

***Propalaeoryx* Stromer 1926 (Ruminantia, Pecora, Giraffomorpha) revisited: systematics and phylogeny of an African palaeomerycid**

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Abstract: We describe new mandibular and dental material of *Propalaeoryx stromeri* from Langental (early Miocene, Sperrgebiet, Namibia), and re-describe the cranial anatomy of this genus of African giraffomorphs. The occipital and nuchal anatomy of the two *Propalaeoryx* species are described and emended differential diagnoses are presented. Several cranial and postcranial characters are crucial for understanding the position of *Propalaeoryx* as a basal member of the Palaeomerycoidea within the Giraffomorpha. We define the clade Palaeomerycoidea as the least inclusive clade of giraffomorphs containing *Triceromeryx* and *Propalaeoryx*. Finally, the phylogenetic position of *Propalaeoryx* unveils a putative early African-Eurasian vicariance event among basal palaeomerycoids that probably took place around the Oligo-Miocene boundary, a time when other ruminant lineages were also splitting.

Key Words: Ruminants; Early Miocene; Namibia; Sperrgebiet; Evolution; Phylogeny.

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Introduction

Propalaeoryx (Fig. 1) is a genus of African pecorans first described by Stromer (1926) on the basis of dental and postcranial material from Elisabethfeld (early Miocene, Sperrgebiet). Stromer noted the morphological differences between *Propalaeoryx* and extinct and extant ruminants, but he did not elaborate a clear hypothesis of relationship with any of them. He described *Propalaeoryx* as a ruminant as large as a fallow deer (*Dama dama*) with premolar series as long as the molar series and wrinkled enamel in the lower molars (Stromer, 1926). On the basis of new material collected in the Sperrgebiet by the Namibia Palaeontology Expeditions, Morales *et al.* (2008) described abundant material attributed to the type species *P.*

austroafricanus and to a new species *P. stromeri*, which differed from the former in being more microdont (smaller teeth and larger postcranial skeleton) and with a more derived lower dentition (flatter cuspids, higher crowns, less developed stylids) besides another characters (Morales *et al.* 2008). The authors also described much of the postcranial skeleton of *Propalaeoryx* highlighting several characters in the navicular-cuboid in the tarsus that later proved relevant for resolving pecoran phylogeny at a large-clade level (see Sánchez *et al.* 2015). Morales *et al.* (2008) referred to *Propalaeoryx* as a probably hornless pecoran (no cranial appendages or frontal bone fragments have been found) with large sabre-like upper canines in the

males. These canines are of the moschid-type a very conspicuous morphology among pecorans (Sánchez *et al.* 2010a). Morales *et al.* (2008) attributed *Propalaeoryx* to the Climacoceratidae, a Miocene African group of giraffoids also including forms such as *Orangemeryx* and *Climacoceras*. However, they did not offer a phylogenetic analysis. Recently, the total-evidence tip-dating phylogenetic analysis of

Sánchez *et al.* (2015) recovered *Propalaeoryx* as the sister-group of the Palaeomerycidae within the Giraffomorpha as the basal offshoot of the Palaeomerycoidea, thus rejecting the climacoceratid hypothesis and offering a new and more complex evolutionary scenario for the large clade of pecorans of which giraffes (*Giraffa* and *Okapia*) are the only living representatives.

