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Leaf epidermal micromorphology of *Beilschmiedia* Nees (Lauraceae) from Africa

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ABSTRACT: Leaf cuticular anatomy of the *Beilschmiedia* Nees group were studied for taxonomic purposes and species from America, Asia, and Australia were well represented, however species sampling from the Africa mainland was rarely sampled. Here we studied 14 species of *Beilschmiedia* from the Africa mainland using light and scanning electron microscopy. The leaves of all the studied species are hypostomatic with paracytic stomata. The presence or absence of peristomatal ridges constitutes a distinctive character of taxonomic significance. Stomatal orientation is sunken, superficial or raised; lower stomatal ledges are narrow lip-shaped and stomatal rim surface is smooth or rough. The anticlinal wall is uniformly straight and angular on the adaxial surface and curved, sinuous or undulate on the abaxial surface. Uniformity of thickness of the anticlinal walls is variable, beaded or not beaded, rarely buttressed or unevenly thickened. The periclinal wall is usually smooth or rarely punctate. Leaf micromorphological characters partially support the existing infra-generic classification that is based on macromorphology. This study provides supplementary data of leaf micromorphology for classification of the *Beilschmiedia* group. We confirmed the taxonomic usefulness of leaf epidermis characters to some extent in grouping of the African *Beilschmiedia* species, especially those of stomata.

KEY WORDS: Anatomy, Lauraceae, light microscopy (LM), scanning electron microscopy (SEM), taxonomy.

INTRODUCTION

There are numerous studies on the taxonomy of the family Lauraceae e.g. macromorphology (Gangopadhyay, 2008; Kostermans, 1938, 1952a,b, 1957; Rohwer, 1993; van der Werff and Richter, 1996; van der Werff, 2001), wood anatomy (Richter, 1981, 1985), palynology (Raj and van der Werff, 1988; van der Merwe *et al*., 1990), leaf anatomy (Christophel *et al*., 1996; Nishida and Christophel, 1999; Nishida and van der Werff, 2007, 2011, 2014; Kamel and Loutfy, 2001; Yang and Zhang, 2010; Yang *et al*., 2012; Gomes-Bezerra *et al*., 2011), and molecular systematics (Chanderbali *et al*., 2001; Rohwer and Rudolph, 2005; Li *et al*., 2011; Liu *et al*., 2013; Rohwer *et al*., 2014). Yet, there are still some taxonomically difficult genera.

Beilschmiedia Nees belongs to the *Beilschmiedia* group of the Lauraceae which is characterized by the fruit lacking a cupule and usually seated unprotected on the pedicel without any remnants of tepals or with only minute remnants of tepals at the base of the fruit (van der Werff and Nishida, 2010; Yang *et al*., 2012). Other genera of the group are *Endiandra* R. Br., *Hexapora* Hook.f., *Sinopora* J. Li & al., *Syndiclis* Hook.f., *Potameia* Thouars, and *Yasunia* van der Werff & Nishida, most of them have relatively restricted distribution. Modern molecular systematic studies support the *Beilschmiedia* group to be monophyletic (e.g. Chanderbali *et al*., 2001; Rohwer and Rudolph, 2005; Liu *et al*., 2013; Rohwer *et al*., 2014; Li *et al*., 2020) though relationships within the group and the genus *Beilschmiedia* are not yet fully understood.

Beilschmiedia is one of several taxonomically difficult genera in the family, and includes about 250 species that are widely distributed in the tropics (Nishida, 1999, 2008; van der Werff, 2001; Yang *et al*., 2012). *Beilschmiedia* is confronted with problems of (1) overlapping characters, (2) poor sampling, with many species represented by only one or a few specimens in the herbaria, and (3) poorly known flower and/or fruit characters because of small size (Hyland, 1989; Nishida and van der Werff, 2007; van der Werff and Nishida, 2010; Yang and Zhang, 2010; Yang *et al*., 2012).

Leaf epidermal characters have been explored and found to offer useful taxonomic data (Christophel *et al*., 1996; Christophel and Rowett, 1996; Nishida and Christophel, 1999; Nishida and van der Werff, 2007, 2011, 2014; Yang *et al*., 2012; Zeng *et al*., 2014; Trofimov and Rohwer, 2018). For these features, *Beilschmiedia* species from areas such as Asia, Australia, Madagascar, and Neotropics were investigated (Christophel and Rowett, 1996; Nishida and Christophel, 1999; Nishida and van der Werff, 2007; Yang *et al*., 2012), but *Beilschmiedia* species from mainland African

Table 1. Distribution and provenances of the species with their exsiccate data.

