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GEOLOGY AND PALAEOBIOLOGY OF THE NORTHERN SPERRGEBIET, NAMIBIA

by

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Mammalia from the Lutetian of Namibia

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The 2008 field season of the Namibia Palaeontology Expedition was notable for the discovery of four small, but extremely richly fossiliferous carbonate deposits of Palaeogene age. The geology of two of the occurrences was briefly described in the 1970s in unpublished reports by geologists employed by The Consolidated Diamond Mines Ltd., (now Namdeb) but at the time no fossils were recognised in them. The deposits are at Silica North, Silica South, Black Crow and Steffenkop. Mammals have been found in the first three deposits, the last one having yielded only gastropods and plants. Provisional identifications of the mammals indicate the presence of at least 15 taxa. Other vertebrates include fish, crocodiles, ranoids, pipids, amphisbaenians, lizards, snakes and birds. All the deposits are rich in gastropods, ostracods and plant remains. Among the freshwater snails there are lymnaeids, hydrobiids and planorbids, while the land snail fauna is dominated by *Dorcasia*, with some *Trigonephrus*, *Xerocerastus*, *Succinea* and possibly a pupillid. This report provides preliminary descriptions and interpretations of the mammals from the deposits, briefly discusses the palaeobiogeography of the faunas and provides a provisional age determination on the basis of biochronology.

Introduction

Palaeogene marine deposits in the Sperrgebiet, Namibia, were first recorded by German geologists in the 1920s and were correlated to the Eocene using the macrofauna (molluscs, sharks) that they yielded (Beetz, 1926; Böhm, 1926; Kaiser, 1926) an estimate that was confirmed by Siesser and Salmon (1979) on the basis of micropalaeontology. The latter authors estimated a Priabonian age for the Langental deposits (NP 19-20) which suggested an age of 35.5-34 Ma to Pickford and Senut, (2000). Fossils in terrestrial deposits of Palaeogene age have proven to be more elusive, various units such as the doline infilling at Chalcedon Tafelberg and the Blaubock Gravels being mapped as Palaeogene, but because they lacked vertebrate fossils, there was no direct proof of their age. The Chalcedon Tafelberg deposits were later transferred to the Middle Miocene (Liddle, 1971; Stocken, 1978) on the basis of a radio-isotopic age determination of a monchiquite lava considered to predate the 'crater' infilling. We here replace the sedimentary deposits into the Palaeogene. The Pomona Quartzites have generally been correlated to the Late Cretaceous. They are older than the bedded carbonates in the Black Crow Depression, and are thus pre-Lutetian in age, at least at that locality. The Blaubock Gravels unconformably overlie the Black Crow Carbonates (Pickford *et al.*, 2008) and are older than the classic Early Miocene site at Langental. The only fossils known from these gravels consist of tree trunks.

In 2008, the Namibia Palaeontology Expedition mapped six occurrences of stratified carbonate rocks in the Northern Sperrgebiet, all of which have undergone some degree of silicification (Pickford *et al.*, 2008). The sediment patches are small (400-500 metres diameter) and infill depressions in Proterozoic Gariep Dolomites. All six deposits proved to be fossiliferous. Chalcedon Tafelberg has been known to be fossiliferous since the 1920s (Wenz, 1926) as was a restricted deposit of chalcedonic limestone at Gamachab which yielded a single fossil snail (*Dorcasia*) (Wenz, 1926). The main body of calc-sinter at Gamachab is a Pleistocene deposit, not to be confused with the Palaeogene chalcedonic limestone. The four newly recognised deposits are at Silica North, Silica South, Black Crow (Kalbskopf, 1977), and Steffenkop (Kalbskopf, 1977). Of these freshwater carbonate bodies, all six have yielded gastropods and four have yielded vertebrates. Plant fossils are also represented in most of them.

The aim of this paper is to put on record the discovery of the first substantial Palaeogene mammal localities in sub-Saharan Africa, to provide preliminary descriptions and interpretations of the fossils and to discuss the chronological implications and biogeographic affinities of the faunas. Full treatment of the fossil assemblages, which hold much promise for the future, will require a concerted research effort that will take several years to come to fruition.

Palaeogene vertebrates of Africa: a brief review of previous work

Palaeogene mammal-bearing deposits of Africa and Arabia are concentrated in the north of the continent, notably in the Maghreb, Libya and Egypt (Fig. 1) (Annex 1) (Andrews, 1899; Arambourg, 1963; Beadnell, 1905; Bown *et al.*, 1988; Capetta *et al.*, 1978; Coiffait *et al.*, 1984; Cooke, 1972; Crochet, 1986; Gheerbrandt, 1987, 1992; Hartenberger *et al.*, 1997; Jeddi *et al.*, 1991; Mahboubi *et al.*, 1984b;

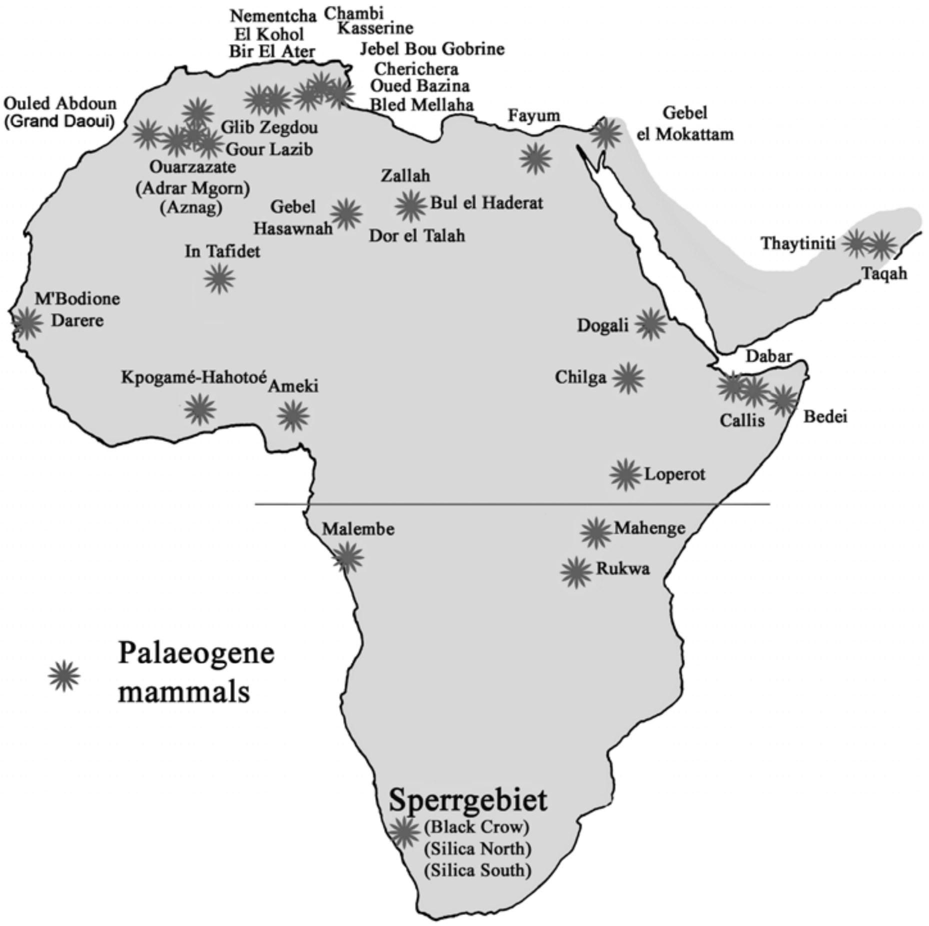

Figure 1. Palaeogene mammal-bearing localities of Afro-Arabia. Currently there are six Palaeogene terrestrial fossil localities known in the Sperrgebiet, three of which have yielded mammals, Silica North, Silica South and Black Crow. Several marine deposits of Palaeogene age are also known in the Sperrgebiet.

Sudre, 1979; Thomas *et al*., 1989, 2004; Vianey-Liaud, *et al*., 1994; Wight, 1980; Wood, 1968). Deposits further south in the continent are known but tend to be poorly fossiliferous (Bellair *et al*., 1954; Gorodiski and Lavocat, 1953; Kappelman *et al*., 2003; Sanders *et al*., 2004; Savage, 1956, 1969; Shoshani *et al*., 2006). Prior to the Sperrgebiet discoveries, only three Palaeogene localities south of the Equator have previously yielded mammals (Gunnell *et al*., 2003; Harrison *et al*., 2001; Hooijer, 1963; Pickford, 1986; Stevens *et al*., 2005a) and all of them are rather poorly fossiliferous.

The literature on Palaeogene mammals of Africa is dominated by a single locality, the Fayum, Egypt, (Fig. 1) which comprises a thick sequence of strata spanning the Late Eocene to Early Oligocene period. Discovered towards the end of the Victorian Era, the Fayum continues to yield large quantities of fossils belonging to many groups of mammals and other vertebrates (Abel, 1913; Anapol, 1983; Andrews, 1899, 1900, 1901a, 1901b, 1901c, 1902a, 1902b, 1902c, 1903a, 1903b, 1903c, 1904a, 1904b, 1905, 1906, 1907a, 1907b, 1908a, 1908b, 1909a; Andrews and Beadnell, 1902; Ankel-Simons *et al*., 1998; Beadnell, 1901, 1902, 1903, 1905; Black, 1978; Bown and Simons, 1984a, 1984b, 1987; Bown *et al.,* 1982, 1988, 1990; Cote *et al*., 2007; De Blieux and Simons, 1999; De Blieux *et al.,* 2006; Delmer, 2005; Depéret, 1907; Ducrocq, 1998, 2001; El Khashab, 1974, 1977, 1979; Fischer, 1986; Fleagle, 1980, 1983, 1986a, 1986b, 1988, 1994; Fleagle and Kay, 1983, 1985, 1988, 1994; Fleagle and Simons, 1979, 1980, 1982a, 1982b, 1983; Fleagle *et al.,* 1975, 1980, 1986a, 1986b, 1996; Ford, 1994; Gagnon, 1992, 1993, 1997; Gebo, 1988, 1989, 1993; Gebo and Rasmussen, 1985; Gebo and Simons, 1984, 1987; Gebo *et al.,* 1994; Gingerich, 1973, 1978, 1990, 1992b, 1993; Gunnell and Miller, 2001; Gunnell and Rose, 2001; Harris, 1978; Holroyd, 1994, 1995, 1999; Holroyd and Mussell, 2005; Holroyd *et al.,* 1996, 2006; Hooker *et al*., 2008; Kälin, 1960, 1961; Lewis and Simons, 2007; Matsumoto, 1922a, 1922b, 1923, 1924, 1926; Matthew, 1910; Meyer, 1973, 1978; Miller and Simons, 1997; Miller *et al*., 2005; Muldoon *et al.,* 2002; Osborn, 1906, 1907a, 1907b, 1908, 1909a, 1909b, 1910, 1912, 1919, 1921, 1922a, 1922b, 1923, 1934, 1936 + 1942; Petronievics, 1923; Pontier, 1907, 1909; Radinsky, 1967, 1973, 1974, 1977, 1979;

Rae and Simons, 1992; Rasmussen, 1986, 1989, 2001; Rasmussen and Nekaris, 1998; Rasmussen and Simons, 1988a, 1988b, 1991, 1992, 2000; Rasmussen *et al.,* 1990, 1992; Robinson and Seiffert, 2004; Rossie and Seiffert, 2006; Sanchez-Villagra *et al*., 2007; Sanders and Kappelman, 2002; Sanders *et al.,* 2004; Savage, 1956, 1965b, 1969, 1971; Savage and Coryndon, 1972; Savage and White, 1965; Schlosser, 1910, 1911, 1912; Schmidt, 1913; Seiffert, 2006, 2007a, 2007b; Seiffert and Simons, 1999, 2000; Seiffert *et al.,* 2000*,* 2003, 2004, 2005a, 2005b, 2007; Shoshani, 1992; Shoshani and Tassy, 1992; Shoshani *et al.,* 1989, 1996; Sigé, 1985a; Simons, 1959, 1960a, 1960b, 1961, 1962a, 1962b, 1963a, 1963b, 1965, 1967a, 1967b, 1967c, 1967d, 1967e, 1968a, 1968b, 1969a, 1969b, 1970, 1971a, 1971b, 1972, 1974a, 1974b, 1976a, 1976b, 1984, 1986, 1987, 1989, 1992, 1995a, 1995b, 1995c, 1996, 1997a, 1997b, 1997c, 1998; Simons and Bown, 1984, 1985; Simons and Chatrath, 1996; Simons and Delson, 1978; Simons and Gingerich, 1974, 1976; Simons and Kay, 1981, 1983, 1988; Simons and Miller, 1997; Simons and Rasmussen, 1989, 1990, 1994a, 1994b, 1996; Simons and Seiffert, 1999; Simons *et al.,* 1986, 1987, 1991, 1994, 1995, 1996, 1999, 2001, 2007; Stromer, 1903a, 1903b, 1908; Tassy, 1979, 1981, 1982; Tassy and Shoshani, 1988; Thewissen and Simons, 2001; Tobien, 1971, 1973a, 1973b, 1978; Van Couvering and Harris, 1991; Wood, 1968; Zittel, 1883).

The literature on other North African and Arabian Palaeogene deposits has grown in recent decades and includes descriptions of faunas similar in age to the Fayum deposits, but also material from much older strata spanning the Palaeocene and Eocene (Adrover *et al.,* 1977; Arambourg, 1951, 1963; Arambourg and Burrollet, 1962; Arambourg and Magnier, 1961; Arnould-Saget and Magnier, 1962; Barghoorn, 1977; Batik and Fejfar, 1990; Bellair *et al.,* 1954; Capetta *et al.,* 1978, 1987; Coiffait *et al.,* 1984; Cooke, 1968, 1972; Court, 1989, 1990, 1992a, 1992b, 1993, 1994, 1995; Court and Hartenberger, 1992; Court and Mahboubi, 1993; Crochet, 1984, 1986, 1988; Crochet *et al.,* 1990, 1991, 1992; De Bonis *et al*., 1988; Delmer, 2006; Delmer *et al.,* 2006; Fejfar, 1987; Gevin *et al.,* 1975; Gheerbrant, 1987, 1988, 1989, 1990, 1991, 1992, 1993, 1994, 1995, 1998; Gheerbrant and Hartenberger, 1999; Gheerbrant and Russell, 1989; Gheerbrant, *et al.,* 1993a, 1993b, 1995, 1996a, 1996b, 1998a, 1998b, 2001, 2002, 2003, 2005a, 2005b, 2006; 2007; Godinot, 1994, 1998; Godinot and Beard, 1993; Godinot and Mahboubi, 1992, 1994; Hartenberger, 1986; Hartenberger and Marandat, 1992; Hartenberger *et al.,* 1985, 1997a, 1997b, 1998a, 1998b; Holroyd and Maas, 1994; Jaeger *et al.,* 1985; Jeddi *et al.,* 1991; Kowalski and Rzebik-Kowalska, 1991; Lavocat, 1950, 1953a, 1953b, 1954; Mahboubi *et al.,* 1983, 1984a, 1984b, 1986, 1997; Noubhani, 1988; Noubahni *et al*., 2008; Sassi *et al.,* 1984; Shoshani *et al.,* 2001, 2006; Sigé, 1985b, 1991, 1993; Sigé *et al.,* 1990, 1994; Spinar and Rocek, 1978; Sudre, 1975, 1979; Sudre *et al.*, 1993; Tabuce, 1998; Tabuce and Marivaux, 2005; Tabuce *et al*., 2000, 2001a, 2001b, 2002, 2004, 2005, 2007a, 2007b; Thomas and Gheerbrant, 1992; Thomas *et al.*, 1989, 1988a, 1988b, 1991, 1992, 2004; Vianey-Liaud and Jaeger, 1996; Vianey-Liaud *et al.*, 1994; Wight, 1980; Zalmout, 2005).

Further south in Africa, Palaeogene mammals are poorly represented, and the literature is correspondingly brief (Andrews, 1920; Arambourg *et al.,* 1951; Arroyo-Cabrales *et al.,* 2003; Conraux, 2004; Dartevelle, 1935; Gingerich, 1992a; Gorodiski and Lavocat, 1953; Gunnell, *et al.,* 2003, 2005; Harrison, 2001; Harrison *et al.,* 1998, 2001; Hooijer, 1963; Kappelman *et al.,* 1992, 2003; Lavocat and Radier, 1953; Leakey *et al.,* 1995; Pickford, 1986; Pickford *et al.,* 1994, 1997; Stevens *et al.,* 2005a, 2005b, 2006).

Since the mid-1980s Palaeocene and Eocene localities have been reported in the Maghreb. In sub-Equatorial Africa, only one pre-Miocene mammal-bearing locality (Cabinda, Angola) (Pickford, 1986) was recorded prior 2000. At the beginning of this Century, two mammal-bearing localities were found in Tanzania (Gunnell *et al*., 2003; Harrison *et al*., 2001; Stevens *et al*., 2005a, 2005b). There was thus a major bias in the African Palaeogene palaeontological record to the Eocene-Oligocene boundary zone and the northern fringe of the continent and these biases have greatly influenced biogeographic and biochronological interpretations of the faunas. The Sperrgebiet discoveries should redress this imbalance to some extent, the occurrences being richly fossiliferous with well-preserved remains of a diversity of mammals of likely Lutetian age (Table 1).

Table 1. Ordinal and family level representation of mammals in the Sperrgebiet Carbonate deposits at Silica North, Silica South and Black Crow.

- Mammalia Linnaeus, 1758
  - Eutheria Gill, 1872
    - Order Cimolesta McKenna, 1975
      - Family Todralestidae Gheerbrant, 1991
    - Order Erinaceomorpha Gregory, 1910
    - Order Macroscelidea Butler, 1956
    - Order Creodonta Cope, 1875
      - Family Hyaenodontidae Leidy, 1869
        - Subfamily Hyaenodontinae Leidy, 1869
        - Subfamily Proviverrinae Schlosser, 1886
    - Order Pholidota Weber, 1904
    - Order Hyracoidea Huxley, 1869
    - Order Embrithopoda Andrews, 1906
      - Family Arsinoitheriidae Andrews, 1904
    - Order Primates Linnaeus, 1758
    - Order Rodentia Bowdich, 1821
      - Family Zegdoumyidae Vianey-Liaud, Jaeger, Hartenberger and Mahboubi, 1994
      - Family Myophiomyidae Lavocat, 1973
      - Family Diamantomyidae Schaub, 1958
      - Family Phiomyidae Wood, 1955
      - Family Bathyergidae Waterhouse, 1841

Systematic descriptions

Mammalia Linnaeus, 1758
Order Cimolesta McKenna, 1975
Family Todralestidae Gheerbrant 1991
Genus *Namalestes* nov.

Type species. *Namalestes gheerbranti* sp. nov.

Diagnosis. Large todralestid with cusplets on the anterocristid of the entoconid of the lower molars.

Derivatio nominis. The genus name combines *Nama* for the region of discovery with *lestes* the Greek word for thief, often used as the termination for genus names of insectivorous micromammals.

Species *Namalestes gheerbranti* nov.

Holotype. BC 3'08 right molariform tooth (m/1 or m/2).

Type locality. Black Crow, Sperrgebiet, Namibia.

Diagnosis. As for the genus.

Differential diagnosis. *Namalestes gheerbranti* differs from *Todralestes variabilis* by its greater dimensions (ca 3 times bigger) and by the presence of additional cusplets on the anterior cristid of the entoconid, such that the talonid valley is completely closed.

Derivatio nominis. The species is named in honour of Emmanuel Gheerbrant, for his contributions to our understanding of Palaeogene African Mammals.

Description. BC 3'08 is a right molariform tooth (m/1 or m/2) with the following dimensions : maximum length = 3.89 mm, breath of trigonid = 2.86 mm, width of talonid = 2.35 mm, maximum length of talonid (buccal) 2 mm, minimum length of talonid (lingual) = 1.57 mm. In occlusal view the trigonid is a closed V-shape (Fig. 2). The protoconid is very high (H = 3.62 mm) and pyramidal. The metaconid is significantly lower (H = 2.27 mm) than the protoconid and is also pyramidal in shape, and is situated in a more posterior position than the protoconid, such that the posterior wall of the protoconid-metaconid is oblique with respect to the antero-posterior axis of the tooth. The paraconid is somewhat damaged, and occupies an antero-lingual position, but was probably quite a bit lower than the metaconid. It has a pseudo-pyramidal form. The central valley of the trigonid is quite high. The talonid is slightly narrower and smaller than the trigonid. It is dominated by a strong hypoconid sporting a cristid obliquid which contacts the base of the posterior wall of the protoconid-metaconid at a right angle beneath the notch which separates these two cusps. A deep hypoflexid is present on the buccal side between the base of the protoconid and the hypoconid. The entoconid is smaller than the hypoconid, and its anterior cristid shows two well formed small cusplets. A small hypoconulid closes the talonid valley posteriorly. This valley is

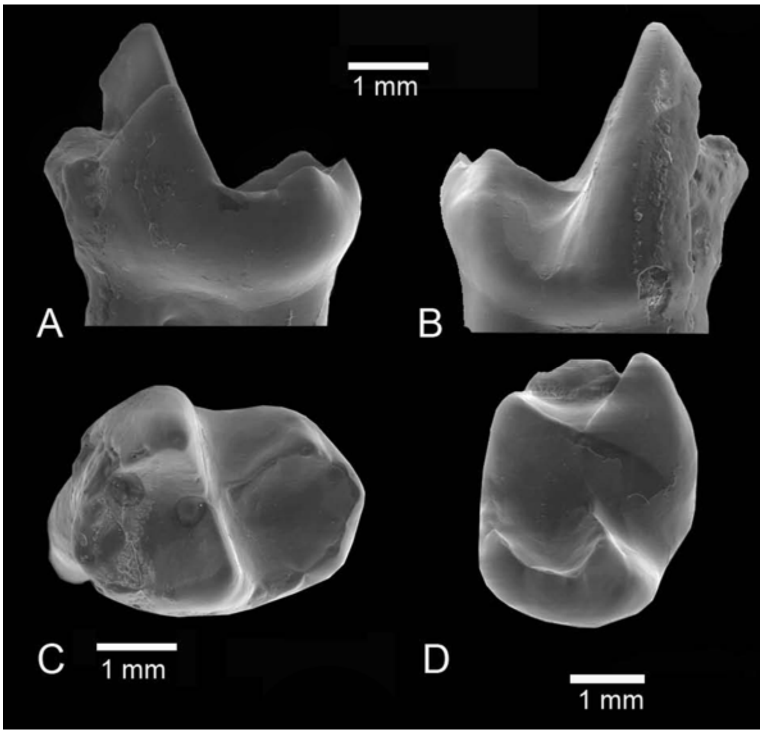

Figure 2. BC 3’08, *Namalestes gheerbranti* nov. gen. nov. sp., right lower carnassial from Black Crow, Northern Sperrgebiet, Namibia. A) lingual view, B) buccal view, C) occlusal view, D) oblique disto-occlusal view.

quite deep and is completely surrounded by cusplets.