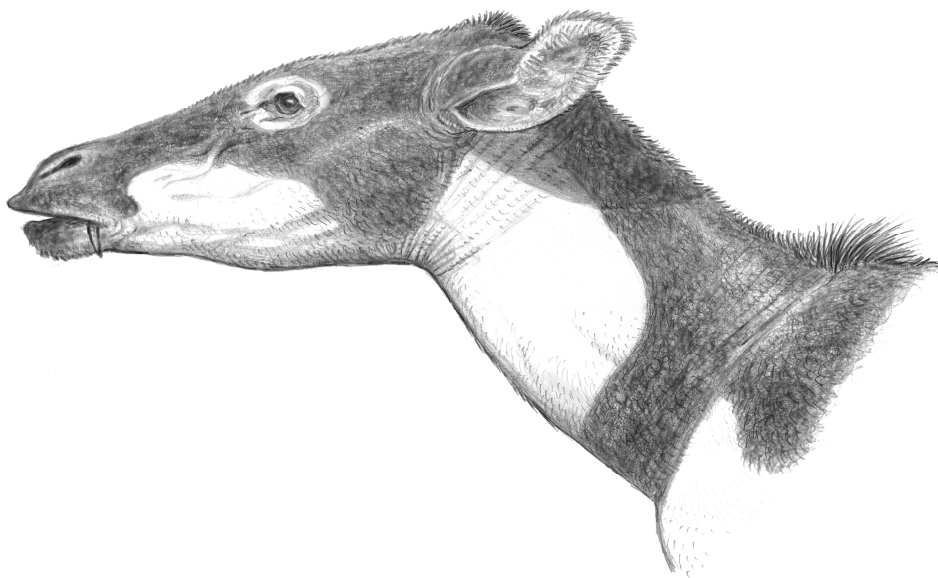


Figure 1. Reconstruction of an adult male of *Propalaeoryx stromeri*. Illustration by Israel M. Sánchez.

In this paper we aim a) to describe new *Propalaeoryx austroafricanus* material from Langental, b) to describe new cranial characters that differentiate the two species of *Propalaeoryx*, offering emended diagnoses in detail, c) to describe both the

cranial and postcranial morphological characters that unite *Propalaeoryx* with the Palaeomerycidae and d) to discuss the evolutionary hypotheses derived from the phylogenetic position of *Propalaeoryx* as published by Sánchez *et al.* (2015).

Material and methods

Material. In this work we studied *Propalaeoryx austroafricanus* mandibular and cranial material from Elisabethfeld and *P. stromeri* cranial material from Langental. These fossils are curated by the Geological Survey of Namibia (Windhoek, Namibia) and are currently on study loan in the MNCN-CSIC (Madrid, Spain).

Nomenclature. Postcranial anatomical terms are based on Barone (1999). Azanza

(2000) - English version in Sánchez & Morales (2008) - has been followed for nomenclature of the dentition.

Abbreviations. **EF** - Elisabethfeld; **LT** - Langental; **GSN** - Geological Survey of Namibia; **MNCN-CSIC** - Museo Nacional de Ciencias Naturales-CSIC (Madrid, Spain).

Systematic Palaeontology

Ruminantia Scopoli, 1777

Giraffomorpha Sánchez, Cantalapiedra, Ríos, Quiralte & Morales, 2015

Palaeomerycoidea Ríos, Sánchez & Morales, 2017

Genus *Propalaeoryx* Stromer, 1926

Emended diagnosis.- Palaeomerycoid giraffomorph with deep rectilinear groove behind the temporal fossa; enlarged upper canines of moschid-type in males; presence of lateral notch in the facet for the semilunate in the radius; distally closed

metatarsal sulcus; small metatarsal tuberosity; semicircular P4/ with flat cones; lower molars with flattened cuspids, especially the lingual ones. Based on Sánchez *et al.* (2015).

Type species.- *Propalaeoryx austroafricanus* Stromer, 1926

Additional species in the genus.- *Propalaeoryx stromeri* Morales, Soria & Pickford, 2008

Species *Propalaeoryx austroafricanus* Stromer, 1926

Emended diagnosis.- *Propalaeoryx* with ventrally narrowed foramen magnum that displays an almost closed state; slightly developed posterior basioccipital tuber-

osities anterior to the occipital condyles; presence of deep lateral fossettes over the occipital condyles in the nuchal plane.

