, the impressions for the origin of the interdigital (or cruciate) ligaments and the insertion of the flexor tendon are weak. The dorsal extensor process is high and rugose. The distal articular surface is triangular and somewhat asymmetrical, due to the smaller interdigital half, which is reduced. In interdigital view, its outline is oval and it extends palmarly/plantarly and dorsally over the distal half of the diaphysis, almost reaching the dorsal extensor process, reflecting the ample range of movement of the third phalanx.

**Third Phalanx**—In both lateral and dorsal views, the third phalanges are long and transversely narrow, with strong proximal and distal ends (Fig. 7J1–J3). In lateral view, they show a triangular outline, although in the middle of the dorsal ridge there is a weak angle. Despite this, the outline is slightly convex and it bends to the interdigital side. *Birgerbohlinia schaubi* is very similar, although it shows a straighter dorsal border. There is also a well-developed dorsal process for the insertion of the extensor digitorum (longus or comnis depending on whether it is the anterior or the posterior phalanx) that is even more prominent than in *G. camelopardalis* and *B. schaubi*, where it is barely present. The articular surface is rounded. It lies over a plantar wedge that is moderately high. This wedge does not form a platform, although it is visible in dorsal view. There is a moderately strong plantar process for the insertion of the deep flexor tendon. The interdigital border of the plantar surface is angled. The proximal articular surface is similar in proportions to that of the species of *G. camelopardalis*, with a bigger external proximal articulation facet and a smaller interdigital one, both concave and bending towards the interdigital side. *Birgerbohlinia schaubi* is very similar, although it shows a straighter dorsal border. There is also a well-developed dorsal process for the insertion of the extensor digitorum (longus or comnis depending on whether it is the anterior or the posterior phalanx) that is even more prominent than in *G. camelopardalis* and *B. schaubi*, where it is barely present. The articular surface is rounded. It lies over a plantar wedge that is moderately high. This wedge does not form a platform, although it is visible in dorsal view. There is a moderately strong plantar process for the insertion of the deep flexor tendon. The interdigital border of the plantar surface is angled. The proximal articular surface is similar in proportions to that of the species of *G. camelopardalis*, with a bigger external proximal articulation facet and a smaller interdigital one, both concave and bending towards the interdigital side, and much more inclined than in *G. primaevus* (Churcher, 1970; Solounias, 2007; Harris et al., 2010). The central crest of the facet is not very marked in any of the specimens. Over the dorsal border of the facet, the strong process we just commented on stands out, and in the distal border, there is a small rhomboidal facet for a sesamoid bone. The palmar/plantar surface of the phalanges is narrow and resembles a deformed isosceles triangle. Overall, they are tall specimens, as in *O. johnstoni*, differing from *B. schaubi* and *G. camelopardalis* where they are shorter.

**Distal Sesamoid (DS)**—Small sesamoid attached palmarly/plantarly to the second phalanx. It has two dorsal facets side by side, both oval in shape but differing in size. The interdigital surface also presents some rugose areas for the interdigital ligament, although this surface is almost even, implying that it was not very strong. The distal articular surface is trapezoidal and asymmetric, with the lateral half almost twice as wide as the interdigital one. The general shape of *D. pachecoi* first phalanges is closest to that of *H. schlosseri*, whereas those of *O. johnstoni, P. microdon*, and *G. camelopardalis* are more slender and *He. duvernoyi* first phalanges are more robust and transversely wider.

**Exterior Proximal Sesamoid (EPS)**—Large sesamoid originally attached palmarly/plantarly to the exterior facet of the metapodial trochlea. The articular facet is longish and oval (Fig. 7G).

**Interdigital Proximal Sesamoid (IPS)**—Large sesamoid originally attached palmarly/plantarly to the interdigital facet of the metapodial trochlea. The articular facet is semicircular. It is proximodistally shorter and dorsopalmarly/plantarly wider than the external proximal sesamoids (Fig. 7I).
PHYLOGENETIC ANALYSIS

We performed a cladistic analysis at the species level. Our aim was to improve resolution of the phylogenetic position of *Decennatherium pachecoi* within Giraffidae, to test previously proposed hypotheses regarding the relationships of *D. pachecoi* with respect to other Spanish taxa, and with other Middle Eastern material tentatively assigned to *Decennatherium* (Bosscha Erdbrink, 1976).

