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# ■ Endocarpic trichomes in Vandeae (Orchidaceae)



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## Abstract

Endocarpic trichomes have been analyzed in fruits of 267 species from 80 genera of the orchid tribe Vandeae, using light and scanning electron microscopy. They have been observed for the first time in 56 genera and confirmed in the rest. The present study describes their microstructure in Vandeae and suggests a standardization for its terminology. Endocarpic trichomes are unicellular, thin, tightly cylindrical, hollow, with an obtuse apex and an expanded foot. The outer surface shows a helicoidal micro-ornamentation, usually covered by waxes. Perforations of the walls have been mainly observed at the outer surface in the foot, and the basal and apical regions. The inner wall is formed by helicoidal thickenings which are responsible for the movement of the endocarpic trichomes. These are present in all the species studied of Vandeae, irrespectively of the life form.

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**Keywords:** Elaters; Fruit; Micro-ornamentation; Waxes; Perforations; Epidendroideae

## 1 Introduction

Endocarpic trichomes associated to the seeds of epiphytic orchids have been observed inside the fruits and named using different terms, such as “filet capillacés” ([Petit-Thouars, 1822](#)), “élatères” ([Prillieux, 1857](#); [Hallé, 1986](#)), “cils soyeux” ([Barbosa, 1883](#)), “Schleuderhaare” ([Horowitz, 1902](#)), “elaters” or “spring hairs” ([Cribb, 1999](#)), and “endocarpic trichomes” ([Rasmussen and Johansen, 2006](#)). [Blanco et al. \(2006\)](#) assigned the term “elater” to a single trichome and “capillitium” to the aggregation of trichomes.

The first mention of these structures in Orchidaceae appeared in [Petit-Thouars \(1822\)](#), who described them as small and elastic, showing an illustration of *Angraecum recurvum* [currently *Jumellea recurva*]. [Prillieux \(1857\)](#) mentioned their presence in certain representatives of the current tribes Epidendreae, Cymbidieae and Vandeae, describing them as long hairs with thickened walls, with the foot inserted in the endocarp. Analysing the “élatères” in Sarcanthinae, [Hallé \(1986\)](#) improved the previous descriptions providing data about their size (length and width) and qualitative characters (anatomy, tip, base), such as the lack of ornamentation and the presence of an oblique base and a slightly attenuate apex. [Veyret \(2001\)](#) stated that the diameter was practically constant among species and the diameter at the tip could be six times smaller than at the base. These trichomes are formed along the midline of the carpels ([Hallé, 1977](#); [Rasmussen and Johansen, 2006](#)) and during its development, they became lignified approximately 6-11 weeks after pollination at least in the fruits of *Erycina pusilla* (Cymbidieae) ([Dirks-Mulder et al., 2019](#)).

[Prillieux \(1857\)](#) reported the hygroscopic properties of these trichomes, which in contact with moisture, caused a contraction force which contributed to the release of seeds. This statement was corroborated by [Hallé \(1986\)](#), who

considered a resemblance in their function with the elaters in the sporangia of liverworts and some pteridophytes. Blanco et al. (2006) also observed the hygroscopic movement in *Maxillaria nardoides* under light microscope.

So far, endocarpic trichomes have been reported in 87 genera and 44 species belonging to the current tribes Collabieae, Cymbidieae, Diurideae, Epidendreae, Podochileae and Vandaeae (Petit-Thouars, 1822; Blume, 1848; Beer, 1857; Prillieux, 1857; Horowitz, 1902; Hallé, 1977, 1986; Pedersen, 1993; Freudenstein and Rasmussen, 1999; Blanco et al., 2006; Rasmussen and Johansen, 2006; Mayer et al., 2011; Chase et al., 2015; Dirks-Mulder et al., 2019; Mosquera-Mosquera et al., 2019).

The tribe Vandaeae is one of the major groups within the subfamily Epidendroideae (Orchidaceae), with more than 2300 species in 135 genera (Chase et al., 2015; Govaerts et al., 2020). Freudenstein and Chase (2015) recognized four subtribes: Adrorhizinae, Polystachyinae, Aeridinae and Angraecinae, with 3, 2, 83 and 47 genera, respectively. Farminhão et al. (2018) lumped the genera *Cribbia*, *Margelliantha* and *Rhaesteria* with *Rhipidoglossum*. Recently, Farminhão et al. (2021) supported the exclusion of the genera *Afropectinariella*, *Conchograecum*, *Dolabrifolia* and *Eichlerangraecum* of the genus *Angraecum*. After these proposals, the current number of genera in Vandaeae is 136.

The tribe is distributed in tropical and subtropical areas, mainly in Africa, Madagascar and neighbouring islands, and Asia. According to the life form, Pridgeon et al. (2014) and Govaerts et al. (2020) considered that almost all the representatives of Vandaeae are epiphytes, whereas a reduced number are lithophytes, and only five species of the genera *Bromheadia*, *Cleisostoma*, *Papilionanthe* and *Phalaenopsis* are exclusively terrestrial.

Endocarpic trichomes have been mentioned in 28 genera and 19 species within Vandaeae, in the current genera *Acampe* (Beer, 1857; Prillieux, 1857), *Aerides* (Beer, 1857), *Angraecum* (Petit-Thouars, 1822; Prillieux, 1857; Veyret, 2001), *Pteroceras* (Pedersen, 1993), *Saccolabium* (Beer, 1857), and *Vanda* [Instruction: We would recommend to join the parentheses with the citation: (Mosquera-Mosquera...)](Mosquera-Mosquera et al., 2019). Hallé (1986) published the main and specific work on these structures, describing them in 13 genera of Sarcanthinae from New Caledonia (*Chamaeanthus*, *Cleisostoma*, *Drymoanthus*, *Hymenorchis*, *Luisia*, *Micropera*, *Robiquetia*, *Sarcanthopsis*, *Sarcochilus*, *Schoenorchis*, *Taeniophyllum*, *Thrixspermum* and *Trachoma*); besides, he mentioned its presence in the genera *Diaphananthe*, *Microcoelia*, *Polystachya* and *Papilionanthe*, and hypothesized that they could be generalized in the current Vandaeae. Freudenstein and Rasmussen (1999) included in a table the character “endocarpic trichomes” for the genera *Acampe*, *Aerangis*, *Angraecum*, *Bromheadia*, *Phalaenopsis*, *Polystachya* and *Sirhookera*. Rasmussen and Johansen (2006) included cross sections of fruits with trichomes in *Micropera fasciculata* and *Trachoma subluteum*.

This study is part of our ongoing research on fruits and seeds in Orchidaceae. We aim to provide a detailed study on the anatomy of endocarpic trichomes, by means of light and scanning electron microscopy, contributing to the characterization and standardization of the terminology in these structures. We also intend to know if these trichomes are present in all the subtribes within Vandaeae.

## 2 Material and methods

Endocarpic trichomes were obtained from specimens housed in the herbaria of the Royal Botanic Gardens at Kew (K) and Madrid (MA). Samples of 267 species (264 epiphytic - seven of them also lithophytic -, two lithophytic and one terrestrial) from 80 genera (about 60% of the recognized genera in Vandaeae) were analysed using light (LM) and scanning electron microscopy (SEM). A list of species studied with countries, collector with number and voucher is given in Appendix 1, with scientific names and authorities according to Govaerts et al. (2020) and Farminhão et al. (2021), and subtribes according to Freudenstein and Chase (2015).

For sampling, we selected capsules with mature seeds following the methodology in Gamarra et al. (2018), to ensure the full development of the trichomes. For each genus, we have selected a small portion of the inner surface of one fruit to check the emergence of the trichomes. Samples were carefully taken from the walls of the fruits; we also collected those which were free and surrounding the mature seeds. An average of 10 trichomes from each species was analysed under SEM and LM.

For SEM observations, the samples were fixed on SEM stubs and coated with gold in a sputter-coater (SEM Coating System, Bio-Rad SC 502). The SEM micrographs were taken with a Philips XL30, with a filament voltage of 20 kV at SIDI-UAM (Interdepartamental Service of Investigation, Universidad Autónoma de Madrid). Samples for light

microscopy were previously mounted with PVA (polyvinil alcohol). Images under light microscope were taken in an Olympus BX-41 with a digital camera ColorView1 using software cellSens version 1.4.