Discussion. The tooth from Black Crow shows affinities to *Todralestes variabilis* from the Palaeocene of Morocco (Gheerbrant, 1991), the two species sharing lower molars with the same primitive tribosphenic pattern. The trigonid has the same length and almost the same breadth as the talonid. The metaconid is smaller than the protoconid and is displaced slightly posteriorly, which makes the posterior wall of the trigonid oblique. The proportions and disposition of the cusps is similar in the two species, except for the presence in *Namalestes* of cusplets on the anterior cristid of the entoconid. This is the main character which distinguishes *Namalestes* from *Todralestes* and other incipiently carnivorous forms such as *Cimolestes* (Gheerbrant, 1992), *Palaeosinopa* (Smith, 1997) or primitive creodonts (Smith and Smith, 2001). For the same reason it differs from *Widanelfarasia* from the Eocene of Egypt, which is considered to be a Tenrecomorpha (Seiffert and Simons, 2000; Seiffert *et al*., 2007). Cusplets appear to be present on the entocristid of a new Kelbidae from locality BQ-2 of the Fayum and is a character used in the diagnosis of the new family Kelbidae (Cote *et al*., 2007), which are also present in *Qarunavus* (Simons and Gingerich, 1974). The phylogenetic relationships of the Kelbidae and the Ptolemaiidae remain to be resolved ; the two families present an interesting mixture of derived and primitive characters to the extent that almost any relationship to primitive forms, such as described here, is possible.

Glibzegdouia differs from *Namalestes* by the more anterior position of the metaconid, such that the posterior wall of the metaconid-protoconid is transverse to the antero-posterior axis of the tooth (in *Namalestes* this wall is obliquely oriented). As a consequence the morphology of the talonid is different, being wider and more symmetrical in *Glibzegdouia*. In the latter feature, *Namalestes* resembles more closely *Ketketictis* from the Middle Miocene of Wadi Moghara, Egypt (Morlo *et al*., 2007), but in *Ketketictis*, the trigonid is much lower in comparison with the talonid. The genera *Glibzegdouia* and *Namalestes* share a well developed entoconid with the presence of an additional cuspid on the anterior cristid. Despite the resemblences, however, the structure of the teeth in these two genera is quite divergent, more carnivore-like in *Glibzegdouia* than in *Namalestes*.

Order Erinaceomorpha Gregory, 1910
Family Erinaceidae Fischer de Waldheim, 1817

Material. BC12’08, left M3/.

Locality. Black Crow, Sperrgebiet, Namibia.

Age. Probably Lutetian.

Description. BC 12’08 is a slender, three cusped tooth, lacking part of the lingual cusp (Fig. 3). It is 4.7 mm long and 1.6 mm broad and has two roots, the lingual one, which is substantially larger than the buccal one, flares strongly towards the palate. The buccal cusp is the tallest, the lingual one the lowest. The tooth possesses a wear facet along its mesial side at cingulum level, indicating that this tooth was transversely oriented in the maxilla, as are the third upper molars of Erinaceidae (Butler, 1948, 1984; Frost *et al*., 1991; Rich, 1981).

Discussion. Erinaceidae are known from deposits as old as the Palaeocene of North America and the Eocene of Asia and Europe (McKenna and Bell, 1997). In Africa, erinaceids have not previously been positively identified in Palaeogene deposits, but they are common from the Early Miocene onwards (Butler, 1984). The only previous report of a possible Palaeogene African erinaceid is *Chambilestes foussanensis* from Chambi, Tunisia, which was tentatively classed as an erinaceid by Miller *et al*., (2005) although the original authors (Gheerbrant and Hartenberger, 1999) classed the fossil as ?Lipotyphla or ?Erinaceomorpha. The Black Crow specimen, which was found in the same block of carbonate rock as an arsinoithere skull and a proviverrine tooth, indicates that the passage of

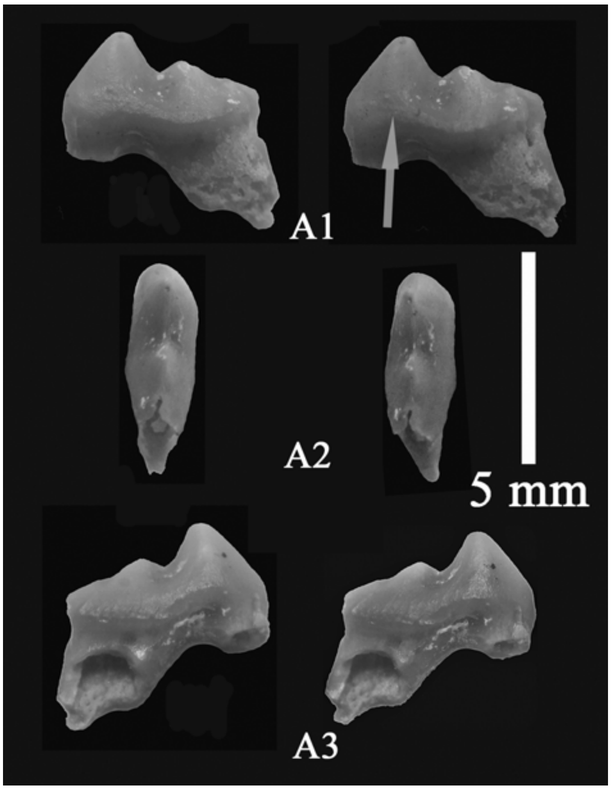

Figure 3. BC 12’08, Erinaceidae left M3/ from Black Crow, Sperrgebiet, Namibia. A1) stereo mesial, A2) stereo occlusal, A3) stereo distal views. The grey arrow shows the position of a wear facet that runs almost the entire length of the base of the crown on its mesial side.

hedgehogs into Africa occurred as early as the Eocene.

Order Macroscelidea Butler, 1956
Family Macroscelididae Bonaparte, 1838

Material. SN 10'08, left upper molariform tooth.

Locality. Silica North, Sperrgebiet, Namibia.

Age. Probably Lutetian.

Description. SN 10'08 is a quadricuspidate tooth with a trapezoidal occlusal outline measuring 1.8 x 1.7 mm (Fig. 4). There is a prominent paraconule joined to the oblique preprotocrista and a low metaconule is positioned near the centre of the crown. The postprotocrista is directed distally where it ends in the median transverse valley, being quite swollen low down. The paracone is missing much of the buccal enamel, but it appears to have possessed a strong preparacrista joined to a distinct but low parastyle. The postparacrista joins the premetacrista at about half the height of the crown. There is no sign of a mesostyle, although there is a tiny cingular remnant low down near the cervix of the tooth. The postmetacrista is directed slightly distolingually and ends in a low metastyle. The hypocone is smaller than the other three cusps which are sub-equal in stature. It has a rounded prehypocrista directed towards the posterior end of the postprotocrista, but does not join it, and it has a posthypocrista that descends obliquely across the tooth towards the metastyle, closing off the distal fovea posteriorly. In the centre of the crown, there is a raised portion separating the lingual notch from the mesial fovea anteriorly and the distal fovea posteriorly. This structure is likely to represent a metaconule. There is no sign of a buccal cingulum, but the mesial cingulum is strong, even though narrow.

Discussion. The trapezoidal outline of SN 10'08 (Fig. 4) suggests that it might be a deciduous upper molar, but it could also represent a permanent upper molar or a P4/ (Butler, 1995; Simons *et al*., 1991; Tabuce *et al*., 2007). The slight reduction of the hypocone with respect to the other cusps is suggestive of the macroscelidean affinities of the specimen as is the presence of a low metaconule complex near the centre of the crown.

Comparison with previously described Palaeogene Macroscelidea (*Chambius*, *Nementchatherium*, *Herodotius*, *Metoldobotes*) reveals that SN 10'08 does not closely resemble any of them. It differs from the three herodotiine genera by its more elongated crown, the low stature of the metaconule and by the lack of a buccal cingulum (Butler, 1995) (condition unknown in *Nementchatherium* due to breakage of the paracone and metacone, Tabuce *et al*., 2001) and it differs from Metoldobotinae by its less bundont molars. Tabuce *et al*., (2001) report that *Nementchatherium* has no paraconule or metaconule, which would represent a significant difference from the Namibian specimen, but it should be borne in mind that SN 10'08 has a rather cryptic metaconule, expressed more as a swelling in the middle of the crown than as a distinct cusplet. The paraconule in SN 10'08, in contrast, is a cusplet that is clearly distinct from the preprotocrista. If the tooth from Silica North is a deciduous one, then this might account for some of the differences from other herodotiines, notably the more elongated occlusal outline.

All known herodotiine macroscelideans possess enlarged buccal cingula in the upper molars, whereas Neogene macroscelideans do not. In this character, therefore, the specimen from Silica North appears to be more derived than other Palaeogene macroscelideans. It remains to be determined whether the fossil belongs to the Herodotiinae or to one of the subfamilies known from the Neogene of Africa. For this uncertainty to be resolved, a more comprehensive fossil sample is required from Namibia, but our preliminary assessment is that herodotiines did not give rise to

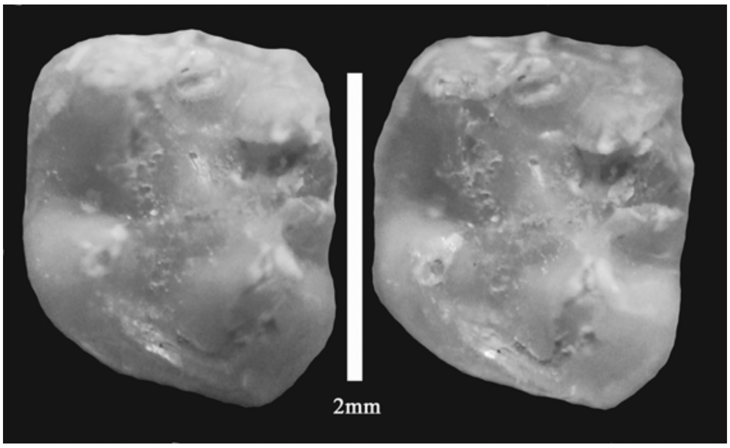

Figure 4. SN 10'08, macroscelidean upper molariform tooth from Silica North, Northern Sperrgebiet, Namibia, stereo occlusal view.

any Neogene macroscelideans. If this is so, then the hypothesis that the macroscelideans originated from a group of Eurasian mammals such as the condylarths (Tabuce *et al*., 2001; Hartenberger, 1986) may require nuancing.

The tooth is brachyodont with pointed cusps, a morphology that could represent the ancestral morphotype for *Myohyrax* and *Protypotheroides* which are hypsodont Early Miocene macroscelideans known in Namibia and East Africa (Senut, 2008).

Order Creodonta Cope, 1875
Subfamily Hyaenodontinae Leidy, 1869
Genus *Pterodon* de Blainville, 1839
Species *Pterodon* sp. indet.

Material. BC 15’08, right maxilla with alveolus of P3/, complete P4, alveolus (containing root fragments) of the M1/ and damaged M2/.

Locality. Black Crow, Sperrgebiet, Namibia.

Age. Probably Lutetian.

Description. The infraorbital foramen is wide and located above the gap between the P3/ and P4/. The P3/ is biradiculate. The P/4 is triradiculate (L x B = ca 17 x ca 12mm), with a high and robust main cusp, a small anterior cusplet which is eroded, a posterior cusplet comprising a quite developed cutting blade (Fig. 5). It probably had a lingual cuspid of small size, of which only the root remains. Of the M1/ only the alveoli are preserved (L x B = 16 x 14 mm) with some fragments of roots. The length of the buccal alveoli is greater than that of the anterior alveoli. The M2/ (L x B = ca 21 x ca 21 mm) which has the crown worn into a chisel, preserves much of the buccal wall, and there is a small parastyle. The protocone is quite strong and anteriorly projected.

Discussion. As far as can be judged, the dimensions of the dentition of the maxilla from Black Crow correspond closely to those of *Pterodon dasyuroides*, the type species of the genus (Lange-Badré, 1979). As such it is much smaller than that of *Pterodon africanus* (Andrews, 1906) from Egypt and is close in size to other species of *Pterodon* from the Fayum, Egypt, *P. syrtos* Holroyd (1999) and *P. phiomiensis* Osborn (1909a). *P. syrtos* differs from the Black Crow species by the presence of three roots in the P3/. Comparison with *P. phiomiensis* can only concern the dimensions, because the upper dentition of this species is unknown.

Subfamily Proviverrinae Schlosser, 1886
Genus and Species indet.

Material. BC 2'08 left D4/.

Locality. Black Crow, Sperrgebiet, Namibia.

Age. Probably Lutetian.

Description. BC 2'08 is badly damaged, in particular

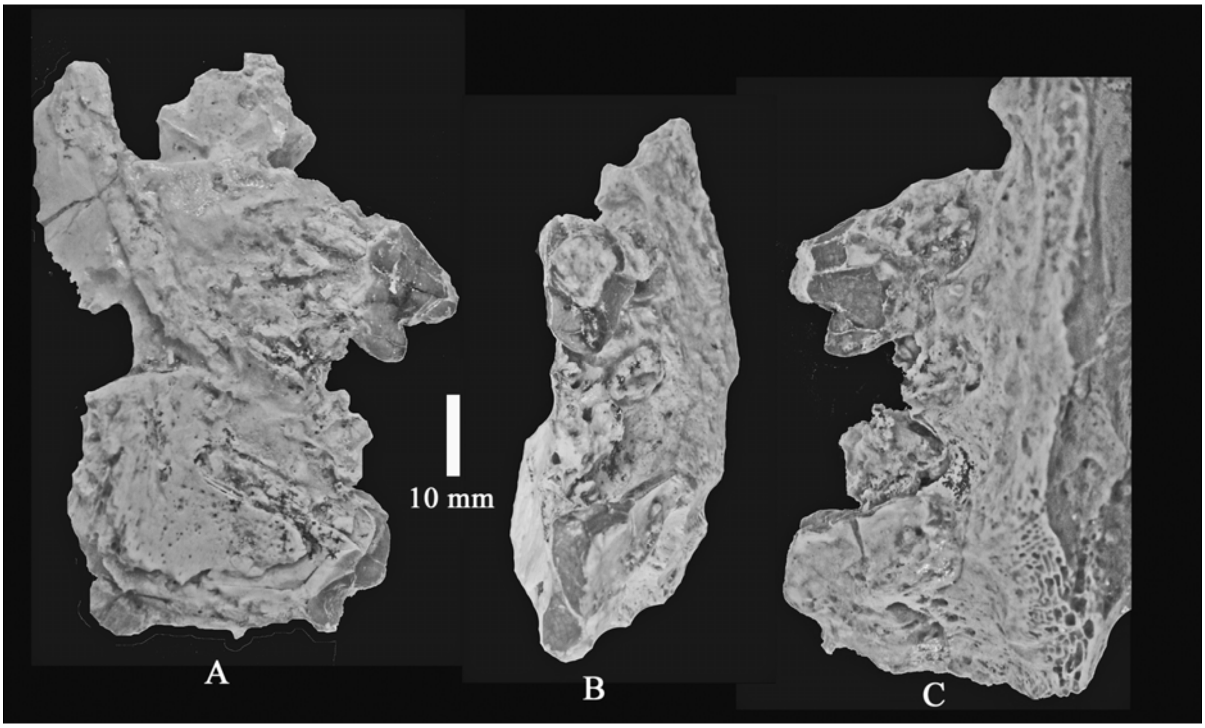

Figure 5. BC 15’08, right maxilla, *Pterodon* sp. from Black Crow, Northern Sperrgebiet, Namibia, A) buccal, B) occlusal, C) lingual views.

in the area of the parastyle and the base of the lingual wall of the metastyle, metacone and protocone (Fig. 6). This damage prevents confident identification of the specimen, but enough remains to reveal the presence of a small proviverrine at Black Crow. The fossil was found while cleaning an arsinoithere skull and was close to an erinaceid tooth.

The occlusal outline of the tooth is subtriangular, due to the posterobuccal projection of the metastyle. The paracone and metacone are well separated from each other, the former is massive and rounded, whereas the latter is sectorial, and somewhat higher than the paracone. The metastyle forms a well developed cutting blade, similar in length to the metacone. The buccal cingulum is well developed forming a relatively tall crest extending from the posterobuccal base of the paracone to the base of the metastyle. Between the cingulum and the external wall of the metacone-metastyle there is a clear valley and an incision. The lingual part of the crown is poorly preserved, which makes interpretation delicate. The protocone is quite well developed and appears to have had no signs of a paraconule or metaconule. The tooth is 2.97 mm long by 2.33 mm wide, and the length of the protocone-metastyle is 3.33 mm.

Discussion. We interpret the specimen from Black Crow as a D4/ on the basis of the great width of the protocone and the subtriangular occlusal outline of the tooth, in which the antero-posterior length is greater than the transverse breadth. Similar morphology can be observed in D4/s of *Prototomus minimus* and *Arfia gingerichi* from the Tienen Formation, Belgium (Smith and Smith, 2001). The specimen from Black Crow is closer to *A. gingerichi* than to *P. minimus* by the separation and individualisation of the paracone and metacone and by the better development (above all in height) of the buccal cingulum. Because the difference in size between D4/ and M1/, at least in the species mentioned above, is small, we can affirm that the Black Crow tooth represents one of the smallest members of the order, some of which are known from the Palaeocene and Eocene of Morocco, where they are represented only by elements of the lower dentition (Gheerbrant *et al*., 2006), which makes comparisons difficult.

Order Pholidota Weber, 1904

Material. BC 16’08, second phalanx, probably manual.

Locality. Black Crow, Sperrgebiet, Namibia.

Age. Probably Lutetian.

Description. BC 16’08 is a second phalanx of a medium-sized mammal, in which the distal epiphysis is medio-laterally compressed and with a pulley-like articular surface (Fig. 7). The medial and lateral sides of the distal epiphysis possess large but shallow depressions, there is a low depression on the dorsal surface of the diaphysis near its distal end, and in lateral view the distal epiphysis is seen to bend down palmarly to a marked extent. The proximal end is symmetrical indicating that the bone is from the axial part

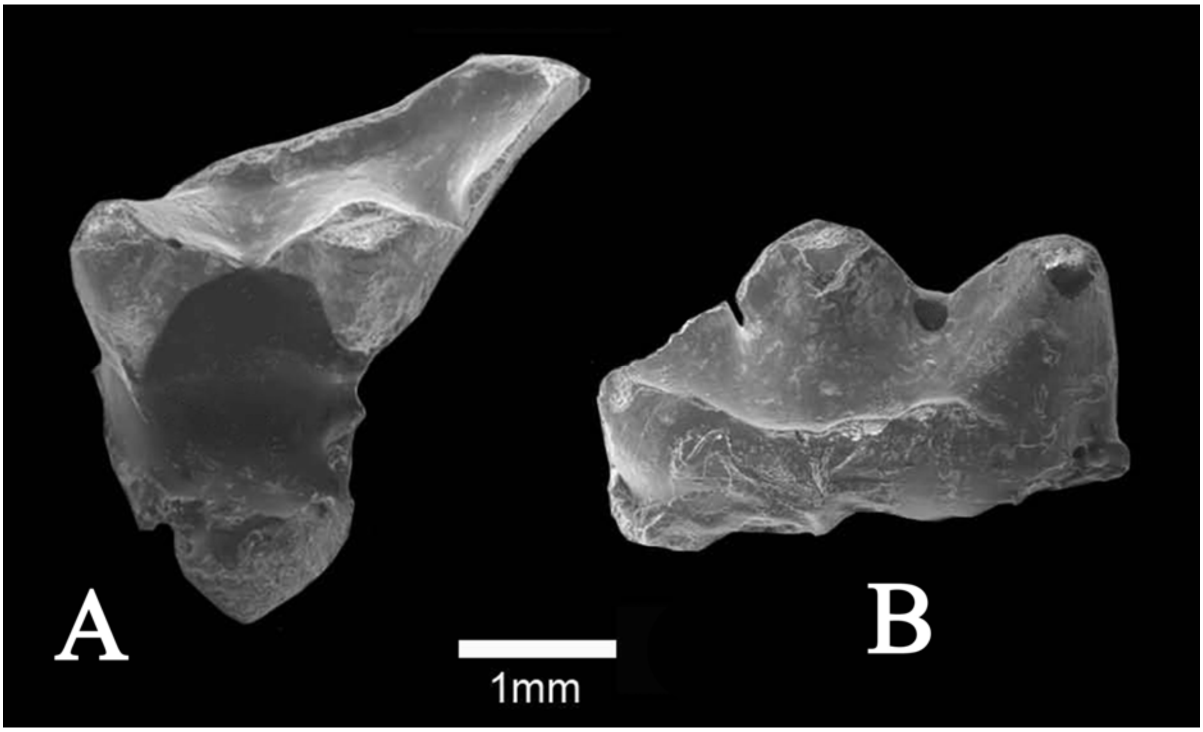

Figure 6. BC 2’08, Proviverrinae left D4/ from Black Crow, Namibia, A) occlusal view, B) buccal view.

