

# A FOSSIL *ANTHONOTHA* (LEGUMINOSAE: DETARIOIDEAE: AMHERSTIEAE) SPECIES FROM THE EARLY MIOCENE (21.73 MA) OF ETHIOPIA

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**Premise of research.** Several morphotypes of well-preserved legume leaflet compressions are known from the early Miocene Mush plant assemblages from the northwestern plateau of Ethiopia. One of these morphotypes represents a member of the Amherstieae tribe (subfamily Detarioideae) and is prevalent in the assemblage. Morphological and epidermal micromorphological characteristics are sufficient to identify it to genus. The evolutionary and biogeographic significance of the early Miocene occurrence of this genus in the uplands of Ethiopia is explored.

**Methodology.** Fossil laminae were compared with herbarium specimens and leaf cuticle preparations to determine their likely identity.

**Pivotal results.** Morphological and micromorphological characteristics support recognition of a new fossil species of *Anthonotha* (Leguminosae: Detarioideae: Amherstieae: Berlinia clade), herein named *Anthonotha shimaglae* Pan, Jacobs, Currano, Estrella, Herendeen et Burgt sp. nov. Characteristics include symmetrical, untoothed leaflets with pulvinate petiolules, short acuminate leaflet tips, eucamptodromous secondary venation, an abaxial epidermal surface possessing sinuous anticlinal cell walls, paracytic stomatal complexes, abundant trichome bases, papillate periclinal cell walls, and an adaxial epidermal surface possessing highly sinuous anticlinal cell walls. *A. shimaglae* represents the earliest-known macrofossil of the genus. The occurrence of this new species with other Detarioideae legumes, including *Englerodendron mulugetanum*, and a morphotype representing *Berlinia* or *Isoberlinia* in the early Miocene Mush plant assemblages is more analogous to high-rainfall evergreen forests of Central Africa today than East African forest types.

**Conclusions.** Early Miocene Mush fossils include the common occurrence of an extinct species of legume, herein named *Anthonotha shimaglae*. Prehistoric forests of the Ethiopian plateau may represent ancestral sources of currently disjunct and perhaps relictual wet forest taxa in tropical montane and coastal forests of eastern Africa today, as well as potential evolutionary sources of the Guineo-Congolian forested region.

**Keywords:** Africa, evolution, forest, legume, prehistoric.

**Online enhancements:** appendixes.

## Introduction

Within the tribe Amherstieae (Leguminosae: Detarioideae), the African endemic *Berlinia* clade represents a diverse and ecologically important group of trees found in tropical forest and

woodland (including miombo) communities (Estrella et al. 2017, 2020; Boom et al. 2021). The fossil record indicates that this group also has had a long and substantial role in prehistoric African ecological communities throughout much of the Cenozoic, first occurring in the Paleocene and becoming ecologically prominent in the early to middle Eocene (Herendeen and Jacobs 2000; Pan et al. 2010; Romero et al. 2020).

The *Berlinia* clade can be subdivided into two major monophyletic branches, designated by Estrella et al. (2020) as *Berlinia*

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subclades A and B. Subclade A consists of the bambij group (seven genera: *Brachystegia*, *Aphanocalyx*, *Michelsonia*, *Bikinia*, *Icuria*, *Julbernardia*, and *Tetraberlinia*), *Microberlinia*, *Didelotia*, and *Gilbertiodendron*. These are the dominant arborescent constituents of today's miombo communities and many African Guineo-Congolian moist and wet forest types, including almost all tropical monodominant forest formations (Bonnefille 2007; Boom et al. 2021; Pan et al. 2023). Subclade B also consists of important tropical moist and wet forest and woodland taxa, but they generally do not currently form monodominant forest formations, although the gregariousness of some species has been noted (Lebrun and Stork 2008). *Berlinia* subclade B includes *Anthonotha*, *Berlinia*, *Englerodendron*, *Isoberlinia*, *Librevillea*, and *Oddoniodendron* (Breteler 2010; Estrella et al. 2019, 2020; Ojeda et al. 2019).

