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Floral morphology and micromorphology of selected *Maxillaria* species (Maxillariinae, Orchidaceae)

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Summary: The genus *Maxillaria* s.l. constitutes the core of the subtribe Maxillariinae Benth. It is estimated that ca 56% of the *Maxillaria* species attract pollinators by 'empty promises'. Among the rest, there are three types of reward: nectar, pseudopollen and wax-like substances. In this paper we present the results of the investigation of lip epidermis of 20 species from 11 sections and one complex. For the study, we used scanning electron microscope (SEM). In all studied species, the presence of the papillae in various shapes has been demonstrated. Obpyriform papillae seem to be the most common and their presence has been noticed on the labellar surface of 15 species from all investigated sections. Conical papillae have been found on the lip surface of 10 species from 8 sections, villiform – in 10 species from 9 sections, clavate papillae – only in 4 species, each from different sections and elliptic papillae have been noticed only in a single species. Trichomes are limited to 7 species. Pseudopollen has been recorded only in species from the *Grandiflora*-complex. Residues of some kind of secretion were observed on the lip surface of 7 species from different sections. In 5 species papillae occurred also on the outer surface of the lip.

Keywords: morphology, micromorphology, *Maxillaria*, Maxillariinae, Orchidaceae

The genus *Maxillaria* Ruiz & Pav. constitutes the core of the subtribe Maxillariinae Benth. and the tribe Maxillarieae Pfitzer (Orchidaceae Juss.). Its representatives, in the broad sense, are distributed from South Florida through Central America and the Caribbean Islands to South America, southern to northern Argentina. The genus was first described by Hipólito Ruiz López and José Antonio Pavón Jiménez in 1794 in *Flora Peruviana et Chilensis Prodromus*. The publication included a brief description of the genus and an illustration with various views of the flower and its parts. Unfortunately, the authors did not indicate which of the sixteen species mentioned in the text is illustrated. This oversight resulted in the later taxonomic problems of the entire subtribe Maxillariinae.

Investigations conducted since the middle of the 20th century revealed a great diversity of labellar epidermises in many groups of orchids. Such characters as papillae and trichomes could potentially be used to serve as taxonomic characters. The importance of foliar micromorphology is well known and has already been utilized in the taxonomy of Orchidaceae Juss. (cited in Davies & Winters 1998). In contrast, SEM studies on labellar epidermis are still quite neglected, there is only one study presented by Davies & Winters (1998). The main aim of this paper was the investigation of the micromorphology of labellar epidermis in selected species of the genus *Maxillaria* s.l.

Classification

Generic classification of the subtribe Maxillariinae has been a challenge for the taxonomists since its formal description by Ruiz and Pavón (Blanco et al. 2007). For a long time, it has been suspected that it is an assemblage of taxa, consisting of morphologically disparate groups of species (Whitten et al. 2007). Establishing the exact number of species, belonging to the various

genera or even the subtribe itself, is extremely difficult, since it depends mainly on the adopted classification system and the concept of a genus. It is said that *Maxillaria* s. l. covers about 4/5 of the species belonging to the subtribe (Senghas 2002). According to various researchers, it contains 420 (Dressler 1993) to 750 species (Senghas 2002). Over the last 150 years, *Maxillaria* has been expanded and contracted based on morphological features to embrace or reject a number of taxa (e.g. Dressler 1981; Carnevali 1991; Senghas 2002; Christenson 2002; Chase et al. 2003; Blanco et al. 2007; Whitten et al. 2007; Szlachetko et al. 2012). More recently, phylogenetic analyses based on molecular techniques have redefined this subtribe and realigned the species, genera and sections which it contains (Davies 2017, pers. comm.).

In the latest classification, Schuiteman & Chase (2015) suggested another way of classifying *Maxillaria* s. l. They concluded that narrowly defined genera are often difficult to diagnose, especially when the material is designated only to the genus level. They have decided to merge all the presently recognized taxa under a megagenus *Maxillaria*.