Figure 7. BC 16'08, second axial phalanx (possibly manual) of a pholidote from Black Crow, Sperrgebiet, Namibia. A) dorsal, B) medial, C) volar, D) lateral, E) distal and F) proximal views.

of the manus or pes, and it has a strong central ridge with a central depression (Fig. 7F) separating the two parts of the articular surface. The specimen is 16.5 mm long and is slender (the medio-lateral mid-diaphysis diameter is 2.6 mm).

Discussion. The second phalanx from Black Crow (Fig. 7) is from a mammal in which the phalangeal movements were largely constrained to the parasaggital plane. The depth of the central gulley of the distal pulley suggests an animal that is using its fingers for heavy duty actions such as digging in the earth, prising open bark on trees or breaking open nests of ants and termites (Fig. 7E). The strong keel separating the two parts of the articular surface at the proximal end suggest the same thing.

Gebo and Rasmusssen (1985) reported on two distal phalanges from the Fayum, Egypt, which they attributed to pangolins, but the proximal articulations appear to be devoid of the central ridge that would articulate with the distal pulley of the second phalanx. For this reason, the two Fayum specimens (DPC 3972 and DPC 4364) are probably not from a pholidote, but could be from a small creodont, an order of carnivorous mammals that possess bifid terminal phalanges. BC 16'08, in contrast, possesses most of the morphological hallmarks of pangolin axial manual phalanges (Pickford, 1976), but the shaft is relatively long compared with phalanges of extant *Manis*.

The fossil record of Manidae is rather poor, on account of the fact that they do not possess teeth. Hitherto, the earliest known manid fossils were from Eocene deposits in North America and Europe (McKenna and Bell, 1997). The Black Crow fossil is thus one of the earliest known manids, and the earliest known from Africa. It should be pointed out that other families of Pholidota such as Epoicotheriidae and Metacheiromyidae occur in North America, having a fossil record that extends back into the Late Palaeocene.

Storch (1981) described *Eurotamandua joresi* from the Eocene of Messel (Germany) and classed it in the Xenarthra, an order of South American mammals comprising anteaters, armodillos and sloths, etc. There has been a debate about the affinities of this mammal, with some researchers (Gaudin and Branham, 1998) supporting a phylogenetic relationship to Xenarthra, whereas others consider it to be closer to Pholidota (Delsuc *et al*., 2001). Its phalanges in particular, show morphological features similar to those of sloths. The phalanx from Black Crow also shows characters comparable to those expressed in sloths, such as the ventrally offset distal articulation, the dorsal depression at the distal end of the diaphysis and the presence of a fissure separating the proximal articulation into two halves.

In view of the fact that the debate about the affinities of the European species is not yet settled we adopt a conservative interpretation of the Black Crow fossil, but note that whether it eventually turns out to be a pholidote or a xenarthran, it is a particularly interesting specimen on account of its geographic position.

Order Hyracoidea Huxley, 1869
Family *incertae sedis*
Genus *Namahyrax* nov.

Type species. *Namahyrax corvus* sp. nov.

Diagnosis. Bunodont, extremely brachyodont hyracoid with molars endowed with a greatly enlarged

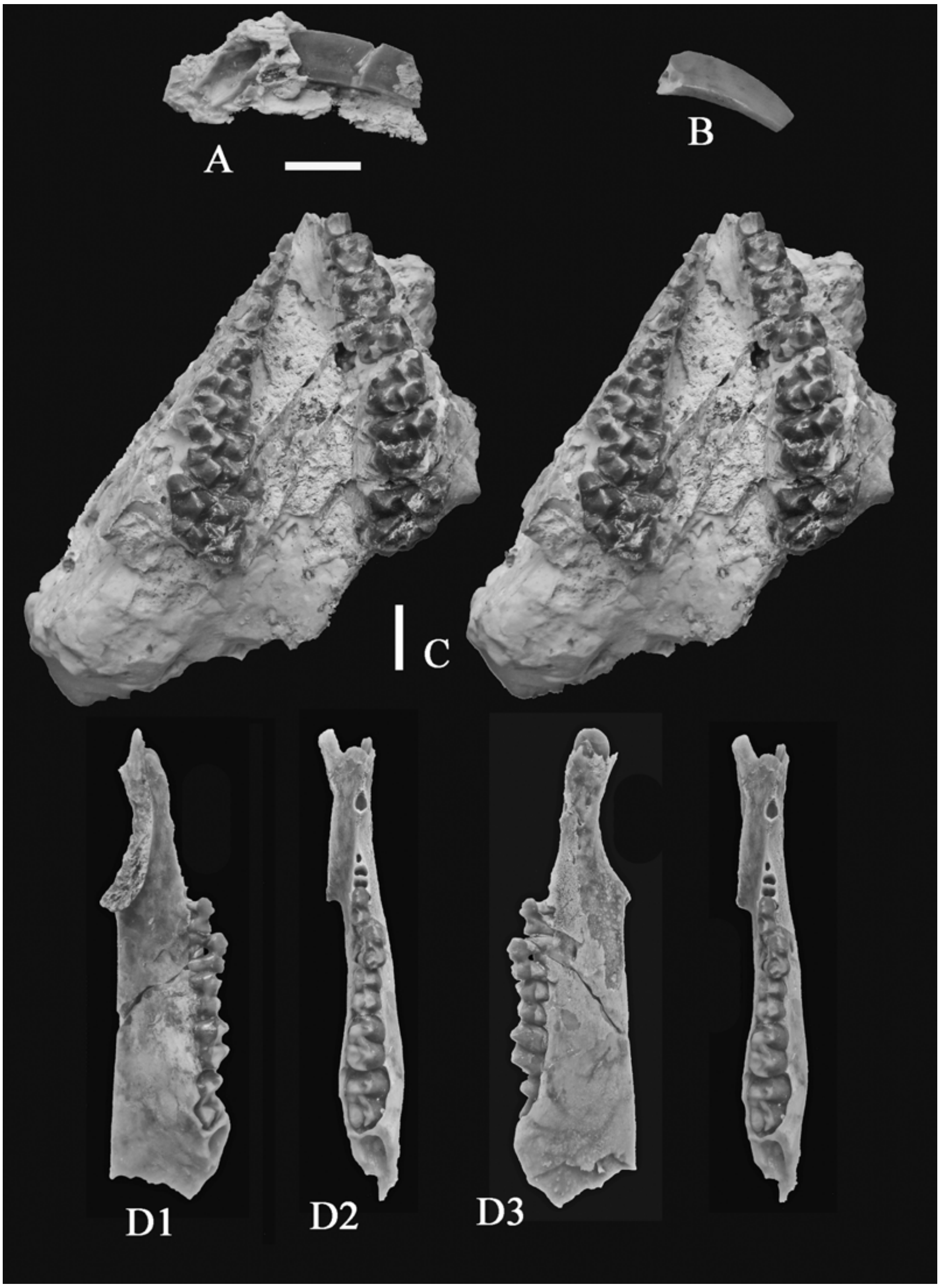

Figure 8. BC 14'08, *Namahyrax corvus* gen. et sp. nov., from Black Crow, Northern Sperrgebiet, Namibia. A) upper central incisor fragment, B) upper central incisor fragment; C) stereo view of palate; D) BC 10'08, right mandible containing i/1, d/2-d/4, m/1-m/2; D1) lingual, D2) stereo occlusal, D3) buccal views. (Scale 10 mm).

parastyle, a moderate mesostyle, and a small metastyle; well developed posterior hypocone cingulum, small spurs leading into longitudinal valley opposite the parastyle and metacone. Sharp buccal cingulum in P3/-M3/. Lower lateral incisor (i/2) with weakly expressed tine incisions. Ventrally concave symphysis.

Differential diagnosis. Differs from most hyracoids except *Seggeurius* and some species of *Bunohyrax* by its extreme molar brachyodonty, and by the presence of a greatly enlarged parastyle in the upper molars. *Namahyrax* differs from *Seggeurius* by the presence of a prominent posthypocone cingulum, a parastylar spur and a metaconal spur. It differs from *Bunohyrax* by the lack of deep indentations in the apex of the i/2.

Derivatio nominis. The genus name is composed of *Nama*, the region where the fossil was found, and *hyrax*, the extant dassie of South Africa.

Species *Namahyrax corvus* nov.

Holotype. BC 14'08, snout with left and right cheek tooth rows in light wear, plus two fragments of central upper incisors found in the same block of rock.

Paratype. BC 10'08, right mandible containing i/2, d/2-d/4, m/1-m/2 and permanent premolars in crypt. The molars have been abraded by wind blown sand.

Type Locality. Black Crow, Sperrgebiet, Namibia.

Age. Probably Lutetian.

Diagnosis. As for the genus.

Derivatio nominis. The species name is the Latin word for a Crow or Raven, *corvus*, in allusion to the name of the depression where the holotype and paratype fossils were found.

Description

The dental nomenclature of hyracoids used in this description is based on Rasmussen and Simons (1988a) and Court and Hartenberger (1992) to which has been added the angulations present in the protocone and hypocone (Fig. 9).

The holotype snout possesses both cheek tooth rows (Fig. 8), the right premolars, having been sand abraded, are poorly preserved, and the left ones better preserved but have suffered some damage, especially the P4/ (Fig. 8C). The left P1/ is damaged anteriorly, the posterior part preserves a buccal postparacone crista bordered lingually by a depression which is encircled by a low cingulum, forming a shallow occlusal basin. The left P2/ possesses three cusps, the two anterior ones (protocone, paracone) forming a transverse loph with a central depression between the two cusps, and the metacone is closely applied to the paracone in such a way that the buccal surface of the crown presents a vertical valley between the barrels of the cusps. The parastyle has broken off. The distolingual basin is larger than that of the P1/ and is also surrounded by a cingulum. The P3/ is a larger version of P2/ with all the structures more defined. The parastyle is large but low, the paracone and metacone are close together and joined by crista, and the protocone shows a well developed, obliquely oriented pre-

Table 5. Measurements of the teeth of *Namahyrax corvus* gen. et sp. nov.

Tooth	Length (mm)	Breadth (mm)
i/2 right	6.0	-
d/2 right	6.1	3.0
d/3 right	6.8	3.7
d/4 right	7.4	4.5
m/1 right	8.9	6.2
m/2 right	9.8	-
P1/ left	-	4.8
P2/ left	7.0	7.4
P3/ left	8.6	9.3
P4/ left	-	10.2
M1/ left	10.0	10.0
M2/ left	11.5	11.7
M3/ left	12.0	13.5
P3/ right	7.2	-
P4/ right	7.6	-
M1/ right	9.0	10.7
M2/ right	11.0	11.8
M3/ right	11.8	14.0

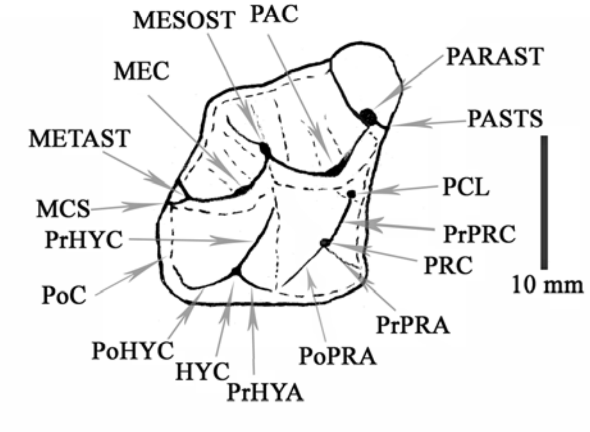

Figure 9. Nomenclature of the right upper third molar of *Namahyrax corvus* gen. et sp. nov. occlusal view. (Abbreviations: HYC – Hypocone, MCS – Metacone spur, MEC – Metacone, MESOST – Mesostyle, METAST – Metastyle, PAC – Paracone, PARAST – Parastyle, PASTS – Parastyle spur, PCL – Paraconule, PoC – Posthypocone cingulum, PoHYC – Posthypocone crista, PoPRA – Postprotocone angulation, PRC – Protocone, PrHYA – Prehypocone angulation, PrHYC – Prehypocone crista, PrPRA - Preprotocone angulation, PrPRC – Preprotocone crista).

protocrista, a crista directed centrally and a weaker postprotocrista which terminates at the lingual margin of the crown. In this tooth, the anterior and lingual cingula are clear, even though small in stature. Both P4/s are damaged, but in different places, so that a more or less complete tooth can be envisaged (the metacone is not preserved in either tooth). The anterior half is well preserved on the left side, and the posterior half on the right. The paracone is large and sports a well developed parastyle which is about half the height of the paracone. Its anterior and posterior crests curve onto the anterior and buccal margins of the tooth respectively. The paracone possesses clear preprotocrista and postprotocrista. The protocone has a sharp preprotocrista, a buccally directed crest and a posterior angulation. The distal basin of the right P4/ shows a small, low cusplet, probably an incipient hypocone, and there is a well developed posterior cingulum bordering the basin. The protocone is encircled lingually and mesially by a low, sharp cingulum.

The upper first and second molars are constructed on the same plan, the M2/ being larger than the M1/. These teeth are close enough morphologically to be described along with the M3/.

The M3/ is basically similar to the other molars (Fig. 9), but is more trapezoidal in occlusal outline, and it possesses five roots instead of four. It differs from the anterior molars by the presence of a well developed posthypocone cingulum and by the presence of parastylar and metaconal spurs which enter the longitudinal valley at the mesial and distal extremities of the ectoloph respectively (Fig. 9). The parastyle in all the molars is very large and almost as high as the paracone. It has two crista, one lingually directed to form the mesial spur, the other bucco-distally which descends to the buccal cingulum. The paracone is conical with clear pre- and postparacrista directed mesially and distally respectively. It also has a buccal barrel. The protocone is lower than the paracone and is pyramidal in shape, with a strong preprotocrista directed antero-centrally, a postprotocone angulation (not forming a crest) directed postero-centrally and a preprotocone angulation lingually. There is a semi-detached paraconule at the end of the preprotocrista (Fig. 8C, 9). The mesostyle is pinched in at its apex which is tall, and it swells basally where it joins the buccal cingulum. There is no sign of a spur opposite the mesostyle, nor opposite the paracone and metacone. The metacone is appreciably smaller than the paracone, and is slightly more obliquely oriented with respect to the tooth row. It has sharp pre- and postmetacrista, a weak metastyle and a small but clear metaconal spur which ends at the base of the posterior cingulum, without fusing with it. The hypocone is slightly lower than the metacone and is a compressed pyramidal shape. The prehypocrista is sharp and mesio-centrally directed. In line with the prehypocrista is the posthypocrista which descends towards the disto-lingual corner of the crown. At the base of the posthypocrista, a prominent posthypocone cingulum takes root and traverses the back of the crown, closing off a narrow, transversely elongated distal basin. This cingulum ends at the base of the metastyle. The anterior cingulum is prominent, but fades out on the lingual side of the protocone. A cingular remnant occurs between the lingual sides of the protocone and hypocone.

In the same block of rock as the holotype snout, there were two fragments of upper central incisors (Fig. 8A, 8B). These are sharply triangular in section, with slight, shallow longitudinal grooves mesially and distally. Enamel occurs only on the mesial and distal surfaces, the lingual side being devoid of this substance.

The juvenile mandible BC 10’08, which is the paratype of the species was found a few metres from the holotype (Fig. 8D). It is a right mandible containing i/2, d/2-d/4, m/1-m/2 and with its permanent premolars in their crypts.

The mandible has some unusual features. The symphysis is concave ventrally, the incisors being lower than the cheek tooth row (Fig. 8D1, 8D3). This could be partly due to the juvenile status of the individual, but is in any case a striking feature of the jaw. The main mental foramen is high, being positioned just beneath the anterior root of the d/3. There are three smaller mental foramina below the posterior diastema between i/3 and c/1 and there is an additional foramen with an anterior groove beneath the mesial diastema (between i/2 and i/3). The symphysis was unfused at the time of death, and this too is somewhat unusual, most other hyracoids showing precocious fusion of the mandibular symphysis, at least by the time the m/2 has erupted, as in BC 10’08. The symphysis is elongated, stretching as far back as the mesial end of the d/2, which makes it at least 30 mm long, which is as long as the distance from the front of d/2 to the rear of m/1. There is no sign of an internal mandibular pocket or fossa beneath the molar row in this specimen, nor is there any buccal inflation of the jaw. The ramus is shallow; 12.7 mm beneath the d/1, 15.2 mm beneath the m/2.

The i/2 is in its crypt but its apex is visible. It is unusual in a hyracoid context by the lack of tining at the apex. There are short, shallow grooves scoring the labial and lingual surfaces of the crown near the apex, but there is no sign that these cut into the crown deep enough to isolate tines from each other. The morphology of this tooth suggests that the individual was a male (De Blieux *et al*., 2006).

There is a single alveolus 7 mm behind the second incisor, presumably for the i/3 (or di/3 in this juvenile individual). Behind this alveolus there is a second diastema 6.7 mm long which ends at a single alveolus for the canine (or deciduous canine). The two alveoli for the d/1 are immediately posterior to the single alveolus for the canine and the remaining teeth in the dentition are in contact with one another. The d/2-d/4 are similar to each other morphologically, but each tooth is larger than its predecessor.

These teeth are comprised of two selenes, one behind the other. The anterior selene possesses a high paraconid located in the midline of the tooth. The protoconid produces an angle buccally that descends distobuccally towards the cervix, outlining a sloping valley between it and the cristid obliquid. The hypoconid and entoconid are separated from each other by a valley, the hypocristid being directed towards the distal end of the tooth in its midline, and not towards the entoconid. The d/3 and d/4 are too worn to reveal fine details of crown morphology.

Prior to collection, the m/1 and m/2 suffered abrasion by wind-driven sand, but several important morphological details are preserved. In m/1 and m/2, both the protoconid and hypoconid possess a mesiolingually directed cristid that descends into the longitudinal valley but does not cross it. This cristid is homologous to the structure found in *Saghatherium*, but in the latter genus the cristid swells basally, whereas in *Namahyrax* it fades out basally. These cusps also possess pre- and post- cristids which terminate near the midline of the tooth. The only cristid that reaches a neighbouring cusp is the prehypocristid which joins the base of the metaconid. The lingual cusps are only marginally behind the buccal ones, such that the trigonid and talonid basins are reduced in size. The buccal cusps flare at quite an angle from apex to cervix, the apices being near the midline of the crown. The buccal cingulum is weakly expressed between the bases of the protoconid and hypoconid, but the mesial and distal cingula are clearly developed. The lingual cusps have almost vertical lingual surfaces. The molar enamel is lightly wrinkled.

Discussion

Namahyrax shows a number of features that are unusual for hyracoids. The lower second incisor has no tines, but only short, shallow grooves buccally and lingually, which would disappear with even a minor degree of apical wear. The symphyseal shape is peculiar, with the incisor row being lower than the cheek tooth row and the ventral margin of the symphysis markedly concave. The upper molars are extremely brachyodont, and the parastyle is enlarged, almost to the point of comprising a separate cusp. These characters serve to distinguish *Namahyrax* from most other hyracoids, including all Procaviidae, Pliohyracinae, Saghatheriinae, and Geniohyinae. Some of the features including extreme molar brachyodonty are shared with *Seggeurius*, and there is a close resemblance between these two forms, despite the marked difference in size. However, the presence of spurs in the upper molars and a large distal cingulum on the hypocone of the M3/ of *Namahyrax* differentiates these two genera. For these reasons the Namibian fossils are attributed to a new genus, *Namahyrax*.

Tabuce *et al.*, (2001b) performed a cladistic analysis of Palaeogene hyracoids, and found support for a Saghatheriinae clade (*Antilohyrax*, *Titanohyrax*, *Saghatherium*, *Selenohyrax*, *Thyrohyrax*, *Pachyhyrax* and *Bunohyrax*). *Geniohyus* was classed in its own subfamily, and *Megalohyrax* was considered to be a sister group to an *Antilohyrax*-*Titanohyrax*-*Saghatherium*-*Selenohyrax* clade. In their study, *Microhyrax* and *Seggeurius* emerged as basal hyracoids and were left unclassified at the subfamily level. It is interesting to note that in their analysis "*Bunohyrax" matsumotoi* was classed with a question mark, as a basal member of the genus *Bunohyrax*. However, in its extreme brachyodonty, its enlarged parastyle and the presence of small spur-like ridges opposite the parastyle and metacone in the M3/, *B. matsumotoi* recalls *Namahyrax corvus*, and when more comprehensive material of the Algerian species is known, it might be necessary to reclassify it. However, it is unlikely to belong to *Namahyrax* because the lower incisor of "*B*". *matsumotoi* (i/1 or i/2 in Tabuce *et al.*, 2000) has three well developed tines separated from each other by deep incisions in the apex of the crown. The lack of tining in *Namahyrax* is unlikely to reflect sexual dimorphism in i/2 morphology (De Blieux *et al.*, 2006) as male hyracoids possess tined second incisors, even if the incisions are less indented than in females.

