SINET: Ethiop. J. Sci., 46(2): 154-162, 2023 ISSN: 0379–2897 (PRINT)

eISSN: 2520–7997

Date received: April 03, 2023; Date revised: October 24, 2023; Date accepted: November 05, 2023
DOI: https://dx.doi.org/10.4314/sinet.v46i2.4

A New Record for *Scolopia Sp. Nov*. (Salicaceaesensulato) from the Early Miocene of Ethiopia: Identification and Classification of Fossil Leaves into their Living Relatives

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ABSTRACT: Early Miocene sedimentary layersfrom the Mush Valley in the Ethiopian Highlands located northeast of Addis Ababa preserve compressed fossil leaves and seeds with abundant organic matter in carbonaceous lacustrine shales. Fossil leaf morphotypes, preserved in those sediments, allow compilation of data and provide information on species richness and species relative abundance without the need for lengthy investigation to determine their taxonomic identity. Moreover, identification of fossil plants with respect to their nearest living relatives provides additional data critical for understanding their phylogenetic history, paleoclimate, and concentration of atmospheric CO_2. Here a previously unnamed taxon from the Mush Valley site was described; the taxon has a distinctly acrodromous primary venation, a pulvinus base, brachyparacyticstomatal complexes, and a suite of other characters of higher order venation and epidermal cells. The comparison of venation patterns and cuticular features among the fossil leaves and herbarium leaves using categorical variables shows that the fossil shares several characters with trinerved species in the genus *Scolopia*, but does not share all characters with any living species. Therefore, an extinct species found in the genus *Scolopia* (Scolopieae, Salicaceae) is described; the genus *Scolopia* is found today in Madagascar, the Solomon Islands, the Comoros, Southeast Asia, and eastern Australia. Two species of *Scolopia* occur today in Ethiopia, but these appear distantly related to the fossil based upon their pinnate, rather than acrodromous, primary venation. The fossil leaves are 21.73 ± 0.03 million years old, based upon $^{206}Pb/^{238}U$ geochronology, which can provide a precise date pointfor phylogenetic analysis. The taxonomic identification of this fossil leaf has important implication for reconstructing concentration of atmospheric CO_2 and paleo temperature of the time and hence, to understand the response of plants to the early Miocene global warming.

Keywords/phrases: Fossil leaves, Mush Valley, Scolopia, Stomatalfeatures, Trinervedvenation

INTRODUCTION

Fossil leaves are vital to reconstruct ancient environments including concentration of atmospheric CO_2 and past climatic conditions (Tekie Tesfamichael et al., 2017; Currano et al., 2020; Currano and Jacobs, 2021). They also reveal evolutionary history of plant groups if the fossils can be identified and placed into their specific taxonomic group (Pan et al., 2023). In nearly all cases, fossil leaf identification requires excellent preservation that includes fine details of higher order venation and perhaps epidermal characters as well. Here exquisitely preserved early Miocene leaves are reported and these fossil leaves are found in the Highlands of Ethiopia, Mush Valley, approximately 160 km northeast of the capital city, Addis Ababa (Fig.1). The presence of higher order venation on many complete leaves of a single taxon, along with intact cuticles that are often pristinely preserved, allows detailed description of characters and close comparison with modern plant relatives. The comparison of venation patterns and cuticular features among fossil leaves and herbarium leaves using categorical variables allows the identification of the nearest living relatives for the fossil leaves. The description of these fossil leaves and the placement of these fossils into their specific taxonomic classification provide critical information about past climatic conditions and serve as an age reference point for phylogenetic analysis conducted to understand plant evolution since the age of the fossil leaves (21.73 ± 0.03 Ma) is determined (Mulugeta Feseha, 2015;TekieTesfamichael et al., 2017).

