

Primitive Adapidae from Namibia sheds light on the early primate radiation in Africa

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Abstract: The initial radiation of primates is best documented on Northern continents, in which two groups are abundant and well-known : the Omomyiformes, often considered to be primitive haplorhines, and the Adapiformes, usually considered to be strepsirrhines. The extinct Adapidae is one of the families of the Adapiformes, which was first documented in Europe and more recently found in Asia and North Africa. The late Eocene African adapids, from the Egyptian Fayum deposits, appear as a group of three genera constituting with the European genus *Caenopithecus*, a monophyletic subfamily, the Caenopithecinae, sister group to the otherwise exclusively European Adapinae. We report here the discovery, in the Middle Eocene locality of Black Crow in Namibia, of an undoubted primitive adapid, *Namadapis interdictus* nov. gen. nov. sp., which compares closely with the European genus *Microadapis* and the Chinese genus *Adapoides*. It also appears smaller, more primitive, closely related to the Fayum caenopithecines, being broadly ancestral to them but not directly in line with the three genera. The three primitive middle Eocene adapid genera present in Europe, Asia and Africa lead us to recognize an early differentiation between European Adapinae and African Caenopithecinae, the latter becoming more cristodont at smaller size than the former. A dispersal of an early adapid to Africa is confirmed, however we suggest an Asiatic instead of a European origin for the colonizer. The new Namibian fossil provides clues to interpret the enigmatic *Notnamaia* found in the same locality : it is probably an adapid. These two forms contrast with the late early or early middle Eocene primates recorded in North Africa, documenting an unsuspected degree of diversity and endemism within middle Eocene African primates. A new look at two poorly known late Eocene primates from the same region in Namibia allows the recognition of a proteopithecoid and emphasizes the distinctiveness of the lemuriform. In contrast with the poor understanding of the origin of African anthropoids and associated dispersals, the new adapid described herein confirms and helps to delineate better one of the early primate dispersals from Eurasia to Africa.

Key Words: Primates; Adapoidea; Biogeography; Dispersal; Eocene; Eurasia; Africa.

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Introduction

In northern continents the fossil record of Primates is rich during the warm Eocene, with more than 200 species described in Europe and North America (Szalay & Delson, 1979; Godinot, 2015). A less comprehensive record exists in Africa and Asia, which is regularly increased by new field work and discoveries (Chaimanee *et al.* 2012; Gunnell *et al.* 2018; Jaeger *et al.* 2010; Marivaux *et al.* 2013, 2014; Ni *et al.* 2010, 2013, 2016; Seiffert *et al.* 2010, 2018). Despite these advances, the fossil record remains insufficient on the two latter continents to allow the reconstruction of a consensual history of the origin and dispersals of the major groups of living and fossil primates. Among the best documented groups,

Omomyiformes are documented in Europe and North America, where they underwent a broad diversification, and Asia, in which their record is fragmentary. Until now they have not been reliably reported from Africa. In contrast, the Adapiformes, which constitute with living and fossil Lemuriformes, the suborder Strepsirhini, are documented on the same continents and also in Africa. Adapiformes are a broad radiation of “lemur-like” primates, which include several families and include some of the best-known fossil primates. The Notharctidae comprise classic fossils from North America (Gregory, 1920) and the European Cercamoniinae. The Sivaladapidae are exclusively Asiatic and survived until the

late Miocene, the Asiadapinae are also Asiatic (Rose *et al.* 2009) and another family was recently identified as Asiatic with a late dispersal to North America, the Ekgmowechashalidae (Ni *et al.* 2016). The family which gave its name to the group, the Adapidae, also appears to have had a broad geographic distribution, being represented in Europe by the classic Adapinae (Stehlin, 1912), in Europe and Africa by the Caenopithecinae (Seiffert *et al.* 2009, 2016; Stehlin, 1916), and in Asia by the primitive genus *Adapoides* (Beard *et al.* 1994). The North-American *Mahgarita* was considered to be a primitive adapid (Szalay & Delson, 1979; Godinot, 1998) but the discovery of its sister taxon *Mescalerolemur* revealed that it has different affinities, and acquired adapid characters by convergent evolution (Kirk *et al.* 2011). The phylogenetic analysis of the Caenopithecinae present in Europe and Africa led to a scenario of dispersal to Africa of an unknown stem genus, an African diversification and a subsequent return across the Tethys seaway by an ancestor of

Caenopithecus (Seiffert *et al.* 2009, 2018). The fossil described below yields evidence to test this scenario.

The new fossil primate comes from the locality of Black Crow in the Sperrgebiet of Namibia, in the southern part of Africa. The fossils were found in a small cliff of limestone (Fig. 1-3), which is a palustral, partly silicified limestone (Pickford, 2015a). They were extracted by acid attack of stone blocks. Mammals from this and from two other localities were described and initially all of them were considered to be Lutetian (Pickford *et al.* 2008).

However, the geochronological distribution of several taxa led to question this age (Seiffert 2010; Coster *et al.* 2012). Further work led to the realisation that the localities are of different ages, Black Crow probably being early Lutetian, whereas Silica North, Silica South and Eocliff are probably Bartonian (Pickford, 2015a) although there is debate about this (Seiffert, 2010). The primitiveness of the fossil described herein confirms a Lutetian age for the Black Crow fauna.

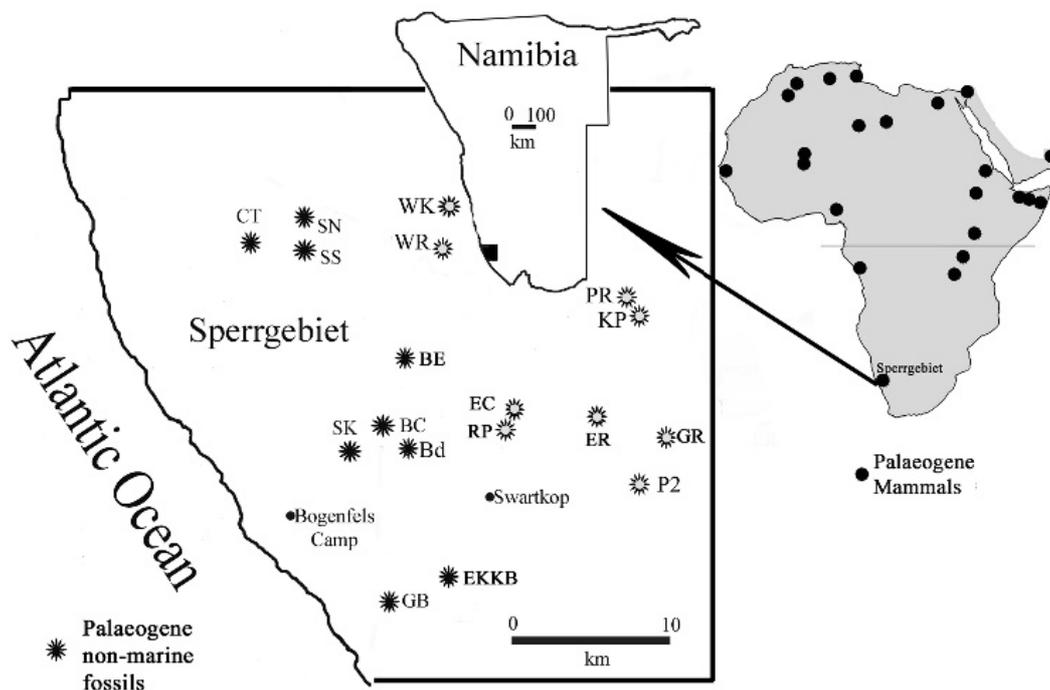


Figure 1. Small Eocene basins in the Sperrgebiet, Namibia, infilled with limestone and chalcedonic limestone derived directly or indirectly from volcanic activity at the Ystervark Carbonatite Centre near Phytoherm Ridge. BC - **Black Crow** ; Bd - Bedded limestone ; BE - Bull's Eye ; CT - *Chalcedon Tafelberg* ; EC - **Eocliff** ; EKKB - *Eisenkieselklippenbake* ; ER - **Eoridge** ; GB - *Gamachab* ; GR - Graben ; KP - Klinghart's Pan ; PR - *Phytoherm Ridge* ; P2 - Pietab 2 Limestone ; RP - *Reuning's Pan* ; SK - *Steffenkop* ; SN - **Silica North** ; SS - **Silica South** ; WK - Werf Kopje ; WR - White Ring. (**Bold Roman** are localities that have yielded mammals, **Bold Italics** are those which have yielded invertebrates and/or plants, the remainder being unfossiliferous; solid stars are located in the Trough Namib, hollow stars are in the Plain Namib).

Black Crow and other limestones of the Sperrgebiet

Black Crow is one of eighteen mapped outcrops of bedded limestone of Eocene age in the Sperrgebiet, Namibia, nine of which crop out in the Trough Namib and nine in the Plain Namib (Kaiser, 1926). Of these, fossils have been found in ten (Fig. 1). On the basis of the mammalian fossils, the limestones fall into two biostratigraphic groups, Black Crow is the oldest of the occurrences (Lutetian), while

Silica North, Silica South, Eocliff and Eoridge are considered to be Bartonian or perhaps Priabonian, the other sites having yielded only molluscs and plants, remain undated but most are likely to be Lutetian on the grounds that the basal well-bedded limestone layers in them resemble those at Black Crow, and differ from the facies developed at Silica North and Eocliff.

Geological Context

Black Crow is a small depression in Proterozoic dolomitic bedrock north of Bogenfels in the Sperrgebiet, Namibia, which filled with limestone during the Lutetian. The source of the limestone was likely the Ystervark Carbonatite Volcano located 15 km to the east on the western outskirts of the Klinghardt Phonolite Cluster. Much of the limestone represents fine-grained aeolian

volcanic ash (in some cases subsequently converted to chalcedonic limestone), but the fossiliferous limestone accumulated in a palustral setting. There are abundant plant root systems in it, a few frog bones, many fish teeth and dozens of small crocodile teeth. However, the bulk of the vertebrates and molluscs are of terrestrial taxa.