Species	Collector and Date	Locality	Herbarium
Beilschmiedia gaboonensis (Meisn.) Benth. & Hook. f.	Onochie, 26 Sept. 1958	Cameroon, Central Africa	FHI
ex B.D. Jacks	Osain & Opbe, 28 June 1966	Nigeria, West Africa	FHI
	Emwiogbon, 14 March 1968	Nigeria, West Africa	FHI
B. hutchinsoniana Robyns & R. Wilczek	Taylor, 11 March 1934	Nigeria, West Africa	FHI
	Latilo, 21 Nov. 1962	Nigeria, West Africa	FHI
	Daramola, 16 Aug. 1971	Nigeria, West Africa	FHI
B. louisii Robyns & R. Wilczek	Germain, 7 Aug. 1949	Cameroon, Central Africa	FHI
B. mannii (Meisn.) Benth. & Hook. f.	Eimunjeze & Ekwuno, 19 Nov. 1973	Nigeria, West Africa	FHI
	Hall, -	Ghana, West Africa	UIH
	Adebusuyi, 11 Apr. 1961	Nigeria, West Africa	FHI
	Ujor, 14 May 1952	Nigeria, West Africa	FHI
	Daramola, 6 March. 2002	Nigeria, West Africa	IFE
B. mannioides Robyns & R. Wilczek ex B.D. Jacks	Adamu, 8 Oct. 1971	Liberia, West Africa	FHI
B. oblongifolia Robyns & R. Wilczek	Pierlot, 22 May 1952	Congo, Central Africa	FHI
B. preussii Engl.	Onochie, 4 March 1957	Nigeria, West Africa	FHI
	21 Feb. 1957	Nigeria, West Africa	FHI
	Okafor, 2 Feb. 1957	Nigeria, West Africa	FHI
B. pubescens Teschner	Devred, 4 Feb. 1960	Congo, Central Africa	FHI
B. staudtii Engl.	Latilo & Onyeachusim, 12 March 1964	Cameroon, Central Africa	FHI
	Ariwaodo, 3 May 1977	Nigeria, West Africa	FHI
B. talbotiae (S. Moore) Robyns & R. Wilczek	Olorunfemi & *al.*, 7 May 1975	Nigeria, West Africa	FHI
	Osanyinlusi & Okoro, 14 Apr. 1980	Nigeria, West Africa	FHI
	Onochie & Brenan, 13 Feb. 1948	Nigeria, West Africa	FHI
	Binuyo & Daramola, 13 March 1956	Nigeria, West Africa	FHI
B. sp. A	Binuyo, 16 July 1959	Nigeria, West Africa	FHI
	Akinsoji, 19 Feb. 2009	Nigeria, West Africa	LUH
B. sp. B	Leonard; 17 July 1958	Gambia, West Africa	FHI
B. sp. C	Olorunfemi, 3 Oct. 1967	Nigeria, West Africa	FHI
	Chizea, 10 Feb. 1946	Nigeria, West Africa	FHI
	Daramola, 30 May 1966	Nigeria, West Africa	FHI
	Odiachi, 1953	Nigeria, West Africa	FHI
B. sp. D	Kadiri & *al.*, 7 Sept. 2011	Nigeria, West Africa	LUH

Note 1. Species' names are alphabetically arranged. Six out of the 14 taxa were represented by only a single collection.
Note 2. Abbreviation of Herbarium Code: FHI: Forestry Research Institute of Nigeria, Niageria; IFE: Obafemi Awolowo University, Nigeria; LUH: University of Lagos, Nigeria; UIH: Herbarium of the Department of Botany, University of Ibadan, Nigeria.

have not been studied as yet. There are about one fifth of the species occurring in the African mainland; 12 species in West Africa and ca. 41 species in Central Africa (Robyns and Wilczek, 1949, 1950; Hutchinson and Dalziel, 1958; Hutchinson, 1964; Fouilloy *et al*., 1974; Verdcourt, 1996), but more than half of them are poorly known.

This study was conducted to document the leaf epidermal characteristics of *Beilschmiedia* species from mainland Africa and to validate the existing infra-generic classification that is based on macromorphology. The taxonomic significance of leaf epidermal micromorphology of *Beilschmiedia* from the mainland Africa is to assist better understanding of this difficult genus.

MATERIALS AND METHODS

Plant materials and sampling: Fourteen species of *Beilschmiedia* (10 well established and four badly delimited species) from Africa were sampled from the herbarium specimens (Table 1). We tried to examine several specimens per species, but six of the 14 taxa were represented by only a single collection and 10 mature leaves obtained from each of them were dissected for the study. The methodology of Nishida and van der Werff (2007) was adopted for leaf epidermal study of all specimens.

***Light microscopy (LM)*:** Leaf portions ca 2–3 cm^2 were cut from the median portion of the leaf lamina near the mid-rib, boiled in water for 30 minutes, and then soaked for two to four hours in concentrated nitric acid (HNO_3) to macerate the mesophyll tissue. Tissue disintegration was indicated by air bubbles; the stage at which the leaf tissues were transferred into petri dishes containing water for separation of the epidermis and tissue debris was cleared off the epidermis with an artist's fine-hair brush and washed in several changes of water. Then, 2–3 drops of sodium hypochlorite solution were dropped onto the epidermis on the slide to bleach opaque areas (i.e. the modification introduced), and allowed to soak for 30–120 seconds until the color changed from bright yellow to white when washed in

Table 2. Measurements of epidermal cells of African *Beilschmiedia*.