Morphology

Representatives of *Maxillaria* s. l. vary widely both vegetatively and florally and are characterized by the wide range of combinations of both set of features. Plants are usually epiphytic, sometimes lithophytic or terrestrial. They are always herbaceous with monopodial, sympodial or dimorphic growth forms. Habit may be caespitose or rhizomatous, erect or less frequently, pendent. Some species are caespitose at the juvenile stage becoming rhizomatous with age. Roots are glabrous, velamentous and usually branching. The stem is rhizomatous, mainly branching or erect, cane-like and lacking pseudobulbs. When present, pseudobulbs are usually ovoid to cylindrical, laterally compressed, unifoliate, often clustered along the rhizome and subtended by several imbricating sheaths, either foliaceous or not. Leaves are variable in form: conduplicate to semiterete, articulate with the sheaths or with the apex of the pseudobulb. They can be sessile to petiolate, oblong, oblong-elliptic or often linear, subterete, elliptic or obovoid, acute to obtuse, symmetrical to unequally bilobed at the apex. The abscission layer of the apical leaf often projects above the pseudobulb in a persistent stalk (phyllopodium). Inflorescences are always single-flowered, arising from the base of the pseudobulb or laterally from the non-pseudobulbous stem, singly or fasciculate. The peduncle is usually enclosed in equidistant, bract-like scales. Floral bracts are either similar in size and shape to the peduncle scales, larger or much smaller. The flowers are minute to large with sepals and petals being free to the base, glabrous, often ringent. The vascular bundles of the tepals are often elastic, fibrous and very strong. The lip is usually much shorter than the tepals, often hinged with the column-foot or sometimes rigidly attached to it, entire or 3-lobed, glabrous or pubescent. The gynostemium is stout, usually with or occasionally without a prominent foot. Four pollinia are superposed, in two pairs, those of a pair are equal or unequal, attached via sticky caudicles to a distinct, often more or less lunate viscidium. The fruit is subglobose to ellipsoid, dehiscing laterally or apically.

Reproductive biology of *Maxillaria* s. l.

The main pollinators of *Maxillaria* are stingless bees (Meliponini) (Singer & Cocucci 1999; Roubik 2000). Apart from them, visits of bees from the subtribe Euglossini, ants from the subfamily Ponerinae and hummingbirds have also been observed (Roubik 2000). According to van der Pijl & Dodson (1969), *Maxillaria fletcheriana* Rolfe is pollinated by the bumblebee

Bombus volucelloides, *Maxillaria rufescens* Lindl., *M. grandiflora* (Kunth) Lindl. and *M. sanderiana* Rchb. f. ex Sander by *Eulaema cingulata* and *Maxillaria reichenheimiana* Endres & Rchb. f. by *Trigona testacea* and *T. amalthea*.

It is estimated that as much as 56% of the *Maxillaria* species attract pollinators with 'empty promises', which are the combination of visual, tactile and olfactory stimuli (Davies et al. 2005). Among the species which offer some kind of reward, there are three types: nectar, pseudopollen (farina) and wax-like substances (Davies et al. 2003a). It is believed that orchids which secrete nectar can even double their chances of pollination and thus the formation of the fruits and seeds. Its production, however, is costly in terms of expended energy and used materials. Until recently, it has been believed that none of the species included in *Maxillaria* s. l. produces nectar. Notwithstanding, it has been found in several taxa, e.g. *Ornithidium coccineum* (Jacq.) Salisb. ex R. Br. and *Maxillaria anceps* Ames & C. Schweinf. Davies et al. (2005) estimate that within the genus only 8% of the species produce nectar.

On the lip surface of some *Maxillaria* species, there is a whitish mealy coating called pseudopollen as it resembles real pollen. It is produced by fragmentation of the trichomes. According to many researchers, it is produced in species which do not produce nectar or any other reward. Farina is common in the representatives of the *M. grandiflora*, *M. splendens* and *M. discolor* alliances. It is believed that bees collect it from flowers because of the nutrients it contains (Davies et al. 2000). These include starch, oils and proteins (van der Pijl & Dodson 1969). According to Davies et al. (2005), 16% of the taxa studied by them produce pseudopollen and 7% have trichomes with a slightly different construction, but similar function.