It may eventually be necessary to create a subfamily for these extremely brachyodont hyracoids with enlarged parastyles in the upper molars.

Order Embrithopoda Andrews, 1906
Family Arsinoitheriidae Andrews, 1904
Genus *Namatherium* nov.

Type species. *Namatherium blackcrowense* sp. nov.

Diagnosis. Arsinoithere in which the zygomatic arches flare strongly laterally; infra-orbital foramen opens above the P4/, anterior margin of orbit positioned above the anterior loph of M1/; posterior palatine foramen on a line just posterior to, and lingual from the M3/; post-glenoid process not greatly projecting ventrally, glenoid articulation slightly superior to the occlusal surface of the cheek teeth; upper premolars monolophodont with large posterior shelf and shallow fossette, posterior interloph crest in upper molars absent or much reduced, cheek teeth moderately hypsodont; intermaxillary suture complexly zigzag and broad opposite the P3/-M1/; maxillo-jugal suture complexly zigzag; presence of low dorsally directed jugal tubercle close to maxillo-jugal suture; maxilla comprises anterior part of orbital margin, the jugal comprises the posterior part.

Differential diagnosis. *Namatherium* differs from Eurasian arsinoitheres *Crivadiatherium* and *Palaeoamasia* by its more hypsodont cheek teeth, from *Palaeoamasia* by the absence of the interloph crest in the upper molars and by the M3/s being offset lingually (conditions unknown in *Crivadiatherium*). *Namatherium* differs from Turkish *Hypsamasia* by its more reduced protocone and hypocone, and by the lack of a centrocrista in the upper molars. *Namatherium* differs from *Arsinoitherium* by its widely flaring zygomatic arch, the anterior root of which is located in line with the middle of P4/ (at the front of M3/ in *Arsinoitherium*) and its posterior root in front of M3/ (at rear of M3/ in *Arsinoitherium*), its less hypsodont cheek teeth, its monolophodont upper premolars with a shallow posterior fossette (deep fossette in *Arsinoitherium*), its slightly larger protocone and hypocone (very reduced in *Arsinoitherium*), the more anterior position of the infraorbital foramen (above P4/ in *Namatherium*, above the middle of M2/ in *Arsinoitherium*), the more anterior position of the orbit (anterior margin is above the front of M1/ in

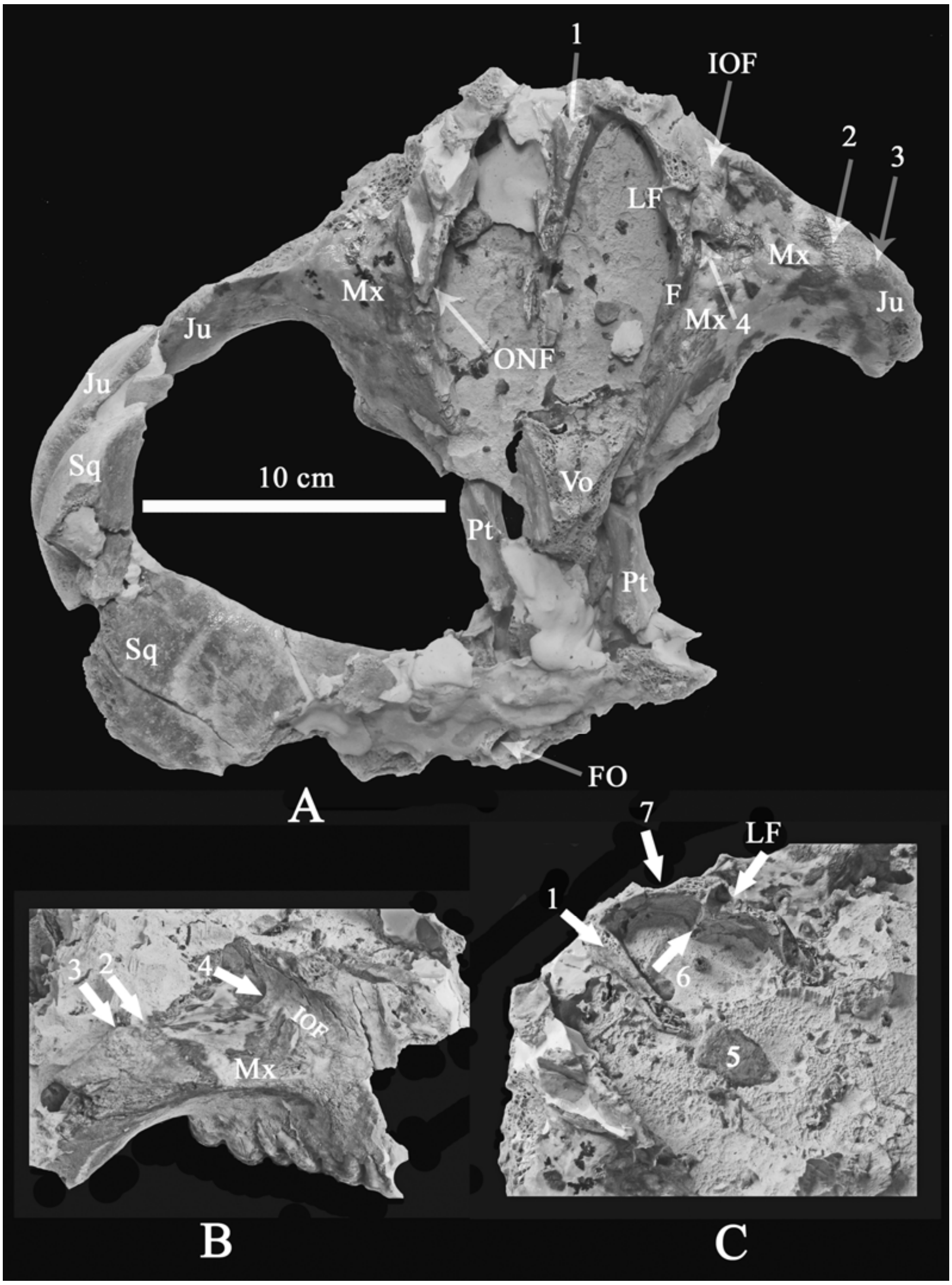

Figure 10. BC 13'08, *Namatherium blackcrowense* gen. et sp. nov., from Black Crow, Northern Sperrgebiet, Namibia, A) dorsal view, B) oblique anterior dorsal view, C) oblique posterior dorsal view (1 – ridge rising from floor of nasal cavity, 2 – maxillo-jugal suture, 3 – jugal tubercle, 4 – three foramina at internal termination of the infraorbital canal, 5 – flat flake of bone possibly from nasal horn, 6 – buttress in lateral wall of nasal cavity, 7 – anterior margin of nasal cavity, F – frontal, FO – foramen ovale, IOF – infra-orbital foramen, Ju – jugal, LF – lacrimal foramen, Mx – maxilla, ONF – orbito-nasal foramen, Pt – pterygoid, Sq – squamosal, Vo - vomer).

Namatherium, above the front of M3/ in *Arsinoitherium*); the lesser ventral projection of the postglenoid process and the lower position of the glenoid articular surface relative to the occlusal surface of the tooth row (high in *Arsinoitherium*). Intermaxillary suture is complexly zigzag and broad opposite the premolars in *Namatherium*, simple, narrow and sinuous in *Arsinoitherium*. Maxillo-jugal suture in *Namatherium* is complexly zigzag, simple in *Arsinoitherium*; jugal tubercle low and dorsally directed in *Namatherium*, extensive in *Arsinoitherium*, and as a result, the anterior part of the orbital opening lies on the maxilla in *Namatherium*, and on the jugal in *Arsinoitherium*.

Derivatio nominis. *Nama* is for the region in Namibia where the fossil was found, *therium* – Greek for beast.

Species *Namatherium blackcrowense* nov.

Holotype. BC 13’08, partial skull containing right P3/-M3/ and left M1/-M3.

Type Locality. Black Crow, Sperrgebiet, Namibia.

Age. Probably Lutetian.

Diagnosis. As for the genus, smaller than *Arsinoitherium zitteli*.

Derivatio nominis. The species name is for the type locality, Black Crow.

Description. BC 13’08 is a partial skull (Fig. 10-15) found teeth downwards in the Black Crow Carbonate. The carbonate is traversed by vertical tubes which are lined with micro-crystalline quartz and manganese, possibly hollows left by plant stems, less likely ant or termite foraging tunnels. The skull was freed from its matrix using 10% solution of formic acid, buffered with calcium tri-phosphate. Examination of the fine residue left by the acid treatment led to the discovery of some interesting small bones and teeth (pholidote phalanx, proviverrine upper carnassial, todralestid lower carnassial).

The palate and zygomatic arches are largely preserved. The bones are undistorted, but the specimen was in the process of breaking into pieces at the time it was buried, with the consequence that some pieces of bone are not in their correct anatomical position. The maxillae have drifted slightly apart, giving the false impression of a much widened palate, and the right maxilla has shifted a small extent distally with respect to the left one. The nasal cavity contained many flakes of bone with sinuous markings on one surface of which one is illustrated in Fig. 10. The palate contains the right P3/-M3/ and left M1/-M3/ in moderate wear. The distal part of the crown of the left P4 was *in situ* at the time of discovery, but since its roots had already been sand-blasted away, it is now loose. The sutures in the rear of the skull are open.

In palatal view the anterior root of the zygomatic arch departs from the facial surface of the maxilla in line with the P4/ and the posterior part is opposite the front of M3/ (Fig. 11). The infraorbital foramen opens above the P4/. The anterior palatine foramen is

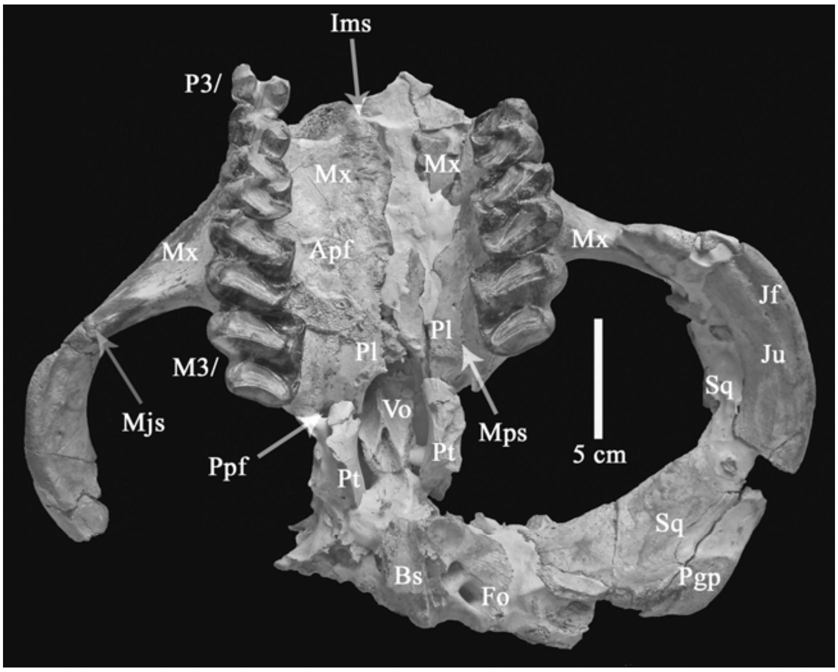

Figure 11. BC 13’08, *Namatherium blackcrowense* gen. et sp. nov., from Black Crow, Northern Sperrgebiet, Namibia, ventral view of skull. (Apf – anterior palatine foramen; Bs – basisphenoid; Fo – foramen ovale; Ims – intermaxillary suture; Jf – jugal fossa; Ju – jugal; Mx – maxilla; Mjs – maxillo-jugal suture; Mps – maxillo-palatine suture; Pgp – postglenoid process; Pl – palatine; Ppf – post-palatine foramen; Pt – pterygoid; Sq – squamosal; Vo – vomer).

located opposite the anterior lobe of the M2/ and the posterior palatine foramen is located on the posterior projection of the palatine slightly behind the level of the M3/ and lingual to it. The maxillo-palatine suture is located just to the rear of the posterior palatine foramen (Andrews, 1906). The maxillo-jugal suture is heavily zigzag trending almost dorso-ventrally some distance from the root of the zygomatic arch, immediately medial to the jugal tubercle; the maxilla thus contributes largely to the zygomatic arches, unlike *Arsinoitherium* in which the contribution is limited (Court, 1992). The intermaxillary suture is complexly zigzag opposite the premolars unlike the sinuous or almost straight suture that typifies most mammals. Not only is it complexly zigzag, but also the total breadth of the suture is extreme (8-9 mm). The zone covered by the complex zig-zagging suture in *Namatherium* is reflected in the base of the nasal cavity as a low, broad wall of bone, narrowing posteriorly, unlike the thin crest of bone that occurs in most mammals. The maxillo-palatine foramen is at the junction of the maxilla, the palatine and the pterygoid. The posterior nares are broadly U-shaped and open opposite the middle of M3/. The zygomatic arches are strongly flaring. The distance between the buccal edges of the left and right M3/s is 144 mm, compared with the total skull width at the zygomatic arches of 360 mm. The arches thus comprise more than half the breadth of the skull. The ventral surface of the jugal is hollowed out into a shallow elongated jugal fossa (Fig. 11) which terminates anteriorly in the vicinity of the maxillo-jugal suture. The ventral margin of the maxilla rises sharply in this zone of the zygomatic arch.

The post-glenoid process projects only moderately ventrally from the glenoid fossa (Fig. 12). The vomer is small with a narrow V-shaped encoche distally. The basisphenoid is damaged but shows two large foramina medial to the glenoid fossa. The anterior one is interpreted to be the alisphenoid canal and the posterior one is probably the foramen ovale (Fig. 12). The anterior margin of the otic vacuity is preserved in the basisphenoid immediately behind the foramen ovale. The pterygoids are damaged but enclose an oval fossa in which the vomer is located.

In dorsal view it is possible to see that there are three foramina penetrating the floor of the orbit at the internal termination of the infraorbital canal. The latter forms a broad, shallow furrow in the floor of the orbit, its roof being eroded away. Further distally on the maxillary dental capsule (the rear of the floor of the orbit) there are several additional foramina.

On the right side 14 mm above the distal part of the infra-orbital canal there is a large foramen passing from the orbital surface into the nasal cavity, but its upper parts are broken away (Fig. 10). This is the lacrimal foramen.

The nasal cavity is large, with a broad bony ridge narrowing distally in its floor separating its base into two halves. The internal vertical wall of each half of

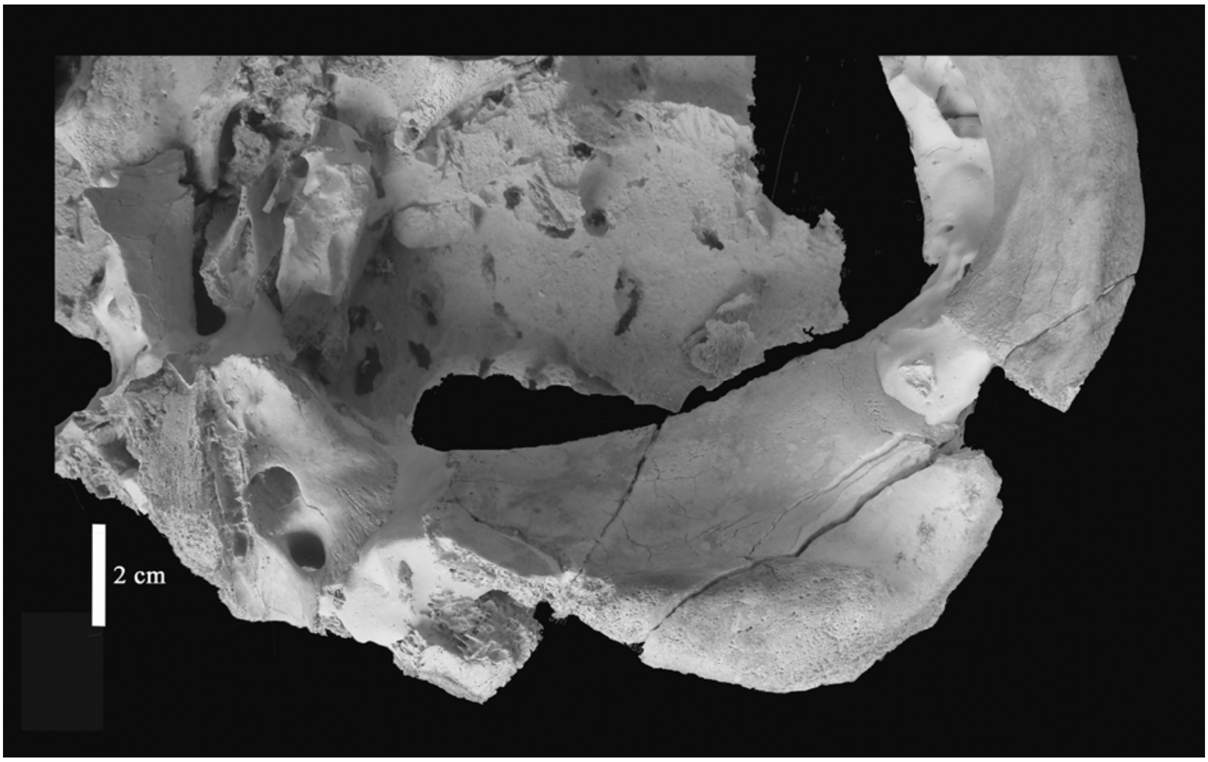

Figure 12. BC 13'08, *Namatherium blackcrowense* gen. et sp. nov., from Black Crow, Northern Sperrgebiet, Namibia, close up ventral view of the squamosal and basi-sphenoid, to show the form of the articulation for the mandible, the ventrally short post-glenoid process, and the two large foramina in the basi-sphenoid.

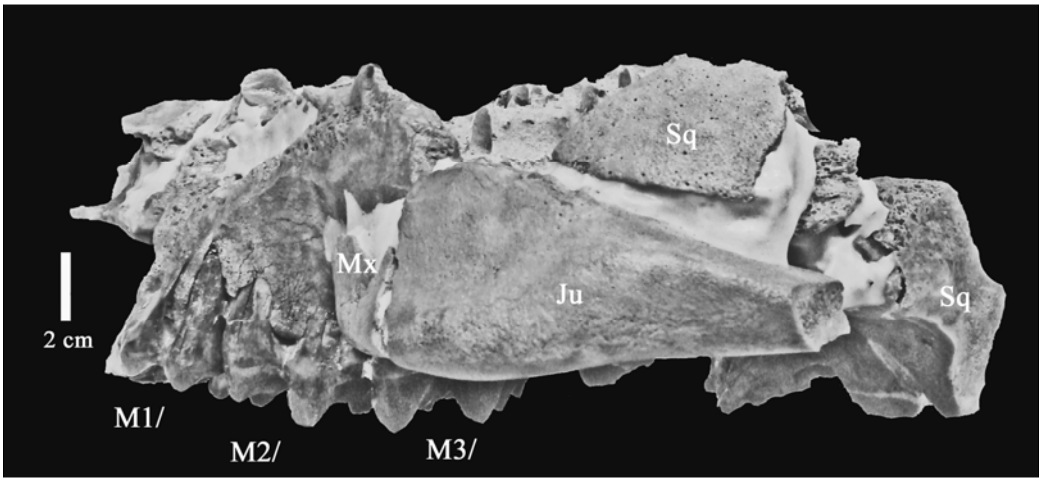

Figure 13. BC 13’08, *Namatherium blackcrowense* gen. et sp. nov., from Black Crow, Northern Sperrgebiet, Namibia, left lateral view. (Ju – Jugal; Mx – Maxilla; Sq – Squamosal)

the nasal cavity is marked by a low vertical buttress of bone. The anterior edge of the nasal cavity is preserved for a short extent in front of the pillar that encloses the infra-orbital foramen. This reveals that *Namatherium* possessed a remarkably retracted nasal opening, as in *Arsinoitherium*. In its anterior part, near the sphenopalatine foramen, the floor of the orbit is not separated from its palatine part by a deep gulley as in hyracoids; instead the bone in this area rises slightly towards the vertical wall of the orbit, as in *Arsinoitherium* (Court, 1992). About 42 mm to the rear of the lacrymal foramen, there is a foramen that extends from the orbital surface through the frontal bone and into the nasal cavity descending palatewards as it goes (Fig. 10). This appears to be the same structure that Andrews (1906) called the orbito-nasal foramen. Immediately lateral from this foramen, the fronto-maxillary suture is visible extending backwards. A heavily zig-zag maxillo-jugal suture is present to the medial side of a bony process on the dorsal surface of the anterior extremity of the jugal (3 in Fig. 10). The anterior margin of the orbit lies above the front of M1/.

