A new adapisoriculid mammal (Eutheria) from the early-middle Eocene of Namibia

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Abstract :- Adapisoriculidae, a family of primitive eutherian, insectivore-like small mammals, is known from Europe, mainland Asia, India and Africa (Morocco, Namibia) but not thus far from the New World. Previous discoveries of this family in Africa were restricted to Morocco, but in 2019 a specimen was found in early to middle Eocene freshwater limestones at Black Crow, Namibia, thereby greatly extending the geographic range of the family well to the south of all other records of the group, even taking into account the northward drift of India since the early Palaeogene. A new genus and species is described and compared in detail with other members of the family as well as with other small-bodied eutherians and placentals. Its biogeography is discussed, but the limited amount of evidence available, allied with the huge geographic and temporal gaps in its distribution, does not yield a clear picture of where the family originated and when it dispersed to other parts of the Old World.

Key words :- Eutheria, Taxonomy, Phylogeny, Biogeography, Namibia, Eocene

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Introduction

The Adapisoriculidae comprise a group of poorly known, small-bodied eutherian mammals of an inferred shrew-like aspect and insectivorous feeding habits (Smith *et al*. 2010). Their relationships and phylogenetic affinities have been the subject of heated debate (De Bast *et al*. 2012 and literature cited in pp. 35-37); during the last few decades several authors favoured their attribution to the Euarchonta, a group that also includes primates, tree shrews (Scandentia) and colugos (Dermoptera) (Smith *et al*. 2010; De Bast *et al*. 2012). More recently, however, Manz *et al*. (2015) argued that the Adapisoriculidae lie outside the crown-group Placentalia (Wible *et al*. 2007; Goswami *et al*. 2011). Their scarce known remains (isolated teeth, jaws, and some postcranial elements) have been found in latest Cretaceous beds of India, the early Paleocene of Hainin (Belgium), the late Paleocene of Walbeck (Germany), Cernay (France), and Adrar-Mgorn (Morocco), and the early Eocene of Dormaal (Belgium) and Vastan (India) (Smith *et al*. 2010; Kapur *et al*. 2017 and literature cited therein). Here we report on a new taxon of Adapisoriculidae that is significant in two aspects: (1) it is the southernmost record of an adapisoriculid, and (2) it is the youngest record for a member of this family. We describe the new taxon, discuss its affinities and review the possible biogeographic history of the group. We understand that adapisoriculid morphology provides several clues on the early radiation of basal eutherians.

The new taxon recognized herein was found and briefly described previously by one of us (Pickford, 2019). It is based on a single specimen, an isolated upper molar, recovered from a block of freshwater limestone from the Black Crow locality collected in 2019 (Tsau-ǁKhaeb National Park, Sperrgebiet; Fig. 1) in southern Namibia (27°22'38.0"S, 15°27'49.7"E). The geological context and inferred age of the mammal-bearing deposit were detailed previously (Pickford *et al*. 2008a, 2008b, 2014; Pickford, 2015). The method employed in the recovery of the specimen is described in Pickford (2019).