Recently, reevaluation of the early Miocene (21.73 Ma) Mush Valley plant assemblages has provided evidence for the earliest-known structurally and taxonomically modern African tropical monodominant forest, located on the northwestern plateau of Ethiopia and representing a long-lived forest surrounding a volcanic crater lake at an elevation likely exceeding 2000 m (Facenna et al. 2019; Currano et al. 2020; Grímsson et al. 2021; Pan et al. 2023). However, this forest differs from extant African monodominant forest formations in being dominated by an extinct species of *Englerodendron*, *Englerodendron mulugetanum*—a constituent of *Berlinia* subclade B (Estrella et al. 2020; Pan et al. 2023). Another morphotype in this fossil assemblage represents the second-most abundant taxon (comprising 5%–10% of the fossil leaf material in each stratigraphic level) in the assemblages and also belongs in the *Amherstieae* (Bush et al. 2017; Currano et al. 2020; Currano and Jacobs 2021). This morphotype, originally designated as short-drip tip to categorize it for paleoecological and paleoenvironmental studies (Currano et al. 2020; Currano and Jacobs 2021), has now been identified and represents the (currently) Central and West African wet and moist tropical forest genus *Anthonotha*, another member of subclade B. Today, both *Anthonotha* and *Englerodendron* coexist only in Guineo-Congolian moist and wet forest formations (Hawthorne and Jongkind 2006). Here, the new fossil species is described and its context and significance are explored.

### Material and Methods

The Mush Valley plant assemblages are located on the northwestern plateau of Ethiopia between the towns of Debre Birhan and Debre Sina (Pan et al. 2012, 2014, 2023; Bush et al. 2017; Currano et al. 2020). Fossil plant compressions (leaf, wood, fruit, seeds, and pollen), along with vertebrates and insect compressions, are preserved in layers of lacustrine carbonaceous shale interbedded with thin layers of volcanic ash, most of which are less than 3 cm in thickness (Pan et al. 2012, 2014, 2023; Engel et al. 2015; Currano et al. 2020, 2021). The age of the fossils can be narrowed to ca. 21.73 Ma based on  $^{206}\text{Pb}/^{238}\text{U}$  radiometric dates derived from zircons within two ashes, one immediately underlying the fossiliferous shales and the other ash occurring 5 m below that. Zircons from these ashes yield ages of  $21.733 \pm 0.060$  and  $21.736 \pm 0.015$  Ma, respectively (Tsfamichael et al. 2017).

Plant compression fossils from multiple carbonaceous shale layers were collected for paleoecological, paleoclimate, systematic, taxonomic, and floristic studies. To document and describe

micromorphological characteristics of the fossil material, small (approximately 0.5-cm<sup>2</sup>) cuticle samples were removed from the fossil leaves. Fossil specimens are permanently housed at the National Museum of Ethiopia, Addis Ababa. Prepared fossil cuticle microscope slides and modern leaf cuticle microscope slides from herbarium comparative samples are housed in the Roy M. Huffington Department of Earth Sciences at Southern Methodist University, Dallas, Texas and the Chicago Botanic Garden, Glencoe, Illinois, respectively (app. A1; Pan et al. 2012, 2014, 2023; Currano et al. 2020).

Fossil specimens were compared to extant Leguminosae specimens from herbaria at the United States National Museum of Natural History (US), Missouri Botanical Garden (MO), and Botanical Research Institute of Texas (BRIT) and from high-resolution digital images from the Muséum national d'Histoire naturelle (MNHN) and Global Plants on JSTOR (app. A2). Supplementary comparisons were based on published material from floras and guides (Brenan 1971; Hawthorne and Jongkind 2006; Breteler 2010). Preparation methods for herbarium and fossil leaflet cuticle and venation are provided in Herendeen and Dilcher (1990) and Pan et al. (2014), respectively.

