Review of Palaeobotany and Palynology 159 (2010) 188–194

Contents lists available at ScienceDirect

Review of Palaeobotany and Palynology

journal homepage: www.elsevier.com/locate/revpalbo

Rutaceae leaf fossils from the Late Oligocene (27.23 Ma) Guang River flora of northwestern Ethiopia

Aaron D. Pan *

Fort Worth Museum of Science and History, 1600 Gendy Street, Fort Worth, Texas 76107-4062, United States

ARTICLE INFO

Article history:
Received 19 June 2009
Received in revised form 17 December 2009
Accepted 19 December 2009
Available online 4 January 2010

Keywords:
Aurantioideae
Clausena
Ethiopia
Kenya
Oligocene
Rutaceae
Vepris

ABSTRACT

Fossil leaf compressions from the Late Oligocene (27.23 Ma) Guang River flora of northwestern Ethiopia include a new record of *Vepris* and the earliest record of *Clausena* and the subfamily Aurantioideae. These fossils, along with most other African rutaceous fossils, are associated with a tropical moist forest community. The large number of Rutaceae taxa in eastern Africa during the Late Oligocene and Early Miocene is likely due to a radiation within Africa or dispersal to Africa associated with the continental expansion of moist tropical forest during this time interval.

1. Introduction

The Rutaceae Juss., including Cneoraceae Link and Ptaeroxylaceae Sond., is a medium-sized cosmopolitan angiosperm family in the Sapindales Dumort. with around 1900 species in approximately 160 genera (Chase et al., 1999; APG, 2003; Groppo et al., 2008). The family is characterized by the presence of scattered pellucid dots (secretory cavities containing ethereal oils) in almost all species, particularly in the leaves and reproductive structures (Groppo et al., 2008; Judd et al., 2008). Rutaceae taxa are particularly diverse and speciose in Asia and Australia–Oceania, and are relatively diverse in Africa and Madagascar with approximately 440 species in 29 to 30 genera (Gilbert, 1958; Dale and Greenway, 1961; Kokwaro, 1982; Gilbert, 1989; Mziray, 1992; Beentje, 1994; Schatz, 2001; Goldblatt and Manning, 2002; Hawthorne and Jongkind, 2006; Lovett et al., 2006). Most extant African Rutaceae species are found in tropical moist and seasonally deciduous forests and woodland communities, or in the case of the Diosmeae, as major components of the unique fynbos vegetation of southern Africa (Goldblatt and Manning, 2002; Cowling et al, 2005; Trinder-Smith et al., 2007).

While the Rutaceae is generally considered to be of Laurasian origin (Morley, 2000; Morley and Dick, 2003) and has an early and prolific fossil record in Europe, Asia, and North America, Africa has a relatively good record including some of the earliest purported occurrences of the family from the Cretaceous or early Paleogene of North Africa, Cameroon, and Ethiopia (Kräusel, 1939; Mädel-Angeliewa and Müller-Stoll, 1973; Koeniguer, 1976; Gregor, 1989; Dupéron-Laudoueneix and Dupéron, 1995). In addition, recent molecular phylogenetic studies of Meliaceae and Simaroubaceae (Muellner et al., 2006; Clayton et al., 2007), the likely sister taxa of Rutaceae, indicate a more generalized Tethyan origin of this Sapindalean subclade rather than a solely, and more restricted Laurasian one. Moreover, phylogenetic relationships within Rutaceae itself suggest that Africa has played a larger role in the evolutionary history of the family than has been realized with basal taxa and some major groups endemic to the continent (ex. *Ptaeroxylon*, Diosmeae; Chase et al., 1999; Groppo et al., 2008). While many major angiosperm families (and groups therein) likely originated in North America, Europe, or Asia and have only recently dispersed or radiated in Africa, much of what is known of the paleobotanical record is due to more extensive and enduring research on those continents compared to Africa. With new research being conducted in the tropics today, it is likely that paleobiogeographical scenarios and minimum ages for angiosperm clades will need to be re-evaluated as new material is discovered.