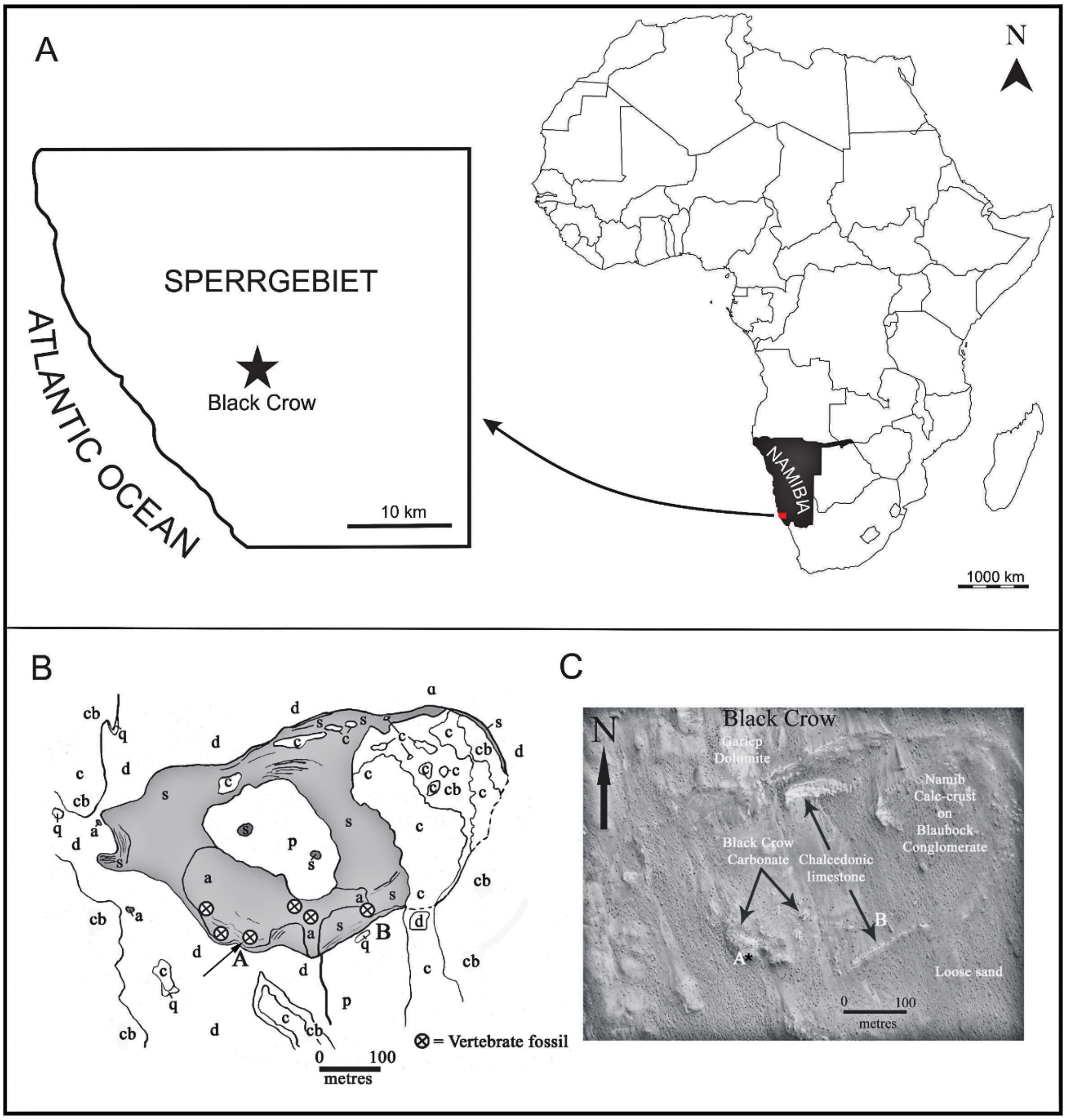

Figure 1. ***A***, right, map of Africa showing the location of Namibia and of the Sperrgebiet (in red); left, location of the Black Crow fossil site in the Sperrgebiet. ***B***, geological sketch map of the freshwater limestone outcrops at Black Crow, showing the locality from which *Namibiodon australis* gen et sp. nov. came (black arrow site "A"). Lower case letters indicate different rock types in the stratigraphic succession; from youngest to oldest: ***c***, Namib 1 Calc-crust; ***cb***, Blaubock Conglomerate; ***p***, conglomerate with phonolite cobbles; ***a***, Black Crow carbonate; ***s***, Black Crow siliceous limestone; ***q***, "Pomona" Quartzite; ***d***, Gariep Dolomite and Quartzite. ***C***, Satellite image of the Black Crow Depression, indicating several rock types cropping out in the area. The site where *Namibiodon australis* gen et sp. nov. came from is indicated by an asterisk (at site "A'). Modified from Google Earth.

Abbreviations

GSN - Geological Survey of Namibia, Windhoek;
BC - Black Crow locality.
St - Stylar cusps (A, B, C, D, and E).
M - Upper molar.

Molar nomenclature follows Goin *et al*. (2016) and Pickford (2019, fig. 2).

Systematic Palaeontology

Class Mammalia Linnaeus, 1758

Infraclass Eutheria Gill, 1872

Order *incertae sedis*

Family Adapisoriculidae Van Valen, 1967

Genus *Namibiodon* nov.

Type species :- *Namibiodon australis* sp. nov.