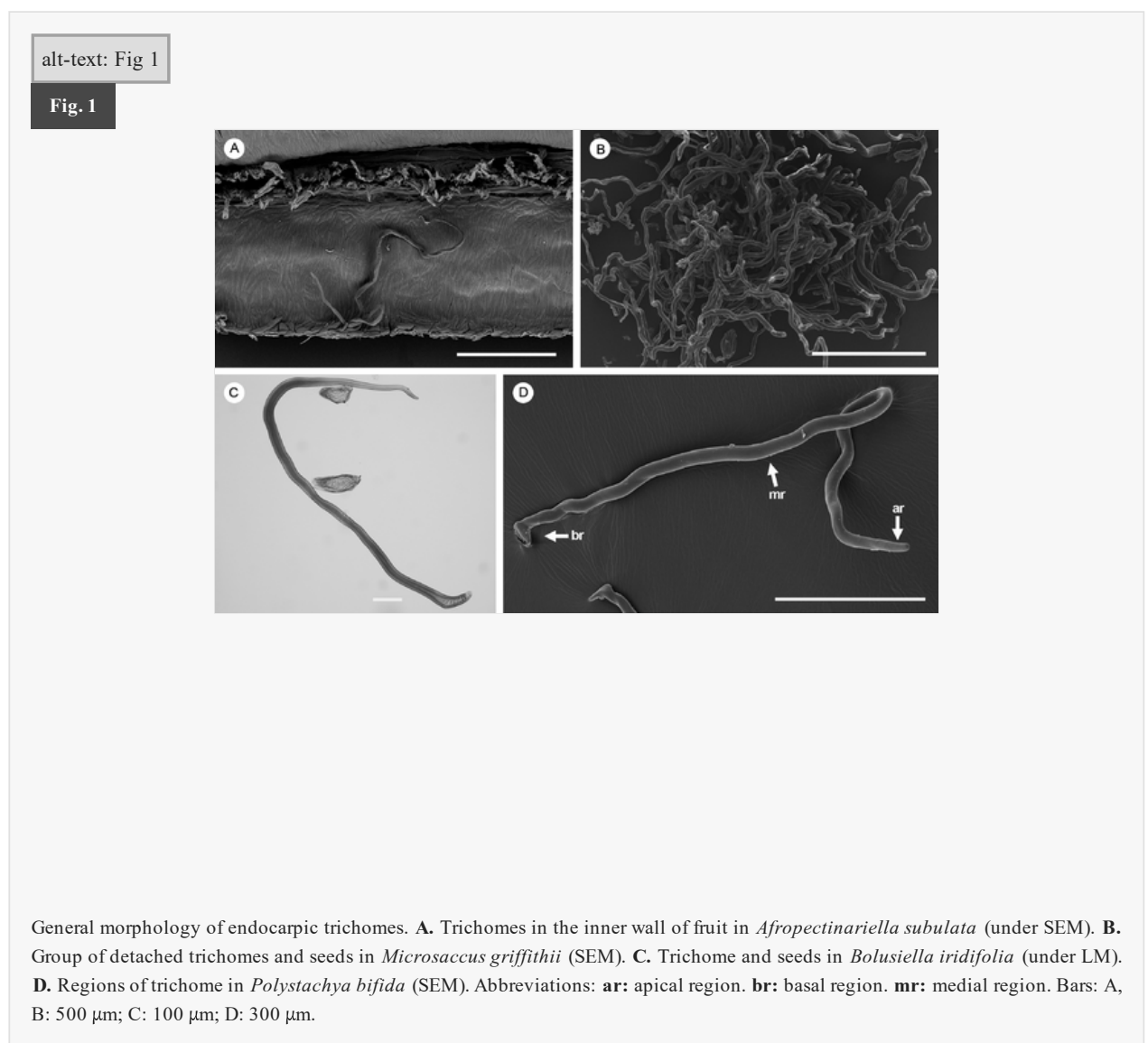
Qualitative data such as foot and apex morphology, presence of surface features (ornamentation, waxes) and perforations of the walls were studied under SEM. Colour was analysed under a stereomicroscope Olympus SZ61 with the software cellSens version 1.4, and was annotated in subjective terms. To detect the presence of waxes in the outer surface, samples were fixed in a solution with Sudan III and ethanol 70% to reveal the presence of lipids, according to [Contín et al. \(2013\)](#).

The terminology was adopted from [Hallé \(1986\)](#), [Stearn \(1992\)](#) and [Blanco et al. \(2006\)](#).

### 3 Results

Endocarpic trichomes have been observed in all the 267 species studied of Vandaeae belonging to 80 genera, which included representatives of the four subtribes (Adrorhizinae, Aeridinae, Angraecinae, Polystachyinae). These trichomes have been observed for the first time in 56 genera and confirmed in the rest.

Endocarpic trichomes developed in the inner wall of the fruit, on the midline of the carpels ([Fig. 1A](#)). At maturity, they detached surrounding the seeds ([Fig. 1B](#)).




All the trichomes observed were simple, filiform, and unicellular ([Fig. 1C](#)), and three regions have been recognized ([Fig. 1D](#)).

The basal region is swollen and oblique, with a foot variable in shape ([Table 1](#)): ovate ([Fig. 2A](#)), lanceolate-ovate ([Fig. 2B](#)), narrowly trullate ([Fig. 2C-D](#)), narrowly lanceolate ([Fig. 2E](#)) and oblong-elliptic ([Fig. 2F](#)). The foot shows two asymmetrical ends. The shorter end is usually obtuse ([Fig. 2A](#)). The longer end is usually acute ([Fig. 2B](#)), gradually attenuate in a pointed tip when the foot is narrowly trullate, such as in the genera *Calymmanthera* ([Fig. 2C](#)), *Cleisostoma*, *Gastrochilus*, *Saccolabiopsis* ([Fig. 2D](#)) and *Uncifera* within Aeridinae, and *Angraecopsis*, *Bolusiella*

*talbotii*, *Conchograecum*, *Nephrangis*, *Solenangis* and *Summerhayesia* within Angraecinae. The longer end is rarely obtuse, only if the foot is ovate or oblong-elliptic in shape (Fig. 2A, F).

alt-text: Table 1

Table 1

 The table layout displayed in this section is not how it will appear in the final version. The representation below is solely purposed for providing corrections to the table. To preview the actual presentation of the table, please view the Proof.

Comparison of the main variable traits (color, foot morphology and placement of the perforations) in the genera studied.

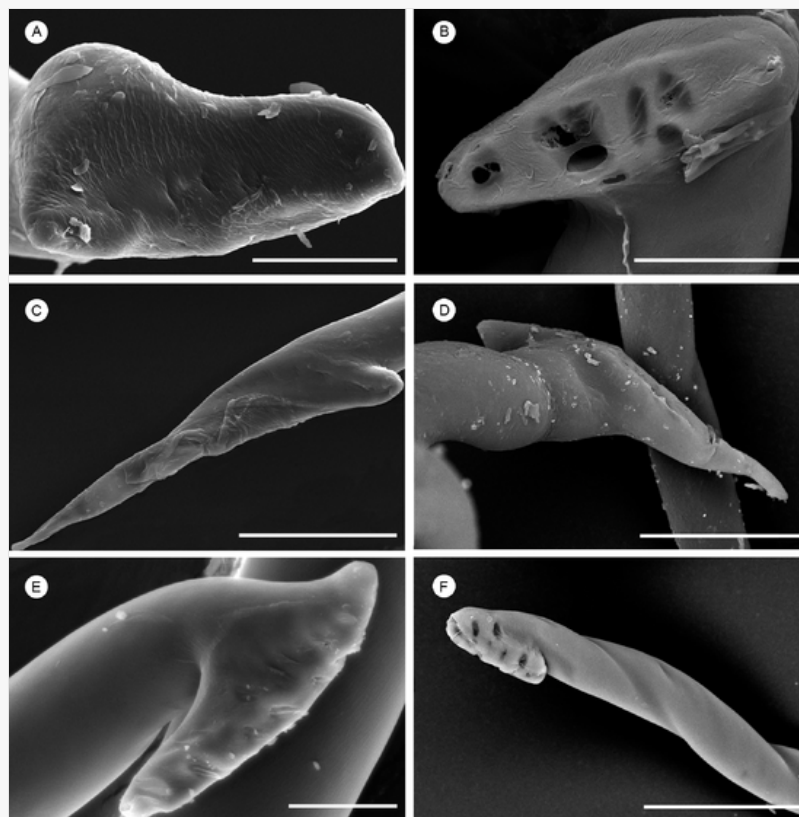
Subtribe/Genus	Color	Foot morphology	Perforations
<b>Adrorhizinae</b>			
<i>Bromheadia</i>	yellowish to pale yellowish	lanceolate-ovate	basal zone, mainly in the foot
<b>Polystachyinae</b>			
<i>Hederorkis</i>	whitish	ovate	along the trichomes
<i>Polystachya</i>	whitish to pale brown	lanceolate-ovate to narrowly lanceolate	mainly in the basal zone
<b>Aeridinae</b>			
<i>Acampe</i>	golden brown	lanceolate-ovate	basal and medial zone, mainly in the foot
<i>Adenoncos</i>	pale yellowish to golden yellowish	narrowly lanceolate	basal zone, mainly in the foot
<i>Aerides</i>	golden yellowish to golden brown	narrowly lanceolate	basal zone, mainly in the foot
<i>Arachnis</i>	golden brown	ovate	basal zone
<i>Brachypeza</i>	whitish	lanceolate-ovate	basal zone, mainly in the foot
<i>Calymmanthera</i>	whitish	narrowly trullate	basal zone, mainly in the foot
<i>Chiloschista</i>	golden yellowish	lanceolate-ovate	along the trichomes
<i>Cleisostoma</i>	pale brown to brown yellowish	narrowly trullate	basal zone, mainly in the foot
<i>Gastrochilus</i>	whitish to pale brown	narrowly trullate	basal zone, mainly in the foot
<i>Holcoglossum</i>	brown yellowish	lanceolate-ovate	basal zone, mainly in the foot
<i>Hymenorchis</i>	golden yellowish	oblong-elliptic	along the trichomes
<i>Jejewoodia</i>	pale yellowish	narrowly lanceolate	along the trichomes, mainly in the foot
<i>Luisia</i>	pale brown to golden brown	ovate to narrowly lanceolate	basal zone, mainly in the foot
<i>Macropodanthus</i>	pale brown	oblong-elliptic	basal zone, mainly in the foot
<i>Micropera</i>	pale brown	narrowly lanceolate	along the trichomes
<i>Microsaccus</i>	pale brown to whitish	oblong-elliptic	basal zone, mainly in the foot
<i>Papilionanthe</i>	golden brownish	oblong-elliptic	basal zone, mainly in the foot
<i>Pelatantheria</i>	pale brown	lanceolate-ovate	basal zone, mainly in the foot
<i>Phalaenopsis</i>	golden yellowish to golden brown	lanceolate-ovate	basal zone, mainly in the foot
<i>Plectorrhiza</i>	golden yellowish	narrowly lanceolate	basal zone, mainly in the foot

