

FOSSIL *NEWTONIA* (FABACEAE: MIMOSEAE) SEEDS FROM THE EARLY MIOCENE (22–21 MA) MUSH VALLEY IN ETHIOPIA

Aaron D. Pan,^{1,*†} Ellen D. Currano,[‡] Bonnie F. Jacobs,[§] Mulugeta Feseha,^{||} Neil Tabor,[§] and Patrick S. Herendeen[#]

*Fort Worth Museum of Science and History, 1600 Gendy Street, Fort Worth, Texas 76107-4062, U.S.A.; †Botanical Research Institute of Texas, 1700 North University Drive, Fort Worth, Texas 76107-3400, U.S.A.; ‡Department of Geology and Environmental Earth Science, Miami University, 250 South Patterson Avenue, Oxford, Ohio 45056, U.S.A.; §Roy M. Huffington Department of Earth Sciences, Southern Methodist University, P.O. Box 750395, Dallas, Texas 75275-0395, U.S.A.; ||Institute of Development Studies and Department of Earth Sciences, Addis Ababa University, P.O. Box 1176, Ethiopia; and #Chicago Botanic Garden, 1000 Lake Cook Road, Glencoe, Illinois 60022, U.S.A.

Numerous fossil winged seeds from the early Miocene (22–21 Ma) of Ethiopia represent the earliest and only definitive record of the ecologically and economically important legume genus *Newtonia* (Fabaceae: “Mimoseae”). These fossils represent a new species and provide evidence that tropical moist forest persisted on the Ethiopian Plateau into the early Miocene.

Keywords: Fabaceae, *Fillaeopsis*, funiculus, Mimoseae, Miocene, *Newtonia*.

Introduction

Recent paleobotanical and palynological discoveries in eastern and northern Africa and the Arabian Peninsula have contributed significantly to our understanding of the composition and extent of Afro-Arabian tropical moist forests from the late Eocene through the early Miocene (Privé-Gill et al. 1999; Herendeen and Jacobs 2000; Morley 2000; Jacobs 2004; Jacobs et al. 2005, 2010; Pan et al. 2006, 2010; Vincens et al. 2006; Eisawi and Schrank 2008; Pan and Jacobs 2009; Bonnefille 2010; García Massini et al. 2010; Pan 2010), a time interval when Afro-Arabia’s humid tropical and subtropical forests were likely at an acme in terms of plant diversity and spatial extent (or at least compared to modern African forests; Saldard-Chebaldaff 1979, 1981; Jacobs 2004; Morley 2007). Within these assemblages, the legume family (Fabaceae or Leguminosae) is well represented in terms of prominence and diversity, patterns that continue among contemporary African tropical forest communities (Gentry 1988; Jacobs 2004). Interestingly, while the African paleobotanical record documents some of the earliest definitive and purported records of the family (Adegoke et al. 1978; Crawley 1988; Giraud and Lejal-Nicol 1989) and evidence of its early importance in African communities (Herendeen and Jacobs 2000), the record also documents shifting generic distributions and extirpation of some ecologically important moist forest genera from large tracts of northern and northeastern Africa after this period of forest expansion (Pan et al. 2010). Many legume taxa are likely to have had a more extensive distribution during the Paleogene and early Miocene than today, including *Afzelia* Sm., *Brachystegia* Benth., *Cynometra* L., *Isobertinia* Craib & Stapf, *Pentaclethra* Benth., and *Sindora* Miq. (Privé-Gill et al. 1999;

Herendeen and Jacobs 2000; Vincens et al. 2006; Danehy 2010; Pan et al. 2010). Newly discovered fossil seeds from early Miocene (22–21 Ma) sediments in the Mush Valley of Ethiopia provide another example: *Newtonia* (Mimoseae), an ecologically and economically important African endemic forest genus that is not present in Ethiopia today (fig. 1). These fossils represent the earliest definitive record of *Newtonia* and document, along with associated sediments, fauna, and flora, the continued presence of tropical moist forest on the Ethiopian Plateau into the early Miocene. In this article we describe the fossils and discuss the fossil record, evolutionary history, paleobiogeography, and paleoecology of *Newtonia*.