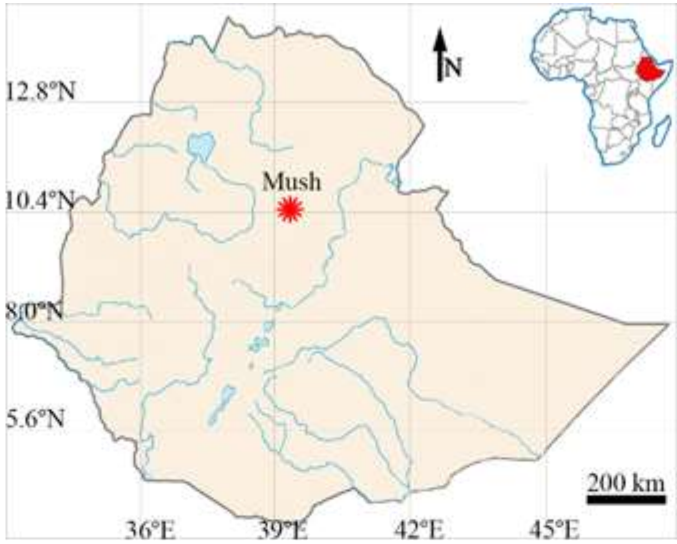

Fig.1. Location map of the early Miocene fossil site at Mush Valley, Ethiopia

Various studies have been conducted on identification and description of fossil leaves as well as comparison of fossil leaves with their corresponding herbarium leaves and played a significant role in providing critical data used to reconstruct palaeo climatic conditions, ecological interactions, and plant evolutions (Steinthorsdottir and Vajda, 2015;TekieTesfamichael et al., 2017;Tarran et al., 2018;Currano et al., 2020; Xue et al., 2020;Song et al., 2022). Currano et al. (2020) classified and analyzed thousands of early Miocene fossil leaves, and these fossil leaves enabled to characterize plant community ecology on a decadal to millennial time scales; Srivastava et al. (2015) described fossil leaves from the family *Moraceae* and based on leaf venation patterns, leaf morphology and other characters, the fossil leaves have a close affinity with the *Ficusracemosa*; the identification of the fossil leaves and the ecological character of *Ficusracemosa* allowed to reconstruct paleoclimate of the early Miocene. Fossil leaves also enabled to estimate ancient atmospheric CO_2 levels, and in turn these estimates show the association of atmospheric CO_2 values to global temperatures (Steinthorsdottir and Vajda, 2015; Tekie Tesfamichael et al., 2017; Liang et al., 2022). All these studies demonstrate the importance of identification and description of fossil leaves to obtain critical information used to reconstruct past climatic and environmental conditions.

Although the Mush Valley stratigraphic layers hold abundant and exquisitely preserved fossil leaves, and more than 2000 fossil leaves have been collected thus far, only few fossil leaves are described, identified, and assigned to their nearest living relatives, and here an early Miocene fossil leaf is described and placed into its nearest living relative. The description and taxonomic identification of the fossil leaves provide critical data used to reconstruct paleoenvironment, establish phylogenetic relations of plants, and understand the evolutionary history of east African forests and forests elsewhere in the world as these fossil leaves provide critical information about the ancestral source information for the evolution of early plants.

Geologic Background and Fossil Locality

The geology of Mush Valley is characterized by a succession of Oligocene flood basalts and felsic volcanic rocks (Coulie et al., 2003;Kieffer et al., 2004; Mulugeta Feseha, 2015). Some areas of the Ethiopian Highlands are overlain by Miocene and younger shield volcanoes and related basalts, and have interbeddedfossiliferous sedimentary rocks that range in age from late Oligocene to Pleistocene (Dereje Ayalew et al., 2002; Kieffer et al., 2004; Mulugeta Feseha, 2015). The Mush Valley sediments, today at 2680 meter above sea level, are associated with the oldest of three volcanic eruptive episodes that took place in 22.63 ± 0.03 Ma, 15.4 ± 0.2 Ma, and 8.0 ± 0.2 Ma (Dereje Ayalew et al., 2002; Solomon Tadesse et al., 2003).