<i>Pomatocalpa</i>	pale brown	oblong-elliptic	basal zone, mainly in the foot
<i>Porrorhachis</i>	pale brown	narrowly lanceolate	basal zone, mainly in the foot
<i>Pteroceras</i>	whitish to pale brown	lanceolate-ovate	basal zone, mainly in the foot
<i>Renanthera</i>	pale brown to golden brown	ovate	basal zone, mainly in the foot
<i>Rhynchostylis</i>	pale brown to brown yellowish	lanceolate-ovate	apical and basal zone, mainly in the foot
<i>Robiquetia</i>	whitish to pale brown	lanceolate-ovate	basal zone, mainly in the foot
<i>Saccolabiopsis</i>	golden yellowish	narrowly trullate	basal zone, mainly in the foot
<i>Sarcanthopsis</i>	golden yellowish	lanceolate-ovate	basal zone, mainly in the foot
<i>Sarcochilus</i>	pale yellow	lanceolate-ovate	basal zone, mainly in the foot
<i>Sarcoglyphis</i>	brown-reddish	lanceolate-ovate	apical and basal zone
<i>Schoenorchis</i>	brown to golden brown	lanceolate-ovate	basal zone, mainly in the foot
<i>Seidenfadenia</i>	brown-yellowish	lanceolate-ovate	basal zone, mainly in the foot
<i>Smitinandia</i>	golden brown	oblong-elliptic	basal zone, mainly in the foot
<i>Taeniophyllum</i>	whitish to pale brown	lanceolate-ovate	basal zone, mainly in the foot
<i>Taprobanea</i>	brown-reddish	oblong-elliptic	basal zone, mainly in the foot
<i>Thrixspermum</i>	whitish to golden brown	lanceolate-ovate	basal zone, mainly in the foot
<i>Trichoglottis</i>	yellowish to pale brown	oblong-elliptic	basal zone, mainly in the foot
<i>Uncifera</i>	pale brown	narrowly trullate	basal zone, mainly in the foot
<i>Vanda</i>	brownish to golden brown	oblong-elliptic	along the trichomes
<i>Vandopsis</i>	pale brown to golden brown	oblong-elliptic	basal zone, mainly in the foot
<b>Angraecinae</b>			
<i>Aerangis</i>	whitish to pale brown	lanceolate-ovate to narrowly trullate	apical and basal zone
<i>Aeranthes</i>	whitish to pale brown	lanceolate-ovate	basal zone, mainly in the foot
<i>Afropectinariella</i>	golden brown to pale brown	lanceolate-ovate	basal zone, mainly in the foot
<i>Ancistrorhynchus</i>	golden brown to golden yellowish	lanceolate-ovate	basal zone, mainly in the foot
<i>Angraecopsis</i>	whitish	narrowly trullate	basal zone, mainly in the foot
<i>Angraecum</i>	pale yellowish to golden yellowish	lanceolate-ovate	basal zone, mainly in the foot
<i>Bolusiella</i>	pale brown to dark brown	lanceolate-ovate	basal zone, mainly in the foot
<i>Calyptrochilum</i>	whitish	lanceolate-ovate	basal zone, mainly in the foot
<i>Campylocentrum</i>	whitish to pale brown	lanceolate-ovate	basal zone, mainly in the foot
<i>Conchograecum</i>	golden yellowish	narrowly trullate	along the trichomes, mainly in the basal zone
<i>Cryptopus</i>	golden brown	ovate	basal zone, mainly in the foot
<i>Cyrtorchis</i>	golden brown to golden yellowish	lanceolate-ovate	basal zone, mainly in the foot
<i>Dendrophylax</i>	pale yellowish to golden yellowish	narrowly lanceolate	basal zone, mainly in the foot
<i>Diaphananthe</i>	pale yellowish to golden	lanceolate-ovate to narrowly	basal zone, mainly in the foot

	yellowish	lanceolate	
<i>Dinklageella</i>	whitish yellow	ovate	basal zone, mainly in the foot
<i>Dolabrifolia</i>	yellowish	narrowly lanceolate	apical and basal zone, mainly in the foot
<i>Erasanthe</i>	whitish yellow to golden yellowish	narrowly lanceolate	basal zone, mainly in the foot
<i>Eurychone</i>	whitish yellow	ovate	basal zone, mainly in the foot
<i>Jumellea</i>	pale brown	lanceolate-ovate	basal zone, mainly in the foot
<i>Lemurella</i>	golden	lanceolate-ovate	apical and basal zone, mainly in the foot
<i>Listrostachys</i>	whitish-yellowish	narrowly lanceolate	basal zone, mainly in the foot
<i>Microcoelia</i>	golden yellowish to golden brown	narrowly lanceolate	apical and basal zone, mainly in the foot
<i>Mystacidium</i>	whitish to pale yellow	narrowly lanceolate	basal zone, mainly in the foot
<i>Neobathiea</i>	golden yellowish	narrowly lanceolate	basal zone, mainly in the foot
<i>Nephrangis</i>	yellowish	narrowly trullate	basal zone, mainly in the foot
<i>Oeonia</i>	pale brown	oblong-elliptic	basal zone, mainly in the foot
<i>Oeoniella</i>	yellow whitish to golden	lanceolate-ovate	apical and basal zone, mainly in the foot
<i>Plectrelminthus</i>	golden, pale brown to brown	ovate	basal zone, mainly in the foot
<i>Podangis</i>	whitish to yellowish	lanceolate-ovate	apical and basal zone, mainly in the foot
<i>Rangaeris</i>	whitish to yellowish	lanceolate-ovate	basal zone, mainly in the foot
<i>Rhipidoglossum</i>	whitish to pale brown	lanceolate-ovate to narrowly lanceolate	basal zone, mainly in the foot
<i>Sobennikoffia</i>	golden	ovate	basal zone, mainly in the foot
<i>Solenangis</i>	brownish to pale brown	narrowly trullate	apical and basal zone, mainly in the foot
<i>Sphyrarhynchus</i>	whitish	lanceolate-ovate	basal zone, mainly in the foot
<i>Summerhayesia</i>	golden	narrowly trullate	basal zone, mainly in the foot
<i>Tridactyle</i>	pale brown	lanceolate-ovate	basal zone, mainly in the foot
<i>Ypsilopus</i>	whitish	lanceolate-ovate	basal zone, mainly in the foot

alt-text: Fig 2

Fig. 2



Variation in foot shape of endocarpic trichomes under SEM. **A.** *Luisia teretifolia*. **B.** *Thrixspermum complanatum*. **C.** *Calymmanthera major*. **D.** *Saccolabiopsis pumila*. **E.** *Neobathiea grandidieriana*. **F.** *Lemurella culicifera*. Bars: A, B, E: 20  $\mu$ m. C, F: 50  $\mu$ m. D: 30  $\mu$ m.

The medial region is elongated, filiform, tightly cylindrical, uniform in width along its length in all the species studied (Figs. 1C-D).

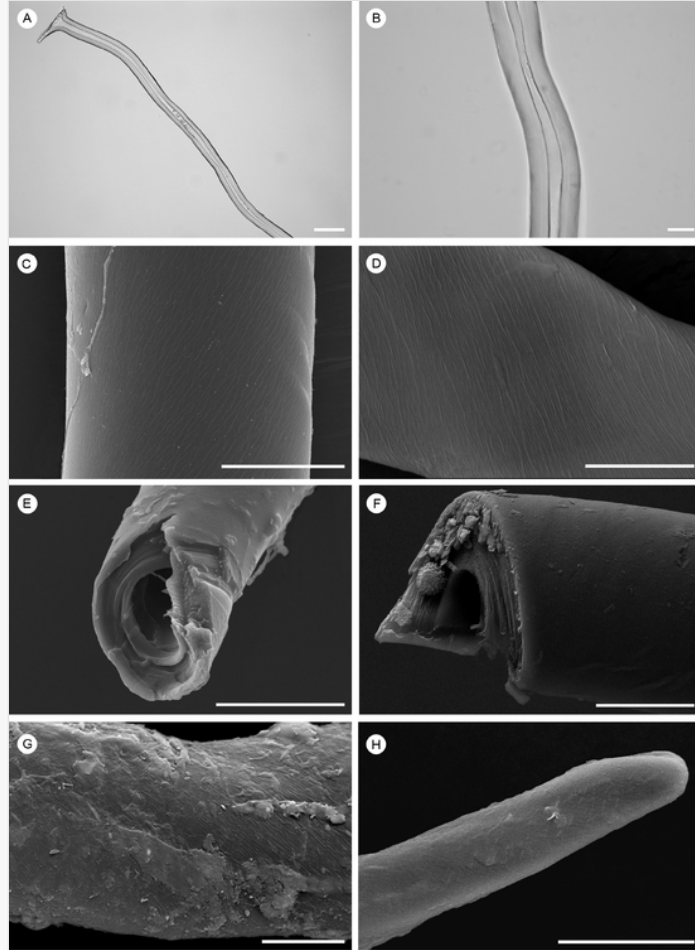
The apical region is gradually tapering until the obtuse apex (Fig. 1D), homogeneous for all the species studied.

Under LM, the endocarpic trichomes were translucent, with a thick wall surrounding an inner hollow (Fig. 3A-B). In general, colour varied from whitish to pale brown or yellowish, rarely golden brown, brown-reddish to dark brown (Fig. 4, Table 1).

alt-text: Fig 3

Fig. 3

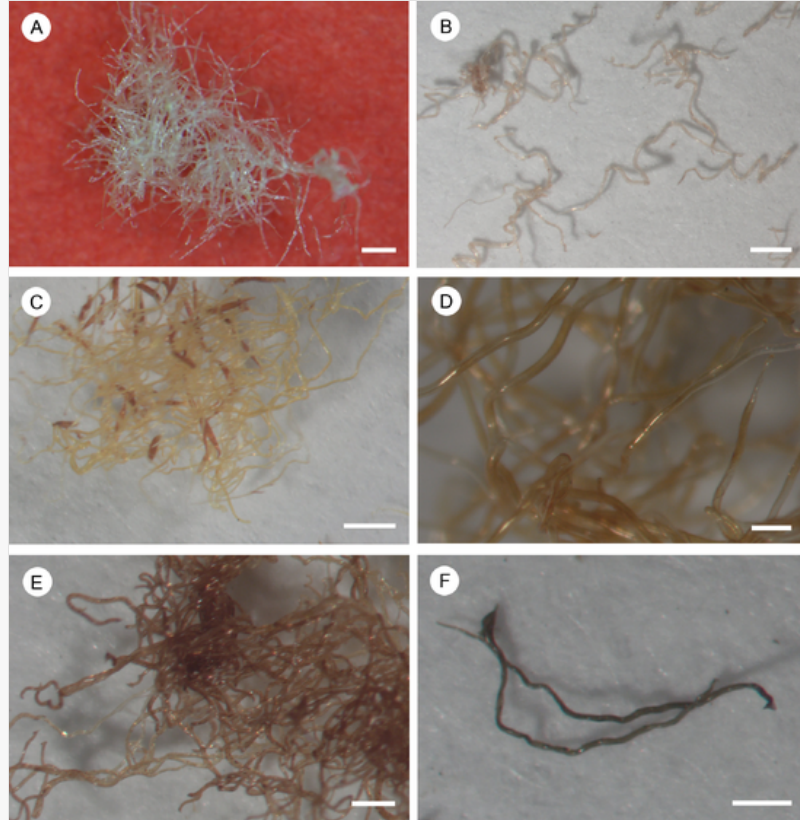




Outer and inner walls of endocarpic trichomes. **A.** Translucent trichome with the inner hollow along the medial and basal region in *Polystachya elegans* (under LM). **B.** Translucent trichome with the inner hollow along the medial region in *Angraecum calceolus* (LM). **C.** Micro-ornamentation of the outer surface in *Arachnis cathcartii* (SEM). **D.** Detail of the helicoidal striations in the outer surface in *Afropectinariella subulata* (SEM). **E.** Transverse view of the inner walls in *Gastrochilus calceolaris* (SEM). **F.** Transverse view of the inner walls in *Dendrophylax porrectus* (SEM). **G.** Detail of the waxes on the outer surface in the medial region in *Listrostachys pertusa* (SEM). **H.** Waxes on the outer surface in the apical region in *Bolusiella iridifolia* (SEM). Bars: A: 100  $\mu\text{m}$ . B, F, H: 20  $\mu\text{m}$ . C, E: 30  $\mu\text{m}$ . D, G: 10  $\mu\text{m}$ .