Description

We restudied the cranial (occipital) fragment GSN EF 34'01, which shows some important, and so far undescribed, features. The most conspicuous character is the presence of a ventrally closed foramen magnum similar to that observed in the Prolibytheriidae (see e.g. Danowitz *et al.* 2016). However, in contrast to the *Prolibytherium* condition, the fusion in *P. austroafricanus* only affects the inner

surface of the condyles. In the outer surface the fusion is not complete and a relatively wide canal appears (see Fig. 2, I). In addition to this, the nuchal plane in *Propalaeoryx austroafricanus* is more convex than in *P. stromeri*, and a pair of well-developed fossettes is present over each occipital condyle. Finally, the posterior basioccipital tubercles are relatively weak (Fig. 2, H-I).

Species *Propalaeoryx stromeri* Morales, Soria & Pickford, 2008

New material.- GSN LT 37'08 + LT 47'06, right hemi-mandible with p/2-m/3 (Fig. 2, A-C).

Emended diagnosis.- In Morales *et al.* (2008) plus: loss of p/1; ventrally wide foramen magnum with open U-shaped morphology; strongly developed and quadrangular posterior basioccipital tuber-

osities anterior to the occipital condyles; presence of shallow, weakly expressed lateral fossettes over the occipital condyles in the nuchal plane.

Differential diagnosis.- Differs from the type species of the genus in the characters listed by Morales *et al.* (2008) plus: more

ventrally open foramen magnum; stronger and quadrangular-shaped posterior basioccipital tuberosities; lack of deep fossettes

over the occipital condyles in the nuchal

plane.

Description

We here describe a new hemi-mandible (GSN LT 37'08 + LT 47'06; Fig. 2, A-C) with the complete lower tooth series and re-

describe the occipital fragment GSN LT 194'96a (Fig. 2, D-G).