The fossils collected for this research is found in carbonaceous lacustrine shales broadly bounded above and below by sediments associated with volcanic activities such as tuffs, ignimbrites, and basalt (Fig.2). The age of the fossils are determined from Zircon that are found on an ash deposit immediately underlying the fossil-bearing strata: $^{206}Pb/^{238}U$ isotopes which provided a date at 21.73 ± 0.03Ma (Mulugeta Feseha, 2015; Tekie Tesfamichael et al., 2017).The shale beds include relatively thin horizons of ash deposits less than 5 cm thick with one exception that is 20 cm thick, and the shales containing the fossil leaves vary in composition from claystone to lignite.

Fig.2. The fossil leaf bearing stratigraphic layers at Mush Valley, Ethiopia.

MATERIALS AND METHODS

The techniques and materials used in this research include desktop study, fieldwork, laboratory work, and data analyses. The materials applied are primarily fossil leaves and associated chemicals used to treat the fossil leaves. Following the collection of fossil leaves from the Mush Valley (Pan et al., 2012; Bush et al., 2017; Tekie Tesfamichael et al., 2017; Currano et al., 2020; Currano and Jabobs, 2021), a thorough formal description of plant fossil specimens were conducted using the protocols provided byEllis et al. (2009) and the International Code of Botanical Nomenclature (Turland et al., 2018). Fossil leaves and their corresponding nearest living relatives were compared, and the nearest living relatives were determined by analyzing various herbarium specimens from the National Herbarium, Addis

Ababa University, Ethiopia (ETH), the Botanical Research Institute of Texas (BRIT), the Missouri Botanical Garden (MO), the digital herbarium collections from the Royal Botanical Gardens Kew (K), and from published floras (Roland, 1996; Hawthorne and Jong kind, 2006). Field work was conducted during several trips between 2012 and 2021, during which time fossil leaves were collected from carbonaceous lacustrine shales that preserve compressions of various fossil leaves, fish, frogs, and seeds of different types of plants. As the shales were moist, blocks of shales that contain fossil leaves were wrapped in tissue paper and then in newspaper to allow them to dry out slowly to limit specimen cracking. The fossil leaf collections were made from bench quarries where slabs of matrix approximately 6 cm thick were removed from the bench quarries, and then the slabs were brought to the National Museum of Ethiopia for a better examination by splitting the slab at every 1cm thickness where they can reveal the fossil leaves. During fossil leaf preparation at the National Museum of Ethiopia, small fragments (≈ 0.5 cm^2) of fossil leaves were collected for further laboratory analyses and for producing high resolution imagesof cuticles.

Cuticle preparation from fossil leaves was carried out as follows: small fragments of fossil leaves were immersed in 10% hydrochloric (HCl) acid for about 50 minutes to remove carbonate matrix associated with the fossil leaves. This was followed by immersion of the fossil leavesin 48% hydrofluoric (HF) acid for 48 hours to remove silicate matrix from the fossil leaves. Then the fossil leaves were rinsed with distilled water repeatedly until the pH test shows neutral value. Preparation of modern leaves for cuticles takes a slightly different approach; the herbarium leaf specimens were immersed in distilled water for two to three days to rehydrate them, and in some cases they were treated with 10% potassium hydroxide (KOH). Then they were washed with a 4% bleach diluted 1:10 with water. Finally high resolution cuticle images ofboth the fossil leaves and the leaves from herbarium were produced using a Leica DM2000epifluorescence microscope.

Gross morphological features of the fossil leaves were described using the protocol of Ellis et al. (2009), and cuticular descriptions follow Dilcher's methods (Dilcher, 1974). The fossil leaves are mainly characterized by having a primarily trinerved venation, a pulvinus base, and brachyparacyticstomatal complexes (Fig.3).