Rewards in form of wax and resinous substances, rich in lipids and aromatic amino acids occur in about 13% of species (Davies et al. 2005). The secretions are produced by floral papillae and trichomes on the surface of the lip. Van der Pijl & Dodson (1969) suggested that these substances are collected by bees as material for nest building. It is probably the correct assumption, but it seems that this may be not the only reason for the insects acquiring waxy substances. As noticed by Davies et al. (2003a), due to the nutritional value, waxes and resins can also be a source of food substances. They were found on lip surface of *Maxillaria cerifera* Barb. Rodr., *Maxillaria divaricata* (Barb. Rodr.) Cogn. and *Maxillaria flavoviridis* Barb. Rodr. According to various authors, the latter two taxa are synonymous with *M. cerifera*. Additional function of waxy substances is predicted in *Maxillaria acuminata* alliance. These secretions result in a glossy surface of the lip which probably is involved in the process of attracting pollinators, just like the speculum in species of the genus *Ophrys* L. (Davies et al. 2003a).

So far, there are no records of pseudocopulation for the genus *Maxillaria* in its narrow sense. Singer (2002) described it for *Trigonidium obtusum* Lindl., which is classified on molecular basis by some researchers as representative of *Maxillaria* s. l. Mechanism of pseudocopulation in this particular case is quite unique, as the deposit of pollinia does not occur as a result of insect mating attempts with one of the elements of the flower, but when it tries to get out of the trap flower. The only observed pollinators visiting the flowers of *T. obtusum* were male bees of *Plebeia droryana* (Meliponini). It seems that a key stimulus in this case is the smell. During very warm days, the flowers of this species emit a sweet scent, to some extent reminiscent of the aroma of lemons (Singer 2002). Since the surface of the sepals and petals is covered by a substance similar to wax, landing insects glide and become trapped inside the flower. They spend from 5 to 30

seconds in the perianth (Singer 2002). To be released, they must enter the space between the gynostemium and lip and receive pollinia resultantly. Pollination occurs when insect falls into the trap flower bearing pollinia brought from another flower. The fact that flying drones try to copulate with males that had landed earlier on the tepals led Singer (2002) to prejudge that this case is actual pseudocopulation .

Flowers of species that are pollinated by birds tend to be coloured from red to pink, from orange up to yellow or white, rarely reddish-purple or blue. They produce abundant nectar, but do not emit odour or create nectar pathways. So far, there is no conclusive evidence for ornithophily in *Maxillaria*. All reports on this topic are based on a single observation made by van der Pijl & Dodson (1969) who observed the hummingbird *Panterpe insignis* visiting an unidentified species of *Maxillaria* with pink, tubular flowers. According to Stpiczyńska et al. (2004, 2009), flowers of *Maxillaria coccinea* and *M. sophronitis*, in terms of morphology, meet a range of criteria characteristic of the hummingbird-pollinated flowers pollinated by birds, but differ from those in the presence of sweet honey scent.

Materials and methods

Lips from flowers of 20 species classified in *Maxillaria* s. l. were studied. The flowers were preserved in Kew (53% ethanol : 5% formaldehyde : 5% glycerol : 37% water) or Copenhagen mixtures (70% ethanol : 2% glycerine : 28% water) and were obtained from Botanical Gardens Heidelberg, Hannover, Marburg and Vienna and were deposited at the Department of Plant Taxonomy and Nature Conservation of the University of Gdańsk. The list of vouchers is presented in Table 1.

Floral material preserved in Kew or Copenhagen mixtures was dehydrated using an ethanol series. Following critical-point drying in a Critical Point Dryer Emitech K850 apparatus, specimens were mounted onto SEM stubs. The stubs were coated with gold using a Sputter Coater Spi-Module. The samples were examined and photographed using a Philips XL-30 Scanning Electron Microscope.

In the SEM study, the terminology of surface characters was used in accordance with previously published literature (e.g. Davies et al. 2003; Davies & Turner 2004; Davies & Stpiczyńska 2012). The scientific names follow the classification of Christenson (2002, 2013).

Results

Maxillaria section *Aggregatae* Pfitzer

Maxillaria callichroma Rchb. f., Bonplandia 2: 16. 1854.

Maxillaria callichroma (Fig. 1) has a 3-lobed lip, elliptic in general outline, up to 2.4 cm long and 1.2 cm wide. The lateral lobes are erect-incurved, obliquely ovate, obtuse-rounded. The middle lobe is elliptic, obtuse and distinctly keeled below. It is up to 0.9 cm long. The callus extends from the lip base to the middle lobe and is broadly obtuse-rounded in front, pubescent throughout. The base of the adaxial lip surface as well as the callus is composed of multicellular trichomes being in different developmental stages (Fig. 1B–E): from clavate papillae to single or clustered filiform and clavate trichomes. Papillae are observed also between the trichomes (Fig. 1C). The difference concerns the coverage density and the length of the trichomes. The highest density and length are at the middle lobe base, whereas at the top of the callus only few unicellular trichomes

Table 1. The vouchers list of the materials used for the research.