alt-text: Fig 4

**Fig. 4**

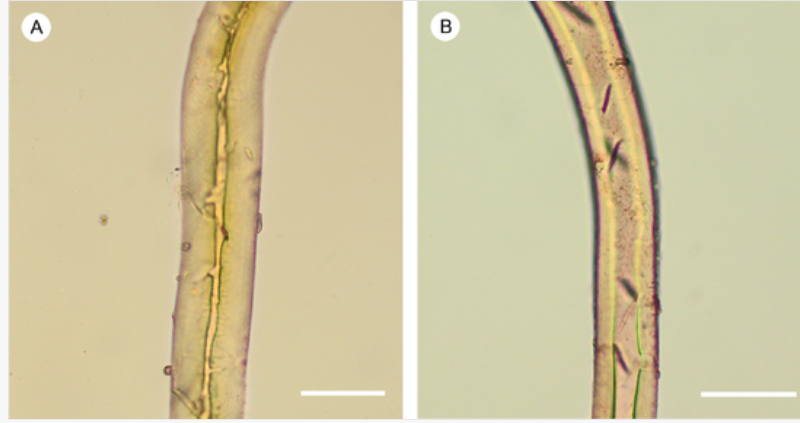


Colour of endocarpic trichomes. **A.** *Brachypeza zamboangensis*, whitish (on red paper). **B.** *Pomatocalpa spicatum*, pale brown. **C.** *Plectorrhiza tridentata*, yellowish. **D.** *Arachnis cathcartii*, golden brown. **E.** *Sarcoglyphis mirabilis*, brown-reddish. **F.** *Bolusiella talbotii*, dark brown. Bars: 50  $\mu$ m.

Under SEM, the outer surface of the cell wall shows micro-ornamentation, formed by thin helicoidal striations (Fig. 3 C-D). Inside, the walls are thickened, fibrous, showing a regular helical microfibril arrangement (Fig. 3 E-F D-E). All the trichomes show a thin covering of wax along the length (Fig. 3 G-H F), more or less visible under SEM. Its presence has been confirmed under LM (Fig. 5).

alt-text: Fig 5

Fig. 5

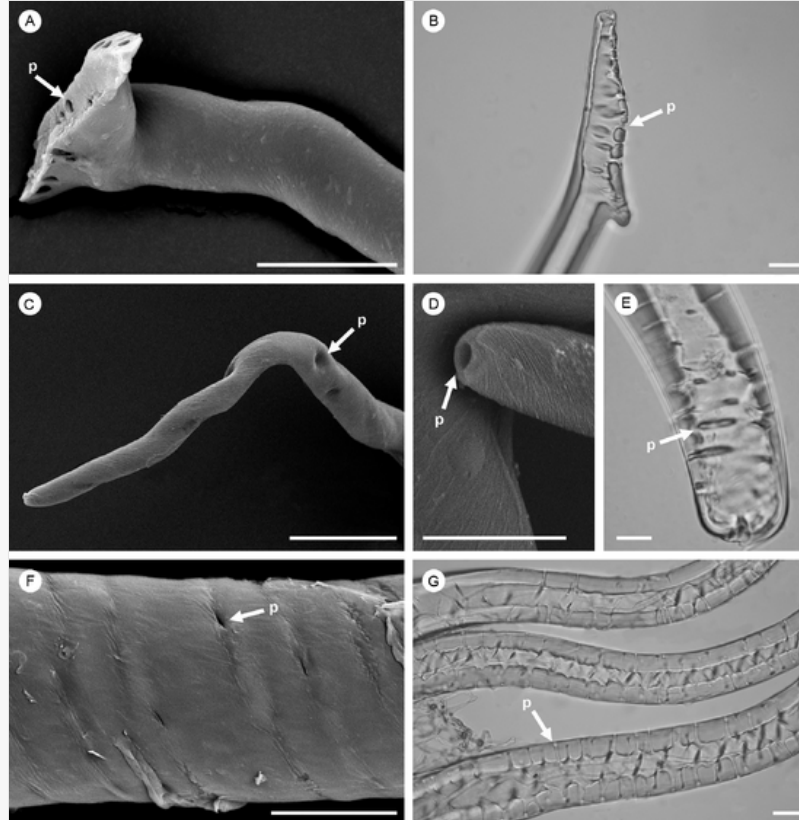


Wax staining of endocarpic trichomes. **A.** *Acampe pachyglossa* (under LM). **B.** *Listrostachys pertusa* (LM). Bars: A, B: 50  $\mu$ m.

Perforations of the walls have been observed under both microscopes. They are common at the foot of the trichomes and the basal region (Fig. 6A-B, Table 1). In the apical region are less common but it is frequent to observe a circular perforation at the tip (Fig. 6C-E). Occasionally, they have been observed scattered along the medial region (Fig. 6F-G). Perforations connect directly with the inner lumen (Fig. 6B, E, G). Its shape is more or less circular (Fig. 2B, Fig. 6C) or longitudinal (Fig. 6E). In the same trichome, both shapes can be present.

alt-text: Fig 6

Fig. 6



Perforations along the wall of endocarpic trichomes. **A.** *Podangis rhipsalisocia*, in the basal region (under SEM). **B.** *Dendrophylax funalis*, connected to the inner hollow in the basal region (under LM). **C.** *Dolabrifolia podochiloides*, in the apical region (SEM). **D.** *Cyrtorchis arcuata*, detail of the circular perforation in the apex (SEM). **E.** *Rhipidoglossum rutilum*, longitudinal perforations connected to the inner hollow in the apical region (LM). **F.** *Hederorkis seychellensis*, longitudinal perforations in the medial region (SEM). **G.** *Hederorkis seychellensis*, connected to the inner hollow in the medial region (LM). Abbreviation: **p**: perforation. Bars: A: 30  $\mu\text{m}$ . B, F, G: 20  $\mu\text{m}$ ; C: 50  $\mu\text{m}$ ; D, E: 10  $\mu\text{m}$ .

## 4 Discussion

Our study reveals the occurrence of endocarpic trichomes in all the species studied of Vandaeae. They have been observed for the first time in 56 genera and confirmed in the rest of 24 genera, which represented about 60% of the tribe.

All the trichomes observed are simple, unicellular, filiform, with three regions: a swollen and oblique basal region, an elongated and tightly cylindrical medial region, and the apical region which is gradually tapering to the obtuse tip. The foot of the basal region shows variability in shape within a genus, also in the same species (Hallé, 1986). The trichomes show a thick wall surrounding the lumen, in concordance with the results of Hallé (1986).

According to [Blanco et al. \(2006\)](#), the trichomes were white in color. Our results reveal that the trichomes vary from whitish to dark brown, more commonly whitish to pale brown or yellowish, but variation in color has been observed within a genus. It would be interesting to check this character in fresh specimens to verify if the color changes during the dried procedure.

In the outer surface of the cell wall, a uniform pattern of micro-ornamentation is observed in all the species studied, formed by thin helicoidal striations. Our results disagree with [Hallé \(1986\)](#), who mentioned the lack of ornamentation, although, a micro-ornamentation is depicted in the figure of its publication, similar to that observed by us.

The outer surface of the cell wall is covered by a smooth layer of wax in all the species studied. This character has been observed for the first time in our study. Waxes are also observed in seeds of epiphytic species in Vandaeae ([Barthlott et al., 2014](#); [Gamarra et al., 2018](#)). They act as hydrophobic surfaces, probably contributing to prevent the influence of moisture in tropical areas during the maturation of the seeds.

Under SEM and LM, perforations of the walls are clearly visible in the outer surface of the trichomes, mainly at the foot, the basal and apical regions. Two main shapes have been observed, circular and longitudinal, independently of the taxonomic level. These perforations were observed and depicted by [Horowitz \(1902\)](#) in representatives of Cymbidieae and Epidendreae. However, [Hallé \(1986\)](#) did not illustrate them in the “elaters” of Sarcanthinae (Vandaeae). [Veyret \(2001\)](#) suggested a relationship between the perforations of walls with the twisting of the trichomes. Probably, these perforations in contact with the lumen, contributed to capture the moisture, inducing the hygroscopic movement of the trichomes due to the helical microfibril arrangement of the thickened and fibrous wall. This movement is a common mechanism involved in seed and spore dispersal ([Blanco et al., 2006](#)), when the tissue desiccates and the cell walls dry and shrink, developing a contraction force whose direction and strength depend on the architecture of the tissue ([Elbaum and Abraham, 2014](#)).

Regarding to the most variable traits observed, such as the foot morphology, the shape of the perforations in the walls and the color of the trichomes, we have not observed patterns related with the taxonomy of the subtribes or genera in Vandaeae.