Material and Methods

The Mush Valley deposits are located approximately 160 km northeast of Addis Ababa in a region located between the towns of Debre Birhan and Debre Sina on the Ethiopian Northwestern Plateau. The geology of the area includes volcanic, volcanoclastic, and clastic sediments including extensive beds of porphyritic basalt, ignimbrites, tuffs, and lacustrine carbonaceous shales commonly interbedded with lignites, mudstones, and fluvial sandstones. The lacustrine carbonaceous shales preserve fossils of mammals, anurans, teleost fish, insects, pollen, and leaf, wood, fruit, and seed compressions. The fossil winged seed compressions described here occur in several fissile carbonaceous shale horizons within a 7-m vertical sequence.

Depositional age of the strata in which the fossils occur is constrained by ²³⁹U/²⁰⁶Pb dates on zircons within volcanic ashes stratigraphically associated with the fossils. The age of an ash layer interbedded with the fossiliferous carbonaceous shales and immediately above the uppermost horizon reported here is 21.73 ± 0.01 Ma, and an ash that occurs 9 m beneath the *Newtonia*-producing fossiliferous layers provides an age of 22.63 ± 0.03 Ma.

Images of herbarium specimens from the Botanical Research Institute of Texas (BRIT) and the fossils were taken using

¹ Author for correspondence; current address: Don Harrington Discovery Center, 1200 Streit Drive, Amarillo, Texas 79106, U.S.A.; e-mail: apan@dhdc.org.



Fig. 1 Distribution map of the genus *Newtonia* based on Villiers (1990), Holmgren et al. (2004), Coates Palgrave (2005), Estrella et al. (2005), Lovett et al. (2006), and Lebrun and Stork (2008). Geometric shapes correspond to the number of species that occur (or co-occur) within an area: circles, 1 or 2 species; triangles, 3 species. The dagger denotes *Newtonia mushensis* sp. nov. and the location of the Mush Valley deposits.

a Canon EOS 20 digital SLR camera. The fossil seed compressions are permanently housed at the National Museum of Ethiopia in Addis Ababa.

Results: Systematic Paleobotany

Fabaceae Lindley 1836

Mimosoideae Linnaeus 1753

Mimoseae Bronn 1822

Newtonia Baillon 1888

Newtonia mushensis Pan, Currano, Jacobs, Feseha,
Tabor et Herendeen sp. nov.

Etymology. The species is named for the Mush Valley where the fossil material and associated paleoflora and paleofauna were collected.

Diagnosis. Flat, elongate tapering seeds bearing a membranous wing that is markedly curved and notched at the attachment of the funiculus. The new taxon is distinguished from extant species of *Newtonia* by a combination of seed size parameters and degree of curvature near the funiculus attachment.

Description. Large, flat elongate seeds surrounded by a chartaceous or membranous wing (fig. 2A, 2B). Complete or nearly complete specimens (including the wing) range in size from 65 to 119 mm in length and 14.6 to 21 mm in width. The embryonic axis runs parallel to the seed length (fig. 2A, 2B). Seed size ranges from 62 to 115 mm in length and 10 to 19 mm maximum width, and seeds are obovate in shape, widest near the rounded apices, and narrowing slightly for much of their length toward the base (fig. 2A, 2B). Near the base, the seed tapers and curves strongly toward the lateral margin, terminating at a notch in the wing (fig. 2C, 2D). The filamentous funiculus attaches to the seed through this notch (fig. 2D). The seed testa is relatively smooth with fine diagonal striations present (fig. 2B, 2D).