Diagnosis :- Adapisoriculid eutherian with M2/ having a full set of stylar cusps, stout protocone, straight centrocrista, incipiently reduced stylar shelf, paracone and metacone well-separated and subequal in size and shape.

Differential diagnosis :- Differs from all other Adapisoriculidae in the following combination of features: well-developed ectoflexus, moderately developed pre- and post-protoconal cingula (pre- and post-cingula), postparaconular crest absent.

Etymology :- The generic name is a combination of "Namibia" and the Greek term "*odontos*" meaning tooth; the gender is masculine.

Species *Namibiodon australis* nov.

Diagnosis :- As for the genus.

Holotype :-. GSN BC 6'19, a left M2/ (Fig. 2).

Locality and age :- Black Crow, Sperrgebiet, Namibia. Early-middle Eocene (Ypresian-Lutetian).

Etymology :- The specific name (*australis*) refers to the extreme southern distribution of this taxon among known adapisoriculids.

Measurements :- Length: 1.49 mm; width: 1.91mm (after Pickford, 2019).

Description

The holotype is roughly trapezoidal in occlusal outline, being wider than long. Its most prominent features are the strong protocone, straight centrocrista, deep ectoflexus, relatively short postmetacrista, asymmetrically placed conulae, absence of a postparaconular crest, presence of incipient anterior and posterior cingula at the base of the protocone, and a full set of stylar cusps at the stylar shelf. The latter is wide and shows five cusps: parastyle ('A'), stylocone ('B'), and the stylar cusp 'D', all three well-developed, as well as reduced stylar cusps 'C' and 'E'. We tentatively refer to StC a cusp located past the ectoflexus, very close to, and at the anterior base of, StD. StC is closer to StD than to StB; StE is paired with StD. The ectoflexus is deep and rather symmetrical. Both stylar lobes are well developed. The preparacrista and postmetacrista are moderately long and they are not perpendicular but slightly oblique to the antero-posterior axis of the tooth. The paracone and metacone are well separated from each other and are connected by a straight centrocrista. The paracingulum is wide near the parastyle 'A', but it is narrow in the middle of the tooth, and it is connected to the paraconule; in turn, the metacingulum is wide, especially in the middle of the tooth, and ends buccally before a point below the end of the postmetacrista. The trigon basin is deep and wide. The metaconule and paraconule are well developed, but only the first conule has an internal crista (the premetaconular crest), while the post-paraconular crest is absent; both cusps are connected to the post- and pre-protocingula. They are not aligned in the antero-posterior axis of the tooth; instead, the metaconule is closer to the metacone than the paraconule is to the paracone; for this reason, the postprotoconal crest is longer than the pre-protoconal one. The former shows, due to wear, a visible thickening near the base of the metaconule. The protocone is wide and is slightly eccentrically placed, closer to the anterior side of the tooth. The pre-cigulum and post-cingulum are incipient, especially the anterior one (named precingular groove in Pickford 2019) but clearly visible. The protocone has a shallow groove on its mesial surface.

Figure 2. *Namibiodon australis* gen et sp. nov. SEM micrograph occlusal stereo pair of the type specimen, GSN BC 6'19, considered to be a left M2/

Reasons for considering that the holotype of **Namibiodon australis** *is an M2/*

In adapisoriculids, as in many other mammals, M3/ is mesiodistally compressed, with the metastylar area highly reduced, in such a way that the buccal edge of the tooth is tilted lingually at the posterior end. In turn, M1/s usually have a poorly defined ectoflexus and the stylar shelf is proportionally wider than in the other molars of the upper series (as compared, for instance, with the protocone width). For these reasons, and because GSN BC 6'19 resembles more the M2/s of other members of this family, we identify it as a left M2/, as hinted previously by Pickford (2019).