### Results

*Leguminosae* Jussieu 1789

*Detarioideae* Burmeister 1837

*Amherstieae* Benth. (Hooker) 1840

*Anthonotha* P. Beauv. 1806

*Anthonotha shimaglae* Pan, Jacobs, Currano,  
*Estrella*, Herendeen et Burgt sp. nov.

**Etymology.** The species name, *shimaglae* (ሸማገሌ), means “elder” in Amharic and references this species as representing the oldest-known macrofossil record of the genus.

**Diagnosis.** Symmetrical, elliptic to obovate untoothed (entire-margined) microphyllous to mesophyllous leaflets with terete pulvinate petiolules and short acuminate leaflet tips. Basal leaflets with reduced length-to-width ratios compared to apical leaflets. Canaliculate leaflet midribs. Secondary venation eucamptodromous. Tertiary venation sinuous and opposite percurrent. Abaxial anticlinal cell walls sinuous. Stomata paracytic. Abaxial trichome bases present and abundant. Papillate abaxial periclinal cell walls. Highly sinuous adaxial anticlinal cell walls.

**Description.** Symmetrical unlobed, untoothed (entire-margined), elliptic to obovate leaflets with terete pulvinate short petiolules (figs. 1, 2). Microphyllous to mesophyllous leaflet lamina generally range in size from ca. 5–17 cm in length and 2.7–7 cm in width, typically with length-to-width ratios ranging from 1.6:1 to 2.6:1. Leaflet midribs are canaliculate. The leaflet apex is obtuse with a short acuminate drip tip. The leaflet base is convex to rounded in shape, is obtuse in angle, and ranges from symmetrical to slightly asymmetrical. Primary venation is pinnate. Secondary venation is eucamptodromous. The secondary veins are regularly spaced, except for three crowded pairs at the base; have excurrent attachment; and generally possess uniform acute angles, except those at the base, which are high angled.



**Fig. 1** Fossil and extant *Anthonotha* apical leaflets. A, *Anthonotha shimaglae* Pan, Jacobs, Currano, Estrella, Herendeen et Burgt sp. nov. (holotype; MU41-54). B, *Anthonotha shimaglae* (paratype; MU41-44A #3). C, *Anthonotha stipulacea* (MNHN-P-P03503989). Scale bar = 10 mm.

Leaflets typically possess (10–)11–14(–15) pairs of secondary veins (fig. 1). Intersecondary veins are present in most intercostal areas, with proximal courses parallel to major secondaries, reticulating distal courses, and lengths greater than 50% of the length of the subjacent secondary. Tertiary venation is sinuous and generally opposite percurrent. Epimedial tertiary veins have admedial courses obtuse to the midvein and exmedial course parallel to intercostal tertiary veins. Quaternary and quinary venation is irregular reticulate, and the areolation is moderately developed.

**Cuticle.** Stomatal complexes are paracytic with one subsidiary cell typically larger than the other (fig. 3A). Stomata are prominent on the abaxial surface and are rare (or absent) on the adaxial surface (fig. 3A, 3B). Subsidiary cells range in size from 15.2 to 22.4  $\mu\text{m}$  in length (fig. 3A). The anticlinal cell walls on the abaxial surface are sinuous, and those on the adaxial leaf surface are highly sinuous (fig. 3A, 3B). The abaxial epidermal cells are generally rectangular in shape and are typically 12–24  $\mu\text{m}$  in length and 4.8–23.2  $\mu\text{m}$  in width (fig. 3A; app. A3). Papillae are present, abundant, and centrally located on abaxial periclinal cell surfaces (fig. 3A; app. A3). Hairs (trichomes) are abundant on the abaxial surface, based on the presence of thickened trichome bases (fig. 3A; app. A3). Hair bases are surrounded by radial basal cells (fig. 3A; app. A3).