Species	Leaf surface	Epidermal cell length (μm)	Epidermal cell width (μm)
B. gaboonensis	Adaxial	47.0±2.0	30.0±1.0
	Abaxial	50.0±2.0	29.0±1.0
B. hutchinsoniana	Adaxial	54.0±2.0	35.0±2.0
	Abaxial	53.0±2.0	36.0±2.0
B. louisii	Adaxial	50.0±2.0	35.0±2.0
	Abaxial	52.5±3.0	45.0±2.0
B. mannii	Adaxial	47.0±2.0	36.0±1.0
	Abaxial	47.0±3.0	37.0±1.0
B. mannioides	Adaxial	47.0±2.0	37.0±2.0
	Abaxial	50.0±3.0	39.0±1.0
B. oblongifolia	Adaxial	38.0±1.0	28.5±1.0
	Abaxial	45.0±2.0	32.0±1.0
B. preussii	Adaxial	49.0±2.0	30.0±2.0
	Abaxial	51.5±3.0	29.0±1.0
B. pubescens	Adaxial	45.5±1.0	32.0±1.0
	Abaxial	50.5±1.0	34.5±2.0
B. staudtii	Adaxial	47.0±2.0	37.0±1.0
	Abaxial	52.5±2.0	39.0±2.0
B. talbotiae	Adaxial	42.5±1.0	29.0±1.0
	Abaxial	49.5±2.0	32.0±2.0
***B.* sp. A**	Adaxial	39.0±2.0	27.0±1.0
	Abaxial	42.0±2.0	34.5±1.0
***B.* sp. B**	Adaxial	41.0±2.0	27.0±1.0
	Abaxial	37.0±1.0	33.0±1.0
***B.* sp. C**	Adaxial	43.5±2.0	30.0±1.0
	Abaxial	39.0±1.0	32.0±1.0
***B.* sp. D**	Adaxial	40.0±2.0	28.5±1.0
	Abaxial	50.5±2.0	33.0±1.0

water. The epidermis was mounted with the outer periclinal wall upwards on the slide and then two to five drops of ethanol in a series of ascending concentrations (50%, 75%, and 100%) were added to harden the cell wall. Two to three drops of 10% aqueous Methylene Blue and one drop of 50% aqueous Safranin were then added in turn to stain for three to five minutes. At the end, 2–3 drops of glycerine were added, then the preparation was covered with a cover-slip and the edges were sealed with nail polish to prevent dehydration. Each slide was observed under magnifications of ×100 and ×400 so as to capture all the features of the epidermis, e.g. epidermal cell size, stomatal number, size and indices, stomatal prominence, stomatal rim, stomatal symmetry, and peristomatal ridge presence. Micrographs were taken using a Zeiss Axio Imager A_1 light microscope with a mounted camera.

Scanning electron microscopy (SEM): Five square millimeter portions of the leaf lamina were dipped into 100% ethanol for 15 minutes and shaken vigorously, air-dried and coated with gold, and then fixed adaxially and abaxially on the stubs. The leaf surfaces were observed and photographed under a HITACHI S-4800 scanning electron microscope at 10kV. LM and SEM photographs were viewed, edited, and merged with Adobe Photoshop CS vers. 8.0.1.

Terminology: Description of epidermal characters for the Lauraceae was established (Metcalfe, 1987; Christophel *et al*., 1996; Nishida and Christophel, 1999; Ceoline *et al*., 2009; van der Werff and Nishida, 2010; Nishida and van der Werff, 2007, 2011; Yang *et al*., 2012). The features being described were actually those of the epidermal cells and the stomatal complex whose impressions were preserved in the cuticle. Peristomatal ledge referred to the ledge nearby the stomatal ledge. Stomatal rim referred to the rim of subsidiary cells surrounding the inner stoma.

RESULTS

All the specimens in Table 1 were examined and the specimens showed constancy in the characters studied. The differences found among individuals of the same species were minor. The overall findings are summarized in Figs. 1–3; quantitative measurements were assembled in Tables 2–3; and micromorphological characters of stomata were tabulated in Table 3, these include stomatal prominence, rim, and symmetry, and peristomatal ridge presence.

The stomata are confined to the abaxial surface (i.e. hypostomatic) and randomly distributed (Figs. 1–3). The stomata may be asymmetric, when the adjoining cell of the subsidiary cell on one side is specialized into a peristomatal ridge as found in *B. hutchinsoniana* Robyns & R. Wilczek (Fig. 1I), *B. louisii* Robyns & R. Wilczek (Fig. 3L), *B. mannii* (Meisn.) Benth. & Hook. f. ex B.D. Jacks (Fig. 3F), *B. mannioides* Robyns & R. Wilczek (Fig. 2F), *B. preussii* Engl. (Fig. 2C), *B. staudtii* Engl. (Fig. 2L), and *B. talbotiae* (S. Moore) Robyns & R. Wilczek (Fig. 1F), or symmetric, i.e. without a peristomatal ridge, like in *B. gaboonensis* (Meisn.) Benth. & Hook. f. ex B.D. Jacks (Fig. 1C), *B. oblongifolia* Robyns & R. Wilczek (Fig. 2I), *B. pubescens* Teschner (Fig. 1L), *B.* sp. A (Fig. 3I), *B.* sp. B (Fig. 3C), *B.* sp. C (Fig. 3O), and *B.* sp. D (Fig. 2O). Concerning stomatal prominence, five species namely *B. gaboonensis* (Fig. 1C), *B. hutchinsoniana* (Fig. 1I), *B. mannii* (Fig. 3F), *B. pubescens* (Fig. 1L), and *B. talbotiae* (Fig. 1F) have raised stomata. Superficial or impressed stomata were recorded in *B. louisii* (Fig. 3L), *B. oblongifolia* (Fig. 2I), *B. preussii* (Fig. 2C), *B. staudtii* (Fig. 2L), *B.* sp. B (Fig. 3C), and *B.* sp. D (Fig. 2O) while the remaining three species *B. mannioides* (Fig. 2F), *B.* sp. A (Fig. 3I) and *B.* sp. C (Fig. 3O) possess sunken stomata. The stomatal type is paracytic in all the species studied.