Comparisons

Namibiodon australis is not a metatherian mammal, even though it superficially resembles one. On the one hand, pre- and post-protoconal cingula are quite infrequent among metatherians – although pre- and/or post-protoconal cingula can be observed in a few taxa; e.g. Protodidelphidae (Oliveira & Goin, 2011). On the other hand, no metatherian known to us shows such disparity in the location of the paraconule (much closer to the protocone) and metaconule, as occurs in *Namibiodon* and other Adapisoriculidae. Among metatherians, when there is a different position of the paraconule and metaconule, it happens to be exactly the opposite way: the metaconule is closer to the protocone than the paraconule. This happens in a few basal metatherians, such as the deltatheridian *Oklatheridium szalayi* (Averianov, 2015), and mainly, in most "pseudodiprotodont" South American marsupials as well as in the Australasian Diprotodontia (Goin *et al.* 2009; Black *et al.* 2012). In most of them, the metaconule is not only lingually placed but is also much larger than the paraconule, forming a hypocone-like structure at the postero-lingual corner of the upper molars.

Regarding similarly shaped Placentalia, *Namibiodon* differs from the representatives of Chrysochloridae and some Tenrecidae (Afrotheria), as well as from Apternodontidae, Oligoryctidae, Parapternodontidae and Solenodontidae (Eulipotyphla) in that these families have zalambdodont molars and lack a metacone in the upper molars. *Namibiodon* differs from the tenrecomorphan *Widanelfarasia*, among other features, in having a wide buccal shelf; also, the metacone and paracone are conical in *Namibiodon*; finally, in *Widanelfarasia* the protocone is triangular in shape. It differs from the probable tenrecomorphan *Dilambdogale* in that the latter genus has narrower upper molars, lacks cingula, the ectoflexus is less developed, and the main cusps of the trigon are not rounded. *Namibiodon* differs from the potamogalid *Namagale* and the primitive tenrecids *Sperrgale* and *Arenagale* in that species of these genera have narrower upper molars that lack cingula and in which the main cusps and the buccal cusps are poorly developed. It differs from Paleogene African mammals with possible afrosoricid affinities, such as *Chambilestes*, in that the latter have narrower molars, the ectoflexus and cusps are less developed (especially the metacone), it has a hypocone and better developed cingula. It differs from *Garatherium* in that in the latter the molar is narrower, it has a mesostyle, the cusps are less rounded, the ectoflexus less invasive and cingula are absent. It differs from *Todralestes* in that the latter has less developed buccal cusps and ectoflexus, as well as a narrower protocone. It differs from "*Aboletylestes*" in that the latter has less developed ectoflexus and buccal cusps, lacks cingula and paraconule. It differs from "*Palaeoryctes*" in that the latter has narrower teeth, poorly developed cusps and buccal cusps and it lacks cingula. It differs from representatives of the Apatotheria, in particular from the genus *Labidolemur*, in the absence (in the latter), of an anterior cingulum, a more developed posterior cingulum and buccal cusps, as well as in the presence of a hypocone. In turn, the more similar apatotherid *Russellmys* has a less pronounced ectoflexus and less developed buccal cusps. It differs from the pentaconid *Eurolestes* in that the latter has more developed buccal cusps and a hypocone, as well as extra cusps in the postprotocrista.

Namibiodon differs from similarly shaped representatives of Chiroptera, Dermoptera and Scandentia, as well as from Soricidae and Talpidae of Eulipotyphla, in that the latter do not have a conical metacone and paracone, their stylar cusps are poorly developed, the centrocristae are not straight (the centrocrista, preparacrista and postmetacrista display a W-shape design in occlusal view). It differs from the Dermoptera *Plagiomene* in having more developed cusps and in the absence of an ectoflexus in that genus. It differs from Dimylidae and Erinaceidae (Eulipotyphla) and Macroscelididae in that the latter two families have a hypocone and, generally, more quadrangular upper molars in occlusal view.

Regarding the other adapisoriculids, *Namibiodon* differs from *Afrodon*, *Proremiculus*, *Remiculus* and *Garatherium* in its more developed ectoflexus; it differs from *Afrodon*, *Deccanolestes*, *Proremiculus* and *Garatherium* in its better developed buccal cusps; it differs from *Bustylus*in its less developed buccal cusps; it differs from *Afrodon*, *Bustylus*, and *Garatherium* in its well-developed pre and post-cingula; it differs from *Afrodon*, *Bustylus* and *Garatherium* in its proportionally more robust protocone; it differs from *Adapisoriculus*, *Remiculus* and *Garatherium*in its less developed dilambdodonty; it differs from *Deccanolestes* in having more developed cuspsand a relatively longer M2/; finally, it differs from *Proremiculus* in the absence of the postparaconular crest.