**Holotype.** MU41-54. National Museum of Ethiopia, Addis Ababa (fig. 1A).

**Paratypes.** MU23-34 (cuticle, fig. 3A; app. A3), MU17-40 (fig. 2A; cuticle, app. A3), MU27-45 #1 (fig. 2B), MU30-8A, MU41-44A #3 (fig. 1B; cuticle, app. A3), MU41-61 (cuticle; fig. 3B).

**Noted additional material.** MU13-18A #4, MU17-15A (cuticle), MU18-2A #1, MU18-9, MU18-11A #4 (cuticle; app. A3), MU23-34 (app. A4), MU23-32B #1, MU23-52 #4, MU23-64, MU29-40 #2 (app. A4), MU30-8A (leaflet and cuticle; apps. A3, A4); MU30-36B (app. A4), MU31-15 #1, and MU41-3A.

#### Comments

Leaflet lamina characteristics of the fossil align with four genera in the *Berlinia* clade of the Amherstieae (Fabaceae: Detarioideae), *Anthonotha*, *Berlinia*, *Englerodendron*, and *Isoberlinia*, which all belong to *Berlinia* subclade B (Estrella et al. 2020; Pan et al. 2023). The entire-margined, symmetrical leaflets possessing eucamptodromous venation, acuminate apices, and terete pulvinate petiolules are particularly similar to those of *Anthonotha* and *Englerodendron*, although the absence of twisted petiolules potentially excludes *Englerodendron* (figs. 1, 2). These characters are also present on the obovate, more rounded leaflets (with length-to-width ratios of around 1.6:1 to 1.7:1; fig. 2), which likely represent basal leaflets (apical leaflets have greater length-to-width ratios), again comparable to *Anthonotha* (fig. 2C). In addition, leaflet cuticle micromorphological characteristics are particularly diagnostic and match





**Fig. 2** Fossil and extant *Anthonotha* basal leaflets. A, *Anthonotha shimaglae* (paratype; MU17-40). B, *Anthonotha shimaglae* (paratype; MU27-45 #1). C, *Anthonotha macrophylla* (MNHN-P-P0085429). Scale bar = 10 mm.

exclusively with the genus *Anthonotha* (fig. 3). These include the presence of abundant trichome bases and periclinal papillae on abaxial leaflet surfaces of the fossil and extant species observed, including *A. cladantha* (fig. 3C, 3D), *A. crassifolia* (fig. 3E, 3F), *A. gillettii* (fig. 3G, 3H), *A. lamprophylla* (not shown), and *A. macrophylla* (fig. 3I, 3J). These characteristics have not been observed in any other members of the *Berlinia* clade or other members of the *Amherstieae* examined in this study or in Pan et al. (2023). *Anthonotha shimaglae* differs from all observed extant species, excluding *A. gillettii*, in having sinuous anticlinal cell walls on the adaxial leaflet surface (fig. 3B, 3H). *Anthonotha gillettii* differs from the fossil taxon in generally having fewer secondary veins (8–11 pairs) on the leaflets (Breteler 2010). The age of the fossil morphotype, its geographic location far from any existing population of *Anthonotha* species, and its laminar morphological and micromorphological characteristics warrant its designation as a new species.