Our data matrix (Appendices 1 and 2; Supplementary Data 5) includes 34 taxa and 47 characters (cranial, dental, mandibular, and postcranial), thus resulting in the largest morphological data set thus far employed in a giraffid cladistic analysis. We performed a run using a traditional search (Wagner trees) of 1000 replicates, with tree bisection reconnection (TBR) that saved 10,000 trees per replication. Twenty-seven most parsimonious trees (MPTs) of 138 steps were found. We obtained the strict consensus (Nelsen) (consistency index [CI] = 0.748; retention index [RI] = 0.748) that showed six internal clades, with low Bremer support values (Fig. 14). There are polytomies involving mostly the basal giraffids (Clade A) and the Samotherini (Clade M), which remained unresolved in our MPTs. The distribution of character states for the internal nodes and the clade (Clade M), which remained unresolved in our MPTs. The distribution of character states for the internal nodes and the clade. Both a higher number of bohlinine taxa and more characters and specimens are needed to fully assess this question in the future.

Our results agree with other recent studies (Solounias, 2007) in considering the depth of the longitudinal palmar hollowing of the metacarpals containing the palmar interosseous muscles, and the specialized tendinous derivatives of these muscles as an important character, especially to discriminate between the Giraffinae (very shallow), the Bohlininae (very deep), and the other subfamilies (characters 32, 44, and 46). However, contrary to the remaining sivathereles, *B. schaubi* has a deep palmar trough (Fig. 9). Although this particular feature of the metapodials is not discussed or figured in the description of *Sivatherium hendeyi* from Langebaanweg, South Africa (Harris, 1976b), it could be present in this taxon as well. This apparent autapomorphic feature of *B. schaubi* could challenge its position in the sivathere clade. Both a higher number of bohlinine taxa and more characters and specimens are needed to fully assess this question in the future.

In our MPTs, *D. pachecoi* is recovered as a member of the samothere clade (node M). Thus, we reject the hypothesis of a direct relationship between *D. pachecoi* and *B. schaubi* (e.g., Montoya and Morales, 1991). This clade comprises all the samothere-like genera, including the Greek species of *Samotherium*, the Asian species of *Schantiferium*, the Spanish *D. pachecoi*, and the Middle Eastern *D. crusafonti*, as well as Eastern European *Palaeogiraffa macedoniae* (Fig. 14). No skull elements can be reliably attributed to *D. pachecoi*. Still, the overall proportions and morphology of the dentition and postcranical skeleton of *D. pachecoi* are very similar to those of *Samotherium*, especially *S. neumayri* (Bohlin, 1926; Morales and Soria, 1981). Although the *Samotherium* species are more robust, the rest of the morphological characters are almost identical (see Supplementary Data 3 and 4). Samotheres were abundant and widespread during the late Miocene, with more than six species currently identified throughout the Anatolian–East Aegean and North Black Sea late Miocene regions to the east as *Maragheh* (Iran) and China, although its presence is rather scarce in the Balkans, and it is absent from the Indo-Pakistani regions (McQuenem, 1924; Bohlin, 1926; Bernet et al., 1996; Solounias, 2007; Kostopoulos, 2009). Thus, recognizing a representative of this lineage in the Iberian Peninsula is not surprising. However, this interpretation must be taken cautiously, due to the high intraspecific variability of several dental features, and also because our MPTs recover the presence of four ossicones as a plesiomorphic state. We currently lack data regarding skull characters such as occipital orientation, the palate indentations, the masseteric angle, and the vertebral morphology of *D. pachecoi* that would help resolve these relationships.

FIGURE 13. Metatarsal proximal morphology. A, *Palaeotragus microdon* (Bohlin, 1926:fig. 33). B, *Birgerbohlinia schaubi* from Piera, IPS-5090. C, *Decennatherium pachecoi* from Los Valles de Fuentidueña, MNCN-42764. D, *Samotherium sinense* (Bohlin, 1926:fig. 127). E, *Giraffa camelopardalis*, AMNH 1435. Images not to scale.