Discussion

Affinities of Namibiodon australis *gen. et sp. nov*.

In his description of the (at the time, unnamed) holotype of *Namibiodon australis*, Pickford (2019) noted overall similarities between it and *Proremiculus lagnauxi* from the early Palaeocene of Hainin (Belgium), including "…a horizontal mesial groove on the protocone and a postcingulum, two structures which also resemble the situation in the todralestid *Todralestes variabilis* from Morocco" (Pickford, 2019, pp. 28-29). We also note these general similarities, especially with *Proremiculus lagnauxi*. The main differences between *Namibiodon* and *Proremiculus* lie in the deeper ectoflexus and lack of a postparaconular crest in the former, while *Proremiculus* has a better developed preparaconular crest which ends buccally forming a thick anterior cingulum. In turn, differences from *Todralestes* (Cimolesta, Todralestidae) are more noticeable: *Namibiodon* has a deeper ectoflexus, more developed metastylar lobe, proportionally larger metacone less antero-posteriorly compressed protocone, and inversely developed protoconal cingula (the precingulum much better developed than the postcingulum in *Todralestes*). Interestingly, however, both genera share quite a derived feature: the lack of a postparaconular crest.

De Bast *et al*. (2012) performed a phylogenetic analysis of all adapisoriculid eutherians known at the time. In it, several taxa form a monophyletic clade on the basis of lower molar features: *Remiculus*, *Proremiculus*, *Adapisoriculus*, *Bustylus*, two species of *Afrodon*, and *Deccanolestes narmadensis*. Even though no lower molars of *Namibiodon* are yet known, we feel confident that eventually it will prove to belong to this clade. Outside this monophyletic unit are the remaining species of *Afrodon* and *Deccanolestes*, suggesting that these two genera are paraphyletic (De Bast *et al*. 2012).

Adapisoriculid affinities

De Bast *et al*. (2012) reviewed the highly contrasting views of adapisoriculid affinities that have been published since their discovery. They have been successively related to marsupials (Didelphidae), then to the eutherian Nyctitheriidae (Eulipotyphla), Leptictidae (Leptictida); Mixodectidae (Dermoptera), Tupaiidae (Scandentia), Palaeoryctidae (Cimolesta), Plesiadapiformes and Euarchonta *sensu lato*. Hooker (2001) noted that both colugos and *Mixodectes* (Dermoptera) shared a series of derived features in the astragalus and calcaneum with the Late Cretaceous adapisoriculid *Deccanolestes*. Later Smith *et al.* (2010, p. 422) stated: "Based on tarsal morphology, adapisoriculids are not lipotyphlan insectivores nor didelphid-like marsupials nor leptictids but instead belong to the Euarchonta" (Boyer *et al*. 2010). This point of view on the affinities of the Adapisoriculidae was followed by subsequent authors (De Bast *et al*. 2012). More recently, however, it was argued that adapisoriculids should not be included even within the Placentalia eutherians. To Manz *et al.* (2015, p. 1) their results "...suggest that similarities in postcranial morphology among nyctitheriids, adapisoriculids and euarchontans represent separate instances of convergence or primitive retention of climbing capabilities." Interestingly, their extensive phylogenetic analysis including both extinct and extant taxa shows a quite basal position of Adapisoriculidae among Eutheria. It should be noted, however, that the position of Adapisoriculidae within Eutheria varies widely in the different phylogenetic analyses performed in the past decade or so (Manz *et al.* 2015; Hu *et al.* 2010; Seiffert, 2010; Goswami *et al.* 2011; Archibald & Averianov, 2012; Chester *et al.* 2015; Halliday *et al.* 2017; Kapur *et al.* 2017).

To Archibald & Averianov (2001) the paraconule closer to the protocone than is the metaconule is the single derived feature in the upper molar morphology that clusters together *Paranyctoides* and *Gallolestes*, apart from other "zhelestids".

This noticeable feature of adapisoriculds is also present in other basal eutherians, such as *Prokennalestes abramovi* and in species of *Daulestes*, both inferred to be members of the Asioryctitheria. Later, in their phylogenetic analysis of this clade of eutherians, *Deccanolestes* appears as the plesiomorphic sister group of a clade that includes *Gypsonictops* + (*Kulbeckia* + (*Zhangolestes* (*Alymlestes*, *Zalambdalestes*, *Barunlestes*))), all of them as sister-group of Cimolesta (Archibald & Averianov, 2012). Summarising, we note that the affinities of basal eutherians is far from clear, and that the position of the Adapisoriculidae is frankly enigmatic. Unfortuntely *Namibiodon australis* adds little to this ongoing phylogenetic discussion, mostly due to the restricted nature of its fossil record.