Section	Species	Accession Number in UGDA spirit collection
Aggregatae Pfitzer	*Maxillaria callichroma*	p-3646
	Maxillaria luteoalba	p-3452
Arachnites Christenson	*Maxillaria reichenheimiana*	p-3449
Cucullatae Christenson	*Maxillaria cucullata*	p-3423
	Maxillaria praestans	p-1492
Ebulbes Pfitzer	*Maxillaria graminifolia*	p-3647
	Maxillaria ramosa	p-3459
Erectae Pfitzer	*Maxillaria ponerantha*	p-3435
	*Maxillaria tenuifolia**	p-3451
Multiflorae Christenson	*Maxillaria ochroleuca*	p-3436
Ornithidium (Salisb.) Christenson	*Maxillaria aurea*	p-3424, p-3445
	Maxillaria purpureolabia	p-3453
Repentes Pfitzer	*Maxillaria marginata*	p-3426
	Maxillaria picta	p-213
	Maxillaria cf. *mosenii**	p-3420
Rufescens Christenson	*Maxillaria rufescens*	p-3410
Urceolatae Christenson	*Maxillaria vitelliniflora*	p-3425
Trigonae Christenson	*Maxillaria pterocarpa**	p-3422
'Grandiflora Complex'	*Maxillaria molitor**	p-3648
	*Maxillaria striata**	p-2590

have been noticed (Fig. 1D). The surface of the callus is built by polygonal, convex cells, covered by the film of secretory material (Fig. 1D). The median part of the lip consists of clavate and obpyriform papillae (Fig. 1E–F). The proximal part is rugose (Fig. 1G), covered by obpyriform papillae. Their accumulation is found near the base of the lip as well as near the apex of the middle lobe, where the shape of these is usually rounded. The surface in some places seems to be folded, what can be due to aggregations of idioblasts with raphides in the subepidermis and in the whole tissue (Fig. 1F). The abaxial (outer) surface of the lip is also covered by few trichomes (Fig. 1H).

Maxillaria luteoalba Lindl., Orchid. Linden. 20. 1846.

Maxillaria luteoalba (Fig. 2A) has a 3-lobed lip, elliptic in general outline. It is about 2.2–2.5 cm long and 1.4–1.8 cm wide. The sidelobes are erect-incurved, rectangular and obtuse. The middle lobe is transverse, broadly ovate and obtuse. The callus is oblong, obtuse, extending from the base of the lip to about ⅓ of its length and abruptly elevates at the apex. The median part of the lip base is densely covered adaxially with trichomes (Fig. 2B). At the base, different developmental stages of the trichomes occur: from obpyriform papillae, elongated two-celled trichomes to long, multicellular, uniseriate and sometimes dichotomously divided (Fig. 2C, D). The sidelobes are glabrous in general view, but their margins on the inner (adaxial) surface (Fig. 2E) are densely covered with obpyriform papillae and single two-celled trichomes (Fig. 2F).