Recently discovered fossil leaf compressions with affinity to the Rutaceae are described from the Late Oligocene (27.23 Ma) Guang River flora of northwestern Ethiopia. They represent the first fossil evidence of *Clausena* Burm. f. and the oldest definitive record of the subfamily Aurantioideae, and a new Oligocene record of the genus *Vepris* Comm. ex A. Juss. The Aurantioideae is most diverse and speciose in Asia today, and has been hypothesized or inferred to have

* Tel.: +1 817 255 9364; fax: +1 817 732 7635.
E-mail address: apan@fwmsh.org.

0034-6667/$ – see front matter © 2009 Elsevier B.V. All rights reserved.
doi:10.1016/j.revpalbo.2009.12.005

originated on that continent (Ehrendorfer, 1988). However, this new record of *Clausena* may indicate that this important group may have originated, or had an earlier presence, in Africa than first conjectured. A review of the African Rutaceae fossil record is also provided here to give insight into the paleoecological and paleobiogeographical importance of the family in African forest communities.

2. Material and methods

The Guang River flora is an autochthonous or parautochthonous fossil assemblage located approximately 60 km west of Gondar in the Amhara District of northwestern Ethiopia. The geology of the area is dominated by Oligocene and Miocene flood basalts with interbedded fluvially reworked volcaniclastic and clastic sediments, airfall tuffs, and lignite deposits (Kappelman et al., 2003; Jacobs et al., 2005). The flora is preserved in a 22 to 36 mm thick massive dark gray to yellow-green mudstone. All macrofossil specimens are permanently housed at the National Museum of Ethiopia, Addis Ababa.

The age of the Guang River flora is well constrained. The fossilferous mudstone layer in which the plant assemblage occurs is part of a 100 m thick section of sedimentary strata which overlie a basalt that has been dated 32.4 ± 1.6 Ma using whole rock K/Ar radiometric dating methods (Kappelman et al., 2003), and underlies an ash dated 27.36 ± 0.11 Ma by $^{40}Ar/^{39}Ar$ radiometric dating of potassium-feldspar. Paleomagnetic reversal stratigraphy also ties the mudstone layer to Chron C9n (Kappelman et al., 2003; Cande and Kent, 1995). In addition, a recent $^{206}Pb/^{238}U$ analysis of zircon crystals extracted from an ash layer that stratigraphically correlates with the Guang River flora is dated 27.23 ± 0.1 Ma and can now be applied with confidence to the flora.

Cuticle was prepared from fossil leaf fragments (0.5–1 cm^2) by first rinsing the material in 10% hydrochloric acid (HCl) for 10–30 min to remove carbonates from the mudstone. The leaf material was then rinsed with distilled water and placed in a solution of 48% hydrofluoric acid (HF) for 24–48 h to dissolve away the silicate matrix. The cuticle was then placed in a 20% bleach (NaClO)–water solution for a brief amount of time (on the order of 20 s to 1 min) to dissolve excess organics. The cuticle was then thoroughly rinsed with distilled water and placed on microscope slides in glycerine. Light microscope slides of both the fossil and herbarium samples are housed in the Huffington Department of Earth Sciences at Southern Methodist University in Dallas, Texas, United States of America.

Modern leaf cuticle samples from 27 species within the Rutaceae and Apocynaceae were collected from the Missouri Botanical Garden herbarium (MO) to compare the epidermal morphology with the fossils. Samples (0.5–1 cm^2) were cleared to remove the mesophyll, and were soaked in distilled water bath for 24 h to re-saturate. The specimens were then treated with a solution of 10% potassium hydroxide (KOH) until they darkened fully, washed with distilled water, placed in baths of 30–60% bleach, stained with a Safranine O solution, rinsed with 90% ethanol (CH_3CH_2OH), and mounted on microscope slides in glycerine jelly.

3. Results

3.1. Systematics

RUTACEAE JUSS., Gen. Pl.: 296. 4 Aug 1789
VEPRIS COMM. EX. A. JUSS. 1825
VEPRIS SP. (Figs. 1–3)