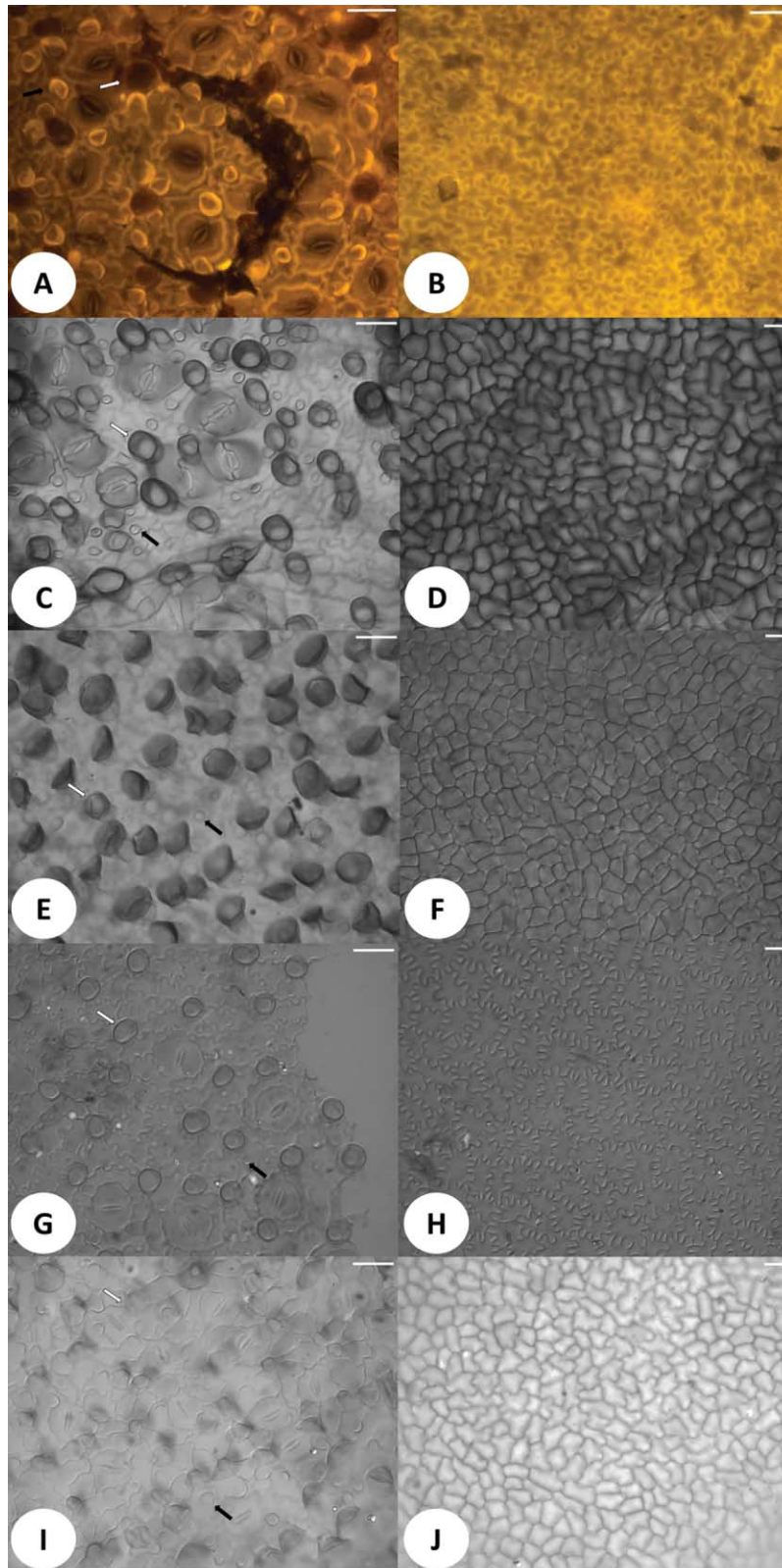
### Discussion

*Anthonotha* sensu stricto is a small genus of ca. 17 species consisting mainly of shrubs and small- to medium-sized trees, although *A. fragrans* can become large trees up to 45 m tall and with stem diameters of 130 cm. Most of the species are found in tropical moist and wet forest formations in the Guineo-Congolian region of Africa, but there are a few exceptions: *A. noldeae*, isolated populations of which are found in central Angola and montane forests of western Tanzania having volcanic soils (fig. 4; Brenan 1971; Breteler 2010), and *A. crassifolia*,

which occurs in moist tropical forests and savannah woodlands (Breteler 2010). *Anthonotha macrophylla* is the most widespread and common species in the genus, occurring mainly in secondary tropical rainforest communities extending from Guinea to the eastern Democratic Republic of the Congo (Breteler 2010). Although *A. shimaglae* lived in an upland moist or wet tropical forest on volcanic-derived soils, a habitat broadly similar to that supporting the extant *A. noldeae*, *A. shimaglae* leaflets are morphologically more similar in appearance to other species of *Anthonotha*, including *A. brieyi*, *A. cladantha*, *A. crassifolia*, *A. lamprophylla*, *A. pellegrini*, *A. pynaertii*, *A. stipulacea* (fig. 1C), and *A. xanderi*.