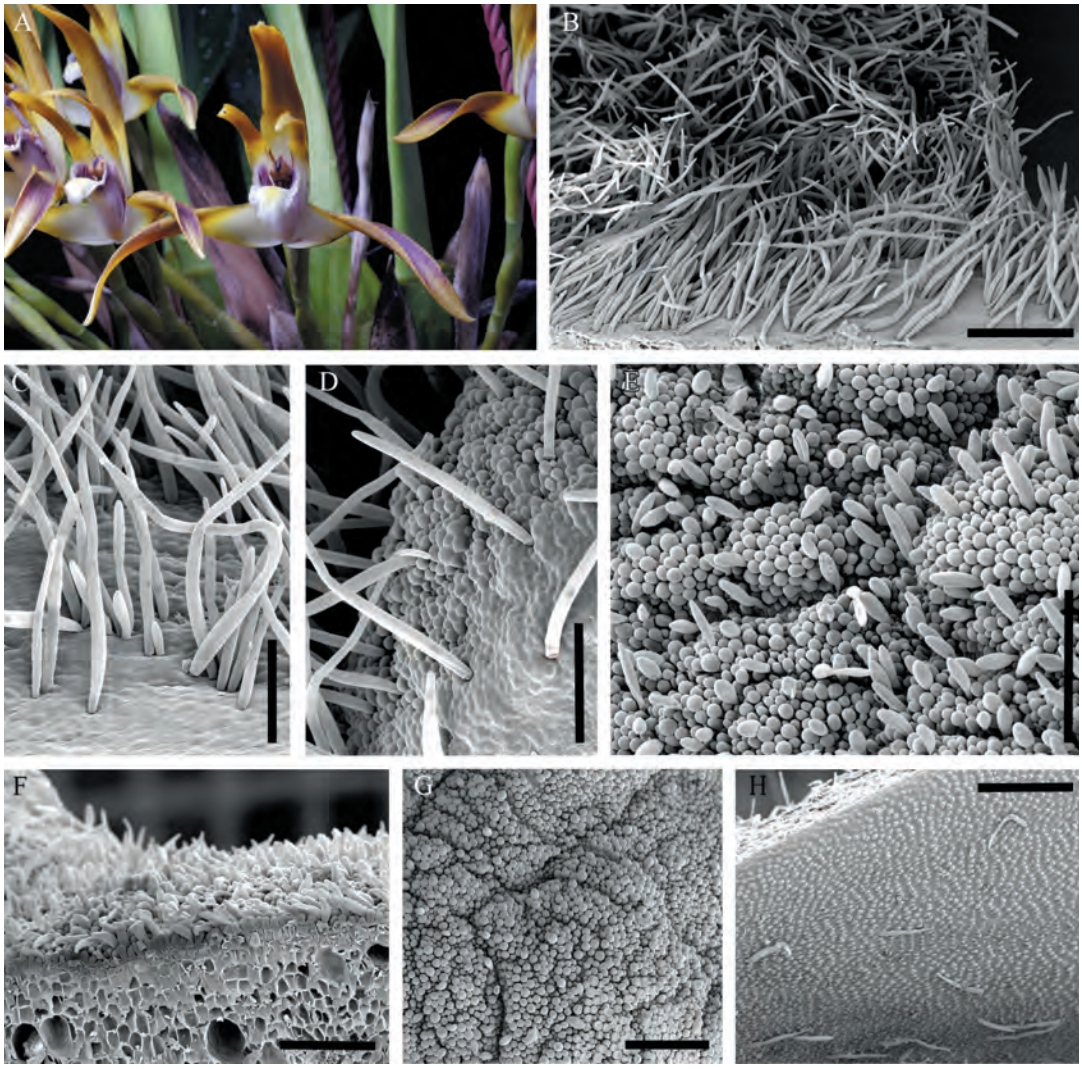

Figure 1. *Maxillaria callichroma* Rchb. f. Overview of the flowers (Photo credit: Markus Angler). A – multicellular trichomes; B – top of the callus with few unicellular trichomes; C – close-up on the callus edge with unicellular trichomes; D – surface of the callus built by polygonal, convex cells, covered by a film of secretory material; E –median part of the lip consists of clavate and obpyriform papillae; F – surface in some places seems to be folded, what can be due to aggregations of idioblasts with raphides in the subepidermis and in the whole tissue; G – proximal part: rugose, covered by obpyriform papillae; H – abaxial (outer) surface of lip covered by few trichomes. Scale bars = 500 µm (B, E–H); 200 µm (C, D).

Maxillaria section *Arachnites* Christenson

Maxillaria reichenheimiana Endrés & Rchb. f., Gard. Chron. & Agric. Gazette 1871: 1678. 1871.