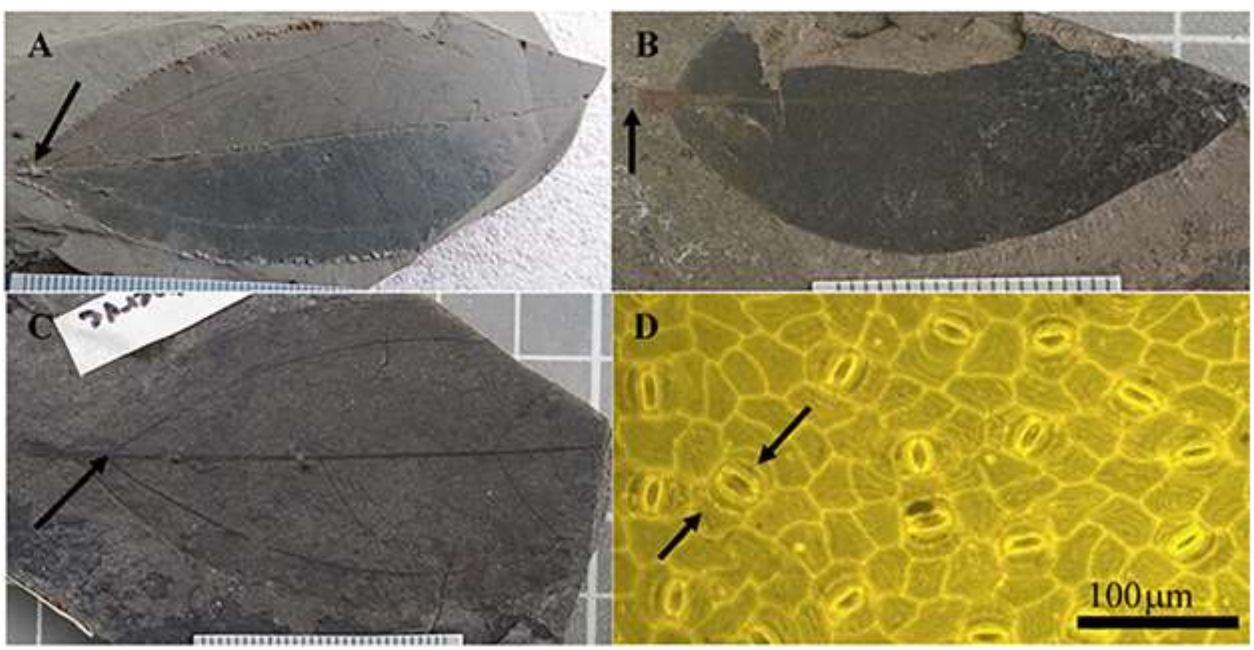

Fig.3. A new record of Scolopiatrinervifolia showing leaf-venation networks and cuticle characters: trinervedsuprabasalacrodromous primary veins (arrows in A and C), pulvinate petiole (arrow in B) and brachyparacyticstomatal complexes (arrows in D)

Based on the fossil leaf characters, a thorough examination of herbarium specimens from the National Herbarium, Addis Ababa University (ETH), the Botanical Research Institute of Texas (BRIT), and the Missouri Botanical Garden (MO), and the Royal Botanical Gardens Kew (K) enabled the identification of numerous plant families from which four genera that have the closest charactersto the fossil leaves were identified.Even though the plant families Fabaceae, Melastomataceae, Loganiaceae, Lauraceae, Salicaceae, Cannabaceae, Connaraceae, and Menispermaceae have a primarlytrinerved venation similar to the fossil leaves, these plant families have, however, different higher order venation networks. The genera that share the most characters with the fossil leaves are found in the following angiosperm families: Loganiaceae – *Strychnos*, Cannabaceae – *Celtis*, Lauraceae – *Cinnamomum*, and Salicaceae – *Scolopia*(Fig.4).