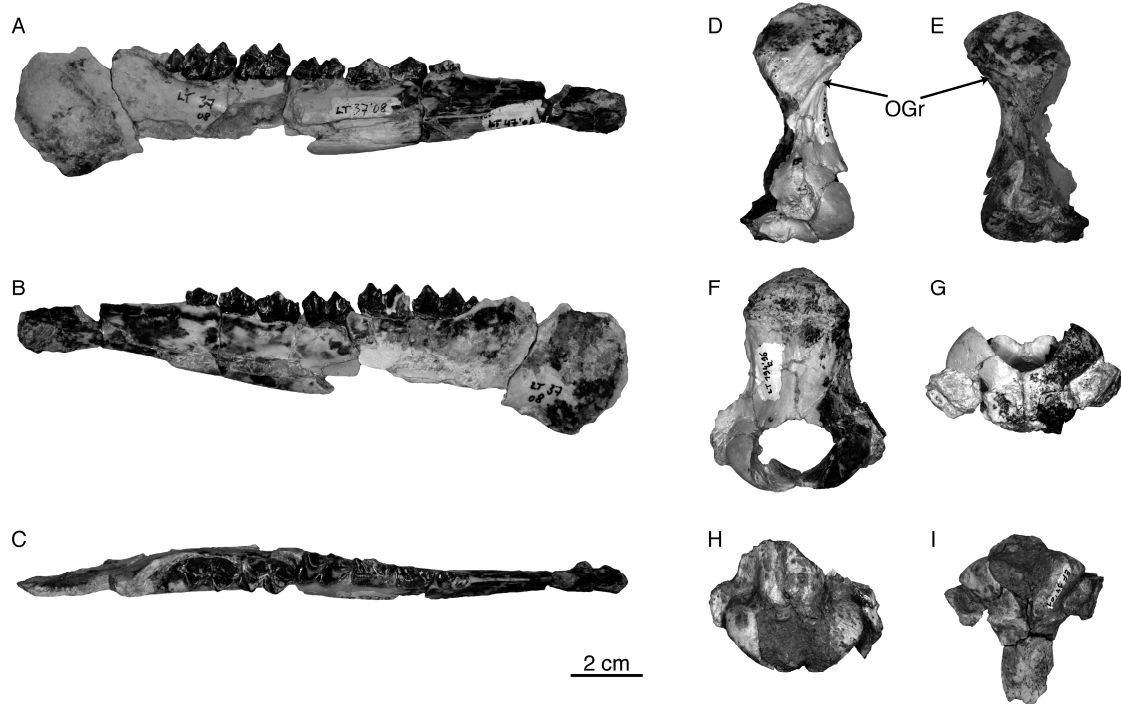


Figure 2. A, *Propalaeoryx stromeri* GSN LT 37'08 + LT 47'06, right hemi-mandible with p/2-m/3 in buccal view; B, *Propalaeoryx stromeri* GSN LT 37'08 + LT 47'06, right hemi-mandible with p/2-m/3 in lingual view; C, *Propalaeoryx stromeri* GSN LT 37'08 + LT 47'06, right hemi-mandible with p/2-m/3 in occlusal view; D, *Propalaeoryx stromeri* GSN LT 194'96a, skull fragment, in left lateral view; E, *Propalaeoryx stromeri* GSN LT 194'96a, skull fragment, in right lateral view; F, *Propalaeoryx stromeri* LT 194'96a, skull fragment, in caudal view; G, *Propalaeoryx stromeri* GSN LT 194'96a, skull fragment, in ventral view; H, *Propalaeoryx austroafricanus* GSN EF 34'01, skull fragment, in caudal view; I, *Propalaeoryx austroafricanus* GSN EF 34'01, skull fragment, in ventral view. *Abbreviation:* OGr, Occipital groove.

Mandible and adult lower dentition. As is usual for the genus, the diastema is short. Most of the ventral border of the mandible is missing, but the anterior portion (diastema to the m/1) is dorso-ventrally narrow. There is no p/1. The p/2 is simple with a single anterior stylid. Both the p/3 and p/4 have an anterior stylid and anterior conid. In both p/2 and p/3 the lingual structures are very simple. The postero-lingual conid is bifurcate in the p/3 and does not reach the lingual wall. In the p/4 the anterior valley is open lingually, the cristid obliqua contacts the mesio-lingual conid, which has a very short antero-lingual cristid and a moderately long postero-

lingual cristid that almost closes the medial valley. The molars have more or less aligned flattish lingual cuspids with relatively high cristids. The metastylid is well-developed. The m/1 is subequal in size to the m/2. The molars do not present a *Palaeomeryx*-fold. The molars are distally open (no contact between the post-entocristid and the post-hypocristid). The anterior cingulid is moderate to strong from m/1 to m/3, being more developed at the protoconid. The ectostylid increases in size from m/1 to m/3. The third lobe of the m/3 is mono-cuspidate, with a robust hypoconulid.

Occipital. Dorsally, a well-developed sagittal crest meets a massive and triangular external occipital protuberance that extends caudally over the nuchal plane. Both the nuchal crest and the external occipital crest are well-developed. Two elliptical shallow fossae extend below the external occipital crest, in the nuchal plane, creating a marked convexity. However this morphology is not as developed as in the nuchal fossa of palaeomerycids (see Sánchez *et al.* 2015). Caudally to the nuchal crest and next to it, just behind the temporal fossa, there is a deep dorso-ventral rectilinear groove on each side of the skull. This groove of

unknown function is also found in palaeomerycids and resembles a robust superficial vascular canal (Sánchez *et al.* 2015). Very shallow fossettes appear in the nuchal plane, immediately above the occipital condyles. The foramen magnum is wide, ventrally open as is the norm in pecorans with the exception of prolibytheriid giraffoids (Sánchez *et al.* 2010b; Danowitz *et al.* 2016). The foramen magnum is wide ventrally, showing an open U-shaped morphology. Also, the posterior basioccipital tuberosities anterior to the occipital condyles are strongly developed with a marked quadrangular morphology.

Table 1. Measurements (in mm) of the dentition of the new hemi-mandible GSN LT 37'08 + LT 47'06 (*P. stromeri*) from Langental, Namibia.