Biogeography

The biogeography of Adapisoriculidae was discussed by Gheerbrant & Russell (1989), Gheerbrant (1991), Prasad *et al*. (2009), Rana & Wilson (2003), and Kapur *et al*. (2017), among others. As it stands, the fossil record of this family is so full of blank spaces and time gaps that it is difficult to propose a coherent biogeographic scenario of its origins and subsequent dispersal. The oldest known fossils of the family are from the Cretaceous of India, but this does not necessarily mean that the group originated there. The terrestrial fossil record of Africa from Late Cretaceous to Ypresian/Lutetian times is practically non-existent, but this does not signify that the continent was devoid of mammals during that span of time.

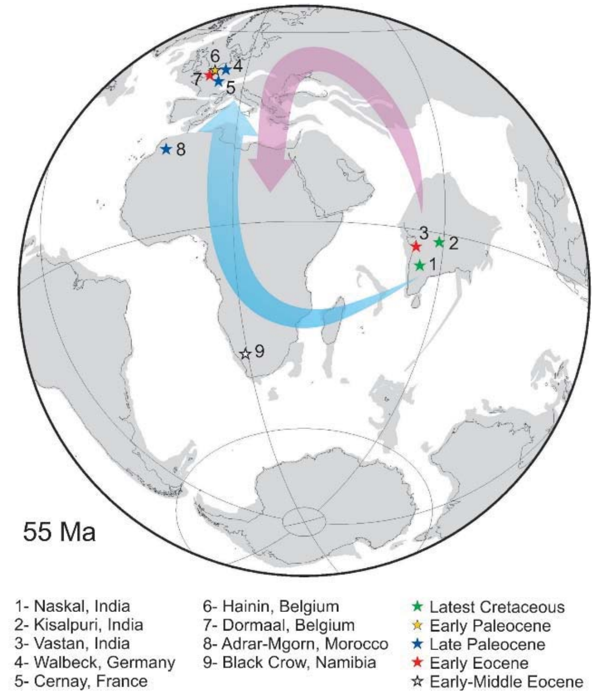

Figure 3. Palaeogeographic representation of Africa and adjacent continents at 55 Ma, indicating localities and ages of the Adapisoriculidae record (modified from Kapur *et al.* 2017). The black triangle in northern Madagascar indicates the presence of a Late Cretaceous, probably zhelestid mammal in that island (Averianov *et al*. 2003; contra Krause, 2001). The coloured arrows indicate possible migration routes of the Adapisoriculidae, assuming an Indian origin for the group. The red arrow suggests dispersal to Africa via Eurasia, while the blue one suggests dispersal to Eurasia via Africa. A third possibility, not shown here, is that dispersal to Africa and to Europe might have been two separate, unconnected events that might have occurred at different times. The palaeogeographic reconstruction was performed with the palaeomap maker of ODSN (Ocean Drilling Stratigraphic Network) Plate Tectonic Reconstruction Service (Research Center for Marine Geosciences, Kiel, Germany and the Geological Institute of the University of Bremen, Germany; https://www.odsn.de/odsn/services/paleomap/paleomap. html).

Figure 3 shows two palaeobiogeographic scenarios accepting that the family originated in India and then spread to Eurasia and Africa, but it is also possible that future discoveries might point to Africa as the source of the family. What is more sure, is that the family seems to have failed to disperse to the New World.

Conclusion and Discussion

The discovery of an adapisoriculid molar in the middle Eocene Black Crow Limestone of Namibia is of interest for a number of reasons; taxonomic, phylogenetic and biogeographic. Comparison with other known adapisoriculids and with related small mammals including marsupials, reveals that the Namibian fossil belongs to a new genus and species of Eutherian, *Namibiodon australis*. The sample is restricted to a single, well-preserved upper molar, but its features are clear and yield important information about its affinities. However, additional material is required, especially of the lower dentition and post-cranial skeleton, in order to throw more light on its affinities, its diet and other aspects of its biology and adaptations. Morphological details issued during the initial announcement the discovery of the fossil (Pickford, 2019) are augmented by a more detailed anatomical description, and by more intensive comparisons with other adapisoriculids and related mammals from the Old World. As it stands, this record from Namibia is the youngest known for the family and it reveals that adapisoriculids likely survived in Africa longer than they did in Europe, mainland Asia or India.