The lower stomatal ledge is visible under LM. Narrow lip-shaped lower stomatal ledges were found in all of the studied species. Half of the species studied sometimes have thicker anticlinal walls on the adaxial surface than abaxial surface viz: *B. gaboonensis* (Figs. 1A, 1B), *B. hutchinsoniana* (Figs. 1G, 1H), *B. louisii* (Figs. 3J, 3K), *B. mannii* (Figs. 3D, 3E), *B. pubescens*

Table 3. Stomatal measurements and comparative characters of African *Beilschmiedia* under SEM.

Species	Stomatal number per mm²	Stomatal length (µm)	Stomatal width (µm)	Stomatal index (%)	Stomatal prominence	Stomatal rim	Stomatal symmetry	Peristomatal ridge presence
B. gaboonensis	16±2	14.0±1.0	13.0±1.0	31	raised	wide/smooth	symmetric	no
B. hutchinsoniana	11±2	16.0±1.0	14.0±1.0	25	raised	wide/smooth	asymmetric	yes
B. louisii	16±2	14.0±1.0	10.0±1.0	22	superficial	wide/rough	asymmetric	yes
B. mannii	12±1	14.0±1.0	11.0±1.0	27	raised	wide/smooth	asymmetric	yes
B. mannioides	18±2	13.0±1.0	11.0±1.0	34	sunken	wide/rough	asymmetric	yes
B. oblongifolia	12±1	14.0±1.0	14.0±1.0	26	superficial	wide/rough	symmetric	no
B. preussii	34±1	14.0±1.0	12.0±1.0	25	superficial	wide/rough	asymmetric	yes
B. pubescens	11±1	16.0±1.0	10.0±1.0	38	raised	wide/rough	symmetric	no
B. staudtii	23±1	19.0±1.0	14.0±1.0	32	superficial	wide/rough	asymmetric	yes
B. talbotiae	12±1	14.0±1.0	9.0±1.0	24	raised	wide/smooth	asymmetric	yes
***B.* sp. A**	12±1	14.0±1.0	11.0±1.0	46	sunken	wide/rough	symmetric	no
***B.* sp. B**	14±1	17.0±1.0	11.0±1.0	27	superficial	wide/rough	symmetric	no
***B.* sp. C**	16±1	14.0±1.0	13.0±1.0	19	sunken	wide/rough	symmetric	no
***B.* sp. D**	20±2	12.0±1.0	10.0±1.0	33	superficial	wide/rough	symmetric	no

(Figs. 1J, K), *B. staudtii* (Figs. 2J, 2K) and *B.* sp. C (Figs. 3M, 3N) while the remaining half appear to have uniformly thickened anticlinal walls on both surfaces. Adaxially, the anticlinal walls are straight and angular in most species (Figs. 1A, 1D, 1G, 1J, 2A, 2G, 2J, 2M, 3A, 3D, 3G, 3J, 3M) but sinuous in *B. mannioides* (Fig. 2D).

Straightness of the anticlinal walls on the abaxial surface varied among the species. Straight and angular walls were recorded in *B. oblongifolia* (Fig. 2H); curved walls occurred in *B. gaboonensis* (Fig. 1B), *B. staudtii* (Fig. 2K), *B.* sp. B (Fig. 3B) and *B.* sp. D (Fig. 2N); slightly or fully undulate walls were found in *B. hutchinsoniana* (Fig. 1H), *B. louisii* (Fig. 3K), *B. mannii* (Fig. 3E), *B. preussii* (Fig. 2B), *B. talbotiae* (Fig. 1E), *B.* sp. A (Fig. 3H), and *B.* sp. C (Fig. 3N), while sinuous walls were recorded in *B. mannioides* (Fig. 2E) and *B. pubescens* (Fig. 1K). Of the wall ornamentation, the adaxial and abaxial surfaces of the epidermis may be identical (beaded or not beaded) or dissimilar (beaded against not beaded or vice versa, and not beaded against unevenly thickened). Beaded walls were recorded in 11 species (Figs. 1A, 1D, 1E, 1G, 1J, 2A, 2B, 2J, 2K, 2M, 2N, 3B, 3D, 3G, 3J); unbeaded walls were encountered in 10 species (Figs. 1B, 1H, 1K, 2D, 2G, 2H, 3A, 3E, 3H, 3K, 3M, 3N) while *B. mannioides* had unevenly thickened and unbeaded walls on the adaxial and abaxial surfaces respectively (Figs. 2D, 2E). The periclinal walls were smooth or nearly so on both leaf surfaces in most species but a punctate adaxial surface was found in *B. mannioides*.