In lateral view it is possible to make out the squamosal-jugal suture which is relatively far back, as in *Arsinoitherium*, the bulk of the orbital margin being formed by the jugal and the maxilla (Fig. 13). The squamoso-jugal suture is flat, long and broad, the two bones lying on top of one another like tiles on a roof. Even in this old individual, the suture is open. The zygomatic arch sweeps slightly downwards from its anterior root, and partly hides the molars in lateral view. On the more complete right side of the skull, the zygomatic process of the maxilla is dorso-ventrally tall, and it slopes at an angle of about 45° from antero-dorsal to ventro-distal.

In anterior view (Fig. 14), the alveolar process is seen to be extremely narrow and deep at the level of the premolars. Indeed the premolars are broader than the alveolar process. The depth of the alveolar process decreases posteriorly, such that the palate is deep anteriorly and shallower opposite the M3/s.

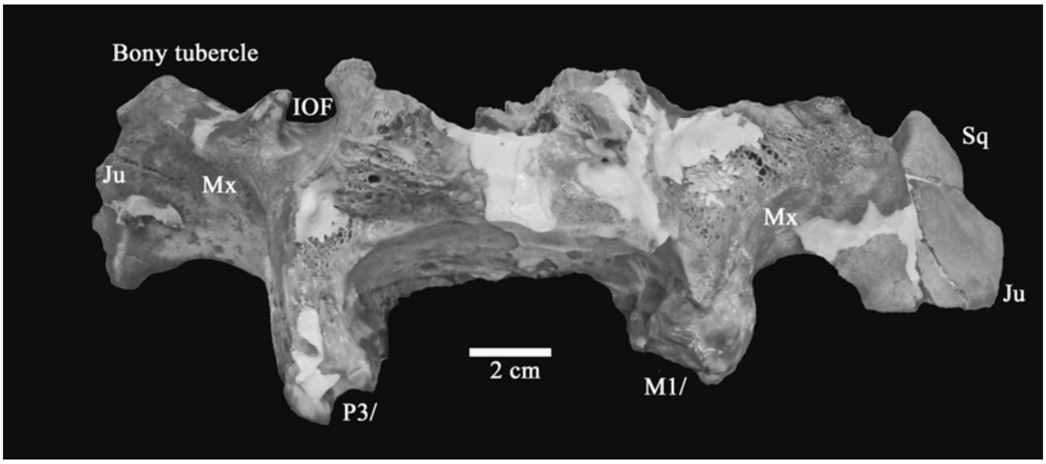

Figure 14. BC 13’908, *Namatherium blackcrowense* gen. et sp. nov., from Black Crow, Northern Sperrgebiet, Namibia, anterior view. (IOF – Infraorbital foramen; Ju – Jugal; Mx – Maxilla; Sq – Squamosal).

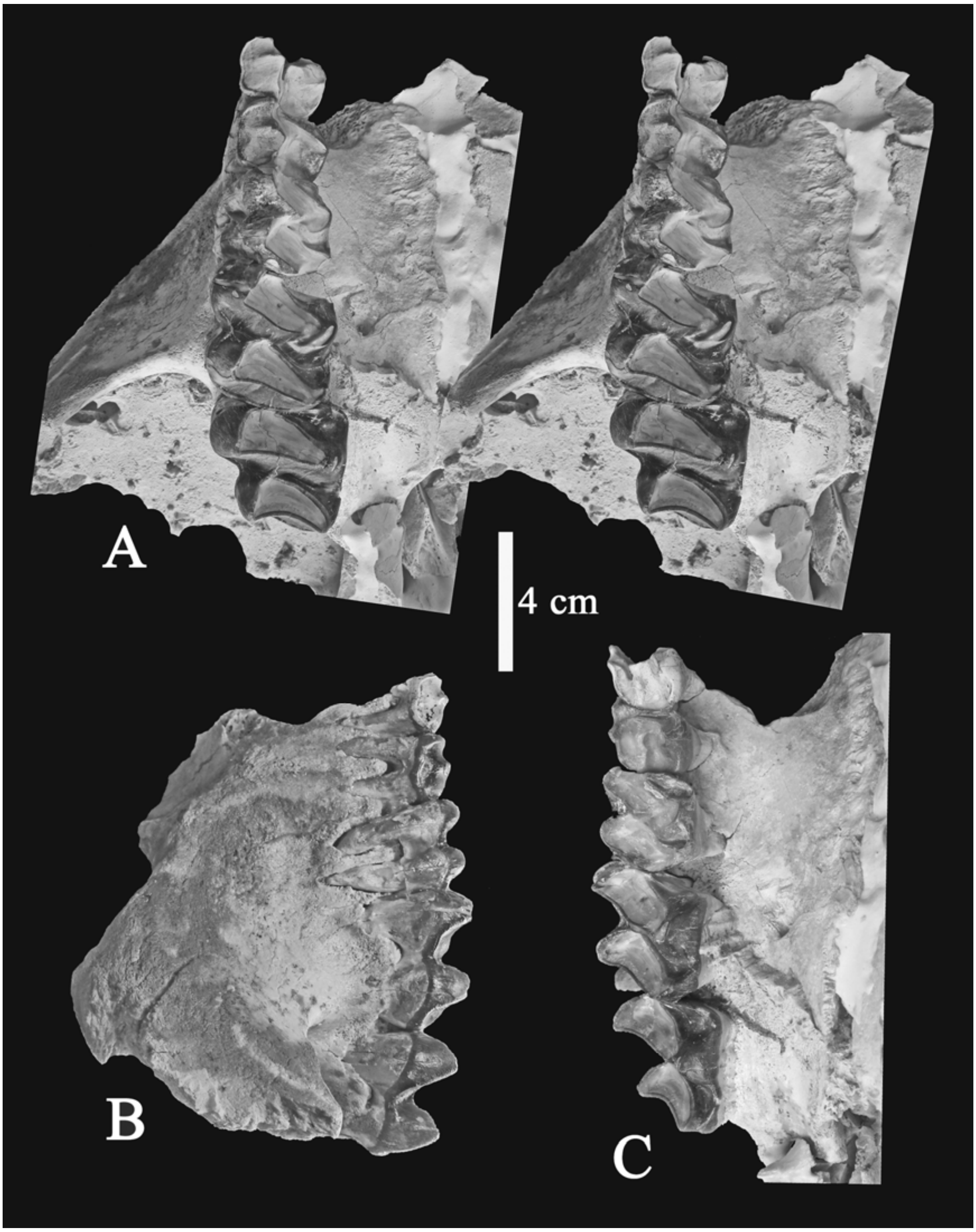

Figure 15. BC 13'08, *Namatherium blackcrowense* gen. et sp. nov., from Black Crow, Northern Sperrgebiet, Namibia, upper right tooth row (P3/ to M3/), A) stereo occlusal view, B) buccal view showing crown-root junction, and C) slightly oblique lingual views. Note the highly zigzag inter-maxillary suture (at top of image A to left of plaster of paris).

Dentition. The upper premolars are monolophodont, with a broad posterior shelf with a shallow occlusal fossa (Fig. 15). The molars are bilophodont with obliquely oriented lophs and the cervix is horizonal all round the crown. The protocone is bucco-lingually compressed and reduced in dimensions (Fig. 15, 16). The parastyle is enlarged and traverses more than half the breadth of the crown, the paracone being located to the lingual side of the midline of the tooth. Similarly the hypocone is reduced in stature, the metacone is lingually displaced and the metastyle dominates the posterior loph of the tooth. There is a prominent anterior cingulum forming a low but sharp ridge-like cusplet at the mesio-lingual corner of the tooth. In the cheek teeth the buccal side of the crown is more hypsodont than the lingual part, but the cervix is horizon-

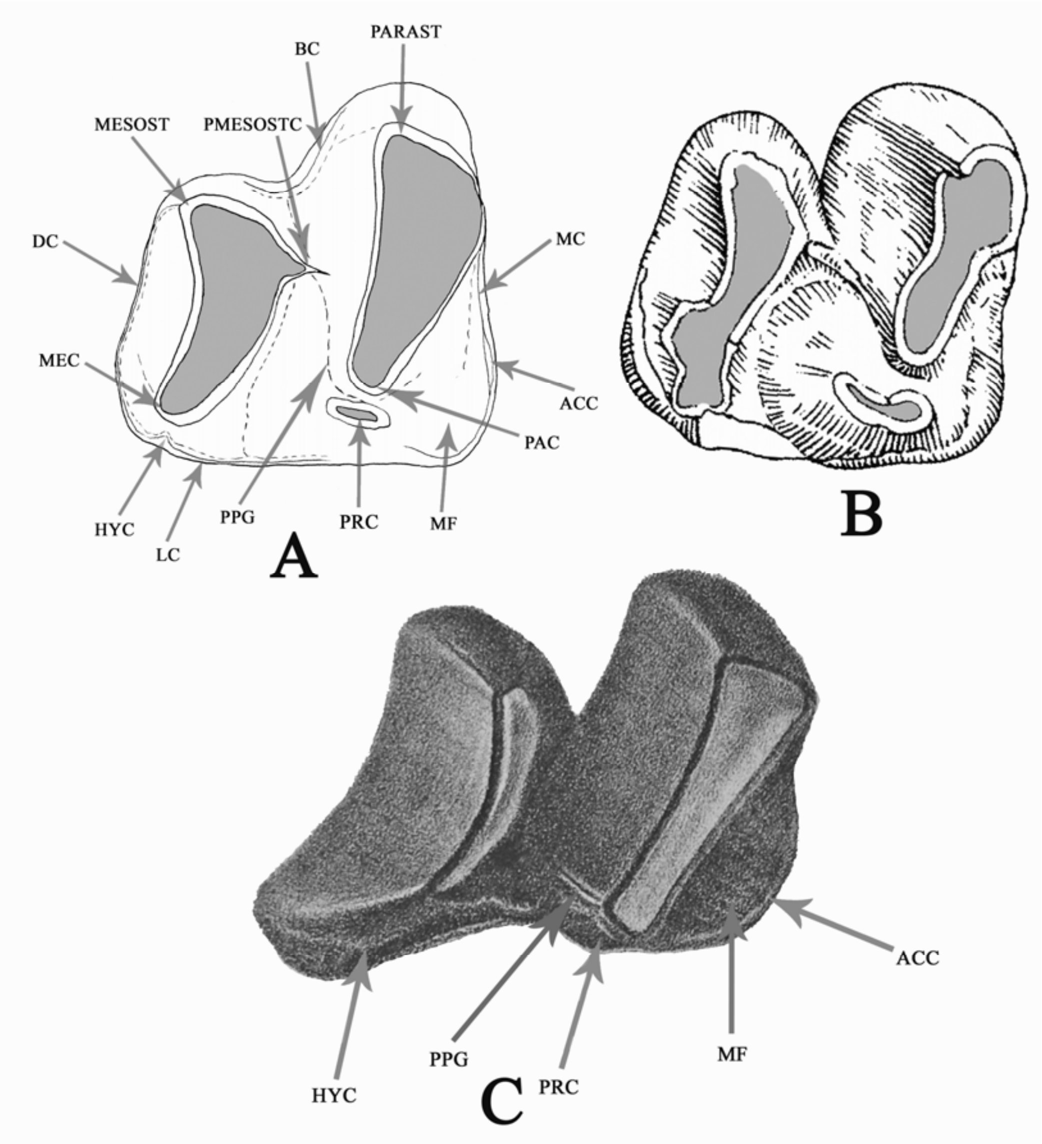

Figure 16. Comparison of upper right 3rd molars of A) *Namatherium*, B) *Palaeoamasia*, C) *Arsinoitherium* (anterior to right of page) The M3/s are reproduced to the same breadth of the protoloph and are oriented with the lingual margin of the protocone approximately parallel to each other (ACC – Anterior cingular cusp, BC – Buccal cingulum, DC – Distal cingulum, HYC – Hypocone, LC – Lingual cingulum, MC – Mesial cingulum, MEC – Metacone, MESOST – Mesostyle, MF – Mesial fossa, PAC – Paracone, PARAST – Parastyle, PMESOST – Premesostylecrista, PRC – Protocone, PPG – Protocone-paracone groove)(B - modified from Sen and Heintz, 1979, C - modified from Andrews, 1906).

tal all round the tooth, unlike *Arsinoitherium* in which only the mesial and lingual parts of the cervix are horizontal, the distal and buccal sides being extremely hypsodont. The anterior loph of the M1/ is slightly narrower than the posterior loph, whereas in the M2/ the anterior loph is slightly broader than the posterior one, and in the M3/ the anterior loph is much broader than the posterior one. The M3/ is appreciably closer to the saggital plane than the M1/ and M2/. This position produces a marked step in the lingual edge of the tooth row, the lingual edges of the other teeth being in line with each other. *Arsinoitherium* also shows this unusual position of the M3/.

The extent of the roots of the upper molars of *Namatherium* differs from that of *Arsinoitherium* although it is easy to envisage how the morphology in the latter genus could be derived from that of the former. In the M3/ of *Namatherium* there are three roots, a mesiodistally elongated lingual root that extends from beneath the anterior cingulum to the hindmost part of the crown, and two moderately compressed bucco-lingually elongated transverse roots. These roots separate from each other about 10 mm beneath cervix on the lingaul side (Fig. 17A). In *Namatherium* the lingual root also shows a solid base beneath the cervix (Fig. 17B) beneath which there are three vertical grooves indicating that there is probably a separation of the root apex into four parts as in *Arsinoitherium*, an anterior part beneath the anterior cingulum, a middle c-shaped part beneath the protocone which is grooved lingually, and a distal part beneath the distal cingulum. However, in *Arsinoitherium* the central part of the lingual root is reduced in mesiodistal dimensions compared to *Namatherium* such that it extends only over the central third of the lingual side of the crown which is why Andrews (1906) called it the "middle root". It has a c-shaped section, the concavity in the "c" facing lingually and it is reduced in cervical-apical dimensions, being about half the height of the other roots, and is inclined towards the rear (Fig. 17A). The "middle root" in *Arsinoitherium* supports the protocone and hypocone both of

Table 4. Measurements of the teeth of the holotype of *Namatherium blackcrowense* gen. et sp. nov.

Tooth	**Length (mm)**	**Breadth 1st loph (mm)**	**Breadth 2nd loph (mm)**
P3/ right	17e	24.4	--
P4/ right	19.0	26.1	--
M1/ right	27.0	28.0	29.3
M2/ right	37.7	37.5	36.4
M3/ right	41.2	40.8	31.0
M1/ left	28.3	28.3	28.8
M2/ left	37.6	37.4	35.6
M3/ left	40.4	40.5	31.0

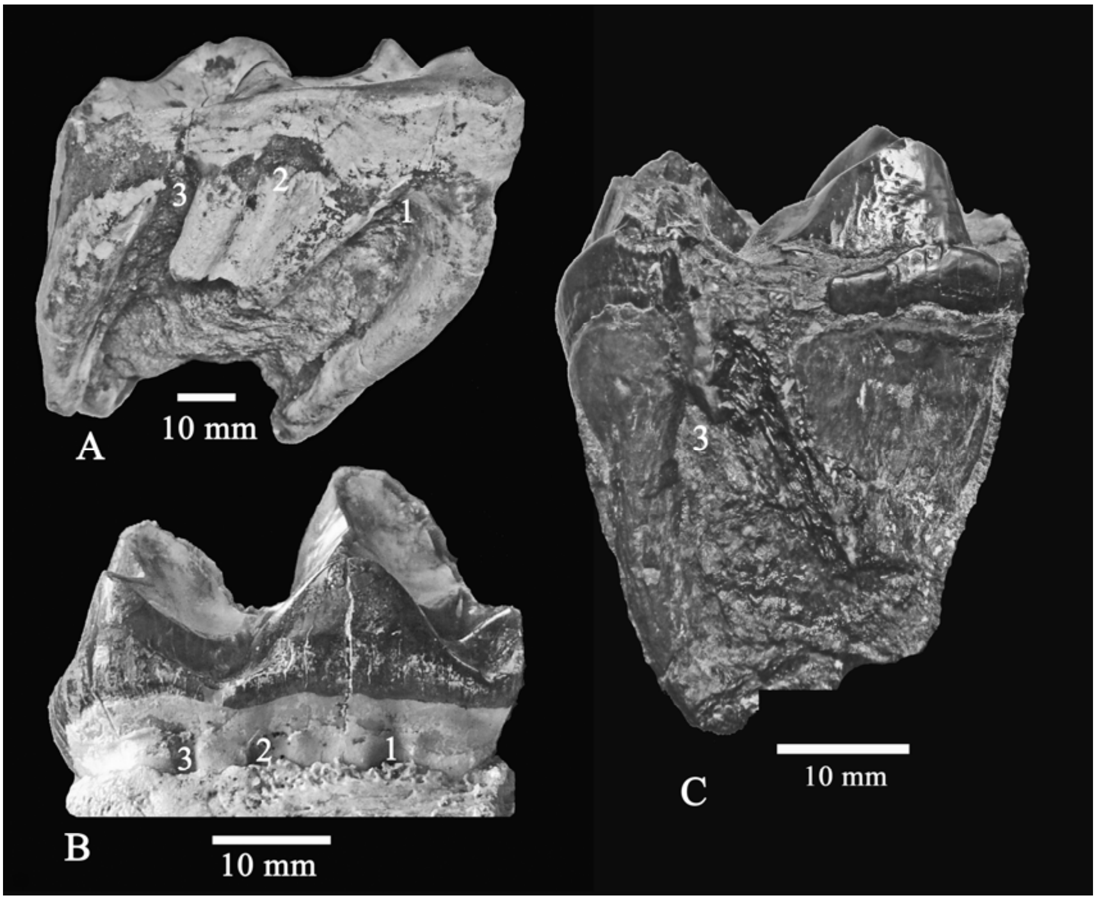

Figure 17. Lingual view of M3/ roots in A) *Arsinoitherium* from Egypt (M 8804) and B) *Namatherium*, C) *Palaeoamasia* from Turkey. To facilitate comparisons the teeth have been brought to the same length and are illustrated as from the right side (anterior to the right). Note the vertical grooves (1-3) in the lingual root complex of *Namatherium* which correspond to the groove (n° 2) in the "middle root" of *Arsinoitherium* and the gaps (1 and 3) between its three roots, and the presence of only a single gap in *Palaeoamasia*, equivalent to n° 3.

which are extremely reduced in stature in this genus.

In the M2/ of *Namatherium* the anterior transverse root stops short well before reaching the lingual margin of the tooth, ending beneath the cingular cusp-like swelling (ACC in Fig. 16), and there is no contact with the anterior part of the lingual root. In contrast, examination of a complete specimen of *Arsinoitherium* M3/ stored in the Natural History Museum, London (M 8804, Andrews, 1906) shows that the anterior transverse root is fused to the anterior part of the lingual root, thereby forming a continuous transverse root complex.

In *Namatherium*, the posterior transverse root of the M3/ is continuous from beneath the mesostyle to the disto-lingual margin of the crown, and it is oriented obliquely with respect to the long axis of the tooth row, running parallel to the rear margin of the tooth (Fig. 16A). The root morphology of *Palaeoamasia* (Fig. 17C) differs markedly from both *Arsinoitherium* and *Namatherium* there being no sign of a third root anterior to that beneath the protocone.

The root layout in the M3/ of *Namatherium* is unlike that of hyracoids, in which there are three lingual roots and two circular buccal ones, but is more similar to that observed in *Phosphatherium* (Gheerbrant *et al*., 2005b).

Discussion

The Black Crow arsinoithere diverges greatly from other genera of embrithopods, both in its cranial features and its dental ones. Its dentition differs from that of *Palaeoamasia* (Ozansoy, 1969; Sen and Heintz, 1979) by the absence of the postparacone crista (centrocrista of Maas *et al*., 1998) in the upper molars, by the greater reduction of the protocone and by its greater hypsodonty. Furthermore, the M3/ in *Palaeoamasia* is not offset lingually from the line of the other cheek teeth. Upper molars of *Hypsamasia seni*, from the Middle Eocene of Turkey, possess larger protocones and metacones than *Namatherium*, and there is a distinct postparacrista, as in *Palaeoamasia* (Maas *et al*., 1998). The upper dentition of *Crivadiatherium* is unknown (Radulesco *et al*., 1976) but is expected to resemble that of *Palaeoamasia (*Radulseco and Sudre, 1985) more than that of *Arsinoitherium*.

Namatherium is closer in dental morphology to *Arsinoitherium* than to *Palaeoamasia* but the premolars are monolophodont with a shallow posterior fossa and low posterior cingulum, unlike the condition in *Arsinoitherium* in which the posterior fossa is deep, so much so that in heavily worn teeth it forms a posteriorly closed fossette. The basic structure of the molars of *Namatherium* resembles that of *Arsinoitherium* (Fig. 16) save for the distinctly lower degree of buccal and distal hypsodonty (Fig. 15B). Other differences include the fine structure of the lophs. In *Arsinoitherium*, the enamel on the anterior surface of the protoloph and metaloph is extremely thin apically (0.4 mm), thickening basally, whereas the enamel on the distal surface is uniformly thicker (1.5 mm). The protocone and hypocone in *Arsinoitherium* are reduced to low, flat swellings on the lingual side of the crown, and the roots that support these cusps are reduced in height, and are fused into a C-shaped complex (the ‘c’ is concave lingually). The transversely fused roots beneath the lophs of *Arsinoitherium* molars are tall and concave mesio-distally. In *Arsinoitherium* the fossette between the protocone and the anterior cingulum and the one between the protocone and the hypocone are deeper than the lingual cervix, in *Namatherium* these fossettes are shallow and do not extend deeper than the cervix. In *Arsinoitherium*, the molars are more hypsodont buccally than lingually, and are more hypsodont distally than mesially. In *Namatherium*, the cervix is horizontal all around the tooth (Fig. 15B, C).