Within Epidendroideae, the endocarpic trichomes were observed in certain epiphytic genera of the tribes Collabieae, Cymbidieae, Epidendreae, Podochileae and Vandaeae ([Beer, 1857](#); [Horowitz, 1902](#); [Hallé, 1977](#); [Pedersen, 1993](#); [Freudenstein and Rasmussen, 1999](#); [Blanco et al., 2006](#); [Rasmussen and Johansen, 2006](#); [Mayer et al., 2011](#); [Mosquera-Mosquera et al., 2019](#)). In our study, we have observed endocarpic trichomes in all the 264 epiphytic species of the tribe Vandaeae. All these results suggest that the endocarpic trichomes are a synapomorphy of a clade encompassing these tribes, according to the phylogeny in [Chase et al. \(2015\)](#).

In our study, the trichomes are also present in the lithophytes *Jumellea papangensis* and *Vandopsis undulata*, and in the terrestrial *Bromheadia finlaysoniana*, which suggests that their presence is independent of the life form in this tribe. The presence of this trait in *Bromheadia finlaysoniana* concurs with the observations of [Hallé \(1977\)](#) in the terrestrial *Dipodium punctatum* (Cymbidieae, Epidendroideae), and [Freudenstein and Rasmussen \(1999\)](#) who mentioned the presence in the terrestrial genus *Prasophyllum* (Diurideae, Orchidoideae), to date the only genus with this character outside of Epidendroideae. These observations challenged [Beer \(1857\)](#), [Dressler \(1993\)](#) and [Cribb \(1999\)](#), who asserted that endocarpic trichomes were absent in terrestrial species.

Endocarpic trichomes have been observed in the four subtribes ([BromheadiAdrorhizinae](#), Polystachyinae, Aeridinae and Angraecinae) recognised by [Freudenstein and Chase \(2015\)](#), which suggest that it is a common feature in Vandaeae and could be regarded as a symplesiomorphic character.

## Author statement

The authors of the manuscript “Endocarpic trichomes in Vandaeae (Orchidaceae)”<sup>[Instruction: In the Reference "Cribb, P.J., 1999. Morphology Pridgeon...", it is necessary to rewrite "Morphology, in:", because is a chapter in an edited book.]</sup>~~characterization and standarization~~, Roberto Gamarra and Emma Ortúñez have absolutely participated in all the statements during the development of the research.

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## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix 1 List of species studied with life form, countries, collector (including collector number) and voucher. E: epiphytic; L: lithophytic; T: terrestrial

 The table layout displayed in this section is not how it will appear in the final version. The representation below is solely purposed for providing corrections to the table. To preview the actual presentation of the table, please view the Proof.

Subtribe / Species	Life form	Country	Collector and number	Voucher
<b>Adrorhizinae</b>				
<i>Bromheadia cecieliae</i>	E	Malaysia, Sarawak	<i>Yahud et al. S.88176</i>	K
<i>Bromheadia finlaysoniana</i>	T	Malaysia, Sabah Papua New Guinea Thailand	<i>K. Murch s.n.</i> <i>R. Brown 1882</i> <i>A.F.G. Kerr 0129</i>	K K000482101 K000594041
<i>Bromheadia truncata</i>	E	Malaysia	<i>A.C. Maingay 1680</i>	K
<b>Aeridinae</b>				
<i>Acampe ochracea</i>	E	Thailand	<i>A.F.G. Kerr 0207</i> <i>Put 507</i>	K K
<i>Acampe pachyglossa</i>	E	Mozambique Mozambique Tanzania	<i>D.J. Goyder 6048 et al.</i> <i>P.C.M. Jansen 262 et al.</i> <i>G.B. Wallace 580</i>	K000787769 K000385154 K000385124
<i>Acampe praemorsa</i>	E	India India Thailand	<i>N.E. Parry s.n.</i> <i>K.M. Mathews et al. s.n.</i> <i>A.F.G. Kerr 0255A</i>	K K K
<i>Adenoncos major</i>	E	Thailand	<i>A.F.G. Kerr 0389</i>	K
<i>Adenoncos parviflora</i>	E	Thailand	<i>Put 2374</i>	K
<i>Adenoncos vesiculosa</i>	E	Thailand Thailand	<i>A.F.G. Kerr 0583</i> <i>A.F.G. Kerr s.n.</i>	K K
<i>Adenoncos virens</i>	E	Malaysia	<i>R.H. Yapp 452</i>	K
<i>Aerides crassifolia</i>	E	Thailand	<i>A.F.G. Kerr 176</i>	K
<i>Aerides multiflora</i>	E	Nepal	<i>Barclay s.n.</i>	K
<i>Aerides odorata</i>	E	Thailand	<i>A. Kostermans s.n.</i>	K
<i>Aerides ringens</i>	E	Sine loc.	<i>R. Wight s.n.</i>	K
<i>Aerides rosea</i>	E	East Himalaya	<i>Griffith s.n.</i>	K

<i>Arachnis cathcartii</i>	E	India	<i>J.D. Hooker s.n.</i>	K
<i>Brachypeza archytas</i>	E	Australia	<i>B.A. Mitchell 102</i>	K
<i>Brachypeza zamboangensis</i>	E	Malaysia, Sabah	<i>A. Lamb et al. 374/85</i>	K
<i>Calymmanthera major</i>	E	Solomon islands	<i>P.F. Hunt 2235</i>	K
<i>Chiloschista lunifera</i>	E	Thailand	<i>Phra Vanpruk 463</i>	K
<i>Chiloschista phyllorhiza</i>	E	Australia	<i>M.O. Rankin 1606</i>	K
<i>Chiloschista usneoides</i>	E	China	<i>T. Zhanhuo 91-573</i>	K
<i>Cleisostoma appendiculatum</i>	E	India	<i>R. Pantling 241</i>	K
<i>Cleisostoma aspersum</i>	E	India	<i>R. Pantling 178</i>	K
<i>Cleisostoma callosilobum</i>	E	Indonesia, Sumatra	<i>J.J. Wood 944</i>	K
<i>Cleisostoma halophilum</i>	E	Malaysia, Sarawak North Borneo	<i>O. Ismawi s.n.</i> <i>Creagh s.n.</i>	K K
<i>Cleisostoma racemiferum</i>	E	China Nepal	<i>A. Henry 13817</i> <i>J.D. Hooker s.n.</i>	K K
<i>Cleisostoma williamsonii</i>	E	Vietnam	<i>M. Poilane s.n.</i>	K
<i>Gastrochilus acaulis</i>	E	India India	<i>E. Barnes 1938</i> <i>A.G. Bourne 1139</i>	K K
<i>Gastrochilus calceolaris</i>	E	India	<i>J.D. Hooker s.n.</i>	K
<i>Gastrochilus distichus</i>	E	China	<i>G. Forrest 7198</i>	K
<i>Gastrochilus inconspicuus</i>	E	Nepal	<i>sine coll.</i>	K
<i>Gastrochilus intermedius</i>	E	India	<i>Griffith s.n.</i>	K
<i>Gastrochilus japonicus</i>	E	Japan	<i>M. Furuse 4775</i>	K
<i>Gastrochilus matsuran</i>	E	Japan	<i>M. Togasi 1585</i>	K
<i>Holcoglossum sinicum</i>	E	China	<i>Sino-British Expedition to Cangshan n. 0380</i>	K
<i>Hymenorchis foliosa</i>	E	Papua New Guinea	<i>J. Croft et al. s.n.</i>	K
<i>Jejewoodia jiewhoei</i>	E	Malaysia, Sabah	<i>J.H. Beaman 10673 et al.</i>	K
<i>Luisia brachystachys</i>	E	India Thailand	<i>M. Clelland s.n.</i> <i>A.F.G. Kerr 0796</i>	K K
<i>Luisia celebica</i>	E	Indonesia, Sulawesi	<i>S.H. Koorders s.n.</i>	K
<i>Luisia macrotis</i>	E	Thailand	<i>K. Larsen 32418 et al.</i>	K
<i>Luisia teres</i>	E	Japan Japan	<i>M. Furuse 12138</i> <i>M. Furuse 4760</i>	K K
<i>Luisia teretifolia</i>	E	Fiji France, New Caledonia	<i>W. Greenwood 298</i> <i>M. Mackee 196</i>	K K
<i>Luisia zeylanica</i>	E	India	<i>K.M. Matthew et al. s.n.</i>	K
<i>Macropodanthus alatus</i>	E	Thailand	<i>A.F.G. Kerr 0850</i>	K
<i>Micropera callosa</i>	E	Indonesia, Java	<i>J.B. Comber 1284a</i>	K
<i>Micropera fasciculata</i>	E	Australia	<i>K. Domin s.n.</i>	K
<i>Micropera pallida</i>	E	Bangladesh Thailand Thailand	<i>Wall. Cat. 7321</i> <i>A.F.G. Kerr 456</i> <i>A. Kostermans s.n.</i>	K K K