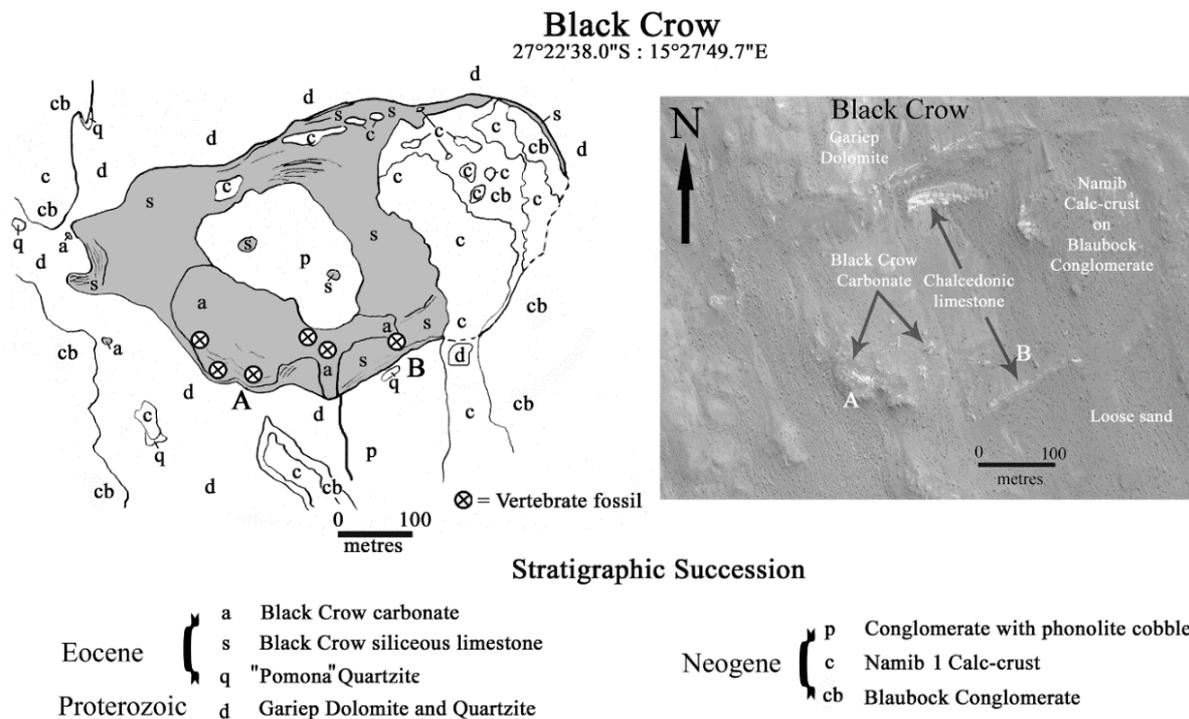


Figure 2. Outcrops in the Black Crow Basin, geological sketch map and image modified from Google Earth. A) Discovery site of *Namadapis*, *Notnamaia*, and *Namahyrax*; B) *Namatherium* locality.

The Black Crow Limestone is unconformably overlain by Neogene deposits Blaibok Conglomerate, Namib 1 Calc-crust, Gemboktal Conglomerate and loose sand (Fig. 2).

The deposits at Black Crow were originally included in the Pomona Schichten by Kaiser &

Beetz (1926; Symbol « bks » in Map sheet 3 - Granitberg), a heterogeneous suite of rock types spanning a considerable period of time (Lutetian to Pleistocene; Pickford 2015a), although in the original publications, they were thought to be of Prämitteleocän age.

The depression was named Black Crow by Kalbskopf (1977) who studied the various disjointed outcrops of Pomona Schichten in the Trough Namib.

The first mammal fossils were found at Black Crow by the Namibia Palaeontology Expedition in 2008 (Pickford *et al.* 2008). A Middle Eocene age was deduced for the fossiliferous limestones on the basis of four observations : 1) the stage of evolution of the

arsinothere, *Namatherium blackcrowense*, which is considerably less hypsodont than the Late Priabonian-Rupelian *Arsinoitherium zittelli* from the Fayum, Egypt, 2) the primitive dental morphology of the hyracoid, *Namahyrax corvus*, 3) the presence of a bunodont rodent, *Zegdoumys namibiensis* and 4) the presence of a Todralestidae (*Namalestes gheerbranti*) (Table 1).



Figure 3. Two views of the freshwater limestone outcrops at Black Crow, Namibia. The holotype of *Namadapis interdictus* was collected at the pile of stones heaped on the lower large white outcrop (centre right of the right hand image).

This correlation was challenged by Seiffert (2010) and others who considered that the deposits were considerably younger, possibly Priabonian or later (see the report of the discussion in Pickford 2015a).

The discovery of a paramyid rodent, *Namaparamys inexpectatus*, and of the

primitive adapid *Namadapis* nov. gen. at the site, the latter most similar to material from the Lutetian of Switzerland and the Middle Eocene of China, confirms that Black Crow is most likely to be of Lutetian age, as originally proposed (Pickford *et al.* 2008).

Abbreviations

BNM: Basel Naturhistorisches Museum, Switzerland.

CGM: Cairo Geological Museum, Egypt.

DPC: Duke Primate Centre, USA.

GSN: Geological Survey of Namibia, Windhoek, Namibia.

GU: Gujarat, used for GU/RSR/VAS, Department of Geology, Garhwal University, Srinagar, India.

IVPP: Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing, China.

Black Crow Fauna

Table 1. Faunal list of the Black Crow Limestone, Namibia

<p>Gastropoda <i>Dorcasia</i> sp. <i>Trigonephrus</i> sp.</p> <p>Subulinidae <i>Lymnaea</i> sp.</p> <p>Pisces Characidae <i>Hydrocynus</i> sp. cf <i>Alestes</i> sp.</p> <p>cf Cichlidae</p> <p>Anura Pipidae</p> <p>Reptilia Crocodylia Amphisbaenia Scincidae Boidae</p> <p>Mammalia Erinaceidae? Genus indet.</p> <p>Primates Adapidae <i>Namadapis interdictus</i> <i>Notnamaia bogenfelsi</i></p>	<p>Rodentia Paramyidae <i>Namaparamys inexpectatus</i></p> <p>Zegdomyidae <i>Zegdoumys namibiensis</i> <i>Tsaukhaebmys calcareus</i></p> <p>Hyaenodontidae Hyaenodontinae Proviverrinae <i>Pterodon</i> sp. Genus indet.</p> <p>Xenarthra? Genus indet.</p> <p>Todralestidae <i>Namalestes gheerbranti</i></p> <p>Chrysochloridae <i>Diamantochloris inconcessus</i></p> <p>Macroscelididae Genera indet.</p> <p>Hyracoidea <i>Namahyrax corvus</i></p> <p>Arsinoitheriidae <i>Namatherium blackcrowense</i></p> <p>Proboscidea Genus indet.</p>
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Systematic Palaeontology

Order Primates Linnaeus, 1758
Family Adapidae Trouessart, 1879
Subfamily Caenopithecinae Godinot, 1998
Genus *Namadapis* nov.

Type species: *Namadapis interdictus* sp. nov.

Diagnosis: As for the type species.

Etymology: ‘Nama’ means desert or wasteland, and *Adapis* is a genus name from Cuvier, 1822.

Distribution: Middle Eocene, Namibia.

Species *Namadapis interdictus* nov.

Holotype: GSN BC 1’17, an incomplete right lower jaw preserving p/3-m/3 and an anterior

alveolus for a uni- or biradicate p/2 (Fig. 4-7; Table 2).

Etymology: the Latin word *interdictus* is a translation of the meaning of the German word

“Sperr” in reference to the Sperrgebiet, the “Forbidden Territory”.

Type locality and horizon: Black Crow, in Southern Namibia. Small Eocene basin in the Sperrgebiet, infilled with limestone indirectly

derived from regional volcanic activity. Associated mammal fauna indicating a Lutetian age.

Diagnosis: Small adapid close in size and morphology to *Microadapis sciureus* and *Adapoides troglodytes*. Differs from both of these genera by a higher degree of cristodonty, a very high and pointed entoconid, the presence of a transverse protocristid and a very narrow groove in the third lobe of m/3. Differs from *A. troglodytes* by a broader talonid basin,

resulting in a greater contrast between trigonid and talonid, by the cristid obliqua more lingually oriented and the entoconid more posteriorly located in m/2; the whole comprises a higher and more extensive posterior shearing crest than in *A. troglodytes*.

Differs from *Microadapis* by its somewhat smaller size, the slightly longer and much

narrower p/3 and p/4 (especially in their posterior part); p/3 is higher than in *Microadapis*, p/4 has a less differentiated metaconid, and appears slightly more molarized by lengthening in GSN BC 1'17, whereas it is molarized by broadening in *Microadapis*.

Differs from the three Fayum caenopithecines by its much smaller size and

accompanying molar proportions. Differs from *Aframoni* by much simpler premolars, p/4 being narrower with less differentiated metaconid and hypoconid. Differs from *Masradapis* by the absence of marked posterior molar size increase, broader p/3 and lack of the salient and curved postprotocristid in the p/4.

Description

This fossil mandible is small, being 1.6 cm in total length. Its corpus is low; its ventral border shows a slight overall convexity, with the maximum height beneath m/2 being 3.5 mm (Fig. 5). On the whole the tooth row is horizontal. In lingual view, the crown of m/3 appears elevated postero-dorsally. In buccal view, only the third lobe of m/3 seems to be dorsally elevated. On the buccal side, two mental foramina open at mid-height of the jaw, one below the posterior extremity of p/3, the other below the anterior alveolus. On the lingual side, the posterior extremity of the symphyseal surface can be seen below p/3. Its

dorsal rim is subhorizontal, indicating a very anteriorly inclined, unfused symphysis. This symphyseal part is not very salient in occlusal view, indicating that the two jaws were not very divergent. Anteriorly, a short space separates the base of p/3 and the incomplete anterior alveolus, however the dorsal rim of the bone is not intact, and the crown of p/2 might have had some posterior extension, so that we cannot affirm whether a small diastema was present or not. The alveolus for p/2 (see stereopairs of the fossil, Fig. 5) appears of normal size for an unreduced p/2.