The architecture of the skull of *Namatherium* differs enormously from that of *Arsinoitherium* (Beadnell, 1902). The zygomatic arches of *Namatherium* are widely flaring, the breadth of the widest part of the skull being more than double the distance between the buccal margins of the M3/s. In *Arsinoitherium* in contrast, the zygomatic arches project only slightly beyond the buccal limits of the M3/s (Andrews, 1906; Court, 1992b). The infraorbital foramen and the anterior margin of the orbit are positioned appreciably further anteriorly in *Namatherium* than they are in *Arsinoitherium*. The intermaxillary suture is complexly zigzag and broad opposite the premolars in *Namatherium*, simple, narrow and slightly sinuous in *Arsinoitherium*. The maxillo-jugal suture in *Namatherium* is complexly zigzag, simple in *Arsinoitherium* and the jugal tubercle is low and dorsally directed in *Namatherium*, being close to the maxillo-jugal suture, whereas the tubercle is elongated and extensive in *Arsinoitherium*, reaching upwards to roof over the infra-orbital foramen. As a result, the anterior part of the orbital opening lies on the maxilla in *Namatherium*, and on the jugal in *Arsinoitherium*.

The post-glenoid process in *Namatherium* descends ventrally to a small extent, much less than the much elongated process that typifies *Arsinoitherium*. In *Arsinoitherium* the glenoid articular surface is a narrow, shallowly excavated banana-shaped depression, the outline of which is concave distally. In *Namatherium* in contrast, the glenoid articulation is flat to convex, and is oval in outline, suggesting a different morphology of the mandibular condyle, and thus the presence of divergent chewing actions in the two genera.

Despite the cranial and dental differences between *Namatherium* and *Arsinoitherium*, it is clear from the overall morphology that they are more closely related to each other than either is to the Eurasian taxa *Palaeoamasia* and *Hypsamasia*. For example, the offset of the upper third molar from the rest of the tooth row is present in both *Namatherium* and *Arsinoitherium*, but is absent in *Palaeoamasia*. Another similarity between the Namibian and Egyptian arsinoitheres concerns the depth of the palate, which is deep anteriorly opposite the premolars, shallowing distally. The fact that most of the skull sutures of *Namatherium* are open at a relatively advanced wear stage of the M3/ provides another similarity to *Arsinoitherium*, but the condition of this feature in Eurasian arsinoitheres is unknown due to imperfection of the available fossils. The nasal cavity in *Namatherium* has vertical lateral walls buttressed by low rounded ridges. These buttresses closely resemble those that occur in the hollow horns of *Arsinoitherium*, and their presence in *Namatherium* suggests that it too may have possessed horns, although the only skull preserved is broken in this area. This suggestion is supported by the discovery of flakes of bone lying in the matrix of the skull, one surface of which is covered with shallow vermiform furrows similar to those that adorn the outer surface of the horns of *Arsinoitherium* (Andrews, 1906).

The dimensions and form of arsinoithere horns have prompted comment by several palaeontologists (Andrews, 1906; Gregory, 1910; Romer, 1946). Despite the impressive dimensions of the nasal horns, they are hollow, the bone is thin (ca 5 mm) and they were covered in skin (Andrews, 1906). They would not have weighed a great deal, nor would they have withstood forceful impacts. It is possible that the horns functioned primarily as resonance chambers, and secondarily as visual signals, whereas intraspecific combat using the horns as weapons was probably not part of arsinoithere behaviour. The possibility that *Namatherium* possessed horns that functioned as resonance chambers, suggests that vocalisation played an important role in interactions between conspecifics, and that the behaviour was maintained over geological time spans.

Andrews (1906) considered that the cheek teeth of arsinoitheres could have been derived from the hyracoid type, but he noted that overall, the skull and teeth of *Arsinoitherium* were so unusual that it was difficult to determine its closest relatives. For this reason, he did not attempt a detailed comparison with other eutherians. Gregory (1910) and Romer (1946) followed Andrews (1906) in locating Embrithopoda closest to Hyracoidea. Court (1992) took up the challenge in the hope of clarifying its phylogenetic relationships. He noted several features that appeared to be closer to the condition in proboscideans than in hyracoids. For instance, in *Arsinoitherium* the premaxilla approaches and sometimes contacts the frontal, a rare condition in mammals, but present in sirenians and proboscideans. The infraorbital canal is very short and has a wide diameter in *Arsinoitherium* as in *Namatherium*. This is likely to be a derived condition (Court, 1992) used to postulate synapomorphy between sirenians and proboscideans by Novacek and Wyss (1986). In *Namatherium*, the layout of the bones of the zygomatic arch and neighbouring regions of the skull resembles more closely that of *Moeritherium* than it does that of hyracoids. The maxillo-jugal suture is in comparable positions and is oriented in the same way in the two genera and the zygomatic process of the maxilla slopes in a similar way, such that the anterior rim of the orbit is shifted forwards relative to the lower margin of the zygomatic arch. The squamoso-jugal suture of *Namatherium* strongly resembles the condition in sirenians, with the exception that it extends further anteriorly in *Namatherium* than it does in *Dugong*. The jugal in hyracoids extends backwards and participates in the glenoid articulation, an unusual situation among mammals, but in *Namatherium*, the jugal terminates before the glenoid as in *Arsinoitherium*. The root system of the M3/ of *Namatherium* resembles that described by Gheerbrant *et al*., (2005b) for *Phosphatherium*, a primitive proboscidean from the Palaeocene of Morocco, whereas it differs from that of hyracoids.

It is thus likely that arsinoitheres are phylogenetically closer to proboscideans than they are to hyracoids, a conclusion already reached by Court (1992).

Order Primates Linnaeus, 1758
Superfamily Simiiformes Hofstetter, 1974
(= Anthropoidea Mivart, 1864)
Family *incertae sedis*
Genus *Namaia* nov.

Type species. *Namaia bogenfelsi* sp. nov.

Diagnosis. Small primate with bunodont upper molars and lower premolar, no buccal or lingual cingulum in upper molars, M2/ with well defined hypocone, clearly expressed paraconule and metaconule, sloping buccal walls of the paracone and hypocone, three cusped M3/.

Differential diagnosis. *Namaia* differs from *Altiatlasius* by the presence of a prominent hypocone in M2/ and by the lack of buccal and lingual cingula in the upper molars and by its less bucco-lingually compressed paracone and metacone. *Namaia* differs from *Biretia*, *Algeripithecus*, *Proteopithecus* and *Catopithecus* by the lack of lingual cingulum on the protocone of the upper molars, by its bucco-lingually narrower crown and its more pronounced hypocone in M2/. Additionally *Namaia* differs from *Proteopithecus* by its possession of a tricuspid M3/ (bicuspid in *Proteopithecus*) and its less compressed hypocone in M2/. *Namaia* differs from *Tabelia* by the more squared occlusal outline in the M2/ and the more sloping buccal walls of the paracone and metacone. *Namaia* differs from *Afromonius* by the lack of buccal cingulum on upper molars, by its more rounded molar cusps, by the more sloping buccal margin of the upper molars and by the absence of a hypocone in M3/. *Namaia* differs from *Plesiopithecus* by the absence of lingual cingulum in the upper molars and by the possession of a more developed and clearly detached hypocone in M2/. *Namaia* differs from *Apidium* by the absence of a lingual cingulum on the protocone of the upper molars and by the absence of a hypocone in M3/. *Namaia* differs from *Propliopithecus* and *Aegyptopithecus* by its much smaller dimensions and by the lack of lingual cingula in the upper molars. *Namaia* differs from *Oligopithecus* by the absence of a lingual cingulum, by its more voluminous, rounded hypocone and the presence of clear paraconule and metaconule. Comparisons with *Arsinoea* and *Serapia* are difficult as these taxa are currently known only by lower dentitions.

Derivatio nominis. *Nama* for the region where the fossil was found to which has been added the suffix –*ia*, often used when naming genera of small mammals.

Species *Namaia bogenfelsi* nov.

Holotype. BC 6'08, right maxilla containing M2/-M3/.

Referred material. SN 15'08, right p/4.

Diagnosis. As for genus.

Differential diagnosis. As for the genus.

Type locality. Black Crow, Sperrgebiet, Namibia.

Other locality. Silica North, Sperrgebiet, Namibia.

Age. Probably Lutetian.

Derivatio nominis. The species name refers to Bogenfels Arch, a prominent landmark on the Namibian coast, not far from the type locality.

Description. BC 6'08 is a right maxilla containing unworn M2/ and M3/ (Fig. 18A). The trigon in the M2/ forms an equilateral triangle, and the hypocone is separated from the trigon by a valley. There is a prominent metaconule between the metacone and the protocone, and the paraconule is well defined, lying slightly anterior to the line of the preprotocone crista. There are clear mesial and distal cingula, but neither of them reaches round onto the lingual or buccal sur-

Table 2. Measurements of the teeth of Black Crow and Silica North primates.

Tooth	Length (mm)	Breadth (mm)
BC 6'08 M2/ right	4.0	4.2
BC 6'08 M3/ right	3.1	3.9
SN 15'08 p/4 right	2.1	1.8

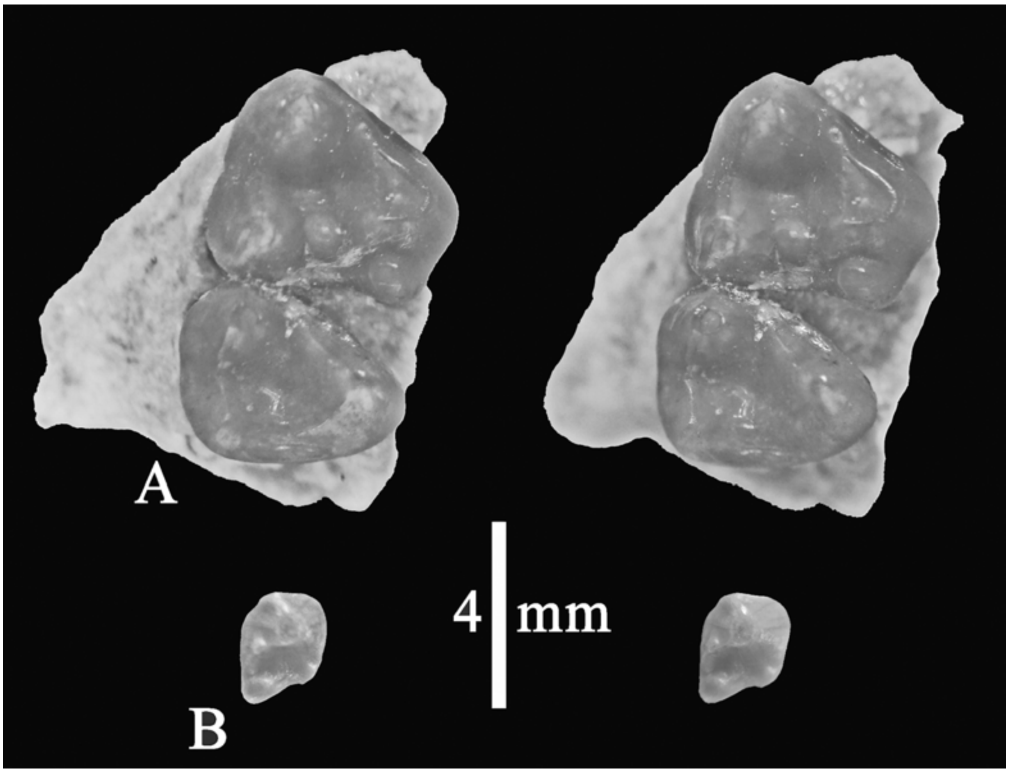

Figure 18. Primate fossils from Black Crow and Silica North, Northern Sperrgebiet, Namibia. A) BC 6'08, *Namaia bogenfelsi* nov. gen. nov. sp. holotype right maxilla containing M2/-M3/, stereo occlusal view; B) SN 15'08, right p/4 referred to *Namaia bogenfelsi*, stereo occlusal view.

faces of the crown. The paracone and metacone are tall slightly bucco-lingually compressed cones, separated from each other by a buccal notch that is about half the height of the tooth. The M3/ is triangular in occlusal outline, being comprised of a trigon without a hypocone. The trigon basin is deep.

SN 15'08 from Silica North, is a right p/4 with a trapezoidal occlusal outline (Fig. 18B). It has a large protoconid and a small but distinct metaconid joined by a low crest to the protoconid. There is a well defined anterior swelling at the mesial end of the preprotoconid cristid, and there is a low posterior cuspid distal to the metaconid. The crown is bunodont.

Discussion. The Black Crow and Silica North primate specimens are not the first Palaeogene African Primates known from south of the Equator, the order being represented at Malembe (Angola) by a lower canine from deposits of likely Rupelian age (Early Oligocene) (Pickford, 1986). However, they are the oldest primate specimens known south of the Fayum, Egypt. The overall aspect of the specimens suggests that we are dealing with a simiiform primate (or anthropoid of some authors). The hypocone in the M2/ is distinct and separated from the trigon by a valley. The paraconule and metaconule in the M2/ are well formed as in many strepsirrhines, but these cuspids also occur in most anthropoids from the Maghreb and Egypt (Godinot and Mahboubi, 1992, 1994; Gunnell and Miller, 2001). *Namaia* differs from most described species of Palaeogene primates from North Africa by the lack of buccal and lingual cingula in the upper molars and by various other features mentioned in the differential diagnosis. For these reasons, *Namaia* appears not to be closely related to basal anthropoids such as *Arsinoea*, *Proteopithecus*, *Catopithecus* and *Serapia*, nor does it fit comfortably within Parapithecidae (*Apidium*, *Parapithecus*, *Qatrania*) or Propliopithecidae (*Propliopithecus*, *Aegyptopithecus*, *Oligopithecus*) as defined by Gunnell and Miller, (2001) which are in any case much larger animals.

The phylogenetic relationships of Palaeogene primates have been widely debated (Godinot, 1994; Gunnell and Miller, 2001) with little consensus emerging (Beard, 2001; Dagosto, 2001; Godinot and Mahboubi, 1992; Kay *et al*., 2004; Miller and Simons, 1997; Seiffert *et al*., 2004, 2005a; Simons, 1989, 1992; 1995a, 1995b, 1995c, 1997a, 1997b, 1997c; 1998; 2001; Simons and Bown, 1985; Simons and Miller, 1997; Simons and Rasmussen, 1994a, 1996; Simons and Seiffert, 1999; Simons *et al*., 1995, 1999, 2001). Cranial characters play an important role in determining whether a fossil may belong to Strepsirrhini or Simiiformes whereas dental features seem to be less informative, at least among Palaeogene primates. This is partly because determining the polarity of dental characters is not always clear cut as a result of the tendency for 'primitive' morphology to be secondarily derived (Gunnell and Miller, 2001). Dentally *Namaia* is highly divergent from all strepsirrhines examined (*Saharagalago*, *Djebelemur*, *Wadilemur*, *Karanisia*) but is closer in general morphology to basal anthropoids such as *Catopithecus* and *Proteopithecus*, but clearly it does not belong to any of the genera described from North Africa (*Serapia*, *Arsinoea*, *Abuqatrania* among others (see annex 1)). A major handicap for determining the higher level relationships of *Namaia* is that its skull and mandible are unknown, yet at Black Crow we are clearly in the presence of an undescribed taxon of primate which we name *Namaia bogenfelsi* nov. gen. nov. sp. Given the fact that *Namaia* does not convincingly fit into any of the named families of Simiiformes, we conclude that it represents an unknown family of basal anthropoids which we refrain from naming until better material becomes available. In Annex 1, we place it without conviction among Parapithecidae, which increasingly appears to resemble a waste basket grouping (Gunnell and Miller, 2001; Miller *et al*., 2005).

From a palaeoecological perspective, *Namaia* is interesting, as its bunodont dentition suggests that its main diet consisted of fruit rather than insects, tree exudates (gum) or leaves. This in turn implies a constant supply of fruit throughout the year.

Order Rodentia Bowdich, 1821

Family Zegdoumyidae Vianey-Liaud, Jaeger, Hartenberger and Mahboubi, 1994

Genus *Glibia* Vianey-Liaud, Jaeger, Hartenberger and Mahboubi, 1994

Species *Glibia namibiensis* nov.

Holotype. BC 1'08, right upper molar.

Type locality. Black Crow Upper Carbonate, Sperrgebiet, Namibia.

Age. Probably Lutetian.

Diagnosis. Larger than known zegdoumyids from North Africa; anteroloph and posteroloph of upper molars have the same breadth; sinus between protocone and hypocone shallow and narrow; posteroloph subdivided by two shallow incisions; enamel in central valley finely pustulate.

Differential diagnosis. *G. namibiensis* differs from the two described species of *Glibia* by its superior dimensions, and by its higher anteroloph and posteroloph and the shallower separation between the protocone and hypocone. *Glibia namibiensis* differs from *Zegdoumys. sbeitlai* and *Zegdoumys lavocati* by its greater dimensions and by the presence of anteriorly directed crests emanating from the centre of the posteroloph and metaloph. *Glibia namibiensis* diverges from *Glibemys* by its superior dimensions (upper teeth of *Glibemys* unknown). *G. namibiensis* differs from *Nementchamys* by its smaller dimensions and by the less complicated wrinkling of the enamel crests.

Derivatio nominis. The species name refers to the country where the fossil was found.

Description. BC 1'08 is a right upper molar (M1/ or M2/) (length x breadth = 2.48 x 2.51) (Fig. 19C). It is brachyodont, with the lingual margin of the crown higher than the buccal one. A posterior contact facet is visible low down near the distal cervix, indicating that this tooth is not an M3/. There are three roots, the lingual one is antero-posteriorly elongated and is inclined towards the palate; the buccal roots are small and circular, and almost vertical. The protocone and hypocone are at the same level. The protocone is longer than the hypocone and extends posteriorly from the protoloph. There is a large mesostyle with a medially directed crest oriented slightly obliquely postero-centrally. At the internal end of the mesostyle crest there is another low crest that runs towards the anterior end of the crest that emanates from the metaloph. The enamel in the bottom of the central basin is finely pustulate (chagriné). The anteroloph and posteroloph are slightly lower than the protoloph and metaloph.

Measurements of the teeth are provided in Table 3.

Discussion. The morphology of BC 1'08 is similar enough to upper molars of *Zegdoumys* and *Glibia* from Glib Zegdou, Algeria (Vianey-Liaud *et al*., 1994) to indicate that it belongs to the same family. Similarities include the brachyodont crown with four lophs, finely pustulate enamel in the central basin, the shallow sinus between the protocone and hypocone, and the presence of a distinct mesostyle accompanied by a low internal crest. The presence of anteriorly directed crests on the posteroloph and metaloph approaches the Namibian specimen to *Glibia*, and distances it from *Zegdoumys* and *Glibemys*. However, there are differences in dimensions and in the development of the crests and the depth and width of valleys between cusps and lophs that indicate that the Namibian specimen belongs to an undescribed species which we name *Glibia namibiensis*.

Glibia namibiensis is slightly smaller than the anomalurid *Nementchamys lavocati* and the morphology of the upper molars is highly divergent, even though in both taxa the crowns are brachyodont. The enamel crests in *Nementchamys* are vermiform and thus more complicated than in *G. namibiensis*. Measurements of two specimens of M1/ or M2/ of *Nementchamys* were published by Jaeger *et al*., (1985) but the only upper teeth illustrated were a P4/ and an M3/, so it is difficult to make detailed metric and morphological comparisons between the fossils from Black Crow and Nementcha.

The presence of a zegdoumyid in Namibia is of biogeographic and biochronologic interest, as it indicates that at the time of deposition there was probably relatively unhindered access between the northern and southern extremities of the continent. The Namibian fossil is larger than the two species of *Glibia* described from Glib Zegdou, Algeria, but in its crown morphology it resembles *G. pentalopha* save for the depth of the sinus and minor details of the shape and positions of minor crests. The available specimens suggest that the Namibian fossil belongs to *Glibia* rather than to *Zegdoumys* or *Glibemys*, but because it is appreciably larger than all known zegdoumyids from North Africa, it is classified in its own species *Glibia namibiensis* sp. nov.

On the basis of the charophyte association, Vianey-Liaud *et al*., (1994) estimated an age of Late Lower Eocene or basal Middle Eocene for Glib Zegdou, Algeria, and on the basis of the evolutionary stage of the mammals they estimated that Chambi, Tunisia, which also yielded zegdoumyids, was Lower Eocene. The rodents from these two localities suggested that they were significantly older than Nementcha, Algeria, which the authors placed in the Upper Eocene. Even though the basis for estimating the ages of the North African localities is slender, we provisionally accept the proposals of Vianey-Liaud *et al*., (1994). Therefore the presence of a zegdoumyid at Black Crow invites correlation to the Early or Middle Eocene (Lutetian).

Family Myophiomyidae Lavocat, 1973
Subfamily Phiocricetomyinae Lavocat, 1973
Genus *Silicamys* nov.

Type species. *Silicamys cingulatus* sp. nov.

Diagnosis. Medium-sized rodent characterised by isolated cusps that point well above the crests; well-developed basal cingulum on buccal and mesial margins, with formation of low cusplets mesially and buccally; m/3 possesses a spur on the posterior crest of the protoconid as in *Paraphiomys*.