DISCUSSION

As a general feature of the Lauraceae, the stomatal complex of the investigated species has sunken guard cells with over-arching subsidiary cells. Similarly, other features of the epidermis reported are in agreement with data already documented for the family. All the African species of *Beilschmiedia* studied here are hypostomatic like all other species of the genus from other regions (Christophel *et al*., 1996; Christophel and Rowett, 1996; Nishida and Christophel, 1999; Nishida and van der Werff, 2007).

Asymmetric stomatal complex and one-sided peristomatal ridge have not been reported in the *Beilschmiedia* group (Nishida and van der Werff, 2007; Yang *et al*., 2012). These features can aid in distinguishing the mainland African *Beilschmiedia* species and they appear to buttress the existing infra-generic classification by Robyns and Wilczek (1949, 1950). Asymmetric stomatal complex and presence of peristomatal ridge support recognition of the section *Eubeilschmiedia*. Bilaterally symmetrical peristomatal ridges were reported in certain *Beilschmiedia* species from other regions e.g. *B. intermedia* C.K. Allen, *B. henghsienensis* S.K. Lee & Y.T. Wei, *B. punctilimba* H.W. Li, *B. roxburghiana* Nees and *B. purpurascens* H.W. Li from Asia (Yang *et al*., 2012), *B. moratii* van der Werff and *B. pedicellata* van der Werff, from Madagascar as well as other members of the *Beilschmiedia* group such as *Endiandra coriacea* Merr., *E. dolichocarpa* S. Lee & Y.T. Wei, *Potameia incisa* Kosterm., and *P. thouarsiana* (Baill.) Capuron. Thus, symmetry of the stomatal complex due to presence or absence of unilateral or bilateral peristomatal ridges is useful for distinguishing taxa from different geographical areas and for showing species affinity.

Ornamentation of the anticlinal walls on the abaxial surface of these species can be beaded, not beaded and unevenly thickened. The species also share straight; undulate to sinuous and sometimes angular anticlinal walls with other genera in the *Beilschmiedia* group (Christophel *et al.*, 1996, Christophel and Rowett, 1996; Nishida and Christophel, 1999; Nishida and van der Werff, 2007, 2011; Yang *et al*., 2012). In the studied species, lower stomatal ledges are generally narrow lip-shaped, while wide lip-shaped, bat-shaped, and butterfly-shaped types can be found additionally in the