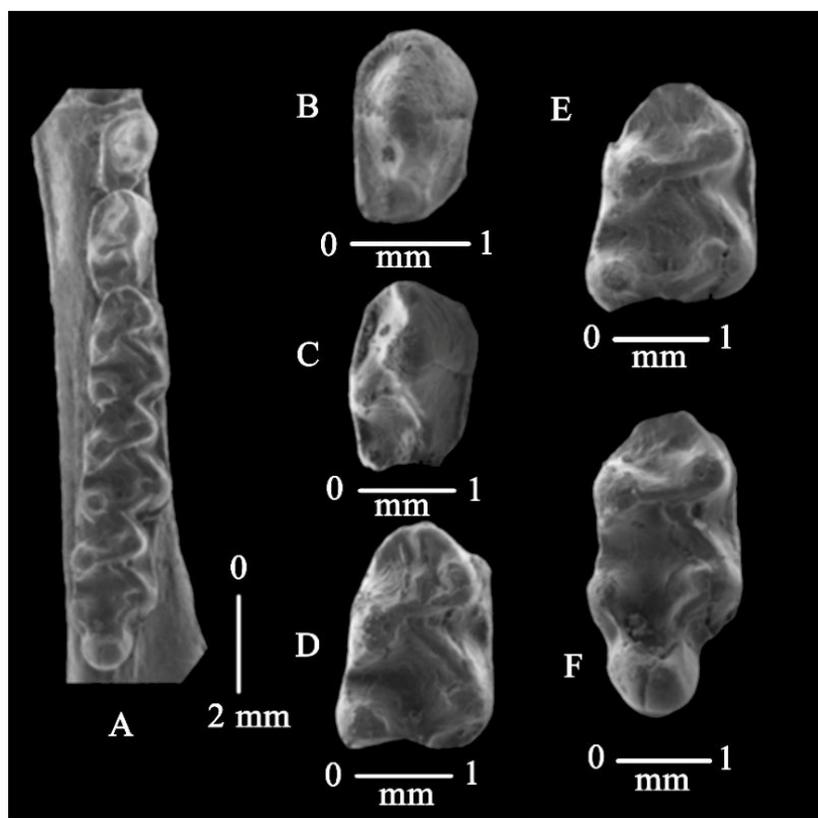


Figure 4. Scanning electron micrographs of the type specimen of *Namadapis interdictus* nov. gen. nov. sp., all in occlusal view. A) the mandible with p/3-m/3; B) p/3; C) p/4; D) m/1; E) m/2; F) m/3 (scales : 1 mm except A which is 2 mm).

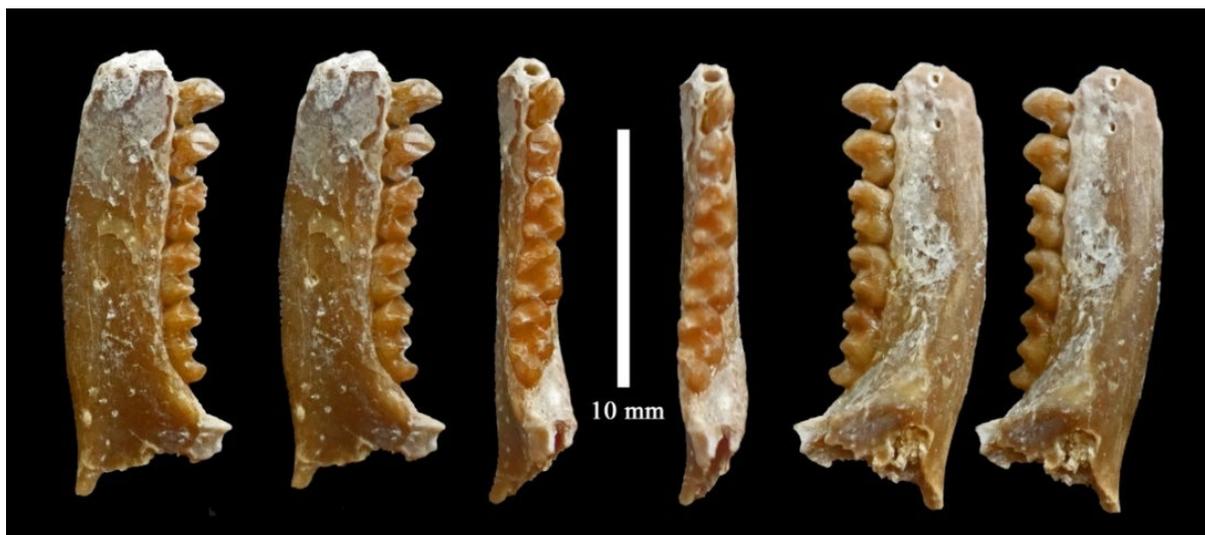


Figure 5. Stereopairs of GSN BC 1'17, type specimen of *Namadapis interdictus* nov. gen. nov. sp. in lingual (left), occlusal (middle) and buccal (right) views (scale : 10 mm).

A small piece of bony septum on its buccal side could indicate that the anterior wall of this alveolus was postero-ventrally inclined (as would be e.g. the alveolus for the posterior root of a biradicate p/2); the included root would have been shorter than the anterior root of the p/3, which appears long and anteriorly inclined

on a radiograph. However, this is not proof that the p/2 was biradicate, and we have no information concerning the presence of a p/1. A canine with a posteriorly inclined root might have reached the space below this alveolus, however this is again very speculative. In fact, the dental formula remains uncertain.

Table 2. Measurements (in mm) of the teeth of GSN BC 1'17, type specimen of *Namadapis interdictus* nov. gen. nov. sp., from Black Crow, Namibia.

Teeth	p/3	p/4	m/1	m/2	m/3	p/3 – m/3	m/1 – m/3
Length	1.66	2.24	2.46	2.81	3.53	11.76	8.02
Width	0.99	1.31	1.73	1.96	1.99	--	--

The p/3 is smaller than the p/4, but it is slightly taller than it. It is biradicate, with a single cuspid, the protoconid, which swells from the apex down to mid-height of the tooth, below which the anterior margin of the tooth curves postero-ventrally. Slightly above mid-height, the postprotocristid splits into two crests, a lingual one which descends abruptly and stops at the base of the protoconid, a buccal one which descends and slopes a little bit posteriorly where it joins the two cingulids. A short, thin and slightly inclined cingulid is visible only at the posterior extremity, close to the crest mentioned immediately above. The lingual cingulid is more developed, almost complete, very thin at the slight median convexity, well-formed on both sides; anteriorly, it makes a concavity in which the cingulid thins out as it rises to mid-height of the crown; posteriorly, it is at first

subhorizontal but then rises more steeply towards the junction between the post-protocristid and the small buccal talonid tip. This way, the lingual cingulid surrounds a short inclined talonid concavity; however, there is no real talonid basin, nor a distinct talonid cusp. A remarkable aspect of p/3 and of p/4, is that in occlusal view the talonid part is transversely narrower than the anterior part. This is in marked contrast with many early primates in which a broadening of the posterior part of p/4 and p/3 occurred early in geological time (earliest Eocene *Teilhardina*, *Donrussellia* and *Cantius*).

The p/4 is much larger than the p/3, not only longer, but also broader (see Table 2), but it is somewhat lower. The protoconid has a rounded apex when seen in profile. The preprotocristid is less steep, directed a bit more anteriorly than in the p/3. Where it joins the

lingual cingulid which is steep anteriorly, a small anterior bulge and a slight swelling suggest the presence of an «incipient paraconid» which begins at mid-height of the protoconid. The antero-lingual cingulid forms a wide curve, rising posteriorly along the metaconid, into which it merges. The metaconid is located postero-lingually and ventrally with respect to the protoconid, and is clearly recognisable by its mass. Its apex is elevated well above mid-height of the crown in lingual view, but it is not bordered by any groove. Instead, it has broad concave surfaces that isolate it from the surface of the protoconid anteriorly and from the lingual surface of the postprotocristid posteriorly. In posterior view, the postprotocristid gives rise to a lingual crest quite high up the cristid, which is slightly ventrally inclined and which caps the metaconid. The main crest extends ventrally, and is slightly inclined buccally. In profile, it descends posteriorly as far as a shallow concavity, whereupon it rises towards the apex of the hypoconid which it almost reaches (thereby corresponding to a cristid obliqua). The hypoconid is not bordered by a buccal groove (no hypoflexid), but its position, more buccal than the protoconid in occlusal view, provides space on the lingual side for a talonid which has an inclined basin opening lingually. A lingual postcristid departs slightly posteriorly and ventrally from the apex of the hypoconid, outlining a small lingual tubercle (incipient entoconid). A short posterior cingulid on one side, and the postmetacristid visible only near the base of the metaconid, on the other, enclose a deep concavity analogous to the lingual notch of the talonid of the molars. The buccal cingulid is only expressed in the posterior part of the tooth; it is not clearly visible because of the slight wear that has affected this part of the tooth. Globally, this p/4 shows a particular type of molarization, marked by its elongation, the anterior extension and the lowering of the protoconid, the development of the hypoconid and an open, inclined talonid basin. It could be described as submolariform. However, in occlusal view, the apex of its trigonid is very narrow transversely, and curiously, its talonid is appreciably narrower at its base than the trigonid.

The three molars increase in dimensions from m/1 to m/3. All three are broader at the level of the talonid than at the trigonid, and this

is more marked in the m/1 than in the other two molars, because this tooth is narrower anteriorly. The trigonid in all three molars is very similar, the main difference being that the metaconid is clearly posterior to the protoconid in the m/1; it is only slightly posterior in the m/3 (in occlusal view the protocristid is almost transversely oriented, but in fact there is a slight posteriorly directed part on the protoconid after which it is oriented clearly transversely over most of its extent); the m/2 shows a morphology intermediate between that of the m/1 and that of the m/3. In posterior view, the protocristid of the m/3 forms a weak asymmetrical concavity (the arm is short on the protoconid side, which is low, whereas the arm is much longer on the side of the metaconid, which is clearly higher than the protoconid). In posterior or anterior view, the protocristid forms a more symmetrical concavity in the m/1 and m/2, a bit deeper in the m/1 than in the m/2 and m/3.