Differential diagnosis. *Silicamys* differs from *Phiocricetomys* by the presence of a spur on the posterior crest of the protoconid, and by a non-reduced m/3.

Derivatio nominis. The genus name combines the name of the type locality, Silica North, and *mys* – Greek for mouse.

Species *Silicamys cingulatus* nov.

Holotype. SN 25'08, unworn right p/4 or m/1.

Paratype. SN 11'08, right m/3.
Diagnosis. As for the genus.

Type locality. Silica North, Sperrgebiet, Namibia.

Age. Probably Lutetian.

Derivatio nominis. The species name refers to the prominent cingulum on the lower teeth.

Description. SN 25'08 is an unworn lower p/4 or m/1 (Fig. 19I). It is wider posteriorly than mesially, with a complete longitudinal crest. It has two anterior cusps, the buccal one is interpreted as the protoconid, and the lingual one as the metaconid. The protoconid possesses a postcristid that descends obliquely into the trigonid basin. The apices of the protoconid and metaconid stand proud. The entoconid has a strong hypolophid which is slightly oblique pointing postero-centrally. Behind the hypoconid there is a posterolophid which is swollen distally to form a cusplet. The posterolophid sends a crest anteriorly which terminates at the base of the entoconid, and the metaconid has a posterior crest which ends at the base of the entoconid. The entoconid thus stands as a conical cusp with low crests at its base.

A prominent cingulum extends continuously from the anterior base of the hypoconid to the lingual base of the metaconid. It gives rise to swellings that resemble small cusplets, notably on its mesial extremity.

SN 11'08 is a right m/3 with four roots, the two posterior roots being joined together by a thin lamella of dentine. The occlusal outline of the crown is trapezoidal with a rounded posterior part (Fig. 19G). The metalophid is straight and extends from the metaconid to the protoconid. The metaconid is the highest of the cusps. The longitudinal crest is oblique and runs from the protoconid to the middle of the hypolophid. The longitudinal crest has a spur in its middle which narrows and changes direction to touch the base of the entoconid. The rear of the tooth is comprised of a posterolophid which extends to the base of the entoconid. The basal cingulum is well developed, but is interrupted at the base of the protoconid.

Measurements of the teeth are provided in Table 3.

Discussion. *Silicamys* differs from *Phiocricetomys* from the Fayum, Egypt, which also has a basal cingulum and conical cusps, by its greater dimensions and by the absence of reduction of the m/3. In addition, the longitudinal crest is better formed in *Silicamys*.

Silicamys differs from Myophiomyinae (*Myophiomys*, *Phiomyoides*, *Elmerimys*) by the presence of a well developed basal cingulum in the cheek teeth, and by its greater dimensions, among other morphological features. In the lower cheek teeth of *Myophiomys* and *Elmerimys* the sinusid is upright, whereas in *Silicamys* it runs obliquely backwards, more so than in *Phiomyoides*. *Elmerimys* possesses an anteroconid in p/4, whereas in *Silicamys* there is only a cingular cusplet growing out of the cingulum.

The only other African rodent that possess a cingulum in the lower teeth as in *Silicamys* is *Phiocricetomys minutus* from the Fayum, Egypt (Wood, 1968). However, in *Phiocricetomys*, the m/3 is reduced and the longitudinal crest is feebler than in *Silicamys*. Because *Silicamys* has a well developed cingulum and cusps that are separated apically from the crests, we consider that it is likely to be related to *Phiocricetomys* from the Fayum, Egypt, which takes these two structures to extreme (Wood, 1968). The unreduced m/3 in *Silicamys*, and the better developed longitudinal crest indicates that we are in the presence of an undescribed genus of rodent, which we name after the discovery locus, Silica North.

Family Diamantomyidae Schaub, 1958
Subfamily Metaphiomyinae Lavocat, 1973
Genus *Prepomonomys* nov.

Type species. *Prepomonomys bogenfelsi* nov.

Diagnosis. Large rodent with four jugal teeth, moderately hypsodont, absence of cement in the cheek teeth, bony boss on lateral surface of jaw beneath the m/1, apex of incisor higher than occlusal surface of the cheek teeth.

Differential diagnosis. *Prepomonomys* differs from *Diamantomys* by the presence of a boss beneath the m/1 on the lateral side of the mandible, and from *Pomonomys* by the lesser hypsodonty and lack of cementum in the cheek teeth. Whilst the cheek teeth are morphologically and metrically close to those of *Metaphiomys schaubi*, the mandibular morphology is divergent, in particular the presence of a bony boss laterally, and the more posterior position of the ascending ramus. In addition, the apex of the incisor is high in *Prepomonomys*, and lower in *Metaphiomys*.

Derivatio nominis. The genus name *Prepomonomys* alludes to the greater age of the material from Silica North compared to the genus *Pomonomys*, with which it shares some morphological characters suggesting its ancestral condition. The name *Pomonomys*, erected by Stromer, 1922, refers to the ghost town of Pomona, with the suffix *mys*, the Greek word for mouse.

Species *Prepomonomys bogenfelsi* nov.

Holotype. SN 8'08, left mandible containing the incisor and p/4-m/3.

Paratype. SN 1'08, left M2/-M3/ in maxilla fragment (possibly the same individual as the holotype).

Referred material. SN 27'08, upper right incisor.

Type locality. Silica North, Sperrgebiet, Namibia.

Age. Probably Lutetian.

Derivatio nominis. The species name refers to the Bogenfels Arch, a prominent landmark on the Sperrgebiet coast.

Diagnosis. Upper molars with five lophs and sinus oblique towards the front, lower molars with sinusid oblique towards the rear.

Description. The mental foramen in mandible SN 8'08 is small and is located in the upper third of the jaw beneath the rear of the diastema (Fig. 19F). The diastema curves sharply ventrally in front of the p/4. The symphysis has a short genial shelf. The masseteric crest is indistinct anteriorly, but posteriorly it forms a prominent tubercle or swelling on the lateral surface of the jaw beneath the m/1. The ascending ramus rises behind the m/3. The depth of the mandible diminishes from p/4 to m/3.

The lower incisor is 2.12 mm in labio-lingual dimension and its mesio-distal breadth is 1.62 mm. Its apex is somewhat higher than the occlusal plane of the cheek teeth. In section, the labial surface is rounded and the enamel surface is finely chagriné.

The p/4 has three roots and the molars four. In m/3 the two distal roots are offset from each other.

The p/4 has a low anteroconid. The two anterior cusps, the protoconid and metaconid, are linked by a transverse crest. The longitudinal crest is almost straight, with a small deviation opposite the hypoconid. Between the protoconid and metaconid there is a longitudinal crest which subdivides the parafossettid into two halves. The posterior arm of the protoconid forms a transverse crest right across the tooth, reaching the posterior crest of the metaconid. The sinusid extends both mesially and distally, making it long near the occlusal surface. The hypolophid touches the longitudinal crest. The posterolophid is wide and closes off a large posterior fossettid.

The m/1 is worn and slightly damaged so it is difficult to interpret. The sinusid is strongly oblique towards the rear and there is a low anteroconid on the mesio-buccal corner of the tooth.

The m/2 is almost rectangular in occlusal outline with four lophids, the posterior arm of the protoconid forms a transverse lophid which joins the posterior crest of the metaconid, closing off a large paraflexid. The mesoflexid is open lingually. There is a small, low anterobuccal cingulum.

The m/3 is triangular in occlusal outline, but it has the same basic structure as the m/2. There is no sign of cementum in the cheek teeth.

The upper molars, M2/-M3/ in the left maxilla, SN 1'08, are moderately hypsodont, especially on the lingual side, but show no signs of cementum (Fig. 19D). The crowns are almost square in occlusal outline. The roots are disposed at an angle to the occlual surface of the teeth. The teeth have five lophs, the M2/ has a straight mesoloph reaching the lingual margin of the tooth, whereas the mesoloph of the M3/ is shorter, ending before the lingual margin. The metaloph, which is oblique in the M2/, extends as far as the lingual edge of the tooth, but in the M3/ it is shorter. The posterior loph of the M3/ is narrower than that of the M2/.

SN 27'08 is an upper right incisor 2.67 mm in labio-lingual dimension, and 1.68 mm mesio-distally. Its labial surface is slightly convex as in Neogene Diamantomyinae.

Measurements of the teeth are provided in Table 3.

Discussion. The lateral surface of the mandible of BC 8'08 shows a prominent boss of bone beneath the m/1, presaging the enlarged tubercle that occurs in *Pomonomys*, a structure which is absent in *Diamantomys*. The p/4 of *Prepomonomys* is close morphologically to that of *Diamantomys* and *Pomonomys*, whereas the molars are simpler than those of *Diamantomys*, being devoid of the supplementary spurs. In *Diamantomys* the sinusids are transversal, whereas in SN 8'08 they are very oblique towards the rear.

In the context of other rodents from Silica North, the cheek teeth of *Prepomonomys* are hypsodont, but they are less hypsodont than those of *Diamantomys* and much less than those of *Pomonomys*. Furthermore there is no cementum in the cheek teeth of *Prepomonomys*, unlike *Pomonomys* which has an abundant endowment of cement in the valleys and fossettes.

Considering the morphology of the teeth and the presence of a tubercle of bone on the lateral surface of the jaw beneath the m/1, it is likely that *Prepomonomys* could be ancestral to *Pomonomys*. If so, then the dichotomy between *Pomonomys* and *Diamantomys* probably occurred earlier than the period of accumulation of the Silica North deposits. The mandibular shape of *Metaphiomys* from the Fayum, Egypt, allies it to *Diamantomys*, which could well be its descendant.

Family Phiomyidae Wood, 1955
Genus *Protophiomys* Jaeger, Denys and Coiffait, 1985
Species *Protophiomys* cf. *algeriensis* Jaeger, Denys and Coiffait, 1985

Material. SS 1'08, left m/1; SN 5'08, left M2/; SN 21'08, left d/4.

Locality. Silica South and Silica North, Sperrgebiet, Namibia.

Age. Probably Lutetian.

Description. SS 1'08 is a moderately worn left lower first molar with three roots (Fig. 19A). The crown is subrectangular, with a rounded posterior margin.

There is a weak cingulum on the antero-buccal corner of the tooth. The protolophid is transversal and the longitudinal crest is oblique, extending from the rear of the protoconid to join the hypolophid in the centre of the crown. On the internal side of the protoconid, there is a crest which extends into the central basin. The sinusid has a transversal posterior margin.

SN 21'08 is a left d/4 in poor condition (the enamel is corroded). It is 1.44 x 1.11 mm (l x b). It is elongated antero-posteriorly, and has a rounded anteroconid, a continuous longitudinal crest which extends to the hypolophid (Fig. 19H). The hypoconid is the largest cusp, and the posterolophid has no swelling. The posterior margin of the sinusid is transversal, whereas the anterior part is oblique. There are two roots. The lingual side of the central basin is closed by a low crest that extends from the metaconid to the hypoconid.

SN 5'08 is a small, moderately worn tooth with the lingual cusps more hypsodont than the buccal ones (Fig. 19B). It measures 1.17 x 1.50 mm. There are four straight lophs, without any trace of a mesoloph or a metaconule. The protocone is larger than the hypocone and as a consequence the metaloph is narrower than the protoloph. The distal margin of the tooth is straight suggesting that it is more likely to be an M2/ than an M3/. There are three roots, two small buccal ones, and a slightly oblique, antero-posteriorly elongated lingual one.

Measurements of the teeth are provided in Table 3.

Discussion. Jaeger *et al*., (1985) provided measurements of four m/1s of *Protophiomys algeriensis* from Nementcha, Algeria (Length mean, min, max, = 1.61, 1.56, 1.68 – Breadth mean, min, max, = 1.52, 1.48, 1.58) which compares with the Namibian specimen (l x b = 1.78 x 1.59). The specimens from Silica North are close in dimensions and morphology to material from Nementcha, and due to the fact that there is some uncertainty about the meristic position of isolated teeth, it is not possible to be dogmatic about the meaning of the slight differences in size between the Namibian and Algerian samples. The slightly greater dimensions of the fossil from Silica South are not sufficient to exclude it from *P. algeriensis*, and until a better sample is obtained we provisionally refer it to the Nementcha species. We note the absence of an antero-buccal cingulum in the Algerian fossils, which is the only significant difference from the Silica South specimen.

Jaeger *et al*., (1985) first classed *Protophiomys* in the Phiomyidae, a view accepted by Hartenberger (1998), but McKenna and Bell (1997) classified it in the Chapattimyidae. We see no reason to classify this genus in the Chapattimyidae, and consequently return it to the Phiomyidae.

Genus *Apodecter* Hopwood, 1929
Species *Apodecter* cf *stromeri* Hopwood, 1929

Material. SN 9'08, left D4/-M1/.

Locality. Silica North, Sperrgebiet, Namibia.

Age. Probably Lutetian.

Description. The D4/ and M1/ in SN 9'08 (Fig. 19E) are markedly more hypsodont lingually than buccally. The D4/ overhangs mesially such that with wear the occlusal length would diminish. The anteroloph is open buccally, whereas the valley between the protoloph and metaloph is closed. The metaloph shows a metaconule at its contact with the posteroloph. The sinus is very oblique anteriorly. There are three roots, an elongated lingual one and two circular buccal ones.

The M1/ is less worn than the D4/ but it has almost the same dimensions as it. The metaloph has a metaconule, and recurves to join the posteroloph, and encloses two small, shallow fossettes. Measurements are provided in Table 3.

Discussion. These two teeth are similar to material of *Apodecter stromeri* from the Early Miocene of the Sperrgebiet, Namibia (Hopwood, 1929). The *Apodecter* lineage appears to have an extremely long duration. Any relationship to *Phiomyoides* is remote, as the latter genus possesses a prominent mesoloph in the molars. Some individuals of *Apodecter* have a small mesoloph, but most individuals do not possess this crest. The Silica North individual possesses a small swelling in the longitudinal crest which could represent a vestige of a mesoloph. More comprehensive material is required to settle the affinities of this small rodent from Silica North.

Family Bathyergidae Waterhouse, 1841
Genus cf *Bathyergoides* Stromer, 1923
Species cf *Bathyergoides* indet.

Material. SN 20'08, right M3/.

Locality. Silica North.

Age. Probably Lutetian.

Description. SN 20'08 is an unworn germ of a right M3/ of a medium sized bathyergid (Fig. 19J, Table 3). The tooth is tetralophodont, with a longitudinal lingual crest and four transverse crests. The anteroloph is almost closed onto the protoloph, behind which there is a broad valley bordered distally by a metaloph which is subdivided before it joins the hypocone, and there is a posteroloph forming the distal margin of the crown. This tooth presents a very oblique sinus which almost joins the anterior fossette, being separated from it by an extremely narrow isth-

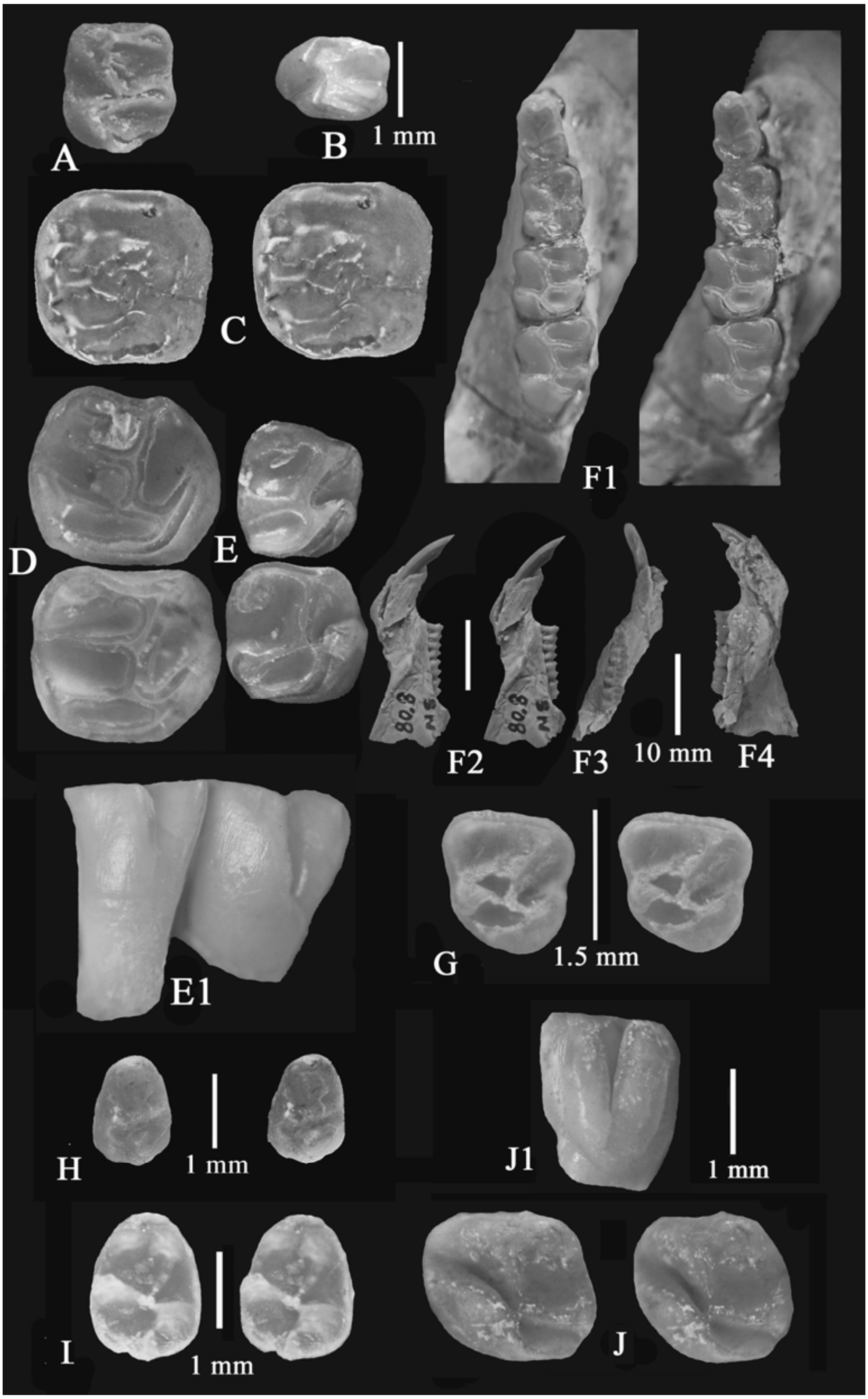

Figure 19. Rodentia from Silica North, Silica South and Black Crow, Northern Sperrgebiet, Namibia. A) SS 1'08, *Protophiomys* cf *algeriensis*, left m/1; B) SN 5'08, *Protophiomys* cf *algeriensis* left M2/; C) BC 1'08, *Glibia namibiensis* right upper molar; D) SN 1a'08 *Prepomonomys bogenfelsi* left M2/ and M3/; E) SN 9a'08, *Apodecter* cf *stromeri* left D4/ and M1/, E1) lingual view of teeth; F) SN 8'08, *Prepomonomys bogenfelsi* left mandible containing incisor and p/4-m/3, F1) stereo occlusal view of cheek teeth, F2) stereo buccal view, F3) occlusal view, F4) lingual view; G) SN 11'08, *Silicamys cingulatus* right M3/, stereo occlusal view; H) SN 21'08, *Protophiomys* cf *algeriensis* left d/4, stereo occlusal view; I) SN 25'08, *Silicamys cingulatus* right P4/ or M1/, stereo occlusal view; J) SN 20'08, cf *Bathyergoides* sp. right M3/, stereo occlusal view, J1) lingual view. For all occlusal views, mesial is towards the top of the page.

Table 3. Measurements of the teeth of rodents from the Palaeogene of Namibia.

Specimen	Length (mm)	Breadth (mm)	Identification
BC 1'08 right M1/ or M2/	2.48	2.51	*Glibia namibiensis*
SN 1'08 left M2/	2.44	2.63	*Prepomonomys bogenfelsi*
SN 1'08 left M3/	2.40	2.90	*Prepomonomys bogenfelsi*
SN 5'08 left M2/	1.17	1.50	*Protophiomys* cf *algeriensis*
SN 8'08 left d/4	2.67	1.97	*Prepomonomys bogenfelsi*
SN 8'08 left m/1	2.45	2.54	*Prepomonomys bogenfelsi*
SN 8'08 left m/2	2.65	2.56	*Prepomonomys bogenfelsi*
SN 8'08 left m/3	3.10	2.76	*Prepomonomys bogenfelsi*
SN 9'08 left D4/	1.92	1.93	*Apodecter* cf *stromeri*
SN 9'08 left M1/	1.90	2.00	*Apodecter* cf *stromeri*
SN 11'08 right M3/	1.71	1.68	*Silicamys cingulatus*
SN 20'08 right M3/	1.88	2.02	cf *Bathyergoides* sp.
SN 21'08 left d/4	1.44	1.11	*Protophiomys* cf *algeriensis*
SN 25'08 right P4/ or M1/	1.80	1.38	*Silicamys cingulatus*
SS 1'08 left m/1	1.78	1.56	*Protophiomys* cf *algeriensis*

mus of enamel. There is no sign of cementum. The anterior height is 2.95 mm, which is greater than the length of the tooth (1.88 mm) which makes this a hypsodont tooth.