Tooth	Mesio-distal length	Bucco-lingual breadth
p/2	8.84	4.26
p/3	11.19	5.35
p/4	12.89	6.21
m/1	14.8	7.87
m/2	16.07	8.69
m/3	20.28	8.29

Discussion

The phylogenetic relationships of *Propalaeoryx* within the Pecora have been subject of debate since its description by Stromer (1926). Arambourg (1933) and Whitworth (1958) described its dentition as cervoid, but some other authors considered *Propalaeoryx* to be a giraffoid (Janis & Scott, 1987; Gentry, 1994) or more specifically a climacoceratid giraffoid (Morales *et al.*, 1999, 2008). Subsequently, Cote (2010) classified *Propalaeoryx* as a pecoran *incertae sedis*, although she admitted that the giraffoid hypothesis was probably the most likely to be valid. However, none of these authors included *Propalaeoryx* in a phylogenetic analysis. When this analysis was done in a work that attempted to check the phylogenetic relationships of the three-horned palaeomerycids, *Propalaeoryx* was recovered with very strong branch support

as the basal off-shoot of the palaeomerycid clade within the Giraffomorpha (Sánchez *et al.* 2015; Fig. 3). Giraffomorpha are the ancient and inclusive clade of crown-pecorans, the only living representatives of which are the giraffes (*Giraffa* and *Okapia*). The phylogenetic structure of the Giraffomorpha encompasses two main lineages, Giraffoidea (Prolibytheriidae, Climacoceratidae and Giraffidae; Fig. 3, clade 2) and Palaeomerycoidea (*Propalaeoryx* plus the Palaeomerycidae - although the European *Sardomeryx* and *Bedomeryx* have recently been recovered as palaeomerycoids by Mennecart *et al.* 2018 - Fig. 3, clade 1). Even though it has been previously mentioned (Ríos *et al.* 2017; Mennecart *et al.* 2018) we explicitly define here the Palaeomerycoidea as the least inclusive clade of giraffomorpha containing *Triceromeryx* and *Propalaeoryx*.