The anterior part of the trigonid is remarkably similar in the m/1, m/2 and m/3. The preprotocristid becomes lower as it curves antero-lingually; it extends as far as the paralophid which continues to decrease in height and thickness; the extremity of the paralophid weakens and fades out completely before reaching the base of the metaconid of the m/1; it almost touches the anterior base of the metaconid in the m/2, whereas in the m/3 it extends a bit further onto the lingual base of the metaconid. A slight difference exists in the m/1, where a light swelling of the paralophid at the base of the preprotocristid represents, with little doubt, a remnant of the paraconid. In lingual view, the extremity of the paralophid is slightly more ventral in the m/2 than in the m/1, and even more ventral in the m/3 than in the m/2.

In the three lower molars, in occlusal view the postmetacristid is strong, oriented postero-lingually. Towards its base it curves and becomes vertical in the m/2 and m/3, due to the narrow U-shaped talonid notch (in lingual view); this curve is absent in the m/1 in which the talonid notch is V-shaped. The hypoconid is the dominant cuspid in the m/1 and m/2; it is less so in the m/3 in which the talonid and its basin are narrower than in the m/2. The cristid obliqua is oriented antero-lingually. It ends slightly below the protocristid in all three molars, in the middle in m/3 and m/2, and more towards the metaconid side in the m/1

(without joining either the metaconid or the protocristid). The cristid obliqua is particularly long and elevated in the m/1 and m/2 and, correlated with this, the hypoflexid is long in m/1, slightly shorter in m/2 and even shorter in m/3. The entoconid is located further posteriorly than the hypoconid, strongly so in the m/1 and m/2, somewhat less so in the m/3. In lingual view it has a pointed silhouette; it is tall in m/1 and m/2, but less so in the m/3. The posterior crest is long (much more than the protocristid) and tall (less so than the protocristid). In occlusal view one observes a long posthypoconid cristid directed posterolingually, then a shorter branch which curves towards the apex of the entoconid. But in anterior and posterior views, it is a large median concavity which is visible, suggesting a longer postentocristid part (because it is

elevated). Of importance is the development of a long, tall postcristid. In the m/2, a slight posterior bulge evokes a hypoconulid, but it does not form a cuspid and is not bordered by grooves, and is thus not a true hypoconulid. The hypoconulid of the m/3 projects strongly dorsally and posteriorly. The crests which depart from its apex border a long, narrow valley.

The buccal cingulid is well-differentiated in the posterior part of the m/3, where it rises quite high. It is attenuated at the base of the protoconid in all three molars. Curiously it is not crested (not underlined by a groove) in the middle of the m/3, at the mouth of the hypoflexid. The cingulid is better differentiated in this zone in the m/2. It is globally more attenuated in the m/1.

Discussion

An interesting palaeobiological issue is raised by this small primate, namely to what kind of adaptation does this adapid morphology correspond? The best known adapines, *Adapis* and *Leptadapis*, weighed between 1 and 2 kg for the first, and 5 to 10 kg for the second (see e.g. Silcox *et al.* 2009). At such body dimensions, these species are clearly above Kay's threshold of 500 g, and their molars with extensive shearing crests and their molarized p/4 are classically explained as implying a folivorous adaptation. The same is true of *Caenopithecus*, *Afradapis* and *Masradapis*, which have much less molarization of the premolars, but have upper

molars with more developed shearing crests than adapines. They also have dental topographic variables indicating folivory with a high probability for the two former taxa, and folivory or insectivory with low probability on the basis of one individual, for *Masradapis* (Seiffert *et al.* 2018). Remarkably, *Namadapis* developed an adapine lower molar morphology at a small body size (88 g for *N. interdictus* when using the equation for m/1 in Gingerich *et al.* 1982). It was too small to be folivorous. Hence what might have been its diet? A high proportion of insects is likely, but this possibility needs to be tested by microwear studies.

Detailed Comparisons

The teeth in the Black Crow mandible show a suite of characters that indicate adapid affinities. The three molars with elevated crests, the long relatively straight paralophid which descends to the base of the metaconid, the large hypoconid and the expansive talonid basin, the deep entoconid notch and the entoconid located posteriorly behind the level of the hypoconid, are all characters which are derived in comparison with the most primitive adapiformes (early Cercamoniinae and Asiadapinae), and contrast with the characters of djebelemurids and other African lemuriformes or stem lemuriformes. These high crests and the long paralophid occur in

adapids in general. In fact, this small African fossil is morphologically closely similar to, and has almost the same dimensions as, *Microadapis sciureus* from Egerkingen γ , Switzerland (MP 14, Middle Eocene, Europe) and *Adapoides troglodytes* from Shanghuang (Middle Eocene, China) (Fig. 7). It also has clear affinities with the much larger Fayum Caenopithecines, being closest to *Masradapis tahai* from BQ-2 (late Eocene, Egypt) (Fig. 7).

The posterior part of the mandible can be compared with the type specimen of *Adapoides troglodytes*, a lower jaw containing m/2 and m/3 (IVPP V11023) from the Shanghuang fissure fillings, Middle Eocene, Jiangsu, China

(Beard *et al.* 1994). The two fossils have the same dimensions. They are close in overall morphology, but several important characters show that they belong to distinct genera (Fig. 6-7). On m/2 and m/3, the protocristid is more transverse in *Namadapis interdictus*, more postero-lingually oriented in *A. troglodytes*. In m/2, the talonid basin is transversely broader and the entoconid more posteriorly located, resulting in a longer and higher postcristid in *N. interdictus*. The entoconid is also more salient into the basin in *A. troglodytes*. In *N. interdictus*, the cristid obliqua is more lingually oriented, whereas it is more anteriorly oriented in *A. troglodytes*, which appears less typically adapine for these characters. In m/3, the talonid basin is much longer in *A. troglodytes*, bordered buccally by the two main crests of the hypoconid which, in occlusal view, make a wide obtuse angle. In *N. interdictus*, the posthypocristid is strongly

lingually directed, abbreviating the basin, before abruptly turning to border the narrow posterior valley. By its longer and broader talonid basin in m/3, *A. troglodytes* resembles more typical adapines, whereas *N. interdictus* is unique in this respect. Other less significant differences include a slightly shorter paralophid in *A. troglodytes*, the posterior wall of the metaconid which appears more vertical in lingual view in *A. troglodytes* than in *Namadapis interdictus*, and its entoconid appears less antero-posteriorly narrow. Another minor difference on the protoconid is probably due to wear on IVPP V11023. On the whole, there is no doubt that these two fossils belong to different genera. *N. interdictus* seems to be somewhat more derived towards adapine characters for its m/2, but it also possesses an unusual m/3 with an abbreviated and posteriorly very narrow talonid basin.

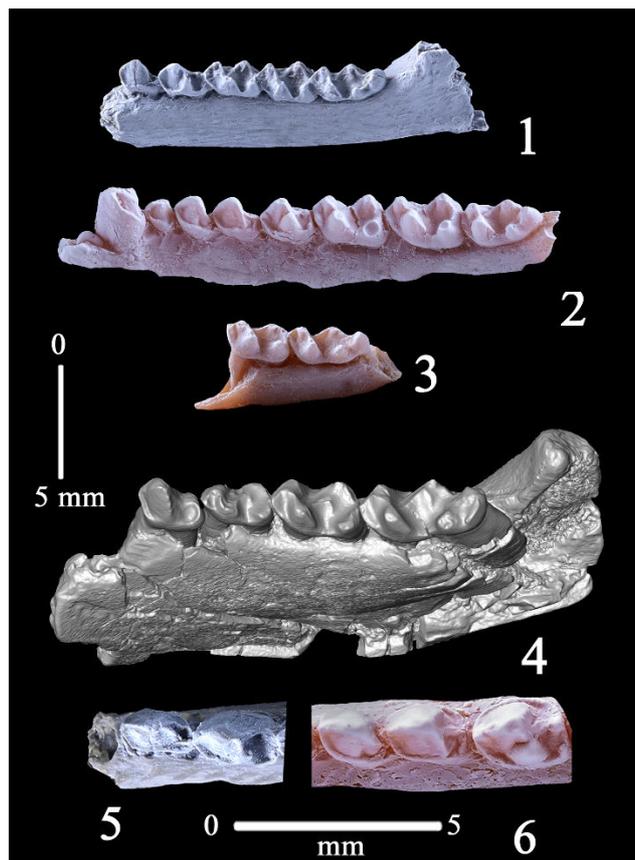


Figure 6. Comparisons of the lower jaws of (1) *Namadapis interdictus* nov. gen. nov. sp. right mandible with p/3-m/3, GSN BC 1'17, (2) *Microadapis sciureus*, left mandible with c/1-m/3, BNM Eh 750 (image reversed), (3) *Adapoides troglodytes*, right mandible with m/2-m/3, IVPP V 11023, and (4) *Masradapis tahai*, right mandible with p/4-m/3, CGM 83720 (from Seiffert *et al.* 2018), oblique lingual views. (1-3) are photographs of white-coated epoxy casts; (5) and (6) are enlarged occlusal views of white-coated epoxy casts of (5) right p/3-p/4 of *Namadapis interdictus* nov. gen. nov. sp. and (6) left p/2-p/4 of *Microadapis sciureus*, (6) has been inverted left-to-right to facilitate comparison (scale : 5 mm).

The type specimen of *Microadapis sciureus* from Egerkingen γ (BNM Eh 750) (Fig. 6, 7) is a beautiful jaw with a complete dentition running from the canine to m/3 (Stehlin, 1916; Szalay, 1974). The specimen is around 20% larger than *Namadapis interdictus*. Its molars show many similarities with those of *N. interdictus* although they also appear to be much less crested. Careful comparison of the specimens reveals that in buccal view, the cristid obliqua appears longer in *M. sciureus*, and the size difference between the protoconid and hypoconid appears more accentuated (hypoconid higher and more voluminous in comparison with the protoconid; or protoconid comparatively reduced, in *Microadapis*). In

lingual view, the talonid notch is longer anteroposteriorly in *M. sciureus*, and the entoconid summit is more rounded than in *N. interdictus*. The posterior walls of their metaconids are remarkably similar, with the same slight posterior bulge of the postmetacristid not far from its summit (a typical adapid character). The differences could be accounted for by a slight further differentiation toward adapine characters, linked with an increase in size in *M. sciureus*. However, there are differences in the shape of the paralophids, linked to a clearly more anteriorly developed preprotocristid in the three molars of *Namadapis*.