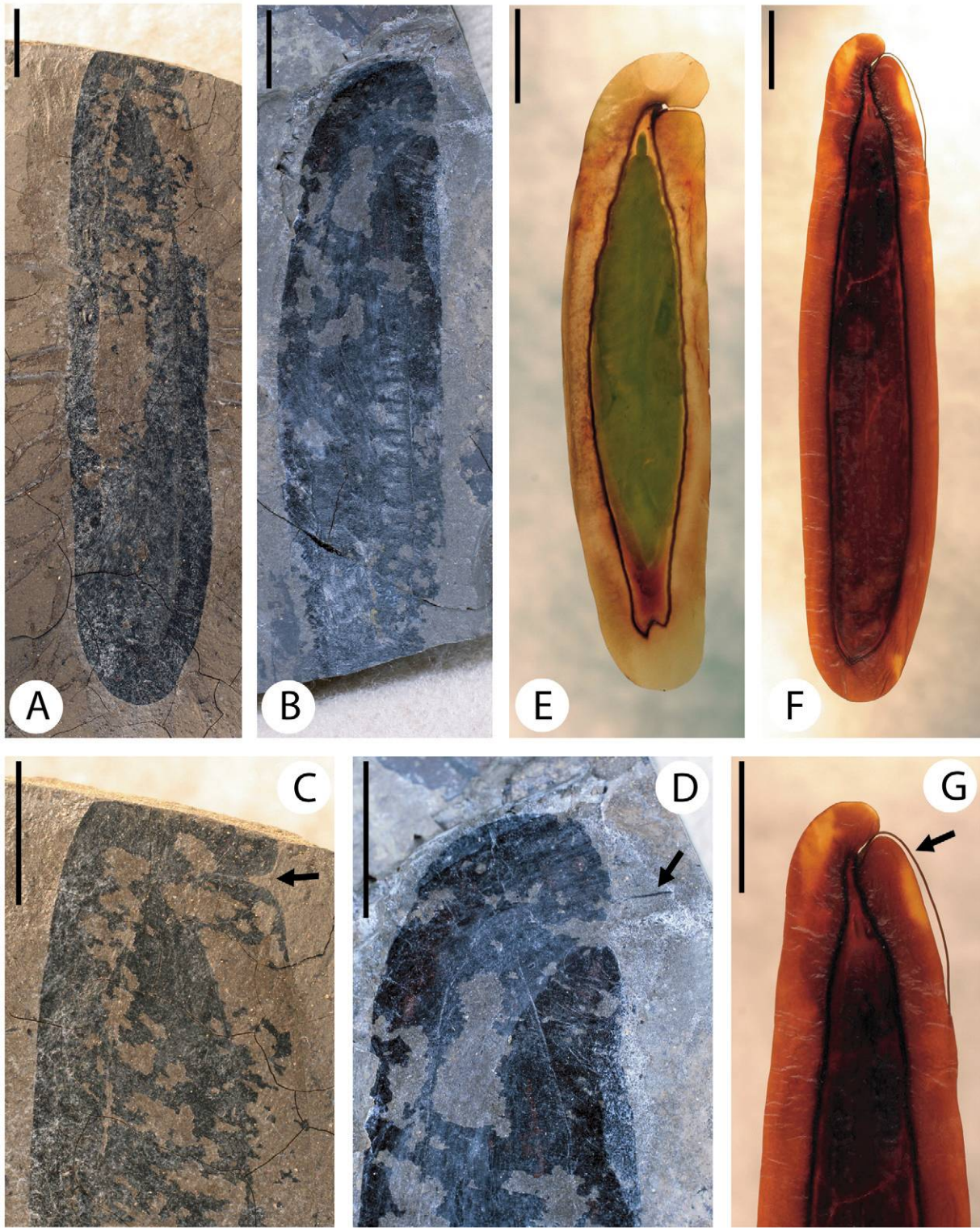


Fig. 2 *Newtonia* seeds. A–D, Fossil *Newtonia mushensis* sp. nov. A, Holotype MU17-31. B, MU18-10. C, D, Seed bases with notched wings. D, Funiculus entering the seed base. E–G, Extant *Newtonia*. E, *Newtonia buchananii*, JA Mlangwa & T Kaniki 1092 (BRIT). F, G, *Newtonia leucocarpa*, JM Reitsma & B Reitsma (BRIT). G, Seed base with notched wing and funiculus. A–G, Scale bars = 10 mm.

The membranous wing surrounds the seed, extending outward 3–4 mm, and lacks reticulate or dividing vasculature. Randomly spaced radial wrinkle impressions are visible on the wing (fig. 2A, 2D).

Holotype. MU17-31

Additional specimens. MU13-29, MU17-4, MU17-31, MU18-10, and MU31-11

Remarks. The following characteristics demonstrate the fossil material represents winged seeds as opposed to winged fruits: (1) no evidence of stigmatic or pedicel structures, (2) lack of vasculature (reticulate or dividing) on the disseminule, (3) the wing and the structure it surrounds are more membranous than those structures found in samaras or fruits, and (4) the presence of a filamentous funiculus.

Elongate, flat seeds fully surrounded by a wing occur in several angiosperm families including (but certainly not limited to) Apocynaceae, Bignoniaceae, Cucurbitaceae, Fabaceae, Lecythidaceae, Lythraceae, Proteaceae, and Rutaceae. However, the presence of a notched wing and filamentous funiculus allows the fossils to be identified readily as winged seeds of the legume tribe Mimoseae (fig. 2C, 2G). Although the hilum and lens are not discernible in the fossils, these structures are typically occluded, and thus obscured, by the membranous wing in the winged-seeded Mimoseae (Gunn 1984).

