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Labellar secretory structures and pollinator food-rewards in representatives of Old World *Bulbophyllum* Thouars

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ABSTRACT

Detailed studies of the floral anatomy, morphology, ultrastructure, and the occurrence of floral food-rewards in *Bulbophyllum* are rare. Here, we investigate the structure of the labellum and secretion of labellar food-rewards for ten Asian species of the genus, representing six sections. Labellar tissue of each of these species was examined using LM, SEM, and TEM, and compared with our previous results for representatives of sect. *Racemosae* and two African species of *Bulbophyllum*. The study indicated that only members of sections *Sestochilos* and *Stenochilus* produced true nectar, and this was present on the adaxial surface of sepals. Lipids occurred only in the labellar secretions of members of sect. *Recurvae*. In members of sections *Sestochilos, Brachyantha* and *Desmosanthes*, labellar secretion was absent. In most investigated sections, secretion, if present, was produced by relatively unspecialized epidermal cells lining a median labellar groove. The labella of most sections contained both ground parenchyma and aerenchyma. This study demonstrates, in conjunction with the results of previous studies, that the structure of the labellum in this genus is highly diverse, especially with respect to the labellar adaxial epidermis, which represents various degrees of secretory specialization.

1. Introduction

Bulbophyllum Thouars is a widely distributed orchid genus comprising about 2200 species, The genus originated in Asia but *Bulbophyllum* occurs throughout tropical Africa, Madagascar and other islands of the Indian Ocean, South-East Asia, Australia, New Zealand and the tropical Pacific islands, as far east as Tahiti to the Neotropics, the main centres of distribution being Madagascar (200 species) and New Guinea (600 species – Pridgeon et al., 2014). Considered to be the largest orchid genus, it contains some of the smallest and most highly morphologically diverse species of orchid, and its flowers are amongst the most intricate, displaying diverse and complex pollination strategies (van der Cingel, 2001). It is entomophilous, and pollinated mainly by Hymenoptera and Diptera (van der Cingel, 2001).

Some Asian *Bulbophyllum* spp. (Pridgeon et al., 2014), e.g. members of sect. *Racemosae*, are pollinated by *Drosophila* fruit-flies that probe the liquid-filled, longitudinal, median labellar groove (Ong and Tan, 2012). Others, produce a phenylpropanoid-rich, fruity or spicy floral scent that attracts only male fruit-fly pollinators, and may be used to make pheromones for the attraction of females (Tan and Nishida, 2000, 2005; Tan et al., 2002; Ong, 2011; Ong et al., 2011 and references therein). Yet other members of the genus, however, are pollinated equally by both male and female dipterans, such as blowflies and flesh flies. The flowers of *B. lasianthum* and *B. virescens* (sect. *Beccariana*) are malodorous and smell of carrion, whereas those of *B. lobbii* (sect. *Sestochilos*) produce a fragrance reminiscent of over-ripe fruit (Ong and Tan, 2011). Some species are very pollinator – specific (Chen and Gao, 2011), and mimicry is frequent, ranging from inflorescences that resemble actinomorphic flowers (Knerr, 1981; Koehler and Davenport 1983), to flowers that mimic spiders, and which may perhaps attract spider-predatory or spider-parasitic flies or wasps (Christensen, 1994). According to Gravendeel et al. (2004) pollinator specialization (as one of the presented hypothesis) can explain the large species richness in this family.

Of the African species, most are pollinated by Hymenoptera such as bees and wasps (including stingless bees and ctenuchid wasps – Johansson, 1974 – cited in van der Cingel (2001), Dressler (1990, 1993), Stewart et al. (2014)), but others are probably sapromyophilous. Rewardless *B. variegatum*, which is endemic to the Mascarenes, is pollinated by a single species of Platystomatidae fly (Humeau et al., 2011).

Attraction of insect pollinators to the *Bulbophyllum* flower is accomplished in a number of ways that may involve a combination of

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Table 1
Investigated *Bulbophyllum* species and their provenance.

Section	Species	Accession Number	Kew (K) and Herbarium of Jagellonian University (UJ) Voucher Number
Asian Taxa			
Stenochilus	*B. macranthum* Lindl.	KLD 201501	K Davies 2017-1
Sestochilos	*B. lobbii* Lindl.	KLD 201204	K Davies 2017-2
	B. facetum Garay, Hamer & Siegerist	KLD 201502	K Davies 2017-3
Recurvae	*B. corolliferum* J.J. Sm.	KLD 201405	K Davies 2017-4
	B. makoyanum (Rchb.f.) Ridl.	KLD 201312	K Davies 2017-5
	B. auratum (Lindl.) Rchb.f.	KLD X02013	K Davies 2017-6
Cirrhopetalum	*B. longiflorum* Thouars	KLD 201414	K Davies 2017-7
Brachyantha	*B. guttulatum* (Hook. f.) N. P. Balakr.	KLD 201314	K Davies 2017-8
Desmosanthes	*B. laxiflorum* (Blume) Lindl.	O/2014/1174	UJ KRA 464136
	B. cf. *leptanthum* Hook. f.	KLD 201316	K Davies 2017-9