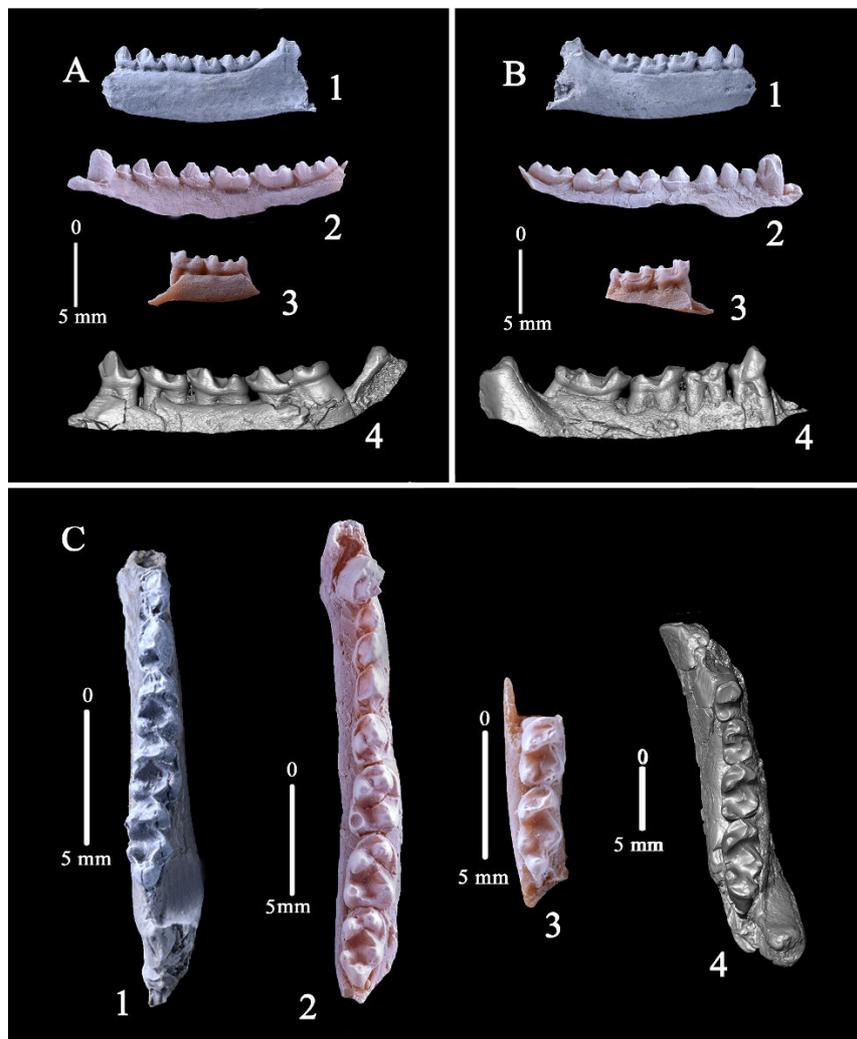


Figure 7. Comparisons of the lower jaws of (1) *Namadapis interdictus* nov. gen. nov. sp. right mandible with p/3-m/3, GSN BC 1'17, (2) *Microadapis sciureus*, left mandible with c/1-m/3, BNM Eh 750 (images reversed), (3) *Adapoides troglodytes*, right mandible with m/2-m/3, IVPP V 11023, and (4) *Masradapis tahai*, right mandible with p/4-m/3, CGM 83720 (from Seiffert *et al.* 2018). (A) lingual views, (B) buccal views, (C) occlusal views of images that have been brought to the same m/2-m/3 length in order to facilitate comparisons (scales : 5 mm).

The paralophid of m/1 is shorter in *M. sciureus*, bearing a slight lingual thickening which could be a remnant of a paraconid, and for this feature *Microadapis* appears more primitive. Furthermore the higher and more pointed entoconids of *Namadapis*, so striking in lingual view, are apomorphic in comparison with cercamoniines, and also advanced over the more bunodont shape in *Microadapis*. The premolars show even more significant differences. Both premolars in *M. sciureus* are broader in outline in occlusal view and have better-developed cingulids (Fig. 6). The p/3 is lower in *M. sciureus*. Its postprotocristid diverges into two crests, a buccal one joining the posterior cingulid as in *N. interdictus*, and a well-expressed lingual one reaching the lingual cingulid, in contrast with *N. interdictus*. In both p/3 and p/4, in lingual view, the anterior cingulid is less dorsally curved in *M. sciureus* than in *N. interdictus*. The posterior part of p/3 is much broader in *M. sciureus*, posteriorly limited by an extensive, well-formed, transverse cingulid; short talonid concavities are thus better developed lingually and buccally in *M. sciureus*. The p/4 is also broader in occlusal view in *M. sciureus*. Its metaconid is more voluminous, salient lingually, and better isolated from the protoconid by a deep anterior groove. The talonid basins have a similar extension, but that of *M. sciureus* appears better differentiated because it is lingually bordered by a high continuous cingulid. Concerning metaconid size and talonid differentiation, the p/4 of *M. sciureus* would appear slightly more molarized than that of *N. interdictus*. However, because it is more elongated, with a lower protoconid in lingual view and a less abrupt preprotocristid, the p/4 of *N. interdictus* appears to be more molarized in a different way (by comparison with primitive cercamoniine p/4). The p/4 of the two taxa appears to be affected by different processes, slight molarization by broadening in *M. sciureus*, and molarization by lengthening in *N. interdictus*.

Comparisons with later African Adapidae (Caenopithecinae) are mandatory, and at the same time are somewhat frustrating. The latest Eocene *Aframonius dieides* and the early late Eocene *Afradapis longicristatus* and *Masradapis tahai* are so much larger and so much more derived in their respective directions (Simons *et al.* 1995; Simons &

Miller, 1997; Seiffert *et al.* 2009, 2018) that proposing close links with one or the other is speculative. *Aframonius* has relatively broad and short p/3 and p/4, which would appear to be more in line with the morphology of *Microadapis* than with that of *Namadapis interdictus*. *Afradapis*, with its long p/4 which is relatively narrow posteriorly, appears more in line with *Namadapis interdictus* for p/4 lengthening. However, the morphological gap between the two taxa is enormous, *Afradapis* having lost p/2, and its specialised p/3 forming an anterior honing mechanism convergent with that of catarrhines (Seiffert *et al.* 2009). *Masradapis tahai* is the closest in overall morphology, probably linked to the fact that it is also the smallest of the three Fayum caenopithecines (Seiffert *et al.* 2018). Concerning premolar morphology, its p/4 has a very similar overall shape, and strangely it does not have a cuspidate metaconid. However, in the two taxa the postero-lingual crest descending from the protoconid is columnar and located exactly at the place of the metaconid, making the morphological difference between their p/4 small (especially as the metaconid of p/4 on GSN BC 1'17 is not isolated by grooves); *Namadapis* p/4 also bears a small entoconid, which is lacking in *Masradapis*. On the whole, *Masradapis* has a somewhat more simplified p/4 and a posteriorly broader p/3 than *Namadapis*, differences which are moderate. Concerning molar morphology, which is quite stereotyped among the group, *Namadapis* appears close in overall proportions to *Masradapis*, but is much smaller. However, it also differs from *Masradapis* by several features: 1) the seemingly broader and more ventro-lingually inclined paralophids of its molars (the groove isolating the paralophid is better formed, more horizontal and isolates a narrower paralophid on *Masradapis* molars); 2) the molars do not show the strong distal increase in size observed in *Masradapis*; 3) the m/1 does not present the cristid obliqua directed toward the summit of the metaconid; and 4) the third lobe of m/3 does not show the transverse broadening present in *Masradapis*. On the whole, *Namadapis*, which is much smaller than *Masradapis*, also appears to be more primitive for the majority of their differences, and ambiguous for a few of them (e.g. the primitive or derived status of the cristid obliqua of m/1

joining the summit of the metaconid would depend on the outgroup: being known in the very primitive *Donrussellia* and *Cantius*, it could be considered primitively retained in *Masradapis* and early lost in *Namadapis*, however, being absent in *Microadapis* and the other caenopithecines, it would appear more likely to be autapomorphic in *Masradapis*. The same is true of the non-cuspidate p/4

metaconid, which could be considered primitive by comparison with some anchomomyines, which have no p/4 metaconid, but which seems more likely to be derived by comparison with a number of other primates including *Microadapis* and other caenopithecines, which have a cuspidate p/4 metaconid).

Phylogenetic assessment of *Namadapis*

Given the variety of methods and results present in the recently published phylogenetic analyses involving fossil Adapiformes, we found it difficult to select the kind of formal phylogenetic analysis that should be done. Concerning the taxa of interest here, we note that many analyses recover a family Adapidae containing the well-supported Adapinae (known since Stehlin, 1912), the Caenopithecinae (*Caenopithecus*, *Aframoni*, *Afradapis*, *Masradapis*), and *Microadapis*. However, even at this level Ni *et al.* (2016) find *Periconodon* and Ekgmowechashalidae within this clade as a sister group of the Adapinae. This surprising result will not be endorsed here because we cannot recognize in *Periconodon* characters which would ally it with adapids. Concerning *Microadapis sciureus*, both of the analyses of Ni *et al.* (2016) recover it as a primitive sister group of *Caenopithecus* + *Afradapis*, however they do not recover *Aframoni* here. In their unconstrained phylogenetic analysis, they find *Aframoni* to be a sister group of *Mahgarita*, both being primitive sister groups of *Djebelemur* and azibiids (but not “*Anchomomys*” *milleri*, despite the fact that it closely resembles *Djebelemur*). In the analysis constrained by a molecular scaffold, they find *Aframoni* in a very basal position, as a primitive sister group of notharctines, azibiids, sivaladapids and adapids. Such enormous discrepancies between two analyses of the same matrix are problematic: one can legitimately ask, what analysis should be preferred and why?