Description: Coriaceous microphyllous to notophyllous asymmetric laminar compressions (Fig. 1). The lamina are 47 to 56 mm long and 24 to 31 mm wide. The fossils are elliptic in shape and have asymmetrical bases which are acutely angled and convex in shape. Apices are acutely angled and convex to rounded in shape. The petiolule is short, about 2 mm in length (CH41-99; Fig. 1). Lamina margins are revolute. Primary venation is pinnate. Secondary venation is brochidodromous, forming submarginal loops. Secondary vein spacing is irregular and the lowermost secondaries have a more acute angle than subsequent ones. Strong intersecondaries are present. Tertiary venation is random reticulate. CUTICLE: Abaxial stomatal complexes are of the polycytic type, most being anomocytic (Fig. 2). Abaxial anticlinal cell walls are straight to slightly rounded in shape and 4 to 7-sided, most being 5-sided. Abaxial cell sizes generally range from 17 to 26 μm long and 8 to 16 μm wide. Adaxial epidermal cells are 4 to 5-sided and anticlinal cell walls are rounded to slightly sinuous (Fig. 3). Adaxial epidermal cells are 11.70 to 41.70 μm long and 8 to 21 μm wide.

Material: CH41-78 and CH41-99 (Fig. 1).

Locality: Sublocality CH41 of the Guang River flora.

Comparisons/comments: The fossils likely represent leaflets due to the asymmetry of the lamina and the short attachments (interpreted here as petiolules). The leaflet morphology and venation of the fossils are also similar to the genus *Alafia* Thouars (Apocynaceae); however species of this genus bear paracytic stomata, while the morphotype and most Rutaceae have anomocytic stomatal complexes.

Assuming that the fossils represent leaflets, and given the following observed characteristics: (1) coriaceous texture, (2) slightly revolute non-crenate margins, (3) short petiolules, (4) glabrous epidermal surfaces, (5) small abaxial cells with straight to slightly rounded anticlinal cell walls, and (6) anomocytic stomata (Figs. 2, 4, and 5), the fossil belongs to the genus *Vepris*, which now includes *Araliopsis* Engl., *Diphasia* Pierre, *Diphasiopsis* Mendonça, *Oricia* Pierre, *Oriciopsis*, *Teclea* Delile, *Tecleopsis* Hoyle & Leakey, and *Toddaliopsis* Engl. (Fig. 6; Mziray, 1992).

Modern Rutaceae are readily identifiable by the presence of oil glands in the leaves, leaflets, and fruits. However, leaf glands are usually present in the mesophyll which is not preserved in these fossils. While the presence of oil glands cannot be confirmed on the fossils, punctuate texture near the margin and within the areoles may indicate the presence of such glands. The characteristic “rutoid” teeth seen in crenulate margined species (Judd et al., 2008) are generally absent or not observable in *Vepris*.

Other taxa of Rutaceae differ from the fossil. The African and Asian monotypic genus *Toddalia* Juss. (*T. asiatica*) has distinctive striations surrounding the stomata which are absent from the fossil cuticle (Mziray, 1992). The random reticulate tertiary venation and absence of hairs on either leaf surface of the fossil indicates that the leaflets do not represent the Afro-Malagasy genus *Fagaropsis* (Mildbr. ex Siebenl.), which is characterized by alternate percurrent tertiary venation and multicellular glandular hairs (Mziray, 1992).

Vepris, with around eighty extant species, includes unarmed shrubs and trees found in numerous types of forests, woodlands, and thickets throughout tropical Africa, Madagascar, the Mascarenes, tropical Arabia, and southwestern India (Mziray, 1992). The fossils look very similar to the extant northeastern African species *Vepris glomerata* and *V. sansibarensis* (Engl.) W. Mziray (Fig. 4). *Vepris glomerata* (F. Hoffm.) Engl. is a shrub or tree found in dry bushland or riparian woodland in Ethiopia, Kenya, Somalia, and Tanzania (Mziray, 1992; Beentje, 1994) and *V. sansibarensis* is a shrub growing in coastal dry forest in Tanzania and southeastern Kenya (Dale and Greenway, 1961; Mziray, 1992). The fossils, which have only anomocytic stomata, differ slightly from *Vepris glomerata*, which can have both anomocytic and paracytic stomata (Mziray, 1992). Since the Guang River *Vepris* differs little from at least two existing East African species (*V. glomerata* and *V. sansibarensis*), a new species is not designated for the fossil leaflets.

RUTACEAE JUSS., Gen. Pl.: 296. 4 Aug 1789
AURANTIOIDEAE EATON 1836
CLAUSENA BURM. F. 1768
CLAUSENA SP. (Figs. 7–11)

Description: Oblong to elliptic microphyllous asymmetrical lamina fragments that are 26 to 55 mm long and 14 to 27 mm wide. Leaf