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References

Archibald, J.D. & Averianov, A.O. 2001. *Paranyctoides* and allies from the Late Cretaceous of North America and Asia. *Acta Palaeontologica Polonica*, **46** (**4**), 533-551.

Archibald, J.D. & Averianov, A.O. 2012. Phylogenetic analysis, taxonomic revision, and dental ontogeny of the Cretaceous Zhelestidae (Mammalia: Eutheria). *Zoological Journal of the Linnean Society*, **164**, 361-426.

Averianov, A.O. 2015. Taxonomic revision of tribosphenic mammals from the Lower Cretaceous Antlers Formation of Texas and Oklahoma, USA. *Proceedings of the Zoological Institute, Russian Academy of Sciences*, **319** (**2**), 141-181.

Averianov, A.O., Archibald, J.D. & Martin, T. 2003. Placental nature of the alleged marsupial from the Cretaceous of Madagascar. *Acta Palaeontologica Polonica*, **48** (**1**), 149-151.

Black, K.H., Archer, M., Hand, S.J. & Godthelp, H. 2012. The Rise of Australian Marsupials: A Synopsis of Biostratigraphic, Phylogenetic, Palaeoecologic and Palaeobiogeographic Understanding. *In*: Talent, J.A. (Ed.) *Earth and Life*. Springer, Dordrecht, pp. 983-1078.

Boyer, D.M., Prasad, G.V.R., Krause, D.W., Godinot, M., Goswami, A., Verma, O. & Flynn, J.J. 2010. New postcrania of *Deccanolestes* from the Late Cretaceous of India and their bearing on the evolutionary and biogeographic history of euarchontan mammals. *Naturwissenschaften*, **97**, 365-377.

Chester, S.G.B., Bloch, J.I., Boyer, D.M. & Clemens, W.A. 2015. Oldest known euarchontan tarsals and affinities of Paleocene *Purgatorius* to Primates. *Proceedings of the National Academy of Sciences of the USA*, **112** (**5**), 1487-1492.

De Bast, E., Smith, T. & Sigé, B. 2012. Diversity of the adapisoriculid mammals from the early Palaeocene of Hainin, Belgium. *Acta Palaeontologica Polonica*, **57** (**1**), 35-52.

Gheerbrant, E. 1991. *Bustylus* (Eutheria, Adapisoriculidae) and the absence of ascertained marsupials in the Palaeocene of Europe. *Terra Nova*, **3** (**6**), 586-592.

Gheerbrant, E. & Russell, D.E. 1989. Presence of the genus *Afrodon* [Mammalia, Lipotyphla (?), Adapisoriculidae] in Europe; new data for the problem of trans-Tethyan relations between Africa and Europe around the K/T boundary. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **76**, 1-15.

Gill, T. 1872. Arrangement of the families of mammals with analytical tables. *Smithsonian Miscellaneous Collection*, **11** (**1**), i-vi, 1-98.

Goin, F.J., Candela, A.M., Abello, M.A. & Oliveira, E.V. 2009. Earliest South American Paucituberculatans and their significance in the understanding of "pseudodiprotodont" marsupial radiations. *Zoological Journal of the Linnean Society*, **155**, 867-884.

Goin, F.J., Woodburne, M.O., Zimicz, A.M., Martin, G.M. & Chornogubsky, L. 2016. *A Brief History of South American Metatherians. Evolutionary Contexts and Intercontinental Dispersals*. Springer Earth System Sciences series, Springer, Dordrecht, 237 pp.

Goswami, A., Prasad, G.V.R., Upchurch, P., Boyer, D.M., Seiffert, E.R., Verma, O., Gheerbrant, E. & Flynn, J.J. 2011. A radiation of arboreal basal eutherian mammals beginning in the Late Cretaceous of India. *Proceedings of the National Academy of Sciences of the USA*, **108** (**39**), 16333-16338.