Among the four analyses provided by Seiffert *et al.* (2015) *Microadapis* is found to be a primitive sister group of adapines + caenopithecines in the parsimony analysis with a number of multistate characters ordered, with the only puzzling aspect that *Europolemur dunaifi* appears here at the base of

caenopithecines, whereas *Europolemur klatti* is at the base of a clade (*Darwinius* (*Mahgarita*, *Mescalerolemur*)). Another analysis with the same characters unordered yields *Microadapis* as a primitive sister group of (*Protoadapis* + *Pronycticebus*), and the latter clade as the sister group of the Adapinae, whereas the Caenopithecinae are not recovered: *Aframoni*, (*Afradapis*, *Caenopithecus*), *Europolemur dunaifi* and the preceding clade (Adapinae, *Microadapis* (*Pronycticebus*, *Protoadapis*)) are in an unresolved polytomy. The majority rule consensus of a Bayesian analysis of the same matrix does not recover caenopithecines because *Aframoni* is found to be a primitive sister group of (Adapinae + (*Afradapis*, *Caenopithecus*)), and *Microadapis* is found in a more basal position, in a polytomy involving a clade with most of the above-mentioned genera, a small (*Pronycticebus* + *Protoadapis*) clade, and a larger clade including anchomomyines (with *Mescalerolemur*!), azibiids and lemuriforms. Finally, in the parsimony and Bayesian analyses of the matrix with standard polymorphic scoring, *Microadapis* has two different positions in two different consensus: it is again a primitive sister group of adapines + caenopithecines (including *Europolemur dunaifi*) in the strict consensus, and, in the majority rule consensus (Seiffert *et al.*, 2015, fig. 17) it is in a completely different place, as a primitive sister group of (*Protoadapis*, *Pronycticebus*), and the latter clade lies in a very basal polytomy. Again, such differences between two kinds of consensus of the very same analysis leave us perplexed as to the significance of these formal analyses.

In the more recent analyses including the new caenopithecine *Masradapis*, Seiffert *et al.* (2018) again provide different kinds of analyses. *Microadapis* is found to be a primitive sister group of adapines +

caenopithecines (with *Europolemur dunaifi*) in a parsimony analysis (in this analysis, *Protoadapis* and *Pronycticebus* appear as primitive sister groups of *Cantius*, something that would seem historically unlikely). *Microadapis* jumps sideways to be a primitive sister group of (*Pronycticebus*, *Protoadapis*) at the base of a clade containing adapids, *Europolemur*, *Mahgarita* and *Darwinius* in a standard Bayesian analysis, and that same clade (*Microadapis* (*Protoadapis*, *Pronycticebus*)) is recovered in an extremely basal position in the Bayesian tip-dating analysis, the one chosen by the authors to discuss biogeographical scenarios.

One way to compare so many different formal analyses would be to compare the characters sustaining the nodes in all of them. Unfortunately the authors do not explicit the characters at the nodes, and it would be a long work to replicate all these analyses in search of these characters. Some difficulties in coding may be suspected for *Microadapis*, which appears especially unstable in these analyses: its molars can be described as relatively generalized, or recognized as incipiently adapid by comparison with the closely similar molars of *Leptadapis priscus*. Furthermore, the preceding analyses did not take into account *Adapoides troglodytes* because it is too fragmentary. However, we used *Adapoides* in our comparisons and we think that it yields crucial information for our inquiry.

We propose a phylogenetic assessment based on our explicit analysis of characters. First, it is clear that *Namadapis* is more primitive than Fayum caenopithecines and at the same time shares with them the adapid pattern of high cusp relief and long crests, lower molars with long and thin, linguo-ventrally inclined paralophid, high protocristid, high hypoconid and postcristid, deep talonid basin and deep lingual talonid notch, high posteriorly placed entoconid, elongated third lobe in m/3. Added to the biogeographic argument, the parsimonious interpretation is evidently that *Namadapis* belongs to the same clade of African Caenopithecinae, of which it represents an early and more primitive member. A more specific relationship with one of them is not straightforward: it could be allied with *Masradapis* with which it shares a p/4 with a non-cuspidate metaconid summit, however the p/4 would have to be secondarily shortened in *Masradapis* relative to

Namadapis (the same secondary shortening would be implied if *Aframoni* is considered, added to the re-development of a well-cuspidate p/4 metaconid); it could be judged more in line with *Afradapis* because the latter further increased its p/4 length, however *Afradapis* would have secondarily re-developed an isolated metaconid summit. Choosing between these hypotheses would require a better understanding of morphological trends and possible reversals in these genera, which are still separated from *Namadapis* by large size and adaptive gaps.

To facilitate the discussion of more distant taxa, we employ the term of cristodont (Rosenberger *et al.* 2015) to characterize molars which emphasize shearing crests, especially the high transverse shearing cristids present on the lower molars of specialized Adapinae (with cuspid merged into the high crests, elongation of the postmetacristid and development of a metastylid in advanced species of *Adapis* and *Leptadapis*, etc.). More or less advanced states of these characters (see also above the list given in caenopithecines) have been recognized for a long time to place some species and genera in a family Adapidae. If we now turn to the more primitive taxa for which we made detailed comparisons above, it is clear that *Namadapis* is more advanced toward cristodontology than the larger *Microadapis*. *Microadapis* itself has molars remarkably similar to those of the larger *Leptadapis priscus*. It is distinct from the later adapines by the retention of a non-molariform p/4, whereas “true adapines” have molarized p/4s. Given the unusual degree of cristodontology reached by *Namadapis* at a very small size, it seems parsimonious to recognize two different lineages (subfamilies), caenopithecines in Africa characterized by their early acquisition of a high cristodontology at small body sizes (added to a precocious molarization of p/4), and adapines in Europe characterized by a lesser degree of cristodontology at larger body sizes (and a later continuous increase in cristodontology in the lineages of *Adapis* and *Leptadapis*; lengthening of p/4 absent in *Microadapis*, and p/4 molarized in the “true adapines”). In summary, *Namadapis* and *Microadapis* belong to two different broad lineages of the same family Adapidae.

It is difficult to assess *Adapoides* in this context, due to the fragmentary nature of the published lower dentition (more has been

announced in an abstract; Coster *et al.* 2012b). *Adapoides* is not as highly cristodont as *Namadapis*, it does not possess entoconids as high and pointed in lingual view. It is still clearly adapid and would appear on the whole to be more similar to the larger *Microadapis*. One exception could be the more anteriorly

projecting preprotocristid of its m/2, which recalls *Namadapis* more than *Microadapis*. In any case the material is insufficient to propose more specific relationships between *Adapoides* and the other small adapids discussed above. The phylogenetic comments will be continued after the reappraisal of *Notnamaia*.

Reinterpretation of *Notnamaia* as an Adapidae and Dispersal of the Family into Africa

A primate maxilla (GSN BC 6'08) with M2/ and M3/ from the same limestone outcrop at Black Crow was described as an anthropoid by Pickford *et al.* (2008), "*Namaia*", and renamed *Notnamaia bogenfelsi* (Pickford & Uhen, 2014) as the name *Namaia* was pre-occupied. Because the molars of this maxilla are generalized, not evidently diagnostic at the family level, Pickford *et al.* (2008) placed it as "family incertae sedis". Few scholars endorsed the attribution of *Notnamaia* to anthropoids. Seiffert (2012) suggested that it was likely a stem or crown strepsirrhine, also noting similarities with some European anchomyiids. It is again mentioned as a possible lemuriform-like strepsirrhine by Gunnell *et al.* (2018). The molars of *Notnamaia* are too large to be ascribed to the same species as *Namadapis interdictus*, but the difference in size is not great. Pickford *et al.* (2008) emphasized their bunodont appearance, however, taking into account a marked degree of wear, and looking at the profile of the molars in buccal view (Fig. 9), they appear as high and as pointed as in many adapiforms (*Europolemur*, *Anchomomys*, etc.) or oligopithecids. The overall shape of the M2/ does not recall that of the M2/ of *Adapoides*, described as an "*Europolemur*-like adapiform" by Beard *et al.* (1994). The M2/ of the latter genus is more transversely elongated and has almost no hypocone. The M2/ of *Notnamaia* has a marked narrowness of its lingual part relative to its buccal part. It looks transversely shortened in comparison with primitive adapiforms and *Adapoides*. However, such proportions are approached in some small cercamoniines, such as *Anchomomys gaillardi* and *A. quercyi* (Stehlin, 1916; Szalay, 1974). The relatively rounded hypocone of *Notnamaia* is unlike the crestiform hypocone found in many adapiforms. However, we know that the hypocone developed with different details in a large number of lineages (Godinot, 1994). The M2/ of *Notnamaia* can be

compared with BNM Eh 772, attributed to *Microadapis sciureus* (Stehlin, 1916; Szalay, 1974) (Fig. 9). The latter is smaller, bears a much larger hypocone and a lingual cingulum, resulting in a more quadrangular tooth with little lingual narrowness and a marked posterolingual bulge. If we make abstraction of the big size of the hypocone, a cusp well known for its growth in many lineages, the overall structure and proportions of the two molars are quite similar (Fig. 9). Other details which differ are the better developed ectocingulum in *Microadapis*, and the paraconule larger than the metaconule in *Microadapis*, whereas the reverse is true in *Notnamaia*. Despite these differences, there are two unusual characters which are shared between *Microadapis* and *Notnamaia*: the fact that the hypocone is rounded, and the presence of a cuspidate metaconule, exceptional in adapiforms, and conspicuous in *Notnamaia* (possibly having contributed to the erroneous impression of bunodonty). These two rare traits might well reflect some phylogenetic relationships between them. Furthermore, there are two important characters of *Notnamaia* which fit with an adapid affinity, the antero-posteriorly broad trigon basin and the unreduced M3/, congruent with the posteriorly elongated m/3 present in the group. For these reasons, we think that *Notnamaia* is best interpreted as a primitive adapid, possibly sharing some rare traits with *Microadapis* in its upper dentition. Consequently, *Notnamaia* and *Namadapis* are probably closely related to each other. Another interesting detail about the upper molars of *Notnamaia* is that their centrocrista is slightly deflected toward the buccal midline of the upper molars, the very character which will be accentuated to make a mesostyle in the Fayum *Masradapis* and *Afradapis* (Fig. 9). There is little doubt that *Namadapis* and *Notnamaia* both represent primitive members of the African caenopithecines discovered in recent decades in the late Eocene of the Fayum

(Simons *et al.* 1995; Seiffert *et al.* 2009, 2018). The primitiveness of the upper molars of *Notnamaia* in comparison with the typical Fayum caenopithecines suggests an age for Black Crow clearly older than BQ2 in the Fayum (37 Ma), and their primitiveness in comparison with *Microadapis* (smaller hypocone in *Notnamaia*) even suggests an age possibly older than the European MP 13-14 levels (42-45 Ma, Escarguel *et al.* 1997), older than the Eckfeld Maar, dated at 44 Ma and which yielded the more derived *Adapis priscus* and possibly *Microadapis sciureus* (Mertz *et al.* 2000; Franzen 2011). However, this age suggestion remains tentative because, as seen above, these fossils clearly belong to different adapid lineages.