<i>Micropera rostrata</i>	E	India	<i>Dr. Prain 111</i>	K
<i>Micropera thailandica</i>	E	Thailand	<i>A.F.G. Kerr 0574</i>	K
<i>Microsaccus griffithii</i>	E	Malaysia Thailand	<i>sine coll.</i> <i>A.F.G. Kerr 0681</i>	K K
<i>Papilionanthe subulata</i>	E	India	<i>Blatter et al. s.n.</i>	K
<i>Papilionanthe teres</i>	E	Thailand	<i>Put 2335</i>	K
<i>Pelatantheria cristata</i>	E	Malaysia	<i>C.E. Carr s.n.</i>	K
<i>Phalaenopsis cornu-cervi</i>	E	Thailand	<i>A.F.G. Baker 0283</i>	K
<i>Phalaenopsis deliciosa</i>	E, L	Philippines	<i>A. Loher s.n.</i>	K
<i>Phalaenopsis mannii</i>	E	Vietnam	<i>M. Poilane 25343</i>	K
<i>Phalaenopsis pantherina</i>	E	Malaysia, Sarawak	<i>P.S. Ashton S.18228</i>	K
<i>Phalaenopsis sumatrana</i>	E	Malaysia, Sarawak	<i>D. Awa et al. S.45280</i>	K
<i>Phalaenopsis taenialis</i>	E	India	<i>J.F. Duthie 5997</i>	K
<i>Plectorrhiza tridentata</i>	E	Australia Australia	<i>W.G. Trapnell s.n.</i> <i>W. Bauerlen 1684</i>	K K
<i>Pomatocalpa diffusum</i>	E	Malaysia Malaysia, Sabah	<i>C.E. Carr 27</i> <i>H.G. Keith 7801</i>	K K
<i>Pomatocalpa maculosum</i>	E	Sri Lanka	<i>Macrae s.n.</i>	K
<i>Pomatocalpa spicatum</i>	E	India Malaysia, Sabah Thailand	<i>R. Pantling 135</i> <i>Amin &amp; Mansus s.n.</i> <i>A.F.G. Kerr 0304</i>	K K K
<i>Porrorhachis galbina</i>	E	Malaysia, Sabah	<i>M.S. Clemens 30162</i>	K
<i>Pteroceras philippinense</i>	E	Philippines	<i>C.M. Weber s.n.</i>	K
<i>Pteroceras teres</i>	E	Malaysia, Sarawak	<i>sine coll.</i>	K
<i>Renanthera elongata</i>	E	Indonesia, Sumatra	<i>J.J. Smith s.n.</i>	K
<i>Renanthera imschootiana</i>	E	<i>sine loc.</i>	<i>Sander &amp; Co. s.n.</i>	K
<i>Renanthera moluccana</i>	E	Indonesia, Sulawesi	<i>S.H. Koorders 29503b</i>	K
<i>Rhynchostylis gigantea</i>	E	Philippines	<i>M. Ramos s.n.</i>	K
<i>Rhynchostylis retusa</i>	E	<i>sine loc.</i>	<i>sine coll.</i>	K
<i>Robiquetia bertholdii</i>	E	Vanuatu Vanuatu	<i>J. Wheatley 173</i> <i>N. Hallé 6446</i>	K K
<i>Robiquetia compressa</i>	E	Philippines	<i>A.D.E. Elmer 5974</i>	K
<i>Robiquetia spathulata</i>	E	Malaysia, Sabah	<i>L. Sailech s.n.</i>	K
<i>Robiquetia succisa</i>	E	China	<i>Tai Zhanhuo 91-247</i>	K
<i>Robiquetia sylvestris</i>	E	Malaysia	<i>C.E. Carr s.n.</i>	K
<i>Robiquetia woodfordii</i>	E	Solomon islands	<i>S. Wickison 212</i>	K
<i>Saccolabiopsis pallida</i>	E	Papua New Guinea	<i>J.R. Croft et al. s.n.</i>	K
<i>Saccolabiopsis pusilla</i>	E	Myamar	<i>C.E. Parkinson 5293</i>	K
<i>Sarcanthopsis hansemannii</i>	E	Papua New Guinea	<i>O. Gideon s.n.</i>	K
<i>Sarcanthopsis warocqueana</i>	E	Vanuatu	<i>L. Bernardi 13082</i>	K
<i>Sarcochilus dilatatus</i>	E	Australia	<i>H.A. Longman s.n.</i>	K



<i>Sarcochilus falcatus</i>	E	Australia	<i>F.A. Weinthal s.n.</i>	K000628045
<i>Sarcoglyphis mirabilis</i>	E	Thailand	<i>M.G. Lakshnakara 1358</i>	K
<i>Schoenorchis gemmata</i>	E	Bhutan China India	<i>H. Kanai et al. s.n.</i> <i>A. Henry 12972</i> <i>G. Craih s.n.</i>	K K K
<i>Schoenorchis jerdoniana</i>	E	India	<i>A. Meebold 13264</i>	K
<i>Schoenorchis juncifolia</i>	E	Indonesia, Java Indonesia, Java	<i>W. Meijer 153</i> <i>Main 178</i>	K K
<i>Seidenfadenia mitrata</i>	E	Thailand	<i>A.F.G. Kerr s.n.</i>	K
<i>Smitinandia micrantha</i>	E	India Thailand	<i>R. Pantling 78</i> <i>S. Bloembergen s.n.</i>	K K
<i>Taeniophyllum fasciola</i>	E	Fiji Solomon islands	<i>J. Hosch s.n.</i> <i>P. Cribb 6008</i>	K K
<i>Taeniophyllum sp.</i>	E	Papua New Guinea Papua New Guinea	<i>H. Streimann et al. s.n.</i> <i>T.M. Reeve 3675</i>	K K
<i>Taprobanea spathulata</i>	E	India	<i>sine coll.</i>	K
<i>Thrixspermum agusanense</i>	E	Philippines	<i>C.A. Wenzel s.n.</i>	K
<i>Thrixspermum centipeda</i>	E	Thailand Thailand	<i>A.F.G. Kerr 98</i> <i>Noe s.n.</i>	K K
<i>Thrixspermum complanatum</i>	E	India	<i>sine coll.</i>	K
<i>Thrixspermum graeffei</i>	E	Samoa	<i>S.J. Whitmee s.n.</i>	K
<i>Thrixspermum japonicum</i>	E	Japan	<i>P. Faurie 15529</i>	K
<i>Thrixspermum trichoglottis</i>	E	Thailand	<i>A.F.G. Kerr 0475</i>	K
<i>Thrixspermum weberi</i>	E	Philippines	<i>C.M. Weber 187</i>	K
<i>Trichoglottis bipunctata</i>	E	Malaysia	<i>sine coll.</i>	K
<i>Trichoglottis lanceolaria</i>	E	Indonesia, Java Thailand	<i>J.B. Comber 1283</i> <i>A.F.G. Kerr 0490</i>	K K
<i>Trichoglottis retusa</i>	E	Indonesia	<i>Kostermans 19168</i>	K
<i>Trichoglottis subviolacea</i>	E	Indonesia, Sulawesi	<i>SBGO 5173</i>	K
<i>Trichoglottis tenera</i>	E	India India Sri Lanka	<i>A.G. Bourne 334</i> <i>L. Anglade 974</i> <i>Thwaites 2341</i>	K K K
<i>Uncifera acuminata</i>	E	India	<i>C.B. Clark 14286</i>	K
<i>Vanda bensonii</i>	E	India	<i>F.K.W. 7846</i>	K
<i>Vanda dearei</i>	E	Indonesia, Borneo	<i>H.N. Ridley s.n.</i>	K
<i>Vanda falcata</i>	E	Japan	<i>M. Togasi 1661</i>	K
<i>Vanda lilacina</i>	E	Thailand	<i>A.F.G. Kerr 0897</i>	K
<i>Vanda miniata</i>	E	Thailand	<i>A.F.G. Kerr 0156</i>	K
<i>Vanda tessellata</i>	E	India	<i>A.G. Bourne 2969</i>	K
<i>Vanda testacea</i>	E	India India	<i>R. Pantling 270</i> <i>H.F. Mooner 206</i>	K K
<i>Vandopsis gigantea</i>	E	Malaysia	<i>sine coll.</i>	K
<i>Vandopsis undulata</i>	L	Bhutan	<i>Y. Dorji 24 et al.</i>	K

Angraecinae				
<i>Aerangis appendiculata</i>	E	Malawi	<i>A.J. Salubeni 459</i>	K
<i>Aerangis biloba</i>	E	Ghana Guinea Conakry Nigeria	<i>W.H. Johnson s.n.</i> <i>C.H. Jongkind 10868 et al.</i> <i>D.E.S. King 104a</i>	K K K
<i>Aerangis brachycarpa</i>	E	Ethiopia Ethiopia	<i>J.W. Ash 697</i> <i>R. Pichi-Sermolli 2530</i>	K000385017 K000385012
<i>Aerangis calantha</i>	E	Equatorial Guinea	<i>W.W. Sanford 6063</i>	K
<i>Aerangis kirkii</i>	E	Tanzania	<i>Kisena 1451</i>	K
<i>Aerangis kotschyana</i>	E	Guinea Conakry Sudan	<i>J.O. Adam 14627</i> <i>coll. illeg. 6</i>	K K
<i>Aerangis luteoalba</i>	E	Kenya	<i>D. Miyawa et al. NMK1244</i>	K000743814
<i>Aerangis montana</i>	E	Zambia	<i>G. Williamson 1055</i>	K
<i>Aerangis mystacidii</i>	E	Tanzania	<i>M.A. Mwangoka &amp; H. Mgalla 6034</i>	K000718246
<i>Aerangis oligantha</i>	E	Tanzania	<i>M.E. Archbold 2611b</i>	K000385044
<i>Aeranthes caudata</i>	E	Madagascar	<i>M.H. Razanajatovo MHR145 et al.</i>	K000395726
<i>Aeranthes polyanthemus</i>	E	Madagascar	<i>C. Rakotovao 3198 et al.</i>	K
<i>Afropectinariella subulata</i>	E	Cameroon Equatorial Guinea Ivory Coast	<i>A.J.M. Leeuwenberg 8704</i> <i>W.W. Sanford 5918</i> <i>L. Ake Assi 6022</i>	K K K
<i>Ancistrorhynchus capitatus</i>	E	Cameroon Republic Democratic of the Congo Uganda	<i>W.W. Sanford 6135</i> <i>C. Evrard 5730</i> <i>D.L.N.Hafashimana 0147</i>	K K K
<i>Ancistrorhynchus cephalotes</i>	E	Ghana Guinea Conakry	<i>D. Westwood 157</i> <i>A. Chevalier 20469</i>	K K
<i>Ancistrorhynchus clandestinus</i>	E	Equatorial Guinea	<i>M. Carvalho 5286</i>	MA 598003
<i>Ancistrorhynchus ovatus</i>	E	Uganda	<i>D.L.N. Hafashimana 0803</i>	K
<i>Ancistrorhynchus schumannii</i>	E	Cameroon	<i>W.W. Sanford 5369</i>	K
<i>Ancistrorhynchus serratus</i>	E	Equatorial Guinea	<i>M. Carvalho 2688</i>	K
<i>Angraecopsis elliptica</i>	E	Cameroon Guinea Conakry	<i>G. Gosline 108a</i> <i>Y.B. Harvey 270 et al.</i>	K000107020 K000339386
<i>Angraecopsis ischnopus</i>	E	Equatorial Guinea Sierra Leone	<i>M. Carvalho 4568</i> <i>P. Jaeger 289</i>	K K
<i>Angraecopsis parviflora</i>	E	Cameroon Ethiopia Nigeria	<i>W.W. Sanford 5660</i> <i>I. Friis 4122 et al.</i> <i>Spumir 14</i>	K K K
<i>Angraecopsis tenerrima</i>	E	Tanzania	<i>W.M. Moreau 14</i>	K000317026
<i>Angraecopsis tridens</i>	E	Equatorial Guinea	<i>W.W. Sanford 4257</i>	K
<i>Angraecum cadetii</i>	E	France, Reunion	<i>J. Bosser 21802</i>	K
<i>Angraecum calceolus</i>	E	Madagascar Mauritius	<i>G.W. Parker s.n.</i> <i>C. Barclay 421</i>	K K
<i>Angraecum chamaeanthus</i>	E	Mozambique	<i>J. Timberlake 5217 et al.</i>	K000718698
<i>Angraecum conchiferum</i>	E	Tanzania	<i>W.M. Moreau 176a</i>	K