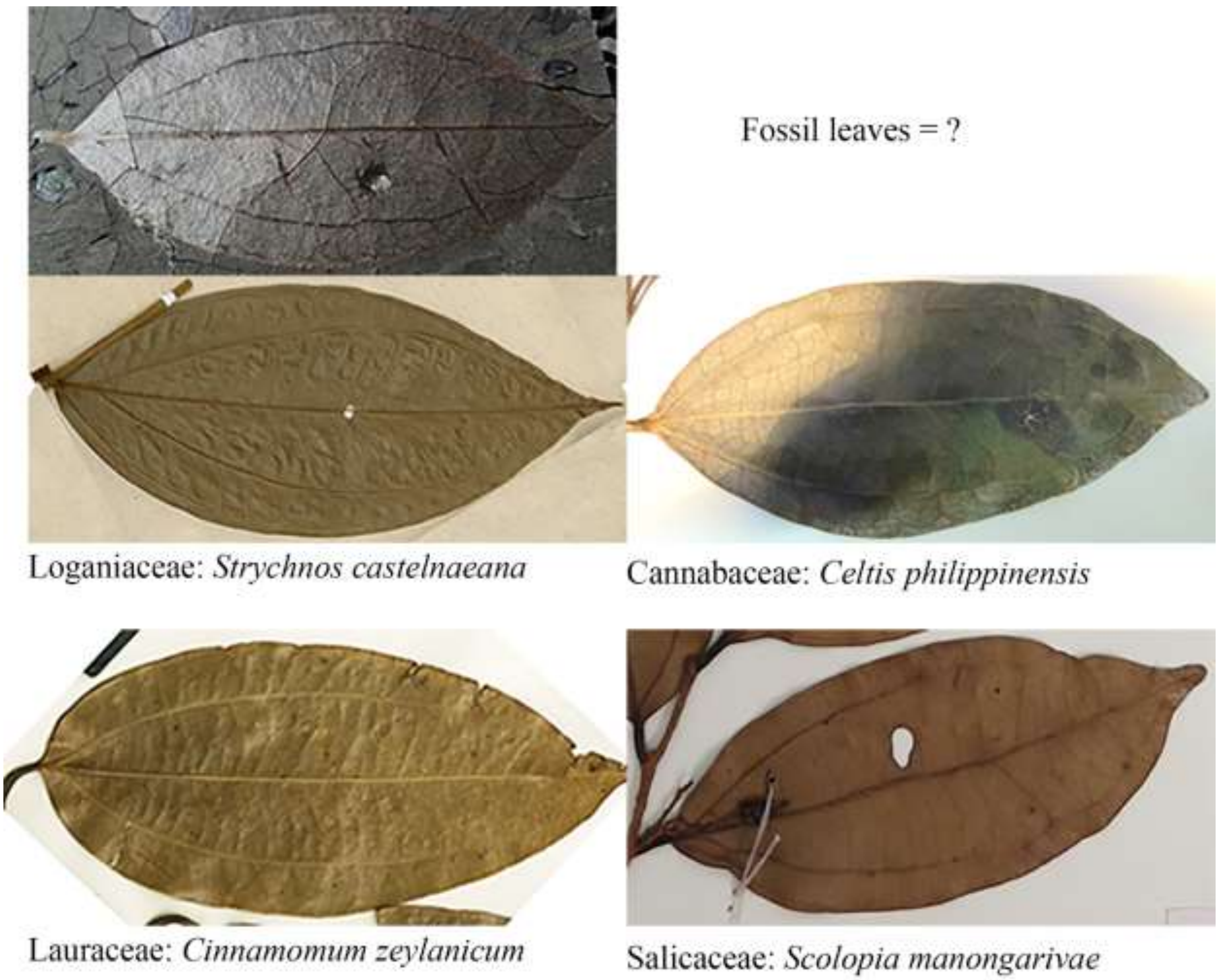

Fig.4. Herbarium specimens that share the most characters with the fossil leaves

Strychnos is the largest genus in the family Loganiaceae, with approximately 200 species of trees and shrubs; these are widely distributed within the tropics, and the genus is commonly found in Africa and Madagascar, Southeast Asia, and Australia (Ohiri et al., 1983;Rasoanaivo et al., 2002;Philippe et al., 2004;John et al., 2015). *Celtis* has about 60 species of shrubs and trees in the family Cannabaceae; they are widely spread throughout warm temperate and tropical regions of South to Central Africa, southern Europe, eastern Asia, and the Americas (Liu et al., 2021). *Cinnamomum* is a genus of evergreen trees and shrubs in the family Lauraceae, and has about 250 species that are widely distributed in tropical and subtropical regions of Asia, the Americas, and Australia (Wang et al., 2020). *Scolopia* is a genus of evergreen trees and shrubs in the family Salicaceae, and has more than 40 species found in Africa and Madagascar, Southeast Asia, and Australia (Chase et al., 2002;Applequist and Schatz, 2016);*Scolopia* is the largest and most widespread genus of the tribe Scolopieae (Steyn et al., 2005).

These four living genera have leaves grossly similar to the fossil leaves and share the following characters: trineved, acrodromous, veins; a marginal petiolar attachment; entire margin; elliptical shape; acute apex angles; and similar angles between the primary and secondary veins (Fig.4). Nevertheless, the fossil taxon differs in significant ways from those living taxa. *Strychnos*, *Celtis*, and *Cinnamomum* all differ from the fossil by the absence of secondary veins that are regularly spaced and tertiary veins that are mixed opposite-alternate percurrent. In addition, *Strychnos*, *Celtis*, *Cinnamomum* and *Scolopia* do