Our discussion relies heavily on the affinities of *Namadapis* and *Notnamaia*. In this context, it is interesting to recall the presence in Chambi, Tunisia (Fig. 8) of two lower molars which were found enigmatic (adapiform or ungulate) when they were described (Court, 1993), which are however considered adapid since the discovery of Fayum caenopithecines (Seiffert, 2012). They are much larger than the lower molars of *Namadapis*, and differ from them at least by their twinned entoconid and hypoconulid. Could they belong to *Notnamaia*? In any case they now confirm a diversification of adapids early in Africa.

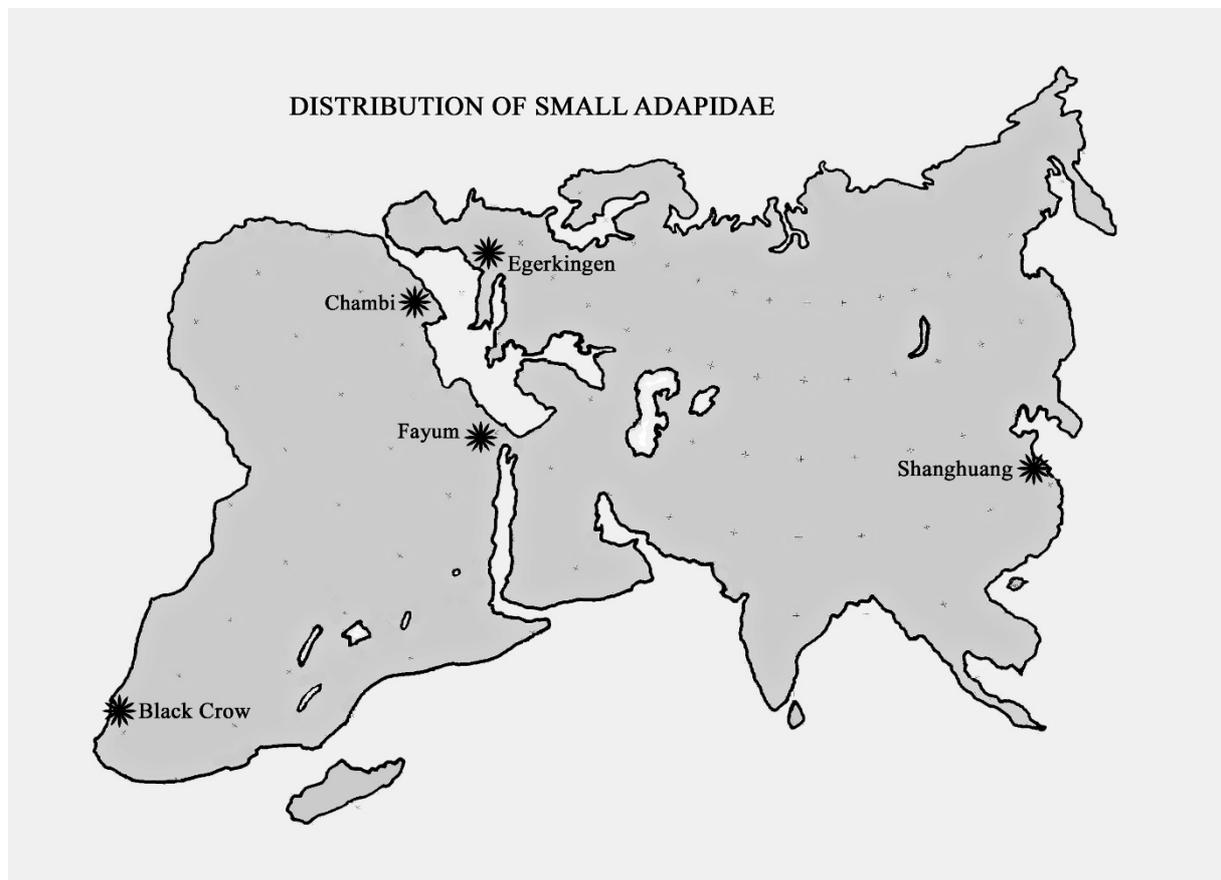


Figure 8. Map showing the location of the small adapids which show some similarities to the Black Crow specimen (*Microadapis* from Egerkingen, Switzerland, *Adapoides* from Shanghuang, China, and fossils from the Fayum and Chambi in North Africa).

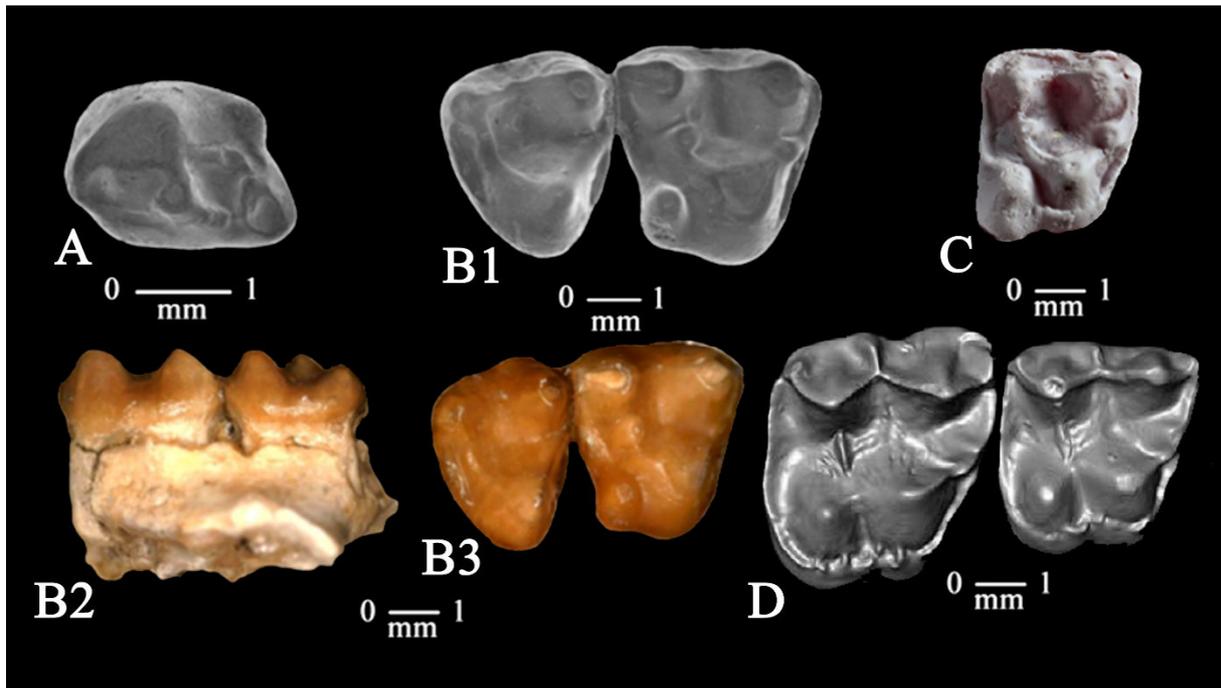


Figure 9. A) Scanning electron micrograph of the GSN SN 15'08, p/4 of a small anthropoid from the late Eocene of Silica North, Sperrgebiet in Namibia, in occlusal view. B1) to B3) are views of GSN BC 6'08, the holotype maxilla with M2/ and M3/ of *Notnamaia bogenfelsi* from the Lutetian of Black Crow, Namibia; B1) scanning electron micrograph in occlusal view; B2) and B3) natural light images, B2) buccal view, B3) occlusal view; C) BNM Eh 772, *Microadapis sciureus* from Egerkingen, occlusal view of left M2/ (image reversed), D), *Masradapis tahai* right M1/ (DPC 26110) and M2/ (DPC 26129) from the Fayum, Egypt, occlusal view (image from Seiffert *et al.* 2018) (scales : 1 mm).

If we now turn to the Chinese *Adapoides troglodytes*, its upper molars increase considerably the morphological gap with *Notnamaia* (Beard *et al.* 1994). Its M2/ is transversely elongated and without hypocone, which makes it much more primitive than *Notnamaia* (a small incipient hypocone is present on one of the upper molars from Shanghuang, possibly an M1/). However, *Adapoides* has already lost its metaconule and it possesses an almost complete lingual cingulum, two characters which would be derived in comparison with *Notnamaia*. Again we are left with the conclusion that they belong to two different lineages, *Adapoides* appearing more primitive through its upper molar proportions and lack of hypocone. This leaves *Adapoides* as the closest sister-group for all other adapids, in agreement with Beard *et al.* (1994) and Gebo *et al.* (2007).

Because they did not take into account *Adapoides* in their phylogenetic analyses, Seiffert *et al.* (2018) postulated a dispersal from Europe to Africa of the ancestor of the African caenopithecines (with a return of *Caenopithecus* in Europe, which sounds very

strange due to the old age of Egerkingen γ relative to Fayum localities). Our comparisons lead us to infer dispersals from Asia to Africa on one side and to Europe on the other side, due to the apparent sudden appearance of adapids around MP 13-14 in Europe (Franzen, 1994; Godinot, 1998). A likely Asiatic origin for the Adapidae is strengthened by the fact that, among the small asiadapines from the early Eocene of India (Rose *et al.* 2009), there are teeth showing the early acquisition of adapid characters, e.g. the m/3 with a long transverse paralophid GU 1619, in figure 10 of these authors.

Thus, although a complete scenario is still far off, we think that there must have been at least one dispersal of an early adapid from Asia to Africa, a dispersal probably older than 44 Ma.