Discussion. SN 20'08 is attributed to Bathyergidae due to the shallowness of the valleys and flexi. The overall morphology resembles that of *Bathyergoides neotertiarius*, but the tooth is smaller. This tooth, even though it is not identified to the species level, is important as it indicates that the family Bathyergidae originated considerably earlier than previously thought (Hartenberger, 1998; Mein and Pickford, 2008).

It is interesting to note that the oldest known bathyergid is from southern Africa, where the family is currently more diverse than in other parts of Africa.

The age of the Sperrgebiet Carbonates

The Phiomyidae rodent assemblage from Silica North has affinities with material from the Nementcha Mountains, East-Central Algeria, Glib Zegdou, West-Central Algeria, and Chambi, Tunisia (*Protophiomys algeriensis* and *Glibia tetralopha*). The deposits which yielded *Protophiomys algeriensis* were correlated to the Late Eocene by Jaeger *et al*., (1985), but they were subsequently correlated to the Early to Middle Eocene by Tabuce *et al*., (2000). The Black Crow deposits which are younger than those at Silica North and Silica South, yielded a tooth similar in morphology to, but larger than those attributed to *Glibia* (Vianey-Liaud *et al*., 1994) from Glib Zegdou, West-Central Algeria. The locality was correlated to the late Early Eocene or the early Middle Eocene (Tabuce *et al*., 2001a, 2001b) as was the Tunisian locality of Chambi that also yielded zegdoumyids (Vianey-Liaud *et al*., 1994). The other rodents from Silica North comprise primitive Diamantomyidae, Bathyergidae, and Myophiomyidae unknown from other localities, making it difficult to perform biostratigraphy. However, they are related to taxa from the Fayum, Egypt, such as *Metaphiomys* and *Phiocricetomys*, or from the Early Miocene of Africa, such as *Bathyergoides*.

The carnivorous mammals from the Sperrgebiet carbonates comprise two hyaenodontines, which are creodonts, and a todralestid. The former groups range through much of the Eocene into the Miocene, but *Pterodon* sp. from Black Crow is comparable in dimensions to species from the Fayum, Egypt. The todralestid from Namibia appears to be more derived than the genotype from the Palaeogene of Morocco (Gheerbrant, 1991). These fossils do not yield precise information about the age of the deposits, but they do not contradict a Lutetian correlation.

The molars of the genus *Namahyrax* gen. nov. are basically upscaled versions of the teeth in *Seggeurius* (Court and Mahboubi, 1993) with the exception that the hypocone in M3/ has a well developed posterior cingulum, not unlike the fossil from Bir el Ater, East-Central Algeria, described as *Bunohyrax* *matsumotoi* by Tabuce *et al*., (2000). Bir el Ater has been correlated to the middle or late Eocene. However, the lower second incisor of *Namahyrax* lacks the deep indentations at the apex of the crown which produce a three-tined tooth, a morphology clearly observed in *Bunohyrax matsumotoi*.

The arsinoithere, *Namatherium*, from Black Crow is highly divergent in cranial architecture from the Fayum, Egypt, genus *Arsinoitherium*, and its cheek teeth are lower crowned. It is also a smaller animal. Its morphology is sufficiently generalised and primitive however, that it could represent the ancestral condition for the highly derived cranial form and hypsodont dentition observed in *Arsinoitherium*. An Early or Middle Eocene age for *Namatherium* would accord with the primitive morphology that it possesses.

The macroscelidean, the primate and the pholidote from the Sperrgebiet Carbonates are too poorly represented to provide any precision concerning the age of the deposits. All that can be said is that they do not contradict a correlation to the Middle Eocene.

It should be noted that there has been a recent trend to shift the Gour Lazib sites downwards in the stratigraphic column (Adaci *et al*., 2007) with sites such as HGL 10 and HGL 52 being possibly correlated to the Ypresian. Considering the presence of closely related taxa in the Black Crow and Silica North sites to those reported from Gour Lazib, it is not unreasonable to keep open the possibility of an Ypresian age for the Namibian sites.

Figure 20 provides a provisional hypothesis of correlation of the Sperrgebiet Carbonates and marine deposits. An Early Lutetian age seems most likely for the doline and kamenitza infillings, although further study of the mammals may modify the conclusions somewhat. It should be borne in mind that the Black Crow Carbonate lies unconformably on the chalcedonic carbonates in the Black Crow Depression. The chalcedonic limestones at Silica North and Silica South are probably contemporaneous with those at Black Crow, Chalcedon Tafelberg, and even Gamachab. There were thus at least two separate periods of carbonate deposition in the Northern Sperrgebiet, an earlier well-bedded succession that infilled dolines and kamenitzas and which underwent slight to pervasive silicification, followed by a period of erosion and a second phase of carbonate deposition. The latter carbonates tend to be poor in silica, except as crystalline linings to small open tubes that traverse the de-

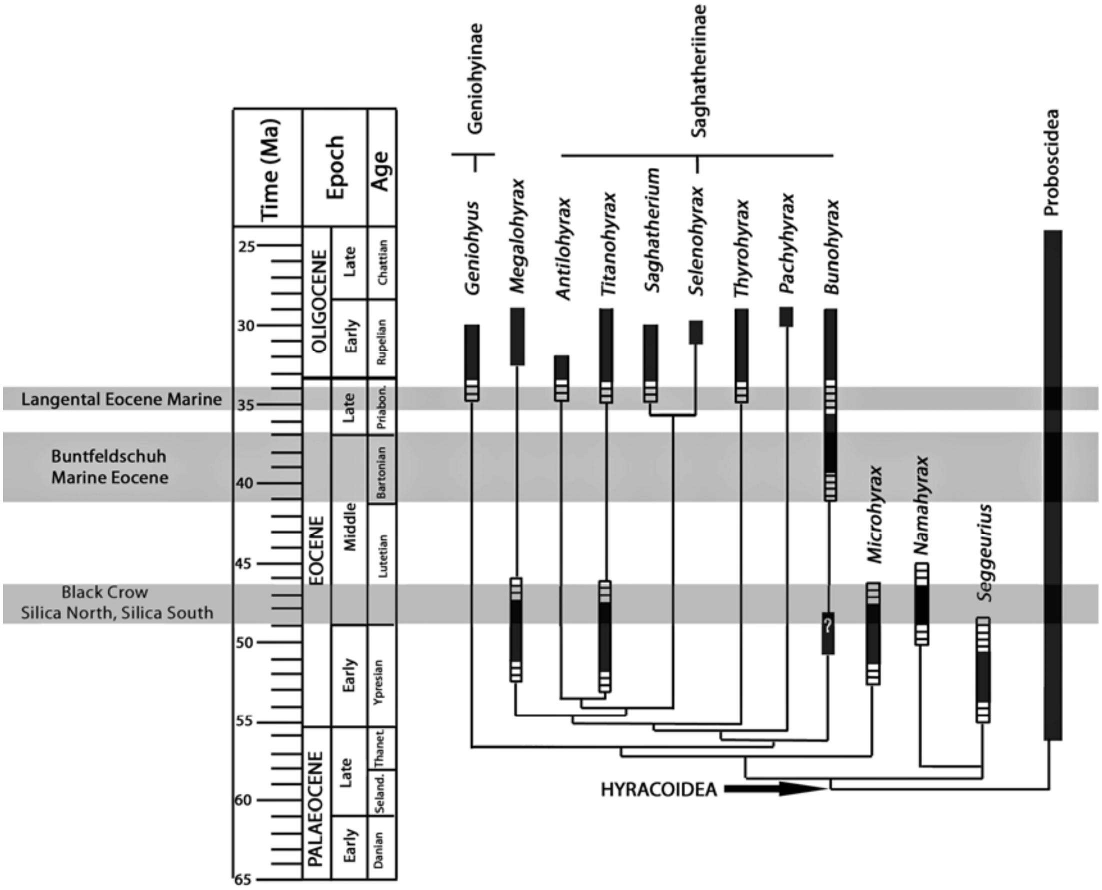

Figure 20. Provisional correlation of the Sperrgebiet terrestrial and marine Palaeogene deposits based on marine invertebrates and mammalian biostratigraphy, in particular the Rodentia, Arsinoitheriidae and Hyracoidea (Chart modified from Tabuce *et al*., 2001: *Namahyrax* added in the position of sister taxon to *Seggeurius*).

posits (root holes, hollow plant stems or termite foraging tubes?). It is thus possible that the Sperrgebiet Carbonates span a significant period of time.

It is clear that the marine Eocene deposits of the Sperrgebiet are younger than the mammal-bearing terrestrial carbonates. The Buntfeldschuh succession was considered by Ward and MacMillan (pers. comm.) to be older than the Langental Eocene sediments, which are correlated to the Priabonian (NP 19-20) (Siesser, 1977; Siesser and Salmon, 1979). These correlations are included in figure 20. It is interesting to have confirmation of the sequence of stratification in the Sperrgebiet inferred by German geologists as early as 1926 on the basis of clast assemblages, in this case the presence of chalcedonic limestone pebbles in the Eocene marine deposits at Langental and Buntfeldschuh.

Biogeographic affinities of the Sperrgebiet Palaeogene mammals

Most, but not all, of the mammals from Silica North, Silica South and Black Crow appear to have affinities with material from deposits in North Africa. The arsinoithere, *Namatherium* has not been recorded from North Africa, but its cranio-dental morphology suggests affinities with the younger genus *Arsinoitherium*, and not with roughly co-eval *Palaeoamasia* from Turkey, and *Crivadiatherium* from Romania. With the exception of the bathyergid, *Prepomonomys* and *Apodecter*, the Sperrgebiet Palaeogene rodents appear to share affinities with fossils from Algeria, Tunisia and Egypt. The hyracoid *Namahyrax* is similar enough to *Seggeurius* and *"Bunohyrax" matsumotoi* for them to be related taxa.

The Sperrgebiet macroscelidid and erinaceid are poorly represented as fossils, but the Macroscelidea is in any case a characteristic African group, also known from North African Eocene deposits (Hartenberger, 1986), and the Erinaceidae were widespread from Palaeocene times onwards in the northern continents, although until the Black Crow discovery, they were not positively identified in Africa prior to the Early Miocene.

As an assemblage, therefore, the Sperrgebiet Palaeogene mammals appear to show close biogeographic affinities with North African lineages, which indicates that the faunal affinities of the southern part of the continent were typically African. Jaeger *et al.*, (1985) discussed the palaeobiogeographic affinities of the Eocene rodents from Algeria, and pointed out some affinities with fossils from Europe and Asia, suggesting the occurrence of faunal exchanges between the continents during or prior to the Eocene. The presence of similar lineages in southern Africa indicates that the lineages concerned dispersed to the latitudinal extremities of the African continent without hindrance, and thus probably without significant delays.

The fact that several of the rodents from Silica North (cf *Bathyergoides*, *Apodecter* cf *stromeri*, *Prepomonomys bogenfelsi*) show closer affinities to Miocene rodents from the same region, than they do to forms from North or East Africa is not surprising considering the vast distances between the localities, but it suggests a certain degree of endemism in the southern African fauna over extended periods of time, in the case of the Sperrgebiet for some 27 million years or so, the time that lapsed between the deposition of the Black Crow Palaeogene carbonates and Langental Early Miocene clastic deposits.

Conclusions

The discovery of fossiliferous terrestrial deposits of Lutetian age in the Northern Sperrgebiet, Namibia, greatly improves the Palaeogene fossil record of sub-Saharan Africa. Prior to the recognition of these sediments, there were only three known occurrences of Palaeogene mammals in the sub-equatorial part of the continent, two in Tanzania (Mahenge and Rukwa) and one in Cabinda, Angola (Malembe) and none of these deposits is very rich in mammals. The Sperrgebiet localities have yielded a moderately diverse mammal fauna along with plants, invertebrates and lower vertebrates. Among the mammals identified there are an erinaceid, a macroscelidean, six genera of rodents belonging to five families (Zegdoumyidae, Diamantomyidae, Myophiomyidae, Phiomyidae, Bathyergidae), two creodonts, a todralestid, a pholidote, a primate, an arsinoithere and a hyracoid. In addition to the mammals there are fish, pipids, ranoids, crocodiles, amphisbaenians, lizards, snakes, birds and a diversity of freshwater and terrestrial gastropods and ostracods.

Preliminary assessment of the age of the deposits on the basis of mammalian biochronology suggests a Lutetian age, more or less equivalent to Bir el Ater, Glib Zegdou and Chambi in the Maghreb, North Africa. The deposits are considerably older than the classic Late Eocene to Early Oligocene mammalian localities in the Fayum, Egypt.

Despite the enormous distance between the North African and Namibian sites (ca 7000 km), the faunas from the two regions, in particular the rodents, appear at first analysis to be rather close to each other, suggesting that there were likely unhindered biogeographic links between the two extremities of the continent at the time, some 47 million years ago, and thus permitting biochronology to yield reasonably reliable age estimates for the Namibian deposits. Nevertheless, three of the rodent lineages suggest that there was already a certain degree of southern endemism to the Namibian faunas.

The Namibian Palaeogene fossils occur in well bedded carbonates that accumulated in dolines and kamenitzas eroded into Gariep Dolomite. The occurrences are small in extent (up to 500 metres diameter), which partly explains why four out of the six occurrences previously escaped notice. The basal layers of carbonate have been silicified to produce chalcedonic limestone. Clasts of chalcedony have long been associated with the presence of diamonds in the Namibian placers, from which it was inferred by geologists that deposits such as those at Chalcedon Tafelberg must be earlier than Priabonian, the age determined for Eocene marine deposits containing marine macro- and microfauna, diamonds and clasts of chalcedony. The dating of the silicified carbonates to the Lutetian supports the conclusions of the geologists.

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Annex I.

Rupelian and Pre-Rupelian Palaeogene Mammals of Africa

(Modified and extended from Miller *et al.*, 2005. Several taxa of Fayum rodents mentioned by Lewis and Simons, 2007, are not included as they appear to be *nomina nuda*) (Namibian mammals are underlined)

- Marsupialia
  - Peradectidae
    - *Kasserinotherium tunisiense*
    - *Peratherium africanum*
- Cimolesta
  - Cimolestidae
    - *Cimolestes* cf *incisus*
    - *Cimolestes euspalus*
  - Todralestidae
    - *Todralestes variabilis*
    - *Todralestes butleri*
    - *Namalestes gheerbranti* n.g.n.s.
  - Palaeoryctidae
    - *Palaeoryctes minimus*
    - *Aboletylestes robustus*
    - *Aboletylestes hypselus ?*
- Lipotyphla
  - Adapisoriculidae
    - *Afrodon chleuhi*
    - *Garatherium mahboubii*
    - *Garatherium? todrae*
    - *Afrodon taghourtensis*
- Afrosoricida
  - Afrosoricidae
    - *Widanelfarasia bowni*
    - *Widanelfarasia rasmusseni*
    - *Jawharia tenrecoides*
    - *Eochrysochloris tribosphenus*
- Erinaceomorpha ?
  - Chambilestidae
    - *Chambilestes foussanensis*
    - Erinaceidae Black Crow
- Macroscelidea
  - Macroscelididae
    - *Chambius kasserinensis*
    - *Nementchatherium senarhense*
    - *Herodotius pattersoni*
    - *Metoldobotes stromeri*
    - Macroscelididae Silica North
- Ptolemaiida
  - Ptolemaiidae
    - *Ptolemaia lyonsi*
    - *Ptolemaia grangeri*
    - *Qarunavus meyeri*
    - *Cleopatrodon ayeshae*
    - *Cleopatrodon robustus*
- Creodonta
  - Koholiidae
    - *Koholia atlasense*
  - Hyaenodontidae
    - *Masrasector aegypticum*
    - *Masrasector ligabuei*
    - *Metasinopa ethiopica*
    - *Apterodon macrognathus*
    - *Apterodon minutus*
    - *Pterodon phiomensis*
    - *Pterodon africanus*
    - *Pterodon leptognathus*
    - *Pterodon* sp. Black Crow
    - *Metapterodon brachycephalus*
    - *Tinerhodon disputatum*
    - *Boualitomus marocanensis*
    - *Glibzegdouia tabelbalaensis*
    - Proviverrinae Black Crow
- Condylarthra
    - *Abdounodus hamdii*
    - *Ocepeia daouiensis*
- Pholidota
  - Manidae
    - Manidae Black Crow
- Hyracoidea
    - *Helioseus insolatus*
    - *Titanohyrax tantalus*
    - *Titanohyrax mongereaui*
    - *Titanohyrax andrewsi*
    - *Titanohyrax ultimus*
    - *Titanohyrax pygmaeus*
    - *Thyrohyrax meyeri*
    - *Thyrohyrxax litholagus*
    - *Thyrohyrax angustidens*
    - *Thyrohyrax domorictus*
    - *Microhyrax lavocati*
    - *Bunohyrax major*
    - *Bunohyrax fajumensis*
    - *Bunohyrax matsumotoi*
    - *Megalohyrax gevini*
    - *Megalohyrax eocaenus*
    - *Pachyhyrax crassidentatus*
    - *Geniohyus magnus*
    - *Geniohyus mirus*
    - *Geniohyus diphycus*
    - *Saghatherium bowni*
    - *Saghatherium antiquum*
    - *Saghatherium humarum*
    - *Selenohyrax chatrathi*
    - *Seggeurius amourensis*
    - *Namahyrax corvus* n.g.n.s.
- Embrithopoda
  - Arsinoitheriidae
    - *Arsinoitherium zitteli*
    - *Namatherium blackcrowense* n.g.n.s.
- Proboscidea
  - Numidotheriidae
    - *Khamsaconus bulbosus*
    - *Daouitherium rebouli*
    - *Phosphatherium escuillei*
    - *Numidotherium koholense*
    - *Numidotherium savagei*
  - Palaeomastodontidae
    - *Palaeomastodon beadnelli*
    - *Palaeomastodon parvus*
    - *Palaeomastodon intermedius*
  - Barytheriidae
    - *Barytherium grave*
  - Moeritheriidae
    - *Moeritherium lyonsi*
    - *Moeritherium trigodon*
    - *Moeritherium chehbeurameuri*
  - Phiomiidae
    - *Phiomia serridens*
    - *Phiomia wintoni*
    - *Phiomia minor*
    - *Phiomia osborni*
- Chiroptera
  - Philisidae
    - *Dizzya exsultans*
    - *Philisis sevketi*
    - *Philisis sphingis*
  - Rhinolophidae
    - *Hipposideros (Brachipposideros) omani*
  - Family ?
    - *Dhofarella thaleri*
    - *Chibanycteris herberti*
    - *Vampyravus orientalis*

    - *Ghamidtherium dimaiensis*
  - Tanzanicteridae
    - *Tanzanicterys mannardi*
- Primates
  - Omomyidae
    - *Altiatlasius koulchii*
    - *Plesiopithecus teras*
    - *Omanodon minor*
    - *Shizarodon dhofarensis*
    - *Djebelemur martinezi*
    - *Anchomomys milleri*
  - Notharctidae
    - *Aframonius dieides*
    - *Azibius trerki*
    - *Dralestes hammadaensis*
  - Afrotarsiidae
    - *Afrotarsius chatrathi*
  - Galagidae
    - *Saharagalago misrensis*
    - *Wadilemur elegans*
    - *Karanisia clarki*
  - Parapithecidae
    - *Apidium moustaphai*
    - *Apidium bowni*
    - *Apidium phiomense*
    - *Parapithecus grangeri*
    - *Parapithecus fraasi*
    - *Abuqatrania basiodontos*
    - *Qatrania wingi*
    - *Qatrania fleaglei*
    - *Algeripithecus minutus*
    - *Tabelia hammadae*
    - *Biretia piveteaui*
    - *Biretia fayumensis*
    - *Biretia megalopsis*
    - *Namaia bogenfelsi* n.g.n.s.
  - Arsinoeidae
    - *Arsinoea kallimos*
  - Proteopithecidae
    - *Proteopithecus sylviae*
    - *Serapia eocaena*
  - Propliopithecidae
    - *Catopithecus browni*
    - *Oligopithecus savagei*
    - *Oligopithecus rogeri*
    - *Propliopithecus ankeli*
    - *Propliopithecus chirobates*
    - *Propliopithecus haeckeli*
    - *Aegyptopithecus zeuxis*
    - *Moeripithecus markgrafi*
- Rodentia
  - Zegdoumyidae
    - *Zegdoumys sbeitlai*
    - *Zegdoumys lavocati*
    - *Glibia namibiensis* n.s.
    - *Glibia tetralopha*
    - *Glibia pentalopha*
    - *Glibemys algeriensis*
  - Anomaluridae
    - *Nementchamys lavocati*
  - Myophiomyidae
    - *Phiocricetomys minutus*
    - *Silicamys cingulatus* n.g.n.s.
  - Diamantomyidae
    - *Metaphiomys beadnelli*
    - *Prepomonomys bogenfelsi* n.g.n.s.
  - Phiomyidae
    - *Protophiomys algeriensis*
    - *Protophiomys* cf *algeriensis.*
    - *Phiomys lavocati*
    - *Phiomys andrewsi*
    - *Phiomys paraphiomyoides*
    - *Apodecter* cf *stromeri*
  - Thryonomyidae
    - *Paraphiomys simonsi*
    - *Gaudeamus aegyptius*
  - Bathyergidae
    - cf *Bathyergoides* sp.
- Artiodactyla
  - Anthracotheriidae
    - *Qatraniodon parvum*
    - *Bothriogenys gorringei*
  - Haplobunodontidae
    - *Rhagatherium aegyptiacum*