not have a pulvinus or brachyparacticstomatal complexes (Table 1). The Lauraceae family is noted for having oil glands on its leaves, which are commonly preserved in older fossils and are readily apparent under the fluorescence imaging used here. These glands are absent in the fossils. Fabaceae leaflets are most noted as possessing a pulvinus, but no living genus shared the trinervedacrodromous character of the major veins. Therefore, the fossil leaves are most similar to the leaves of some species in the living genus *Scolopia* (Salicaceae), though it does not share all characters with any living species (Table 1).

Table 1. Characters and character states of fossil leaves and herbarium leaves; 1 = present, 0 = absent, and – =

unidentifiedSpecimens	1° Veins SuprabasalAcrodromous	2° Veins Brochidodromous-Eucamptodromous	2° Vein Spacing Regular	3° Veins Opp-Alt Percurrent	Petiole Pulvinate	Pavement Cells Pentagonal	Stomatal complex brachy-paracytic	Base Shape: Concave
MU5-6	1	1	1	1	–	1	1	1
MU17-29	1	–	–	–	1	1	1	0
Strychnos splendens	1	1	0	0	0	1	0	0
Celtis philippinensis	1	1	0	0	0	0	0	0
Cinnamomum burmannii	1	1	0	0	0	0	0	0
Scolopia	1	1	1	1	0	1	0	1

RESULTS

Taxonomy

Malpighiales Martius 1835
SalicaceaeMirbel 1815 *sensulato*
Scolopieae Warburg 1893
ScolopiaSchreber 1789
*Scolopiatrinervifolia*Tekie F. Tesfamichael, sp. nov.
Syntypes: MU5-6 and MU17-29#1
Additional specimens:MU36-14(1)#1, MU17-5A#14, and MU17-26A#2

Etymology: The species is named for the most salient character of the fossil leaves, which is its three primary veins originating suprabasally from a single point, converging toward the apex.

Diagnosis: The species has three suprabasal and acrodromous primary veins. Interior secondary veins are both brochidodromous and eucamptodromous and form an acute angle with the midvein. The petiole is pulvinate, and leaves are untoothed.