DISCUSSION

Phylogenetic Position of *Decennatherium* and *Birgerbohlinia* within the Giraffidae

In our study, the two Spanish species *D. pachecoi* and *B. schaubi* belong to a single clade (Samotheriinae + Sivatheriinae; Fig. 14). The clade Samotheriinae + Sivatheriinae (internal node G, clades H + M) is diagnosed in our MPTs by six synapomorphies (Table 3) that include dental and postcranial characters, although it has low Bremer support (Fig. 14). The sivathere clade (node H) groups the most recent African species of *Sivatherium* (nodes I, K) together with the late Miocene Eurasian sivathereles, *Br. megacephalum*, *Br. perimense*, and *He. duvernoyi* (node L). *Birgerbohlinia schaubi* stands as a basal offshore of this sivathere clade (node H). The close relationship of *B. schaubi* with the sivathereles was originally proposed by Crusafont (1952), and later by Morales and Soria (1981) and Montoya and Morales (1991).

In our MPTs, *D. pachecoi* is recovered as a member of the samothere clade (node M). Thus, we reject the hypothesis of
extremely elongated and slender metapodials (characters 30, 31, 34, and 35), shallow palmar/plantar troughs (characters 32 and 36), and long necks. Node D is directly related to node E, which is the one comprising the Spanish giraffids. Finally, node F clusters the bohlinines, which share the common trait of a very deep and wide palmar/plantar metapodial trough (characters 32, 36, 44, 45, 46, and 47), as well as long and slender metapodials similar to those of *Giraffa*.

Our MPTs mostly agree with the working cladogram of Solounias (2007) in the major groupings, although their location within the tree is different. In Solounias (2007), both *D. pachecoi* and *B. schaubi* fall within the bohlinines instead of clustering with samotheres or sivatheres.

**Key Differences between Decennatherium and Birgerbohlinia**

In addition to our phylogenetic analysis, the results of the biometrical, morphological, and statistical analyses show significant differences between *D. pachecoi* and *B. schaubi*. First, *D.
Decennatherium pachecoi has a lower crowned and less complex dentition. In particular, the p3 morphology is different from that of Birgerbohlinia because, despite being a very variable tooth, the p3 of B. schaubi has a mesolingual conid in every morphotype, a feature not shared by D. pachecoi (characters 24 and 25). In contrast to D. pachecoi, the p4 of B. schaubi has the mesobucal and postero-buccal conids completely separated, showing a higher degree of molarization (character 28; Fig. 15). Also, D. pachecoi has more gracle limbs with a lower robusticity index of the metacarpal (proximal TD/total length × 100) (characters 31 and 35), with the metapodials in both species being similar in length. Decennatherium pachecoi also has a shallower palmar/plantar trough in the metapodials, which is very deep in B. schaubi (characters 32, 36, 44, 45, 46, and 47; Fig. 9). Proximally, the articular surface of the metacarpal has a closed synovial fossa in D. pachecoi, but it is palmarly open in B. schaubi.

Phylogenetic Relationships of Alleged Decennatherium Fossils from Eastern Europe and the Middle East

There are some alleged Decennatherium finds from the Vallesian of Greece, Turkey, and Iran (Bosscha Erbrink, 1976; Geraads, 1979, 1989): D. crusafonti from Aliabad (Iran) (Bosscha Erbrink, 1976); cf. Decennatherium from Kayadibi (and Bulumya Ignumbrite), Turkey (Sickenberg et al., 1975; Geraads, 1979); Palaeogiraffa macedoniae (=D. ? macedoniae) from Pentalophos, Greece (Geraads, 1989; Geraads et al., 2005); and Yulafli, Turkey (Geraads et al., 2005); and Palaeogiraffa major (=Decennatherium cf. pachecoi) from Ravin de la Pluie, Greek Macedonia (Geraads, 1979; Yilmaz, 2011), and Yassören, Turkey (Bonis and Bouvrain, 2003). Evidence from the eastern Mediterranean and the Middle East is scanty, with no cranial appendages represented in the samples. With the restricted information at our disposal, the cladistic analysis links most of these findings to the samothere clade with a very low support. Allocation of the new species (Bonis and Bouvrain, 2003) to erect a new genus and species, Palaeogiraffa major, which included these remains, as well as more recent finds from Yassören, Turkey.

Our MPTs poorly link P. major to B. schaubi, at the root of the sivathere clade. The p3 from Ravin de la Pluie RIPI-88 (Geraads, 1979:pl. II, fig. 4) matches B. schaubi in proportions and size, and it has a somewhat similar morphology to CR2-215 from Crevillente-2 (lower Turonian) (Montoya and Morales, 1991) (Fig. 5L). However, the anterior stylid and the anterior conid of P. major are more developed than in B. schaubi, and their lingual wall is connected forming an anterior closed valley.

