First record of *Celtis* (Hackberry) from the Palaeogene of Africa, Sperrgebiet, Namibia

Martin PICKFORD

Sorbonne Universités (CR2P, MNHN, CNRS, UPMC - Paris VI) 8, rue Buffon, 75005, Paris, France, e-mail : martin.pickford@mnhn.fr

Abstract: Small spheres composed of tiny quartz crystals are common in the Ypresian/Lutetian freshwater limestone at Black Crow, Sperrgebiet, Namibia. From the beginning they were thought to be the inner parts of some sort of fruit, but the lack of structure rendered the material unidentifiable. Recently a specimen was found which retains the outer surface of the endocarp of the fruit over most of its surface, but which is broken at one pole to reveal the inner locular structure. The fossil is attributed to *Celtis*, a fruit tree which is common in warm latitudes of the globe. Long known to occur in the Neogene of Africa, the Black Crow record extends its representation in the continent into the Palaeogene, some 30 million years earlier than the previous oldest known occurrence (Napak, Uganda 19-20 Ma) and reveals that the genus was present not only in Eurasia and the Americas during the Palaeogene, but also in Africa. This discovery adds fuel to the debate about the geographic origin of the genus *Celtis* which is thought by some palaeobotanists to have evolved in post-Cretaceous times but whether it originated in the northern or southern hemisphere remains a moot point.

Key words: Eocene; Celtidaceae; Endocarp; Locule; Palaeobotany; Biogeography.

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Introduction

Small spherical fossils composed of masses of tiny quartz crystals have been found in the Black Crow limestone ever since the first samples were dissolved in acid in 2008 to recover the invertebrate and vertebrate fossils (Pickford *et al.* 2008a). The spheres range in diameter from 3.4 to 5.3 mm. As simple spheres the fossils were effectively unidentifiable, but in a recent bout of acid treatment of limestone a specimen was recovered that preserves the external morphology of an endocarp of a fruit, but which is damaged on one side to reveal the inner locular structure identical to that of the previously collected material (Fig. 1).

The specimen has a reticulate, corrugated outer surface similar to that of *Celtis* endocarps from other parts of the world (Chesters, 1957; Manchester *et al.* 2002; Retallack *et al.* 1995) and is accordingly identified as such. One poorly preserved endocarp and 28 natural molds of locules are included in the same taxon.

The significance of the well-preserved specimen is that it extends the geochronological range of the genus in Africa downwards from the Early Miocene (19-20 Ma Napak, Uganda; 18 Ma Rusinga, Kenya) (Chesters, 1957) to the Ypresian/ Lutetian boundary (ca 48 Ma).

A recent review of the worldwide distribution of *Celtis* (Manchester *et al.* 2002) evoked the origin of the genus but did not reach a firm conclusion, although the authors mentioned that the genus was not known from the Palaeogene of Africa but was known to be widespread in Eurasia as well as North and South America during this period. As these authors pointed out, the genus is known from mesophytic to arid habitats in temperate and tropical parts of the northern and southern hemispheres, but currently available evidence does not resolve the question of whether it originated in the northern or the southern hemisphere.

Geological and faunal contexts

The freshwater limestone deposit at Black Crow, Namibia, is a rich source of information about invertebrates and vertebrates of Ypresian/Lutetian age (Pickford *et al.*, 2008a, 2008b). For a recent summary of the geological

and faunal contexts of the limestone, refer to Pickford, 2018a, 2018b).

Palaeobotany

The fossil from Black Crow attributed to *Celtis* is spherical, almost 5 mm in diameter with a coarsely corrugated and reticulate surface sculpture. Part of the surface has spalled away, exposing the inner layers of the specimen, which comprise a thin white layer of small conjoined spherules overlying a large fine-grained core, and underlying the corrugated surface layer. Another specimen preserves the endocarp but in a pitted and eroded state (Fig. 2).

The corrugations on the best-preserved specimen are interrupted by four poorly defined ribs radiating from a pole (Fig. 1) as in specimens of *Celtis rusingensis* from Napak,

Uganda (Fig. 3). Inside there is a single, smooth-surfaced locule.

28 additional specimens lacking the endocarp covering were found at Black Crow, comprising spherical to subspherical natural molds of the locule in minutely crystallised quartz. The locule surface is generally smooth, but some specimens show a thin layer of microspherules covering a smooth inner core. Some specimens are slightly pointed at one pole with a small depression in the apex of the process, interpreted to be the pole by which the locule was attached to the twig. A few specimens are slightly flattened on one side (Fig. 2).