Eight genera of Mimoseae possess flat elongate seeds entirely surrounded by a wing: the African endemic genera *Cylicodiscus* Harms, *Fillaeopsis* Harms, *Newtonia*, and *Piptadeniastrum* Brenan; *Indopiptadenia* Brenan from Nepal and northern India; *Lemurodendron* Villiers from Madagascar; and the Neotropical genera *Parapiptadenia* Brenan and *Pseudopiptadenia* Rauschert. However, characteristics of the fossils allow for their definitive placement within *Newtonia*. *Fillaeopsis*, *Indopiptadenia*, *Lemurodendron*, *Parapiptadenia*, *Piptadeniastrum*, and some species of *Pseudopiptadenia* differ markedly from *Newtonia* and the fossils in possessing seeds where the embryonic axis is perpendicular to the seed length and the funiculus enters the medial portion of the winged seed, not asymmetrically near the base (Gunn 1984). *Cylicodiscus* and the remaining *Pseudopiptadenia* species possess seeds where the embryonic axis runs parallel to the seed length, as in *Newtonia* (fig. 2E, 2F; Gunn 1984), but differ in the shape of the seed, which does not curve and greatly narrows toward the base as it meets the winged margin. Additionally, *Pseudopiptadenia* seeds are small, typically less than 30 mm (and do not exceed 50 mm) in length (Gunn 1984; Cornejo and Janovec 2010). Faint diagonally oriented striations on the fossil seeds and wrinkle impressions on the membranous wings are similar to striations and wrinkle impressions on extant winged seeds of *Newtonia*.

Winged seeds of several extant species of *Newtonia* are much smaller, overall and in their maximum size limits, compared to the fossil, particularly *N. buchananii* (length [l]: 40–70 mm, width [w]: 10–20 mm), *N. camerunensis* (l: 40–80 mm, w: 15–20 mm), *N. duncanthomassii* (l: 50–65 mm, w: 16–18 mm), *N. erlangeri* (l: 40–60 mm, w: 12–20 mm), *N. hildebrandtii* (l: ≤60 mm, w: 12–20 mm), and *N. scandens* (l: 50 mm, w: 15 mm; Hutchinson and Dalziel 1958; Villiers 1990; Mackinder and Cheek 2003; Coates Palgrave 2005). In addition, the apex of the seed in *N. buchananii* can be noticeably forked (fig. 2E) or rounded, but the seed apices of

N. mushensis are always rounded (fig. 2A). Some congeners, *N. aubrevillei*, *N. duparquetiana*, and *N. leucocarpa*, have winged seeds that fall within the size range of the fossil, but these species differ from the fossil *Newtonia* in having a seed with straight or indistinctly curved tapering end at the funiculus attachment (fig. 2G; Hutchinson and Dalziel 1958; Holmgren et al. 2004). The seed of the fossil *Newtonia* tapers and strongly curves at the funicular end of the seed (fig. 2C, 2D). Thus, these distinctions and the age and geographic location of the material suggest a new, extinct species, *Newtonia mushensis* sp. nov. is warranted.

Discussion

Phylogenetic Placement of Newtonia within the Mimosoideae

Recent molecular phylogenetic analyses of the Mimosoideae by Luckow et al. (2003), Luckow (2005), and Bouchenak-Khelladi et al. (2010) differ somewhat in tree topologies but show congruence in the relationship of *Newtonia* to other African mimosoid genera with large (>50 mm), entire-winged seeds: *Cylicodiscus*, *Fillaeopsis*, and *Piptadeniastrum*. Based on these studies, the tribe Mimoseae is clearly paraphyletic. *Fillaeopsis* was consistently found to be sister to *Newtonia* with reasonably strong support. Both *Newtonia* and *Fillaeopsis* comprise the sister group to a clade that includes *Cylicodiscus*, the paraphyletic “Acaceiae” and “Ingeae,” and members of the *Prosopis*, *Leucaena*, *Dichrostachys*, and *Piptadenia* groups (fig. 3; Luckow et al. 2003; Luckow 2005; Bouchenak-Khelladi et al. 2010). Two additional taxa, *Lemurodendron* and *Indopiptadenia*, have been hypothesized to be closely related to *Newtonia* and *Fillaeopsis*; however, no phylogenetic studies have included these two monotypic taxa (Lewis and Elias 1981; Villiers and Guinet 1989; Luckow 2005). The close sister relationship between *Newtonia* and *Fillaeopsis* is interesting because of differences in the embryonic axis mentioned earlier and the closer similarity of *Newtonia* to *Cylicodiscus* based on this character.