The deciduous canines of P. major have a larger second lobe than those of D. pachecoi (Bonis and Bouvrain, 2003). Also, the p3 of P. major (Fig. 5G) is bigger than that of D. pachecoi and its proportions are also different, having a p3 L/W index of ~1.4, slightly lower than that of D. pachecoi (index of ~1.7). In addition, the p3 presents a strong mesolingual conid (Fig. 5L–N; Montoya and Morales, 1991:fig. 5a–c) that contrasts with D. pachecoi, which has an isolated mesolingual conid, and only in two morphotypes. The third lobe of the m3 of P. major is mentioned by Geraads (1979) as similar to D. pachecoi, but this third lobe is highly variable in our sample.

Palaeogiraffa macedoniae (=Decennatherium? macedoniae)—Geraads (1989) assigned some material from Pentalophos (Greece) to a new species, D. ? macedoniae (Fig. 5H–I). In 2003, Bonis and Bouvrain included this material in the new genus and species Palaeogiraffa macedoniae. Our MPTs link Pa. macedoniae to the samothere clade (Fig. 14, node M).

Palaeogiraffa macedoniae resembles D. pachecoi from Spain, but presents some differences. The specimens from Pentalophos have a similar p3 size and proportions to those of D. pachecoi from Spain, but the morphology differs because the p3 from Pentalophos has a non-isolated and more typical mesolingual conid, whereas none of the p3 of D. pachecoi from Spain has such a structure. The p3 from Pentalophos shows three posterior conids, with the exception of one p3 (PNT-138), which has an isolated conid next to the anterior bifurcation (Fig. 5H).

There is no strong argument for placing these eastern Mediterranean forms in Decennatherium (Bonis and Bouvrain, 2003; Geraads et al., 2005). Instead, the morphological features indicate that, for the time being, Decennatherium is known from Spain only, and assigning the eastern taxa to Decennatherium is misleading, especially in terms of biogeography (Geraads et al., 2005). More material from Aliabad (Maragha, Iran) is necessary to clarify the position of D. crusafonti, as well as further analysis on the similarities and differences between the Decennatherium-like eastern and western Mediterranean species.

FIGURE 15. Degree of molarization in p4 in Decennatherium pachecoi and Birgerbohlinia schaubi, outlines in occlusal view. A, D. pachecoi from Los Valles de Fuentidueña, MNCN-43471, left p4. B, B. schaubi from Piera, IPS-936, left p4. Scale bar equals 5 cm.
CONCLUSIONS

The present paper increases our understanding of the anatomy, systematics, and phylogenetic relationships of *D. pachecoi*, providing new evidence that *Decennatherium pachecoi* probably belongs to the lineage of large samintheres. This group of giraffids was widespread during the late Miocene, extending discontinuously from Asia to the Mediterranean region. *Decennatherium pachecoi* extends the paleobiogeographic distribution of the samintheres clade into the Iberian Peninsula. This study does not support a close relationship between *D. pachecoi* and *B. sauphi*. Instead, *B. sauphi* emerges as a basal member of the sivathere lineage. Thus, the history of the late Miocene Spanish giraffids is more complex than previously thought, with the presence on the Iberian Peninsula of two time-successive branches of the great four-horned Miocene giraffes.

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APPENDIX 1. Description of characters used in phylogenetic analysis. Characters are polarized with respect to *Canthumeryx* as the outgroup. All characters are treated as unordered.