The lip of *Maxillaria reichenheimiana* (Fig. 2G) is 3-lobed, elliptic, sparsely pubescent and about 1.3–1.7 cm long and 0.9–1 cm wide. The lateral lobes are erect and obliquely oblong. The middle lobe is broadly ovate with a thinner margin, obtuse. The callus (Fig. 2H) is linear-oblong and extends from the base of the lip to above the middle. The lip apex is rugose, built by obpyriform papillae (Fig. 2I–J). Some trichomes are scattered on the lip and callus (Fig. 2H–K). They consist

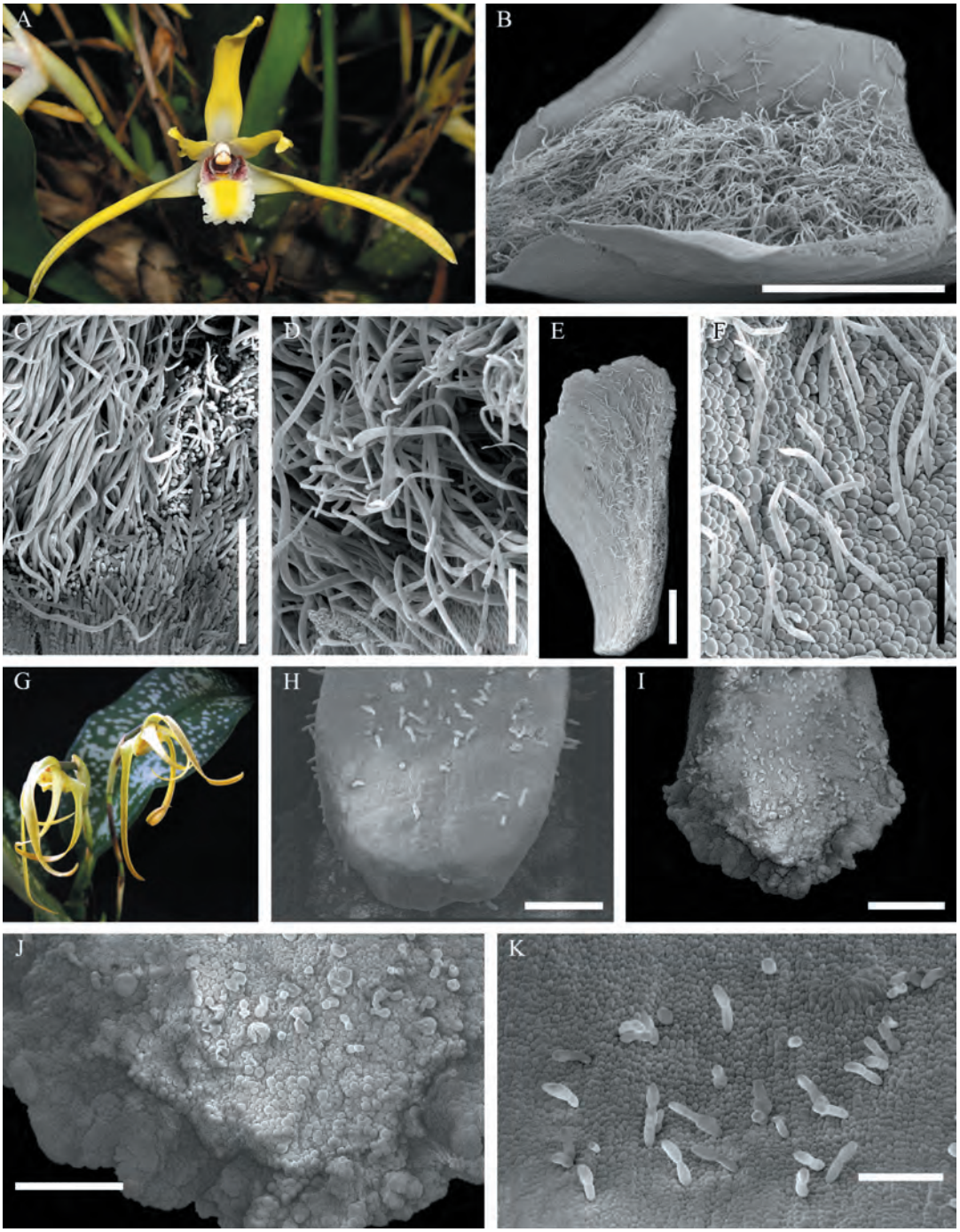

Figure 2. *Maxillaria luteoalba* Lindl. (A–F) and *Maxillaria reichenheimiana* Endrés & Rchb. f. (G–K). A – overview of the flower (Photo credit: John Varigos); B – general view of the lip base, densely covered adaxially with trichomes; C – different stages of trichome development: from obpyriform papillae, elongated two-celled trichomes to long, multicellular, uniseriate trichomes; D – elongated two-celled and long multicellular, uniseriate trichomes, sometimes dichotomously divided; E – overview of the lateral lobe surface; F – close-up of the lateral lobe surface: obpyriform papillae and single two-celled trichomes; G – overview of the flower (Photo credit: Daniel Mclaren); H – close-up of the midlobe surface with callus: scattered trichomes; I – rugose lip apex, built by obpyriform papillae; J – lip surface: rugose, built by obpyriform papillae; K – close-up of the 2- or more-celled trichomes scattered on the lip and callus. Scale bars = 2 mm (B); 1 mm (E, I); 500 µm (C, H, J); 200 µm (D, F, K).

of 2 or more cells (Fig. 2K). Davies & Turner (2004) previously observed bicellular trichomes on the lip and stated that they morphologically resemble the food hairs of *Polystachya* Hook. described by Davies et al. (2002).

Probable pollinators of this species are *Trigona testacea* and *T. amalthea* (Davies & Winters 1998).

Maxillaria section *Cucullatae* Christenson

Maxillaria cucullata Lindl., Edwards's Bot. Reg. 26: t. 12. 1840.

The lip of *Maxillaria cucullata* (Fig. 3A) is 3-lobed and from 1.5 up to 3 cm long. The side lobes are erect-incurved, obliquely elliptic, obtuse-rounded and about ⅓ of the lip length. The middle lobe is elliptic, obtuse-rounded. The callus is conspicuous, broadly oblong and slightly U-shaped in transverse section. The lip surface is glabrous, papillose only at the callus surface. The conical papillae are in different stages of development (Fig. 3B). According to Davies & Turner (2004), *M. cucullata* Lindl., *M. hematoglossa* A. Rich & Galeottii and *M. lexarzana* Soto