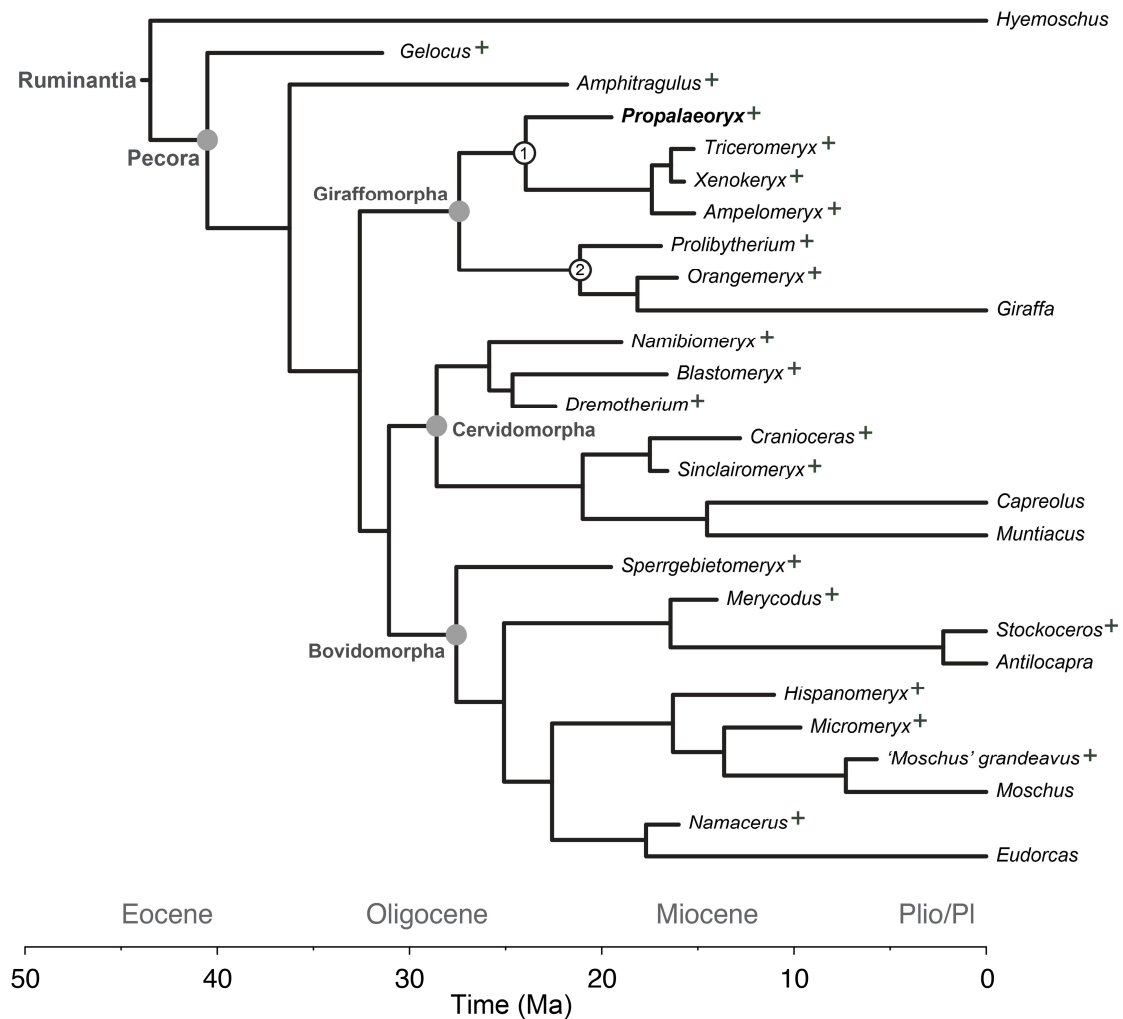


Figure 3. Phylogenetic tree of the Pecora, showing the major clades of crown-pecorans (Giraffomorpha, Cervidomorpha and Bovidomorpha), with special emphasis on giraffomorphs and *Propalaeoryx*. Clade 1: Palaeomerycoidea; Clade 2: Giraffoidea. Based on the tip-dating Bayesian analysis on a combined dataset (morphology + DNA + stratigraphic data) of Sánchez *et al.* (2015). Notice the position of other Sperrgebiet lower Miocene ruminants such as the diminutive stem-cervidomorph *Namibiomeryx* and the stem-bovidomorph *Sperrgebietomeryx*. Both the distribution of the reconstructed morphological character / states for the tip-dating tree, and a description of the tip-dating analysis, are presented in Sánchez *et al.* (2015).

Thus, although definitely related to giraffes the giraffoid/climacoceratid hypothesis for *Propalaeoryx* was rejected, and the African genus proved to be more closely related to the Eurasian branch of the Giraffomorpha. This phylogenetic structure of giraffomorphs showed the existence of complex evolutionary and palaeobiogeographical patterns in the evolutionary history of the group (Sánchez *et al.* 2015). The morphological characters that unite *Propalaeoryx* with palaeomerycids are the presence of a deep rectilinear groove behind the temporal fossa (as described here in GSN LT 194'96a; see Fig. 2, D-E),

enlarged upper canines of moschid-type in males, presence of a lateral notch in the facet for the semilunate in the radius, distally closed metatarsal sulcus, and presence of a small metatarsal tuberosity. Out of these, the most typically palaeomerycid features are the cranial groove and the small metatarsal tuberosity, since these two features are not known in any other pecoran. The upper canines of moschid-type are typical of palaeomerycoids, being absent, as far as we know, in giraffoids. This type of canine is widespread among pecorans (Sánchez *et al.* 2010a), and is known to have secondarily reappeared in