Fossil Record and Evolutionary History

Newtonia mushensis seeds represent the earliest and only definitive record of the genus. Early Miocene fossil wood of the form genus *Mimosaceoxylon* Lakhanpal & Prakash has been compared to both *Newtonia* and *Albizia* Durazz. (Lakhanpal and Prakash 1970; Gros 1992; Herendeen et al. 1992), but definitive placement within either genus is not possible and the fossil could represent a number of other legume taxa. A fossil fruit of *Newtonia* is reported from the late Miocene (6–5.5 Ma) Nkondo Formation in Uganda (Dechamps et al. 1992; Bonnefille 2010). However, the sediment horizon from which it was recovered is not known, and Bonnefille (2010) questioned whether it (and associated remains) may represent modern material. *Fillaeopsis* is represented in the fossil record by pollen tetrads of *Fillaeopsidites* (*Fillaeopsis*) *reticulatus* (Guinet et Salard) Salard-Chebouldaef, which are reported from Oligocene, and possibly late Eocene, sections of the Kwa Kwa drill core from Cameroon (Guinet

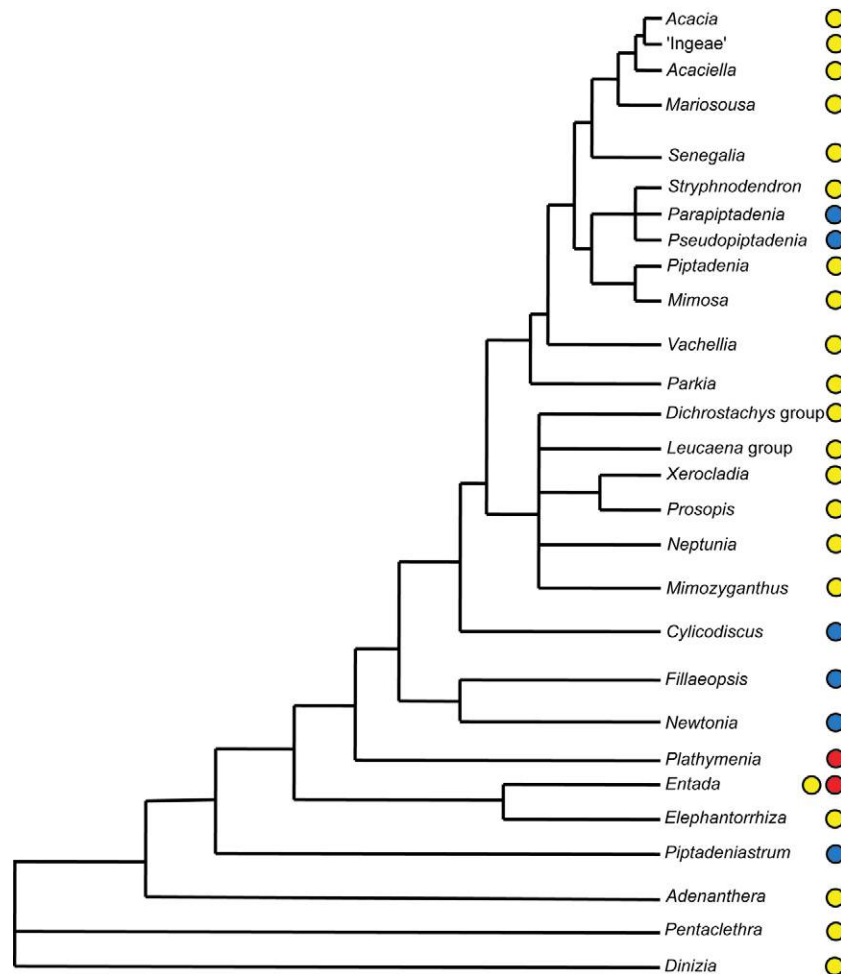


Fig. 3 General relationships within the “Mimoseae” based on Luckow et al. (2003), Luckow (2005), and Bouchenak-Khelladi et al. (2010). Circles correspond to seed types: yellow, seeds not winged; blue, winged seeds; red, seeds not winged, but disseminule is winged.

and Salard-Cheboldaeff 1975; Salard-Cheboldaeff 1979; Muller 1981). No other records of *Newtonia* and *Fillaeopsis* are known.