		Zimbabwe	<i>W.D. Holmes 0153</i>	K
<i>Angraecum dives</i>	E	Yemen, Socotra	<i>A.R. Smith 505 et al.</i>	K
<i>Angraecum eburneum</i>	E	Eswatini	<i>G. MacNaughtan 206</i>	K000317066
<i>Angraecum sacciferum</i>	E	Zimbabwe	<i>N.C. Chase 4098</i>	K
<i>Angraecum tenellum</i>	E	Madagascar	<i>D.J. DuPuy et al. M799</i>	K000453825
<i>Bolusiella iridifolia</i>	E	Equatorial Guinea Gold Coast Tanzania	<i>W.W. Sanford 5765</i> <i>D. Westwood 49a</i> <i>Konstantine 3571</i>	K K MA 802531
<i>Bolusiella talbotii</i>	E	Cameroon Equatorial Guinea Equatorial Guinea	<i>L. Zapjack 650 et al.</i> <i>T.C. Wrigley 33</i> <i>R. Pérez Viso 1481</i>	K000106977 K MA 785018
<i>Bolusiella zenkeri</i>	E	Equatorial Guinea	<i>W.W. Sanford 5756</i>	K
<i>Calyptrochilum christyanum</i>	E	Guinea-Bissau Liberia	<i>Alves Pereira 2816</i> <i>J. de Konig 527</i>	MA 287501 MA 855192
<i>Campylocentrum crassirhizum</i>	E	Brazil Brazil	<i>G.P. Lewis et al. SPF 37051</i> <i>Gardner 5202</i>	K000293861 K000886224
<i>Campylocentrum fasciola</i>	E	Brazil Jamaica Trinidad and Tobago	<i>D.J. Gwynne Vaughan 60</i> <i>D.M. Miab s.n.</i> <i>B. Phillips 8336 et al.</i>	K000886216 K K
<i>Campylocentrum jamaicense</i>	E	Cuba	<i>C. Wright 3298</i>	K
<i>Campylocentrum kuntzei</i>	E	Brazil	<i>G.T. Prance 7372 et al.</i>	K000886209
<i>Campylocentrum mattogrossense</i>	E	Guyana	<i>E.F. im Thurn s.n.</i>	K
<i>Campylocentrum micranthum</i>	E	Trinidad and Tobago	<i>A. Fendler 792</i>	K
<i>Campylocentrum pachyrrhizum</i>	E	Jamaica	<i>Morris 2326</i>	K
<i>Campylocentrum poepiggii</i>	E	Cuba Cuba	<i>J.G. Jack 6633</i> <i>C. Wright 3301</i>	K K
<i>Campylocentrum sellowii</i>	E	Brazil	<i>A. Glaziov 13233</i>	K000886195
<i>Conchograecum erectum</i>	E	Kenya Kenya	<i>G.R. Cunningham-Someren s.n.</i> <i>H. Copley s.n.</i>	K000385070 K000385064
<i>Conchograecum moandense</i>	E	Equatorial Guinea	<i>W.W. Sanford 4299</i>	K
<i>Conchograecum multinominatum</i>	E	Sierra Leone	<i>P. Adames 211</i>	K
<i>Conchograecum stolzii</i>	E	Tanzania	<i>H.J. Schlieben 3855</i>	MA 385935
<i>Cryptopus elatus</i>	E	France, Reunion	<i>M. Boivin s.n.</i>	K
<i>Cyrtorchis arcuata</i>	E	Equatorial Guinea Sierra Leone Tanzania	<i>M. Carvalho 3130</i> <i>D. Small 492</i> <i>W. Donsob 548</i>	K K K
<i>Cyrtorchis aschersonii</i>	E	Nigeria	<i>J.D. Kennedy 234</i>	K
<i>Cyrtorchis chailluana</i>	E	Uganda	<i>B. Drummond et al. 4724</i>	K
<i>Cyrtorchis praetermissa</i>	E	Malawi Malawi Zimbabwe	<i>J. Pawek 13041</i> <i>B. Morris 64</i> <i>G. Pope 1118</i>	K K K


<i>Dendrophylax funalis</i>	E	Jamaica	<i>Purdie s.n.</i>	K
<i>Dendrophylax porrectus</i>	E	USA	<i>P.J. Cribb s.n.</i>	K
<i>Diaphananthe bidens</i>	E	Equatorial Guinea Ivory Coast Liberia	<i>M. Carvalho 5062</i> <i>de Koning 4783</i> <i>J.T. Baldwin Jr. 9209</i>	MA 610097 MA 857399 K
<i>Diaphananthe fragrantissima</i>	E	Ethiopia	<i>F.G. Meyer 7904</i>	K
<i>Diaphananthe ichneumonea</i>	E	Cameroon	<i>M. Etuge 4137 et al.</i>	K000106981
<i>Diaphananthe letouzeyi</i>	E	Equatorial Guinea	<i>W.W. Sanford 4315</i>	K000541485
<i>Diaphananthe odoratissima</i>	E	Equatorial Guinea	<i>W.W. Sanford 5739</i>	K
<i>Diaphananthe pellucida</i>	E	Democratic Republic of the Congo Ivory Coast Sierra Leone	<i>A. Leonard 3210</i> <i>F.N. Hepper et al. 7842</i> <i>G.F. Scott Elliot 5005</i>	K K K
<i>Diaphananthe plehniana</i>	E	Nigeria Nigeria	<i>W.W. Sanford 16/66</i> <i>J.P.M. Brenan 1948</i>	K000541499 K000541503
<i>Diaphananthe sarcophylla</i>	E	Tanzania Uganda	<i>W.R.Q. Luke 8075 et al.</i> <i>Tweedie 312</i>	K000617957 K
<i>Diaphananthe sarcorhynchoides</i>	E	Equatorial Guinea	<i>M. Carvalho 5516</i>	MA 599463
<i>Diaphananthe vesicata</i>	E	Ghana Ivory Coast	<i>D. Westwood 40</i> <i>F.N. Hepper et al. 8057</i>	K K
<i>Dinklageella liberica</i>	E	Ivory Coast	<i>de Koning 6637</i>	MA 857121
<i>Dolabrifolia bancoensis</i>	E	Ghana Sierra Leone	<i>J.K. Morton A2795</i> <i>G. Roberty 17311</i>	K K
<i>Dolabrifolia disticha</i>	E	Ivory Coast Sierra Leone	<i>H.J. Beentje 1065</i> <i>T.S. Bakshi 37</i>	K000743765 K
<i>Dolabrifolia podochiloides</i>	E	Nigeria	<i>P.A. Talbot s.n.</i>	K
<i>Erasanthe henrici</i>	E	Madagascar	<i>C. Rakotovao 3280 et al.</i>	K
<i>Eurychone rothschildiana</i>	E	Ivory Coast	<i>Pérez Vera s.n.</i>	K
<i>Jumellea anjouanensis</i>	E	Comoros	<i>J.N. Labat 3134</i>	K000453821
<i>Jumellea comorensis</i>	E	Comoros	<i>J.N. Labat 3119 et al.</i>	K
<i>Jumellea densefoliata</i>	E	Madagascar	<i>D.J. DuPuy et al. M657</i>	K
<i>Jumellea papangensis</i>	L	Madagascar	<i>D.J. DuPuy &amp; et al. M611</i>	K
<i>Jumellea usambarensis</i>	E	Malawi	<i>B. Morris 161</i>	K000284814
<i>Lemurella culicifera</i>	E	Madagascar	<i>F. Roberts et al. TPPO75</i>	K
<i>Listrostachys pertusa</i>	E	Cameroon Cameroon	<i>W.W. Sanford 5712</i> <i>X.M. Van der Burgt 266</i>	K K
<i>Microcoelia aphylla</i>	E	Tanzania Tanzania	<i>T. Pócs 87018b</i> <i>J.H. Vaughan 2765</i>	K K
<i>Microcoelia caespitosa</i>	E	Ghana Sierra Leone	<i>Ried s.n.</i> <i>F.C. Deighton 717</i>	K K
<i>Microcoelia exilis</i>	E	Kenya Mozambique Tanzania	<i>S.A. Robertson et al. MDE28</i> <i>H. Groenendijk 1026 et al.</i> <i>B.D. Burt 3498</i>	K K K