Description: Elliptic, unlobed, untoothed, microphyllous to notophyllous leaf having a pulvinate, petiolateattachment (Fig.3, A, B and C). The medial section of the lamina is symmetrical. The base is symmetrical, concave and acute; the apex is straight to acute-acuminate. The length to width ratio is 3:2 to 3:1. Primary venation is palmate acrodromous with three suprabasal primary veins (Fig.3, A and C). Interior secondary veins connecting the second and third primary veins are mixed eucamptodromous-brochidodromous (Fig.3, C). Major secondary vein attachment is excurrent. Secondary vein spacing is regular and there is one pair of acutely angled secondary veins. The intercostal tertiary vein network is alternatepercurrent as are epimedial tertiary veins. Exterior tertiaries are alternatepercurrent. Abaxialstomatal complexes are brachyparacytic (Fig.3, D). Anticinal walls of pavement cells primarily form a pentagonal shape, and the cuticle of periclinal cell walls is striate. The adaxial surface is lacking stomata, and duplicates pavement cell wall morphology.

DISCUSSION AND CONCLUSIONS

Comparison of fossil leaf morphological characters and cuticular features against modern herbarium specimens led to four genera in four families among living angiosperms as possible living relatives. Some aspects of the gross morphology and cuticular characters were shared with all of these living taxa, but none of the extant species share all the characters of the fossil leaves. *Scolopia* (Salicaceae) shares the greatest number of characters with the fossil leaves, but it should be noted that only a few species in this genus have the most obvious of characters, trinerved venation. The comparison of morphological features, cuticular characters, and stomatal complexes among the fossil and modern leaves to finding the most likely living relative of the fossil leaves indicates most likely affinity with the genus *Scolopia*.

The living tribe Scolopieae, only has two genera, *Scolopia* and *Hemiscolopia*, but has not been analyzed thoroughly with regard to systematic placement within the family Salicacaceae (Chase et al., 2002; Li et al., 2019). Nor have all the living species of the genus *Scolopia* been analyzed phylogenetically. Nevertheless,Chase et al. (2002) updated the systematics and phylogenetic relationships among taxa within the Flacourtiaceae and Salicaceae. The outcome of that study moved the tribe Scolopieae to the Salicaceae, which is widespread geographically, and includes temperate zone taxa such as *Salix*. Thus, the family designation is *sensulato*. Further studies may benefit from the minimum age for the genus at 21.73 ± 0.03 Ma.

Scolopia occurs today in South Africa, West Africa eastward to the East African Highlands, the Solomon Islands, Madagascar, the Comoros, Southeast Asia, and eastern Australia, and approximately 37 species of *Scolopia*are found in a variety of habitats including montane forest, lowland forest, riverine forest, and drier habitats including wooded savanna (Friis, 1992;Applequist and Schatz, 2016). Two species occur today in Ethiopia, *S. theifolia* and *S. zeyheri*, in single-dominant to undifferentiated montane forests (Friis, 1992); their leaves are pinnately veined rather than trinerved. Trinerved species including *S. madagascariensis* and *S. manongarivae* are endemic to Madagascar, and are found in the eastern forests (Applequist and Schatz, 2016).

The fossil leaves are 21.73±0.03 million years old, based upon $^{206}Pb/^{238}U$ geochronology, which can provide a precise date point for phylogenetic analysis. The taxonomic identification of this fossil leaf has important implication for reconstructing concentration of atmospheric CO_2 and paleotemperature of the time and hence, to understand the response of plants to the early Miocene global warming. In addition to these, the plant species is no longer living in the Mush valley areas, and it can provide critical information about the ancestral source information for the evolution of current forests in East Africa and elsewhere in the world.

ACKNOWLEDGMENTS

This work was supported by the Leakey Foundation:the Francis H. Brown African Scholarship Fund, Addis Ababa University, and Southern Methodist University.The author is grateful to the Missouri Botanical Garden, the Botanical Research Institute of Texas, and Addis Ababa University for providing access to their herbarium collections, and to the Authority for Research and Conservation of Cultural Heritage of Ethiopia for providing access to the laboratory facilities.

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