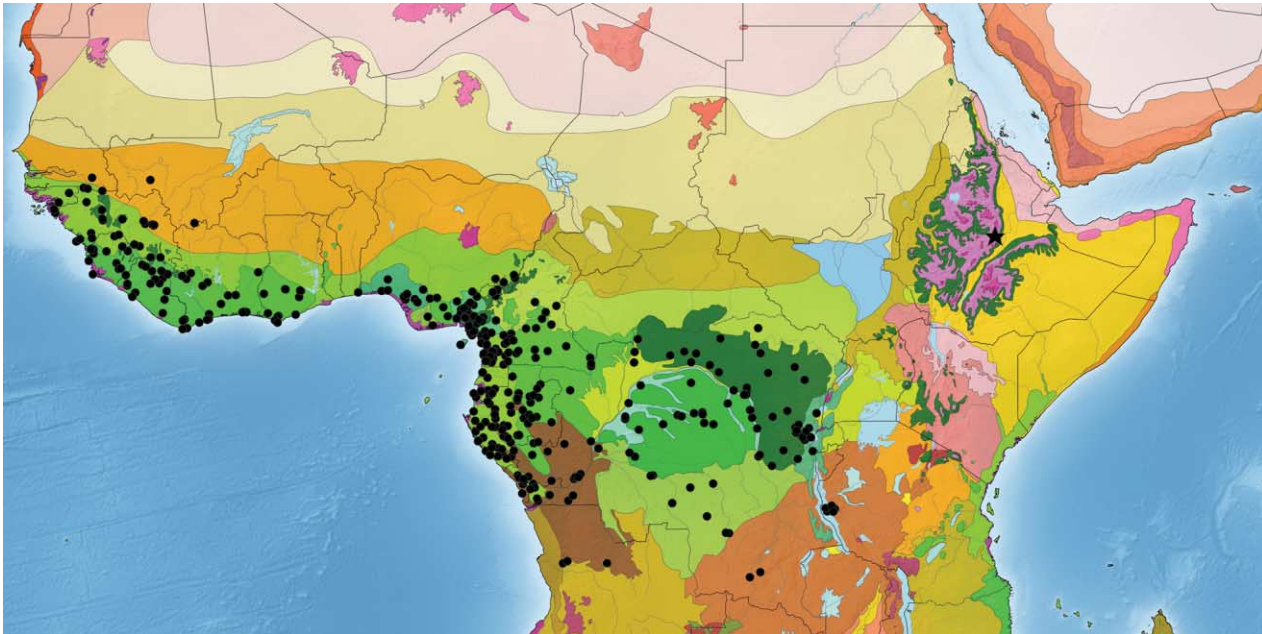
It is significant that the foliar characteristics of *Anthonotha*, particularly the tomentose leaflets of extant species, can be recognized in the fossil record and that an additional characteristic, papillate periclinal abaxial cell walls, is also constant (Brenan 1971; Pan et al. 2023; fig. 3). These leaf micromorphological characters are likely synapomorphies for the genus, and, given their long persistence, likely provide ecological/evolutionary fitness (Lieberman and Lieberman 1984; Wang et al. 2021). If their function was to hinder invertebrate foliar herbivory in the early Miocene Mush forest community, their efficacy is limited as shown by a recent study of *A. shimaglae* leaflets, over 40% of which displayed insect feeding damage (Currano and Jacobs 2021).