Another dispersal from Europe to Africa is implied in the broad phylogenetic analysis of Seiffert *et al.* (2018), who found that a common stem for azibiids, anchomomyines, djebelemurids and lemuriforms dispersed from Europe to Africa, with European anchomomyines later dispersing back to

Europe (unlikely scenario). A close relationship between anchomyiines and djebelemurids is not straightforward because known anchomyiines have large vertical lower canines whereas djebelemurids have small anteriorly inclined canines (Stehlin, 1916; Marigo *et al.* 2010; Marivaux *et al.* 2013). Furthermore, the same phylogenetic analysis led Seiffert *et al.* (2018) to infer an origin of the North American *Rooneyia* among azibiids and an origin of *Mescalerolemur* from the above-mentioned African stem, two hypotheses that we consider extremely

unlikely. Computer-based parsimony can lead to scenarios which are incompatible with the known fossil record (here e.g. the likeliness of *Mahgarita* and *Mescalerolemur* being North-American sister groups; Kirk & Williams, 2011). We refrain from entering into hypotheses concerning earlier dispersals because they are excessively speculative. The minimum sampling simply is not available. By contrast, our inference of one early adapid dispersal into Africa at least concerns one well identified family.

Diversity of Late Eocene Primates in Namibia

The originality of the two adapids from Black Crow studied above prompted us to re-examine two other fragmentary fossil primates from the Palaeogene of Namibia. They came from two different localities, Eocliff and Silica North, which are given the same age because they contain the same taxa of fossil rodents, and must be early Priabonian or Bartonian because silicified portions of the Eocliff unit are overlain unconformably by marine deposits of Nannoplankton zone NP 19-20 (Priabonian, Pickford, 2015a; Berggren *et al.* 1995). If this stratigraphic observation is true, at least the age of Eocliff must be Eocene. Colleagues who questioned this age may have to restudy the mammalian fossils, some of which were determined only in a preliminary way (some wrong identifications?). This question will have to be reassessed.

The lower p/4 from Silica North, which had been earlier ascribed to *Notnamaia* (Pickford *et al.* 2008) appears quite bunodont. We here provide a better illustration of this specimen (Fig. 9), a more complete description and some comparisons.

Even taking into account the wear at the tips of its protoconid and metaconid, this lower p/4 deserves to be called bunodont: it is low and inflated to a degree similar to that of small parapithecids. The azibiids, which have bunodont posterior molars, do not have bunodont premolars (Tabuce *et al.* 2009). A close comparison with the p/4 of *Qatrania fleaglei* (Simons & Kay, 1988) makes sense because they have the same dimensions. However they show morphological differences. In occlusal view, GSN SN 15'08 has a longer and narrower postero-lingual extension (Fig 9). The metaconid appears more

lingually positioned than it is in *Qatrania fleaglei*. It is difficult to say whether it was larger or not, due to wear and the absence of bordering grooves. In lingual view, there is a greater distance between the metaconid and the talonid cusp, which appears relatively high in *Q. fleaglei*, and low in GSN SN 15'08. This talonid cusp is located on the lingual third of the tooth but not at its lingual border (it is slightly buccal in relation to the metaconid). Buccally this low talonid cusp is linked to the crest descending posteriorly in the middle of the protoconid wall, and postero-buccally to a long, sinuous, more or less horizontal posterior cingulid. The posterior part of this p/4 is clearly broader and more complex than in *Q. fleaglei*. It also differs from *Qatrania wingi* and from *Abuqatrania basiodontos* (Simons & Kay, 1988; Simons *et al.* 2001). The marked posterior inclination of the posterior wall of the protoconid and of the posterior wall of the low talonid cusp, bearing a wear facet, all suggest that this p/4 was partly overlapped by the following m/1. It belonged to a species having a more compressed dentition than *Qatrania*. Some of these details, such as the median crest on the posterior wall of the protoconid, are found in *Biretia* (Seiffert *et al.* 2005a). However the overall shape differs a lot, *Biretia* appearing more "classic" in its morphology, GSN SN 15'08 appearing more extremely bunodont, distinct by its lingual talonid cusp, and probably p/4 more compressed below m/1.

A more fruitful comparison is with *Proteopithecus sylviae*, following a suggestion made to us by E. Seiffert (pers. comm.). We could not make precise comparisons under a binocular microscope because we do not have a cast of the lower dentition of *Proteopithecus*

sylviae. We calculated the dimensions of a p/4 of that species from the illustration of the dentition given by Miller & Simons (1997). We found 2.3 x 2.0 mm, very close to 2.1 x 1.8 mm given by Pickford et al. (2008) for the Namibian p/4 (and 2.3 x 1.6 mm if we calculate from our Figure 9). Measurements should be done in the future directly on specimens, with similar protocols, however these specimens are clearly very close in size. The shape of GSN SN 15'08 is indeed extremely similar to that of CGM 42209 as illustrated by Miller & Simons (1997). Their description of the preprotocristid fits exactly with that of the Silica North tooth. These authors mentioned variations of the distal cingulum, which extends around the buccal side of one p/4. The Silica North p/4 appears more slender on our Figure 9, however this is likely due to its different orientation, with less inclination of the buccal side. There is one clear, probably significant, difference between the Namibian p/4 and that of *P. sylviae*: the former has a comparatively smaller metaconid (no variation in metaconid size is mentioned by Miller & Simons, 1997, among their L-41 specimens). For this character, the p/4 of Silica North appears more primitive than that of *P. sylviae* from the Fayum L-41 locality.

It would be important to have more specimens to confirm our identification. We will refer the small Silica North primate to cf *Proteopithecus* pending the recovery of more material. The identification of this p/4 as probably pertaining to a proteopithecid is interesting in relation to the age of the fauna. Until now, *P. sylviae* and the other proteopithecid *Serapia eocaena* are known only from the latest Eocene L-41 locality of the Fayum. A younger age for the Silica North fauna, as suggested by some colleagues, would extend the range of proteopithecids into the Oligocene or even later, increasing the differences between North African and Sub-Saharan fossil faunas. For now, we consider it

more likely that the presence of cf *Proteopithecus* adds to other evidence for an Eocene age for Silica North (and the fact that some other elements of the fauna may need reassessment).

An isolated upper molar (GSN Nr 1) found in the locality of Eocliff is the holotype of *Namaloris rupestris*, which was initially referred to the Lorisidae (Pickford, 2015b). In fact, the affinities of this probable M1/ are not straightforward. It has at the same time a very primitive stamp with its posterior waisting, long postero-lingual postmetacrista suggesting a vestigial styler shelf, and well-formed parastyle projecting anteriorly, and a derived and rare character through the continuous anterior crest joining the protocone to the paracone. Among living lorisoids, we found a parastyle only on the M1/ of *Nycticebus coucang* (Maier, 1980) and among the fossil taxa a parastyle can be seen on the M1/ and M2/ of *Wadilemur elegans*, in which it does not project as far anteriorly (Seiffert et al. 2005b). Even the stem-lemuriform *Djebelemur* does not possess such a salient parastyle (Marivaux et al. 2013). Concerning the continuous connection between protocone and paracone, it is absent in all living and fossil lemuriforms except the extant *Varecia*, in which it is more posteriorly located and the postprotocrista is lost (a different morphology, Maier, 1980). On the whole, *Namaloris* could represent either a lorisoid more primitive than *Wadilemur* and *Saharagalago* from the Fayum on the basis of its global proportions and smaller hypocone (distinct from the latter two genera because of its continuous anterior crest), or a stem lemuriform. We do not know whether some characters such as the projecting parastyle and long postmetacrista could redevelop as part of an insectivorous specialization, thus blurring the phylogenetic signal. However, we want to stress how original this primate is, increasing the endemic aspect of the Namibian Eocene primates.

Conclusions

The Eocene primates from Namibia now comprise two adapids, one probable proteopithecid and an original lemuriform. The middle Eocene Black Crow adapids appear to be markedly distinct from the primates described until now from the late early or early middle Eocene of North Africa (azibiids and

djebelemurids, all considered to be stem lemuriforms; one adapid in Chambi), thus suggesting some degree of endemism of primate fossils in the middle Eocene, persisting in the late Eocene through the Eocliff lemuriform. They also underline how poor our knowledge of African Eocene primates still is.

In this context, we think that it is premature to discuss details of primate dispersals between Eurasia and Africa. The origin and dispersals of anthropoids remain highly controversial, for reasons similar to those mentioned above concerning early adapiform relationships. As an example, we recall that the position of *Afrotarsius* is pivotal to the question of African anthropoid origins. Afrotarsiidae are considered as early anthropoids by Chaimanee *et al.* (2012) and Beard (2016), however *Afrotarsius* is found as a tarsiid, nested among omomyiforms – which would be called tarsiiforms in that case – in the analyses of Seiffert *et al.* (2015, 2018) and Ni *et al.* (2016). Again we are left with enormous contradictions between different analyses of large datasets, all formal and based on computer-aided parsimony analyses, and without detailed discussions of these discrepancies by the authors. In his discussion of anthropoid origins, Beard (2016) did not take into account the hypothesis that an early tarsiiform may have colonized Africa and subsequently given rise to African anthropoids, a scenario which would respect the Tarsiiformes-Simiiformes dichotomy as well

as an early anthropoid colonization of Africa (hypothesis more extensively discussed in Godinot, 2015). A much better record is needed to solve these issues. We know through earlier fossils that dispersals between different continents can be traced to the genus level, with *Teilhardina* on three continents and *Cantius* in Europe and North America at the dawn of the Eocene. Until now, no African fossil has been identified as an amphipithecoid, neither has any Asiatic fossil been attributed to one of the three families of Eocene Fayum anthropoids. Earlier fossils are fragmentary, and in fact the number of dispersal events of putative anthropoids or stem anthropoids between Asia and Africa is unknown (Beard, 2016). Recent scenarios have been based on similarities of one upper molar (Marivaux *et al.* 2014) or a few extraordinary primitive teeth from Myanmar (Burma) (Chaimanee *et al.* 2012). In this context, the new Namibian adapids are important because their similarities to *Adapoides* and *Microadapis* indicate that we are at last coming closer to identifying one of the primate dispersals from Eurasia to Africa, within a well delineated family, in agreement with Seiffert *et al.* (2015, 2018).

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