| Character Description                                                                 | Polarization | Code |
|--------------------------------------------------------------------------------------|--------------|------|
| Number of ossicones: 2 ossicones (0); 4 ossicones (1)                                | (1)          |      |
| Median single ossicone: absent (0); present (1)                                      | (2)          |      |
| Zygomatic ossicones: absent (0); present (1)                                        | (3)          |      |
| Presence of bare ossicone apices: absent (0); present (1)                           | (4)          |      |
| Surface of the ossicone: ornamented with ridges (0); soft, no ridges present (1)   | (5)          |      |
| Bumps in the ossicone surface: absent (0); present (1)                              | (6)          |      |
| Location of the single pair of ossicones: above the orbit (0); posterior to the orbit (1) | (7)          |      |
| Location of the anterior ossicones: anterior to the orbit (0); above the orbit (1); posterior to the orbit (2) | (8)          |      |
| Relationship between the anterior and posterior ossicones: separated (0); united at their base (1) | (9)          |      |
| Orientation of the single pair of ossicones: posteriorly, angle smaller than 90° (0); only slightly posteriorly, almost straight 90° (1); laterally (2) | (10)         |      |
| Orientation of the anterior ossicones: posteriorly (0); anteriorly (1); straight (2) | (11)         |      |
| Morphology of the ossicone: curved (0); straight (1)                                 | (12)         |      |
| Palmate ossicones: absent (0); present (1)                                          | (13)         |      |
| Morphology of the ossicone tip: blunt tip (0); pointy tip (1); very wide tip (2)    | (14)         |      |
| Size of ossicones relative to skull: small (0.5 mm) (0); medium (2 mm) (1); large (1.5 mm) (2) | (15)         |      |
| Presence of ossicones in females: absent (0); present (1)                           | (16)         |      |
| Lower canine: mesial lobe more rounded (0); mesial lobe more pointed (1)             | (17)         |      |
| Adult mandible m1–m3 length: small (~100 mm) (0); medium (100–140 mm) (1); large (~140 mm) (2) | (18)         |      |
| Adult mandible p2–m3 length: small (~170 mm) (0); medium (170–200 mm) (1); large (~200 mm) (2) | (19)         |      |
| Lower premolar row length/lower molar row length index (p/m index): low (~0.625) (0); medium (0.625–0.675) (1); high (~0.675) (2) | (20)         |      |
| Upper premolar row length/upper molar row length index (P/M index): low (~0.70) (0); medium (0.70–0.75) (1); high (~0.75) (2) | (21)         |      |
| p3 anterior stylid: bifurcated (0); not bifurcated (1).                              | (22)         |      |
| m3 length: low (~0.45) (0); medium (0.45–0.55) (1); high (~0.55) (2).               | (23)         |      |
| Presence of a strong real mesolingual conid in the p3: absent (0); present (1).     | (24)         |      |
| p3 with: not small isolated conid probably homologous to the mesolingual conid (0); a small isolated conid probably homologous to the mesolingual conid (1). | (25)         |      |
| Location of p3 isolated conid probably homologous to the mesolingual conid: attached to the base of the post-erolingual conid (0); attached to the base of anterior conid (1). | (26)         |      |
| Morphology of p3 with a bifurcated anterior wing and a strong metaconid, which forms a crest, projects posteriorly until it reaches the lingual end of the entostylid, isolating the entoconid, which is clearly reduced (*Bramatherium*-like): absent (0); present (1). | (27)         |      |
| Degree of p4 molarization: not highly molarized (0); a high degree of molarization with the two lobes well separated, with a very deep groove on the labial wall (1). | (28)         |      |
| Degree of development of the deltoid tuberosity of the humerus: poorly developed (0); well developed (1). | (29)         |      |
| Metacarpal III–IV length: short (~370 mm) (0); medium (370–430 mm) (1); long (430–560 mm) (2); very long (~560) (3). | (30)         |      |
| Metacarpal III–IV robustness index (proximal transverse diameter/total length × 100): very slender (~15) (0); slender (15–20) (1); medium robustness (20–22) (2); very robust (~22) (3). | (31)         |      |
| Metacarpal III–IV palmar trough depth: medium, *Sivatherium*-like (0); medium to shallow, *Samotherium*-like (1); very shallow, *Giraffa*-like (2); very deep, *Bohlinia*-like (3). | (32)         |      |
| Extension of the metacarpal III–IV palmar trough down the shaft: two-thirds (0); one-half (1). | (33)         |      |
| Metatarsal III–IV length: short (~317 mm) (0); medium (317–430 mm) (1); long (430–560 mm) (2); very long (~560) (3). | (34)         |      |
| Metatarsal III–IV robustness index (proximal transverse diameter/total length × 100): very slender (~13) (0); slender (13–14) (1); medium robustness (14–17) (2); very robust (~17) (3). | (35)         |      |
| Metatarsal III–IV plantar trough depth: medium, *Sivatherium*-like (0); medium to shallow, *Samotherium*-like (1); very shallow, *Giraffa*-like (2); very deep, *Bohlinia*-like (3). | (36)         |      |
| Metatarsal III–IV proximal articulation surface with: ectomesocuneiform and entocuneiform facets contacting in a small area or only separated by a few millimeters (0); ectomesocuneiform and entocuneiform facets very separated (1); ectomesocuneiform and entocuneiform facets contacting in the entire contact surface (2). | (37)         |      |
| Medial outgrowth on the posterior edge for the navicular-cuboid in the astragalus: absent (0); present (1). | (38)         |      |
| Astragalus size (medial length): small (~75 mm) (0); medium (75–82 mm) (1); large (~82 mm) (2). | (39)         |      |
| Fusion of cuneiform bones with navicular-cuboid: entocuneiform separated from ectomesocuneiform (0); presence of entomesoectocuneiform (1); fusion of cuneiform bones with navicular-cuboid (2). | (40)         |      |
| Phalanx I robustness: medium, *Samotherium*-like (0); robust, *Helladotherium*-like (1); slender, *Giraffa*-like (2). | (41)         |      |
| Presence of rugose surfaces on the palmar/plantar surface of phalanx I: absent (0); present (1). | (42)         |      |
| Phalanx II length: medium, *Samotherium*-like (0); elongated, *Okapia*-like (1); very short, *Giraffa*-like (2). | (43)         |      |
| Metacarpal III–IV palmar trough width relative to diaphysis dorsopalmar diameter in the middle of the | (44)         |      |