Halliday, T.J.D., Upchurch, P. & Goswami, A. 2017. Resolving the relationships of Paleocene placental mammals. *Biological Reviews*, **92**, 521-550.

Hooker, J.J. 2001. Tarsals of the extinct insectivoran family Nyctitheriidae (Mammalia): evidence for archontan relationships. *Zoological Journal of the Linnean Society*, **132**, 501-529.

Hu, Y., Meng, J., Li, C. & Wang, Y. 2010. New basal eutherian mammal from the Early Cretaceous Jehol biota, Liaoning, China. *Proceedings of the Royal Society, Biology*, **277**, 229-236.

Kapur, V.V., Das, D.P., Bajpai, S. & Prasad, G.V.R. 2017. First mammal of Gondwanan lineage in the early Eocene of India. *Comptes rendus Palevol*, **16,** 721-737.

Krause, D. 2001. Fossil molar from a Madagascan marsupial. *Nature*, **412**, 497-498.

Linnaeus, C. 1758. *Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Vol. 1 (10th Edition) Stockholm: Laurentius Salvius. pp. [1-4], 1-824.

Manz, C.L., Chester, S.G.B., Bloch, J.I., Silcox, M.T. & Sargis, E.J. 2015. New partial skeletons of Palaeocene Nyctitheriidae and evaluation of proposed euarchontan affinities. *Biology Letters*, **11**, 20140911. http://dx.doi.org/10.1098/rsbl.2014.0911

Oliveira, E.V. & Goin, F.J. 2011. A reassessment of bunodont metatherians from the Paleogene of Itaboraí (Brazil): Systematics and age of the Itaboraian SALMA. *Revista Brasileira de Paleontologia*, **14** (**2**), 105-136.

Pickford, M. 2015. Cenozoic Geology of the Northern Sperrgebiet, Namibia, accenting the Palaeogene. *Communications of the Geological Survey of Namibia*, **16**, 10-104.

Pickford, M. 2019. Adapisoriculidae from the Southern Hemisphere. *Communications of the Geological Survey of Namibia*, **21**, 26-31.

Pickford, M., Sawada, Y., Hyodo, H. & Senut, B. 2014. Radioisotopic age control for Palaeogene deposits of the Northern Sperrgebiet, Namibia. *Communications of the Geological Survey of Namibia*, **15**, 3-15.

Pickford, M., Senut, B., Morales, J., Mein, P. & Sanchez, I.M. 2008a. Mammalia from the Lutetian of Namibia. *Memoir of the Geological Survey of Namibia*, **20**, 465-514.

Pickford, M., Senut, B., Morales, J. & Sanchez, I. 2008b. Fossiliferous Cainozoic Carbonates of the Northern Sperrgebiet. *Memoir of the Geological Survey of Namibia*, **20**, 25-42.

Prasad, J.V.R., Verma, O., Gheerbrant, E., Goswami, A., Khosla, A., Parmar, V. & Sahni, A. 2009. First mammal evidence from the Late Cretaceous of India for biotic dispersal between India and Africa at the KT transition. *Comptes rendus Palevol*, **9**, 63-71.

Rana, R.S. & Wilson, G.P. 2003. New Late Cretaceous mammals from the Intertrappean beds of Rangapur, India and paleobiogeographic framework. *Acta Palaeontologica Polonica*, **48** (**3**), 331-348.

Seiffert, E.R. 2010. Paleogene “Insectivores”. *In*: Sanders, W.J. & Werdelin, L. (Eds) *Cenozoic Mammals of Africa*, University of California Press, Berkeley, pp. 253–260.

Smith, T., De Bast, E. & Sigé, B. 2010. Euarchontan affinity of Paleocene Afro-European adapisoriculid mammals and their origin in the late Cretaceous Deccan Traps of India. *Naturwissenschaften*, **97**, 417-422.

Van Valen, L. 1967. New Paleocene insectvores and insectivore classification. *Bulletin of the American Museum of Natural History*, **135**, 221-284.

Wible, J.R., Rougier, G.W., Novacek, M.J. & Asher, R.J. 2007. Cretaceous eutherians and Laurasian origin for placental mammals near the K/T boundary. *Nature*, **447** (**21**), 1003-1006.