*Anthonotha shimaglae* specimens represent the earliest and only known macrofossils of the genus, although the palynological record indicates that it may have a long geologic history in Africa represented by some occurrences of the pollen morphospecies, *Striatopollis catatumbus* (Oboh et al. 2005; Romero



**Fig. 3** Fossil and extant *Anthonotha* leaflet cuticle. A, C, E, G, I, Abaxial epidermal surface. Black arrows indicate an example of a papilla; white arrows indicate an example of a trichome base. B, D, F, H, J, Adaxial epidermal surface. A, *Anthonotha shimaglae* (paratype; MU23-34 #2). B, *Anthonotha shimaglae* (paratype; MU41-61). C, D, *Anthonotha cladantha* (MO3766337). E, F, *Anthonotha crassifolia* (K H440/95 69 and MO5086876). G, H, *Anthonotha gilletti* (MO3254528). I, J, *Anthonotha macrophylla* (US3299348 and MO2111556). Scale bars = 20  $\mu\text{m}$ .





**Fig. 4** Distribution map and terrestrial ecoregion occurrence of extant *Anthonotha* (circles) and location of the fossil species, *Anthonotha shimaglae* (star). Modern distributions derived from Breteler (2010). This map was created with Simplemappr (<https://www.simplemappr.net/>).

et al. 2020). Romero et al. (2020) compared several records of *S. catatumbus* with various extant Amherstieae taxa and provided evidence that they can be differentiated taxonomically to generic affinity with reasonable certainty using airyscanning imaging in conjunction with deep learning classification methods. In the study, Romero et al. (2020) used several Amherstieae genera (and species) including two species of *Anthonotha*, *A. leptorrhachis* and *A. macrophylla*, when trying to identify the taxonomic affinities of *S. catatumbus* from African and South American palynological records. Recently, however, *A. leptorrhachis* has been transferred to the genus *Englerodendron* as *Englerodendron leptorrhachis* (Estrella et al. 2019). With this taxonomic change, African fossil *S. catatumbus* occurrences in the Romero et al. (2020) study that strongly indicate *Anthonotha* affinity should be considered to represent records of the *Anthonotha* clade (*Anthonotha* sensu stricto + *Englerodendron* sensu lato), not the genus alone (Estrella et al. 2019, 2020). With this taxonomic change, a Ypresian occurrence of *S. catatumbus* from the Anambra Basin, Nigeria (Oboh et al. 2005), identified as *Anthonotha* in Romero et al. (2020), represents the earliest record of either *Anthonotha* sensu stricto or *Englerodendron* sensu lato (Estrella et al. 2019, 2020). *Striatopollis catatumbus* and *Anthonotha*-type pollen from the Paleogene and early Miocene of northeastern Africa (Egypt, Ethiopia, South Sudan, and Sudan; Eisawi and Schrank 2008; El Afty et al. 2022; Yemane et al. 1987), while confidently being of Amherstieae affinity, have not been examined in the detail provided by, for example, Grímsson et al. (2019a, 2021), Romero et al. (2020), or Pan et al. (2023), and cannot provide a substantiated generic identification to either confirm or reject the presence of the *Anthonotha* or *Englerodendron* at these localities—although the macrofossil record of both genera at Mush indicates their presence on the Ethiopian plateau in the early Miocene. A taxonomic re-

vision using higher resolution available from combining single-grain light and scanning electron microscopy of these assemblages and others from the Paleogene and Miocene of tropical and northeastern Africa would provide a better understanding of the complex evolutionary history and ecology of Amherstieae in communities of these regions.