Recent investigations of the evolutionary relationships within the mimosoids using molecular phylogenetic analyses (and constrained by the fossil record) provide additional methods to interpret the evolutionary history and radiation of this group. Bayesian *matK* analyses conducted by Lavin et al. (2005) on the entire Fabaceae estimated the family to be 59.0 ± 0.2 Ma in age, with the Mimosoideae crown clade age estimated to be 42.4 ± 2.6 Ma. Bouchenak-Khelladi et al. (2010), using a relaxed Bayesian clock, derived estimates for the Mimosoideae ranging from 61.8 to 58.0 Ma (95% confidence interval). This latter study also estimated an early Eocene divergence between *Fillaeopsis* and *Newtonia*, and their chronogram shows a likely Oligocene divergence within *Newtonia* (Bouchenak-Khelladi et al. 2010). The known fossil record of *Fillaeopsis* and *Newtonia* is younger than the Bayesian clock estimates but does not contradict Bouchenak-Khelladi et al.’s (2010) results.

The development of entirely winged flat seeds within the mimosoid legumes appears to have occurred several times in the evolutionary history of the subfamily (fig. 3; Luckow et al.

2003; Luckow 2005; Bouchenak-Khelladi et al. 2010). Large winged-seeded “Mimoseae” taxa (*Cylicodiscus*, *Fillaeopsis*, *Newtonia*, *Piptadeniastrum*) are all endemic to Africa but do not represent a monophyletic group. However, all of these taxa have growth habits almost entirely composed of medium to large canopy or emergent tree species (excluding the lianescent *Newtonia scandens*; Villiers 1990), whose legume fruits split along the ventral suture and whose seeds dangle from the pods on funicles. When released the seeds drop and flutter away from the parent tree, a dispersal adaptation that may be beneficial within forests, particularly for large trees (Gunn 1984; Villiers 1990). An independent group of derived Neotropical “Mimoseae,” *Parapiptadenia* and *Pseudopiptadenia*, have also developed winged seeds and are also mainly confined to forests, although the seeds of these taxa are much smaller (mainly 9–30 mm in length; Gunn 1984).

Paleobiogeography

The fossil record and recent phylogenetic analyses of the “Mimoseae” mimosoids tentatively support an African origin of the *Newtonia* group (sensu Luckow 2005), although the

sister relationship of the South American genus *Plathymeria* Benth. to *Newtonia* and *Fillaeopsis* and more derived mimosoids (fig. 3; Luckow et al. 2003; Luckow 2005) suggest that a South American origin of the *Newtonia* group is not implausible. The Ethiopian fossil record of *Newtonia* also indicates that the genus had a more extensive distribution in the geologic past.

Paleoecological and Paleoenvironmental Significance

Extant species of *Newtonia* are largely moist tropical forest denizens often found in areas characterized by high water tables (swamp, groundwater, riverine, and lakeside forest formations) or upland forests (Villiers 1990; Mackinder and Cheek 2003; Coates Palgrave 2005; Lovett et al. 2006; Lebrun and Stork 2008). Some species (*Newtonia erlageri* and *Newtonia bildebrandtii*) can be found in both forest and open bushland habitats with high water tables (Coates Palgrave 2005; Lebrun and Stork 2008). The center of distribution of the genus is the Guineo-Congolian region; particularly the forests of Equatorial Guinea, southwestern Cameroon, and Sierra Leone, although a number of species occur in close geographic proximity in the coastal forests of southern Kenya (fig. 1). In some forests, *Newtonia* is widespread and ecologically important. For example, *Newtonia buchananii* is one of the most commonly encountered trees in the East Usambara Mountains (Tanzania), Bwindi forest (Uganda), and swamp and moist forests on Mount Kenya and the Taita Hills (Macharia 1989; Marchant and Taylor 1997; Cordeiro and Howe 2001; Eilu and Obua 2005).

The presence of *Newtonia* seeds in the early Miocene sediments of the Mush Valley and their co-occurrence with a large number of macro- and mesophyllous leaf compressions, a high percentage with entire margins and drip tips, provide evidence that the vegetation of this area represented a tropical moist

forest. The clastic sediments, particularly the laminated carbonaceous shales and mudstones, and the presence of aquatic plants (e.g., Araceae, Nymphaeaceae, and Salviniaceae), teleost fish, and anurans are indicative of a lacustrine depositional environment, likely representing a forest-fringed, hydrologically open pond or lake. The *Newtonia* seeds are a common component in the paleoflora and are found at multiple sublocalities and in numerous strata, suggesting that *Newtonia mushensis* was a common canopy tree constituent of the early Miocene Mush forest.

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