cervids (e.g. *Hydropotes inermis*). Also, the distally closed metatarsal sulcus is a feature that appears to be homoplastic (parallel) among pecorans. As occurs in moschid bovidomorphs (Sánchez *et al.* 2010a), giraffomorphs display the two types of condition of the sulcus, open in giraffoids and closed in palaeomerycoids. This phenomenon occurs when the canal for the digital artery is of moschid-type (see Sánchez *et al.*, 2010a for the definition of the states), which means that it is neither superficial nor deep. When these two extreme cases occur (bovid-type and cervid-type), as in derived bovids and cervoids, respectively, the open and closed states become fixed (open in derived bovids and closed in cervoids and bovidomorph antilocaprids; see Sánchez *et al.* 2010a, 2015). With respect to palaeomerycids, *Propalaeoryx* shows a clear pattern of mosaic evolution, displaying a more derived dentition with a lack of the *Palaeomeryx*-fold and the presence of far more flattened cuspids with higher cristids (Sánchez *et al.* 2015). However, the presence of p/1 in *P. austroafricanus* is a curious retention of a primitive feature that is lost in *P. stromeri* and palaeomerycids. Palaeomerycids are characterized by a highly derived and modified nuchal plane, expanded dorsally, with the presence of novelties such as the nuchal fossa and lateral expansions of the nuchal crest that served as attachments for a reinforced pack of head extensor muscles such as the *rectus capitis dorsalis*, *semispinalis capitis* and *rectus capitis dorsalis minor* (Sánchez *et al.* 2015). *Propalaeoryx stromeri* has a somewhat dorsally expanded nuchal plane that shows well-marked twin attachment areas for the extensor packs. However, the nuchal plane is not heavily modified as in palaeomerycids, and of course no occipital appendages exist.

The main lineages of crown-pecorans apparently experienced a major radiation event about 25 million years ago, when all

the major groups containing the living lineages (giraffomorphs, cervidomorphs and crown-bovidomorphs) appeared (see Fig. 3). By this time, the original palaeomerycoid stock should have entered Europe and Africa, diverging into two lineages. The Eurasian branch was apparently more successful than the African one, producing a high diversity of palaeomerycids plus some forms recently related to *Propalaeoryx* as basal palaeomerycoids, such as *Sardomeryx* and *Bedomeryx* (Mennecart *et al.* 2018). The presence of these basal palaeomerycoids near the Oligocene - Miocene boundary (Burdigalian) of Europe reinforces the hypothesis of an extensive radiation of giraffomorphs taking place ca 25 Ma.

The two species of *Propalaeoryx* from the Sperrgebiet (*P. austroafricanus* and *P. stromeri*) have very conspicuous morphological differences in the occipital area of the skull that were not previously described. In the ventral part of the occipital, *P. austroafricanus* has a narrower foramen magnum, which in fact is almost closed, resembling the *Prolibytherium* condition but not fully closed (Fig. 2, I). Also, the posterior basioccipital tuberosities are far less developed than in *P. stromeri*. Finally, two well-developed fossettes are present above the occipital condyles in the nuchal plane, and the areas of muscular insertion above the foramen magnum are strong and protruding (Fig. 2, H). In *P. stromeri* the fossettes are almost non-existent and the surface above the foramen magnum is clearly flatter. The basioccipital area of *P. stromeri* is much more similar to that of the palaeomerycids than to that of *P. austroafricanus*. We cannot discard the possibility that *P. austroafricanus* and *P. stromeri* belong to different genera, but we need to check this out through a phylogenetic analysis encompassing all published members of the Palaeomerycoidea, including the two Sperrgebiet species of *Propalaeoryx*.

Conclusions

Propalaeoryx has been recovered as a basal offshoot of the Palaeomerycoidea, the branch of the Giraffomorpha that includes the Eurasian Palaeomerycidae. A new and

very complete mandibular fossil of *Propalaeoryx stromeri* yields valuable information about the morphology and variability of the species, and increases its

hypodigm. The occipital area in *P. austroafricanus* and *P. stromeri* are strikingly different, with deep contrasts in the morphology of the basioccipital, the ventral part of the foramen magnum and the structure of the nuchal plane. These newly described characters enrich the diagnoses of

the species, and a generic difference between the two forms cannot be ruled out. Finally, giraffomorphs probably underwent a strong radiation event at the end of the Oligocene (ca 25 Ma) before dispersing through Eurasia and Africa during the early-middle Miocene.

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