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diaphysis: medium, Samotherium-like (0); wide, Bohlinia-like (1).

(45) Metatarsal III–IV plantar trough width relative to diaphysis dorsoplantar diameter in the middle of the diaphysis: medium, Samotherium-like (0); wide, Bohlinia-like (1).

(46) Metacarpal III–IV palmar trough curvature: low, Giraffa-like (0); medium, Samotherium-like (1); acute, Bohlinia-like (2).

(47) Metatarsal III–IV plantar trough curvature: low, Giraffa-like (0); medium, Samotherium-like (1); acute, Bohlinia-like (2).

APPENDIX 2. Character-taxon matrix used for phylogenetic analysis.

| Taxon                              | 10 | 20 | 30 | 40 | 47 |
|------------------------------------|----|----|----|----|----|
| Canthumeryx sirtensis              | 00000000 |     |     |     |    |
| Georgiomeryx georgalasi            | 00000000 |     |     |     |    |
| Giraffokeryx primaevus             | 00000000 |     |     |     |    |
| Giraffokeryx punjabiensis          | 10000000 | 00000000 |     |     |    |
| Injanatherium arabicum             | 10000000 | 00000000 |     |     |    |
| Injanatherium hazimi               | 10000000 | 00000000 |     |     |    |
| Honanotherium schlosseri           | 00000000 |     |     |     |    |
| Birgerbohlinia schaubi             | 00000000 |     |     |     |    |
| Bohlinia attica                    | 00000000 |     |     |     |    |
| Schansitherium quadricornis        | 00000000 |     |     |     |    |
| Schansitherium fuguensis           | 10000000 | 01100101 |     |     |    |
| Schansitherium tafeli              | 10000000 | 11100101 |     |     |    |
| Samotherium boissieri              | 00000000 |     |     |     |    |
| Samotherium neumayri               | 00000000 |     |     |     |    |
| Samotherium major                  | 00000000 |     |     |     |    |
| Samotherium sinense                | 00000000 |     |     |     |    |
| Decennatherium cf. pachecoi        | 00000000 |     |     |     |    |
| Decennatherium macedoniae          | 00000000 |     |     |     |    |
| Decennatherium crusafonti          | 00000000 |     |     |     |    |
| Palaeotragus rouenii               | 00000000 |     |     |     |    |
| Palaeotragus coelophrys            | 00000000 |     |     |     |    |
| Palaeotragus microdon              | 00000000 |     |     |     |    |
| Helladotherium duvernoyi           | 00000000 |     |     |     |    |
| Bramatherium megacephalum          | 10000000 | 21000110 |     |     |    |
| Bramatherium perimense             | 10000000 | 11100101 |     |     |    |
| Sivatherium giganteum             | 10000000 | 10100100 |     |     |    |
| Sivatherium maurosi                | 10000000 | 10100100 |     |     |    |
| Sivatherium olduvaliensae          | 10000000 | 10100100 |     |     |    |
| Sivatherium hendeyi                | 10000000 | 10100100 |     |     |    |
| Okapia johnstoni                   | 00000000 |     |     |     |    |
| Giraffa jumae                      | 00000000 |     |     |     |    |
| Giraffa stillei                    | 00000000 |     |     |     |    |
| Giraffa camelopardalis             | 01000000 |     |     |     |    |