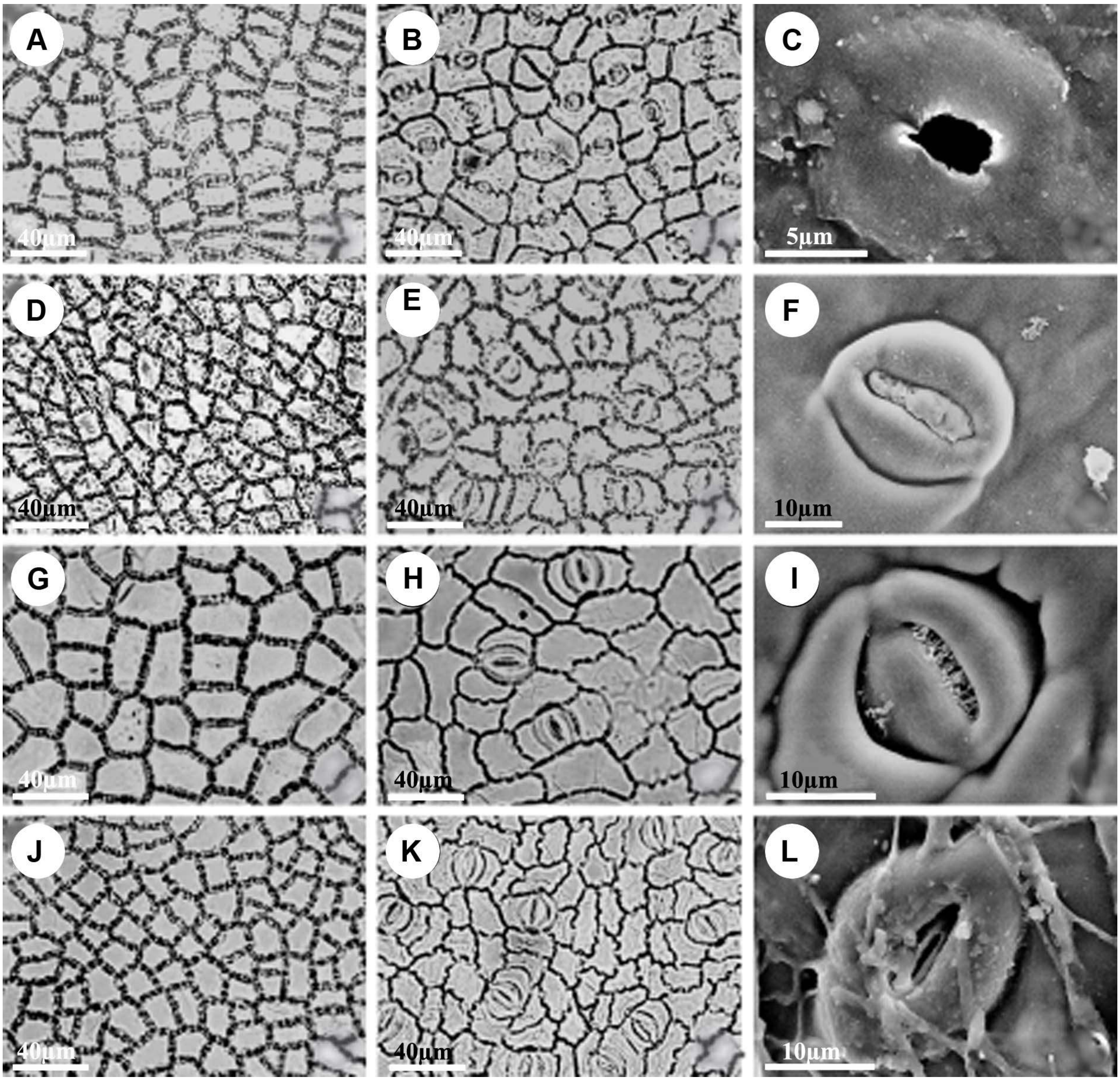

Fig. 1. Comparative epidermal features of African *Beilschmiedia* species. **A**–**C**, ***B. gaboonensis*** showing no peristomatal ridge and beaded adaxial surface; **D**–**F**, ***B. talbotiae*** showing beaded adaxial and abaxial surfaces, and peristomatal ridges; **G**–**I**, ***B. hutchinsoniana*** showing undulate and unbeaded anticlinal walls on the abaxial surface; **J**–**L**, ***B. pubescens*** showing sinuous abaxial anticlinal walls and raised stomata.

species from other regions (e.g. Nishida and Christophel, 1999; Nishida and van der Werff, 2007; Yang *et al*., 2012). Narrow lip-shaped lower stomatal ledges found here have also been reported in the Australian species, lip- and butterfly-shaped types were found in the Malagasy species while lip- and double semi-circle-shaped forms were recorded among Asiatic individuals, and lip-, butterfly- and box-shaped types were found in the species from the Neotropics (Nishida and Christophel, 1999; Nishida and van der Werff, 2007; Yang *et al*., 2012).

The periclinal walls are smooth on both surfaces of the epidermis in all the studied species except *B. mannioides* which has punctate periclinal walls on the adaxial surface. The two character states and their distribution patterns were also observed in the Asiatic species (Yang *et al*., 2012), Neotropical species (Nishida and Christophel, 1999) and Malagasy species (Nishida and van der Werff, 2007).

Beilschmiedia gaboonensis and *B. oblongifolia* are often confused because of incompleteness of macromorphological data (Hutchinson and Dalziel, 1958; Stapf, 1909). The two species can be distinguished using stomatal and epidermal cell features. *Beilschmiedia*