The 30 specimens from Black Crow range in diameter from 3.4 mm to 5.5 mm.



Figure 1. Stereo views of an endocarp attributed to *Celtis*, the hackberry. Left) view of undamaged part of specimen, Right) damaged part of same specimen exposing the single locule of the fruit (scale : 1 mm).

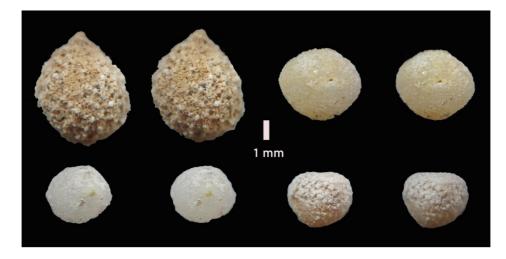


Figure 2. Stereo views of an endocarp and molds of locules of *Celtis* from Black Crow, Namibia. The reticulate surface of the complete endocarp (top left) is somewhat pitted by acid etching, but the structure can be made out satisfactorily, as can the pointed end at one pole. The molds of the locules are either smooth (top right and bottom left) and show a small pit at one pole (centre of images) or are slightly puffy, as in the lightly flattened example (bottom right) (scale : 1 mm).

Discussion

Endocarps of Celtis, the hackberry (also known in Africa as Stinkwood, or False Stinkwood) are often preserved in carbonaterich deposits (Retallack et al. 1995; Manchester et al. 2002). The discovery of an endocarp of the genus at Black Crow, a Palaeogene freshwater limestone in Namibia, is thus not unexpected. Most of the 30 specimens recovered thus far lack the diagnostic outer layer of the endocarp and were essentially unidentifiable natural molds of the sub-spherical locule, but the recovery of an almost complete specimen with a reticulate, corrugated surface sculpture arranged within four poorly defined ribs, removes the uncertainty about the appurtenance of the specimens.

The most complete fossil from Black Crow resembles specimens of *Celtis rusingensis* from

Napak XXI, Uganda (Fig. 3) but the Namibian specimen is about half the diameter of the specimens from Uganda. However, the Namibian fossils are similar in dimensions to Palaeogene specimens from North America (2.9 - 5 mm diameter according to Manchester *et al.* 2002).

At present, *Celtis* is widely distributed in both hemispheres (Manchester *et al.* 2002) in temperate and tropical latitudes. In Africa it grows in a great variety of habitats ranging from tropical forest to arid environments, rocky outcrops and coastal dunes.

The discovery of the genus in the Palaeogene of Namibia (Fig. 4) confirms the longevity of its presence in the continent, similar to that in South America, North America and Eurasia (Manchester *et al.* 2002).

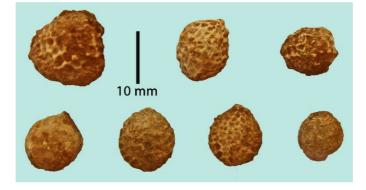


Figure 3. Endocarps of *Celtis* from the Early Miocene locality of Napak XXI, Uganda (scale : 10 mm).



Figure 4. Map showing occurrences of fossilised endocarps of *Celtis* in Palaeogene (yellow dots) and Neogene (red dots) localities. Note the presence of the genus in the Palaeogene of Africa, Eurasia, and North and South America (Distribution in Eurasia and North America based on Manchester *et al.* 2002).

A fossilised endocarp with single locule from Black Crow, Namibia, is identified as *Celtis*, a fruit tree that is widespread in the warmer parts of the northern and southern hemispheres.

Prior to the Black Crow discovery, the oldest known *Celtis* from Africa was from the Early Miocene of East Africa (Chesters, 1957; Retallack *et al.* 1995). This discovery brings the fossil record of the genus in Africa into line with that from South America, North America and Eurasia, where it has long been known to occur in the Palaeogene. The Black Crow occurrence extends the fossil record in Africa downwards by some 30 million years to the Ypresian/ Lutetian boundary.

The presence of this genus of plant at Black Crow accords with the fauna, both invertebrate and vertebrate, which indicates that at the time of deposition, the region lay within a summer rainfall regime, most likely within a temperate climatic zone.

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