The occurrence of *A. shimaglae* in the early Miocene of the Ethiopian Plateau has implications for the evolutionary biogeography of the Berlinia clade and more generally for Africa's tropical vegetation. Today, the distribution of low-latitude, moist forests is characterized by a contrast between the nearly continuous block across the western and central regions (the Guineo-Congolian forests) and the isolated occurrences of submontane, montane, and coastal forests to the east of the Albertine Rift and Lake Victoria (fig. 4, green areas). Eastern Africa's forests are considered to be disjunct from the main forest block, although the phylogenetic histories of East-West relatives are complex and may involve more than one prior connection (e.g., Couvreur et al. 2008, 2021). In this regard, the six extant genera comprising Berlinia subclade B most often occur in forest communities, with the genus *Isoberlinia* differing from the others by its presence as a dominant and widespread component of deciduous wooded savannas of the Sudanian ecoregions (fig. 4, tan and amber regions). The extant forest-dwelling relatives of *Anthonotha shimaglae* repeat the greater disjunct forest pattern: few species exist outside the Guineo-Congolian region of Central and West Africa, and they become particularly rare east of the Albertine Mountains and Congo Basin. In fact, only four species of subclade B occur in the eastern section of the continent, each representing a different genus. *Berlinia orientalis* occurs in coastal forests of Tanzania and Mozambique on sandy soils (Clarke and Robertson 2000; Mackinder and Pennington 2011); *Englerodendron usambarensis* and *Isoberlinia scheffleri*

are endemic to the submontane and montane forests of the Eastern Arcs (Usambaras: *E. usambarensis* and *I. scheffleri*; Udzungwas: *I. scheffleri*) in Tanzania (Brenan 1971; Schulman et al. 1998; Lovett et al. 2006). Interestingly, the sole species of *Anthonotha* found outside the Guineo-Congolian region is *A. noldeae*, which is not the most similar morphologically to the fossil (see above). Nevertheless, the co-occurrence of multiple subclade B taxa from the early Miocene Mush forest—including *Englerodendron mulugetanum*, *A. shimaglae*, and a leaf(let) morphotype referred to as legume 4 that either represents *Berlinia* or *Isoberlinia* (Bush et al. 2017; Currano et al. 2020)—can be found together today only in Guineo-Congolian rainforests, especially the high-rainfall (2000–3000 mm/yr), hygrophilous evergreen forests found in Gabon and Cameroon (Bonnefille 2007).

The forests that grew on the Ethiopian plateau during the late Oligocene and early Miocene need to be considered both as ancestral sources to currently disjunct moist and wet forest taxa isolated in the tropical montane and coastal forests of eastern Africa today and as potential evolutionary sources for the Guineo-Congolian region itself (Yemane et al. 1987; Pan et al. 2006, 2010, 2012, 2014, 2023; Pan 2007; Pan and Jacobs 2009; Bonnefille 2010; Jacobs et al. 2010; Currano et al. 2011, 2020; Grímsson et al. 2019a, 2019b, 2021). As to the modern disjunct subclade B genera in East Africa, it remains to be seen whether they are relicts, the product of long-distance dispersal, or some of both.

The genera today distributed to the north and south of the main Guineo-Congolian forest block are adapted to drier climates. These include members of *Berlinia* subclade A (the bambijt clade [namely, *Brachystegia* and *Julbernardia*]), major components of (Zambebian) miombo woodlands in southeastern and south-central Africa. The genus *Isoberlinia* in subclade B is a major component of northern (Sudanian) woodlands on the continent, convergently filling the similar niche of subclade A members to the

south. A key aspect of the diverse presence of the *Berlinia* clade in the prehistoric forests of Mush and, potentially, other portions of northeastern Africa during the early Miocene is that the northeastern and eastern regions of the continent may be the pivotal focal point from which to examine evolutionary divergence(s) among those taxa adapted to either wetter or drier environments. What remains to be discovered is whether the isolated species of *Berlinia* subclade B found in moist and wet forests in eastern Africa today represent members of Guineo-Congolian genera that reinvaded these forests during optimal environmental conditions or whether they represent the older remnants of clades that had greater ecological impacts in the late Paleogene and early Neogene, now representing shadows of their former glory.

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