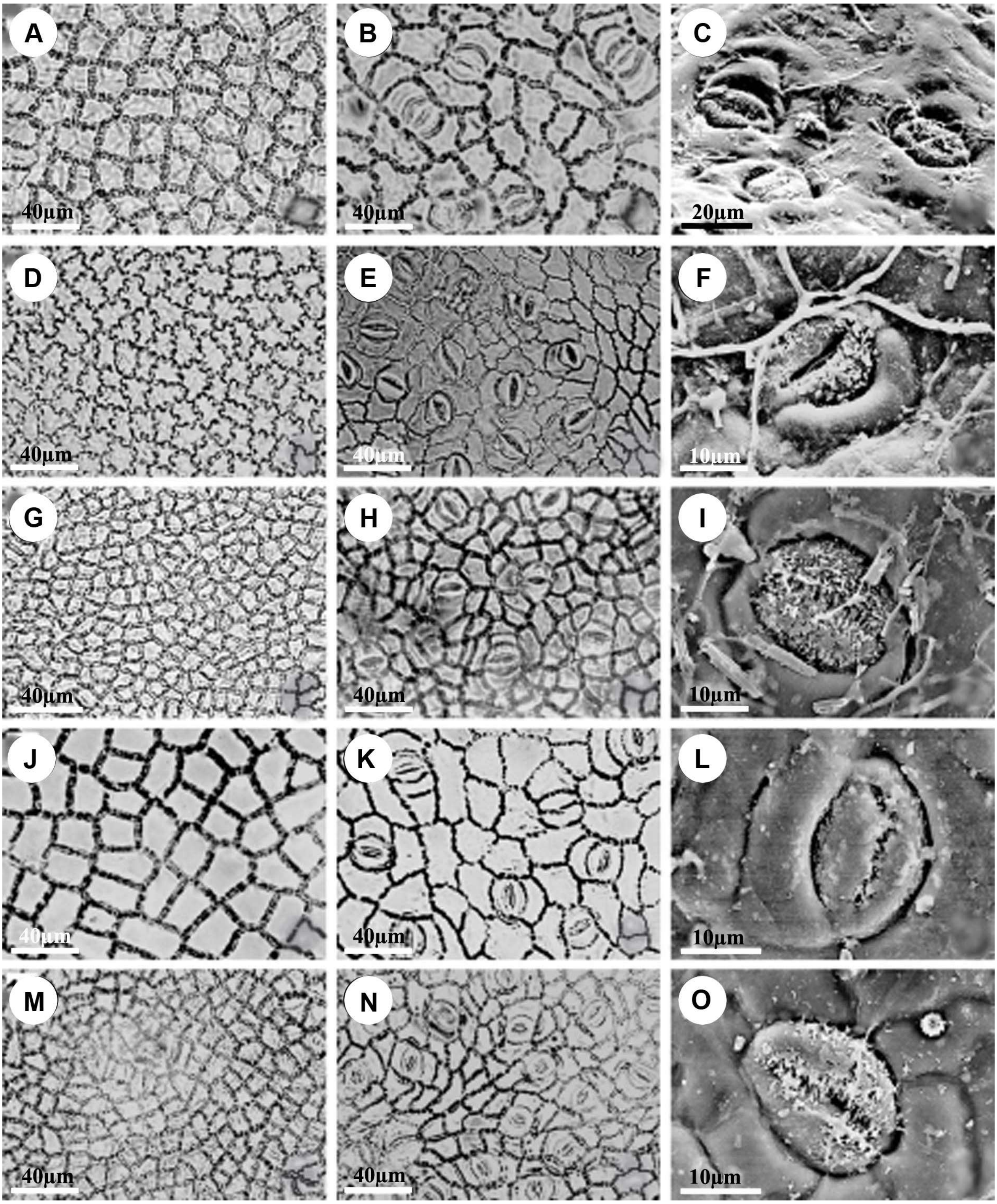

Fig. 2. Comparative epidermal features of African *Beilschmiedia* species. **A**–**C**, ***B. preussii*** showing superficial stomata and peristomatal ridges; **D**–**F**, ***B. mannioides*** showing sunken stomata and peristomatal ridges; **G**–**I**, ***B. oblongifolia*** showing unbeaded anticlinal walls on both surfaces; **J**–**L**, ***B. staudtii*** showing curved anticlinal walls on the abaxial surface and beaded walls on both surfaces; **M**–**O**, ***B.*** sp. **D** showing beaded walls on both surfaces and superficial stomata.