<i>Microcoelia globulosa</i>	E	Cameroon	<i>R. Letouzey</i> 2189	K
		Ethiopia	<i>J.W. Ash</i> 438	K
		Tanzania	<i>G.P. Clarke</i> 3484	K
<i>Microcoelia konduensis</i>	E	Ghana	<i>A.C. Miles s.n.</i>	K
		Ghana	<i>D. Westwood</i> 60	K
<i>Microcoelia physophora</i>	E	Tanzania	<i>G.H. Vaughan</i> 1747	K000284710
<i>Microcoelia stolzii</i>	E	Malawi	<i>B. Morris</i> 74	K
<i>Mystacidium pulchellum</i>	E	Tanzania	<i>W.R.Q. Luke</i> 8114 <i>et al.</i>	K
<i>Mystacidium tanganyikense</i>	E	Zambia	<i>Williamson</i> 1057	K
<i>Neobathiea grandidieriana</i>	E	Madagascar	<i>D.J. Du Puy et al.</i> M632	K
<i>Nephrangis filiformis</i>	E	Liberia	<i>D. Johansson</i> 529	K
		Uganda	<i>D.L.N. Hafashimana</i> 0153	K
<i>Oeonia rosea</i>	E	Madagascar	<i>R. Razakamalala</i> 2943 <i>et al.</i>	K
<i>Oeoniella aphrodite</i>	E	Seychelles	<i>J. Stanley Gardiner s.n.</i>	K
		Seychelles	<i>P.G. Archer</i> 169	K
<i>Plectrelminthus caudatus</i>	E	Ghana	<i>D. Westwood</i> 2	K
		Nigeria	<i>C.F.A. Onochie s.n.</i>	K000541483
<i>Podangis rhipsalisocia</i>	E	Guinea-Conakry	<i>P.M. Haba</i> 171 <i>et al.</i>	K000024173
		Nigeria	<i>D.E.S. King</i> 3a	K
<i>Rangaeris muscicola</i>	E	Uganda	<i>Chandler</i> 2013	K000767289
<i>Rhipidoglossum adoxum</i>	E	South Sudan	<i>I. Friis et al.</i> 1223	K
<i>Rhipidoglossum brachyceras</i>	E	Tanzania	<i>D.K. Harder et al.</i> 1246	K
		Uganda	<i>R.A. Dummer</i> 3686	K
<i>Rhipidoglossum curvatum</i>	E	Ghana	<i>D. Westwood</i> 120	K
		Liberia	<i>J.T. Baldwin Jr.</i> 10795	K
<i>Rhipidoglossum densiflorum</i>	E	Cameroon	<i>W.W. Sanford</i> 6160	K
		Equatorial Guinea	<i>R. Pérez Viso</i> 1513	MA 784997
<i>Rhipidoglossum kamerunense</i>	E	Cameroon	<i>W.W. Sanford</i> 5567b	K
<i>Rhipidoglossum pulchellum</i>	E	Kenya	<i>B. Khayota</i> 300	K000766902
		Malawi	<i>P.G. Adlard</i> 523	K
<i>Rhipidoglossum rutilum</i>	E	Ghana	<i>D. Westwood</i> 278	K
		Nigeria	<i>C.F.A. Onochie s.n.</i>	K
		Tanzania	<i>P.J. Cribb</i> 10267 <i>et al.</i>	K000766995
<i>Rhipidoglossum schimperianum</i>	E, L	Ethiopia	<i>J.E.C.A.M.A.H34</i>	K
		Ethiopia	<i>F.G. Meyer</i> 9045	K
<i>Rhipidoglossum stolzii</i>	E	Tanzania	<i>P. Cribb</i> 10294 <i>et al.</i>	K000766925
<i>Rhipidoglossum subsimplex</i>	E	Kenya	<i>W.R.Q. Luke</i> 4552 <i>et al.</i>	K000766940
		Kenya	<i>Polhill</i> 177	K000766944
<i>Rhipidoglossum tenuicalcar</i>	E	Ethiopia	<i>R. Pichi-Sermolli s.n.</i>	K
<i>Rhipidoglossum xanthopollinium</i>	E	Uganda	<i>D.L.N. Hafashimana</i> 0806	K
<i>Sobennikoffia robusta</i>	E	Madagascar	<i>D.J. DuPuy</i> M701 <i>et al.</i>	K
<i>Solenangis scandens</i>	E	Cameroon	<i>R. Letouzey</i> 10500 <i>et al.</i>	K
		Equatorial Guinea	<i>F. Cabezas</i> 1315 <i>et al.</i>	MA 831762
		Gabon	<i>Reitsma et al. s.n.</i>	MA 456391

<i>Sphyrarhynchus schliebenii</i>	E	Tanzania	<i>P.J. Greenway 12255 et al.</i>	K000390260
<i>Summerhayesia zambesiaca</i>	E	Tanzania	<i>Spurrier 130</i>	K
<i>Tridactyle anthomaniaca</i>	E	Ivory Coast Nigeria	<i>F.N. Hepper 8121</i> <i>H.G. Stubbings 98</i>	K K
<i>Tridactyle bicaudata</i>	E	Malawi	<i>B. Morris 35</i>	K
<i>Tridactyle filifolia</i>	E	Tanzania	<i>B. Pettersson et al. 426A</i>	K
<i>Tridactyle nigrescens</i>	E	Uganda	<i>A.S. Thomas 4088</i>	K
<i>Tridactyle phaeocephala</i>	E	Tanzania	<i>P. Cribb 10462 et al.</i>	K000382786
<i>Tridactyle tricuspis</i>	E	Zambia Zimbabwe	<i>B. Morris 37a</i> <i>Swynnerton 755</i>	K K
<i>Tridactyle tridactylites</i>	E	Cameroon Guinea Conakry Malawi	<i>W.W. Sanford 6265a</i> <i>R. Schnell 1093</i> <i>E. Phillips 4577b</i>	K K K
<i>Tridactyle tridentata</i>	E	Guinea Conakry Nigeria Tanzania	<i>P. Jaeger 2153</i> <i>J.O. Ariwaodo 1107</i> <i>J. Lovett et al. 1075</i>	K K K000618016
<i>Tridactyle virgula</i>	E	Rwanda Uganda	<i>D. Bridson 498</i> <i>W.J. Eggeling 3991</i>	K000592712 K000592718
<i>Ypsilopus amaniensis</i>	E	Kenya	<i>D. Napper 1671</i>	K
<i>Ypsilopus erectus</i>	E	Malawi	<i>B. Morris 122</i>	K000390320
<b>Polystachyinae</b>				
<i>Hederorkis seychellensis</i>	E	Seychelles	<i>P.G. Archer 123</i>	K
<i>Polystachya adansoniae</i>	E	Cameroon Equatorial Guinea Liberia	<i>H. Gregory 294</i> <i>F. Melville 154</i> <i>J. de Koning 517</i>	K MA 294655 MA 855185
<i>Polystachya affinis</i>	E	Sierra Leone	<i>T.S. Bakchi 128</i>	K
<i>Polystachya albescens</i>	E, L	Cameroon Equatorial Guinea	<i>M. Brunt 450</i> <i>W.W. Sanford 4008</i>	K K
<i>Polystachya alpina</i>	E	Equatorial Guinea	<i>W.W. Sanford 5952</i>	K
<i>Polystachya bennettiana</i>	E	Guinea-Conakry	<i>P.K. Haba 309 et al.</i>	K000024096
<i>Polystachya bifida</i>	E	Equatorial Guinea	<i>W.W. Sanford 5965</i>	K
<i>Polystachya calluniflora</i>	E	Cameroon Equatorial Guinea	<i>M. Etuge 4166 et al.</i> <i>W.W. Sanford 5973</i>	K000105956 K
<i>Polystachya caloglossa</i>	E	Cameroon	<i>D.W. Thomas 472</i>	K
<i>Polystachya carnosa</i>	E	Equatorial Guinea	<i>W.W. Sanford 4026</i>	K
<i>Polystachya concreta</i>	E, L	Equatorial Guinea Mozambique	<i>M. Carvalho 2818</i> <i>Schäfer 6844</i>	MA 492359 K
<i>Polystachya coriscensis</i>	E	Cameroon	<i>D.W. Thomas 210</i>	K
<i>Polystachya cultriformis</i>	E, L	Equatorial Guinea	<i>M. Carvalho 2649</i>	K
<i>Polystachya dolichophylla</i>	E	Togo	<i>D. Westwood 66</i>	K
<i>Polystachya elegans</i>	E	Equatorial Guinea	<i>J. Fernández 11918 et al.</i>	K
<i>Polystachya fractiflexa</i>	E	Ghana	<i>Hallo Enti s.n.</i>	K
<i>Polystachya fusiformis</i>	E, L	Cameroon	<i>W.W. Sanford 5668</i>	K
<i>Polystachya galeata</i>	E	Cameroon	<i>de Koning 1564</i>	MA 855251

		Democratic Republic of the Congo	<i>Bequaert 2363</i>	K
<i>Polystachya golungensis</i>	E, L	Ghana Ivory Coast	<i>D. Westwood 61</i> <i>Aké Assi 9341</i>	K K
<i>Polystachya laxiflora</i>	E	Cameroon Equatorial Guinea	<i>W.J. van der Burg 1983</i> <i>M. Carvalho 2700</i>	K K
<i>Polystachya modesta</i>	E	Tanzania Uganda	<i>H.J. Schlieben 5985</i> <i>D.L.N. Hafashimana 0070</i>	K K
<i>Polystachya oblanceolata</i>	E	Sierra Leone	<i>Morton et al. SL1048</i>	K000874544
<i>Polystachya odorata</i>	E	Equatorial Guinea	<i>M. Carvalho 4459</i>	K
<i>Polystachya paniculata</i>	E	Cameroon	<i>W.W. Sanford 6162</i>	K
<i>Polystachya polychaete</i>	E	Equatorial Guinea	<i>E. Guinea 2130</i>	MA 294054
<i>Polystachya puberula</i>	E	Sierra Leone	<i>N.W. Thomas 2573</i>	K
<i>Polystachya ramulosa</i>	E	Gabon	<i>G. Le Testu 5454</i>	K
<i>Polystachya rhodoptera</i>	E	Cameroon	<i>D.W. Thomas 207</i>	K
<i>Polystachya subulata</i>	E	Nigeria	<i>R.W.J. Keay s.n.</i>	K
<i>Polystachya superposita</i>	E	Equatorial Guinea	<i>E. Guinea 2137</i>	MA 785034

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 The corrections made in this section will be reviewed and approved by a journal production editor. The newly added/removed references and its citations will be reordered and rearranged by the production team.

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## Highlights

- Endocarpic trichomes have been observed in all the species studied in Vandeeae.
  - The occurrence of endocarpic trichomes is independent of the life form.
  - Endocarpic trichomes show helicoidal striations in the outer surface.
  - Inner walls are thickened, with a helicoidal microfibril arrangement.
  - Waxes cover the outer surface of the endocarpic trichomes.
-