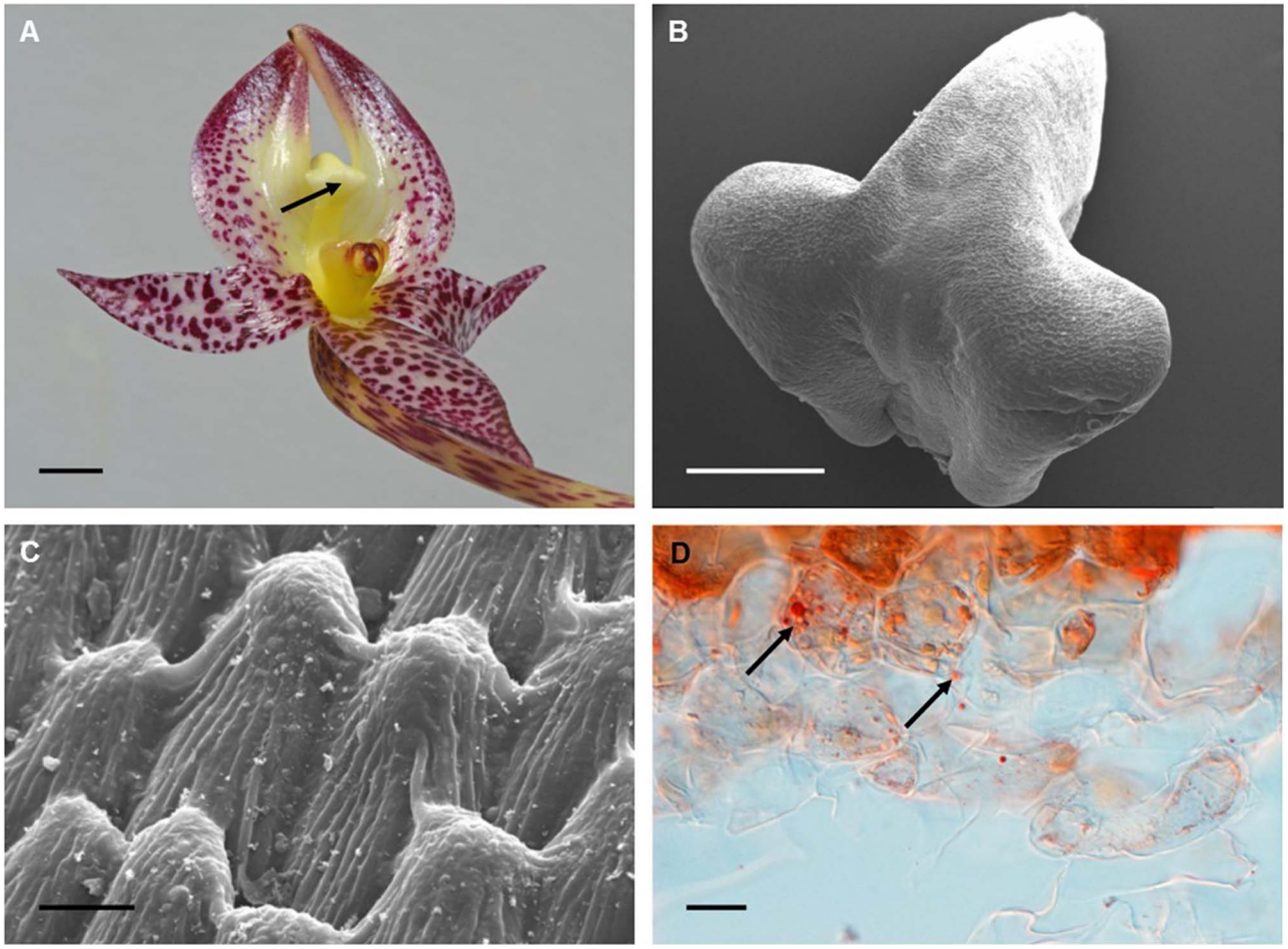

Fig. 1. Flower and detail of labellum of *Bulbophyllum macranthum*. A. Habit of flower with non-resupinate labellum (arrow); B. Labellum with shallow median groove (SEM); C. Squamous epidermal cells with striate and finely-blistered cuticle (SEM); D. Lipid bodies (arrows) in epidermal and subepidermal cells stained with Sudan III (NDIM). Scale bars: A – 5 mm; B – 1 mm; C – 10 μm; D – 20 μm.

fruity or malodorous floral scents (Silva et al., 1999) flower colour, which is usually dull cream or yellow-green to purple-brown and frequently spotted; mobile floral parts, such as hinged labella and appendages, epidermal structures such as hairs or papillae, and secretions, such as fragrant oils and nectar (Teixeira et al., 2004; Kowalkowska et al., 2015; Nunes et al., 2014, 2015, 2017; Stpiczyńska et al., 2015; Stpiczyńska et al., 2017). Floral-food rewards, however, are relatively uncommon amongst orchids. Nectar is the most common of these, although oil and resin-like secretions are also frequently present (van der Pijl and Dodson, 1969; van der Cingel, 2001; Davies and Stpiczyńska, 2008 and references therein). In *Bulbophyllum*, floral food-rewards have hitherto been documented in the field for *B. alticola*, *B. auratum, B. lobbii* and *B.macranthum* (Pohl, 1935; Ridley, 1890; Jongejan, 1994; van der Cingel, 2001). Flowers of *B. lobbii* and *B. macranthum* are said to produce oil and sugar at the base of the lip and adjacent floral parts (Pohl, 1935). True nectar (i.e. one that contains sugar) was detected in African *B. schinzianum* (Stpiczyńska et al., 2015) and *B. saltatorium* (Stpiczyńska et al., 2017), and also occurs on the labellar callus of Neotropical *B. weddellii, B. ipanemense and B. involutum*.

Despite the enormity, diversity and wide distribution of *Bulbophyllum*, few detailed, anatomical studies of the *Bulbophyllum* flower, and even fewer ultrastructural studies to investigate floral secretory processes, have hitherto been undertaken. These include Neotropical species investigated at SEM and light microscopy level