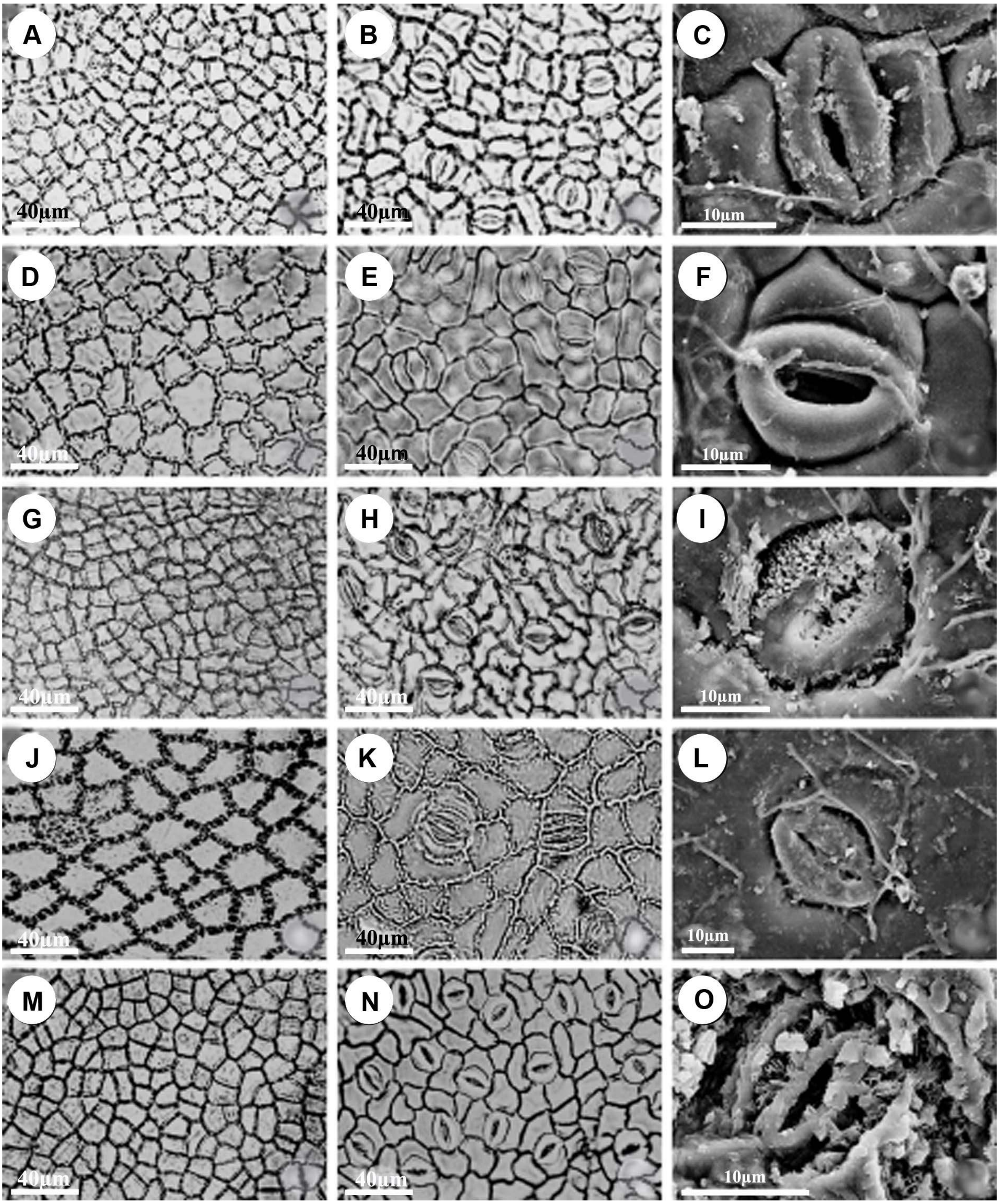

Fig. 3. Comparative epidermal features of African *Beilschmiedia* species. **A**–**C**, *B.* sp. **B** showing no peristomatal ridge, and presence of beaded walls on the abaxial surface; **D**–**F**, ***B. mannii*** showing slightly undulate walls and wide/smooth stomatal rim; **G**–**I**, *B.* sp. A showing sunken stomata and absence of peristomatal ridges; **J**–**L**, ***B. louisii*** showing peristomatal ridges and undulate abaxial anticlinal walls; **M**–**O**, *B*. sp. C: showing unbeaded anticlinal walls on both surfaces and sunken stomata without peristomatal ridges.

gaboonensis has raised stomata and smooth stomatal rim surface, but the stomata are superficial and their rim surface is rough in *B. oblongifolia*. Epidermal cells are larger in *B. gaboonensis* than in *B. oblongifolia* on the adaxial surface. These observations support distinctness of the two species and their grouping in different subgenera by Robyns and Wilczek (1949, 1950) based on floral characters.

Beilschmiedia mannii and *B. mannioides* are difficult to distinguish from each other and were identified as a single species in the Forestry Herbarium in Nigeria (FHI). However, the two species can be easily distinguished by the stomata which are raised with a smooth rim in *B. mannii* but sunken with a rough stomatal rim surface in *B. mannioides*. In addition, mean epidermal cells are longer on both surfaces of the leaf in *B. mannii* than in *B. mannioides*, and on the adaxial surface, the epidermal cell walls are beaded in *B. mannii* but they are unevenly thickened in *B. mannioides*.

Stomatal characters have been reported as valuable to the taxonomy of Lauraceae and other angiosperms (Christophel and Rowett, 1996; Christophel *et al*., 1996; Ghahremaninejad *et al*., 2012; Nishida and Christophel, 1999; Nishida and van derWerff, 2007; Kadiri and Olowokudejo, 2008, 2016; Ogundipe and Kadiri, 2012; Olowokudejo, 1993; Stace, 1965). Robyns and Wilczek (1949, 1950) proposed to classify the African *Beilschmiedia* into two subgenera, namely *Synthoradenia* Robyns & Wilczek and *Stemonadenia* Robyns & Wilczek, based on stamen number, number of lateral nerves and a few other morphological characters of the leaf. Subgen. *Stemonadenia* is further subdivided into two sections *Eubeilschmiedia* and *Hufelandia*, sect. *Eubeilschmiedia* contains *B. hutchinsoniana*, *B. mannii*, *B. mannioides*, *B. preussii*, and *B. staudtii*, and sect. *Hufelandia* includes *B. gaboonensis* and *B. talbotiae*. Subgen. *Synthoradenia* are represented by two of the studied species, i.e. *B. louisii* and *B. oblongifolia*. Our micromorphological data on peristomatal ridge and stomatal rim surface are largely in agreement with the classification (Robyns and Wilczek, 1949, 1950). A rough stomatal rim surface was found in the two species of subgen. *Synthoradenia*, but also in almost half of the species of subgen. *Stemonadenia* examined. In subgen. *Stemonadenia*, a peristomatal ridge is present except in *B. gaboonensis*. In sect. *Hufelandia*, a smooth stomatal rim surface is common, whereas in sect. *Eubeilschmiedia* it is either rough or smooth but all the species have a peristomatal ridge. These important stomatal data can be used together with other features of the epidermis and some other macromorphological characters in order to improve the existing infrageneric classification of Robyns and Wilczek (1949, 1950). Despite this, further studies are need to verify the systematic significance of leaf epidermal characters within a phylogenetic context.

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