Arenas & F. Chiang, all representatives of the *Maxillaria cucullata* alliance, have glabrous labella, completely devoid of papillae. They pointed out that in *M. meleagris* Lindl., which is thought to be closely related to the members of discussed alliance, the labellum is papillose, covered with conical papillae with pointed tips. Since *M. cucullata* is thought to be a quite variable species, this may cause problems with a correct taxonomic identification. Indeed, there was a time when nearly all of the species in the section had been included in the highly variable *M. cucullata* (Christenson 2013). It can be, however, easily distinguished from similar species by almost wholly unmarked sepals and petals (Fig. 3A) and this fits the description of the flower used in this research.

Maxillaria praestans Rchb. f., Gard. Chron., n.s. 23(592): 566. 1885.

The lip of *Maxillaria praestans* (Fig. 3C) is 3-lobed and somewhat curved. It is about 3 cm long. The middle lobe is big, rounded in general outline. The lateral lobes are upcurved. The callus is thick and fleshy, with raised sides from the base and a smooth surface (Fig. 3D). The lip surface of *M. praestans* is papillose, folded-rugose near the apex (Fig. 3E, F), sometimes with 2-celled trichomes. The folds consist of cuboidal cells (Fig. 3F). The lip base is densely covered with obpyriform to villiform papillae (Fig. 3G, H).

Maxillaria section *Ebulbes* Pfitzer

Maxillaria graminifolia (Kunth) Rchb. f., Ann. Bot. Syst. 6: 538. 1863.

The lip of *Maxillaria graminifolia* (Fig. 4A) is unlobed and lightly constricted at the middle to obscurely 3-lobed with the blade narrower above the central constriction. In general outline, it is broadly obtuse, rounded-subtruncate, sometimes slightly notched at the apex and retuse. It is about 0.4–0.6 cm long and 0.3–0.4 cm wide. The callus is fleshy, glossy, with knob-like apex. The lip surface is papillose, densely covered with papillae on both adaxial (inner) and abaxial (outer) surfaces (Fig. 4B). The shape of the papillae varies from obpyriform, conical to villiform (Fig. 4C). Near the median part, trichome-like papillae are observed. The surface of the callus is rather glabrous, but some multicellular, moniliform trichomes are present (Fig. 4D). They consist of at least 4 cells, whereas the apical cell seems to be the secretory one. Based only on their morphology, they could potentially play a similar role as food hairs. Residues of some kind of secretion are observed on both papillae and trichomes (Fig. 4E).

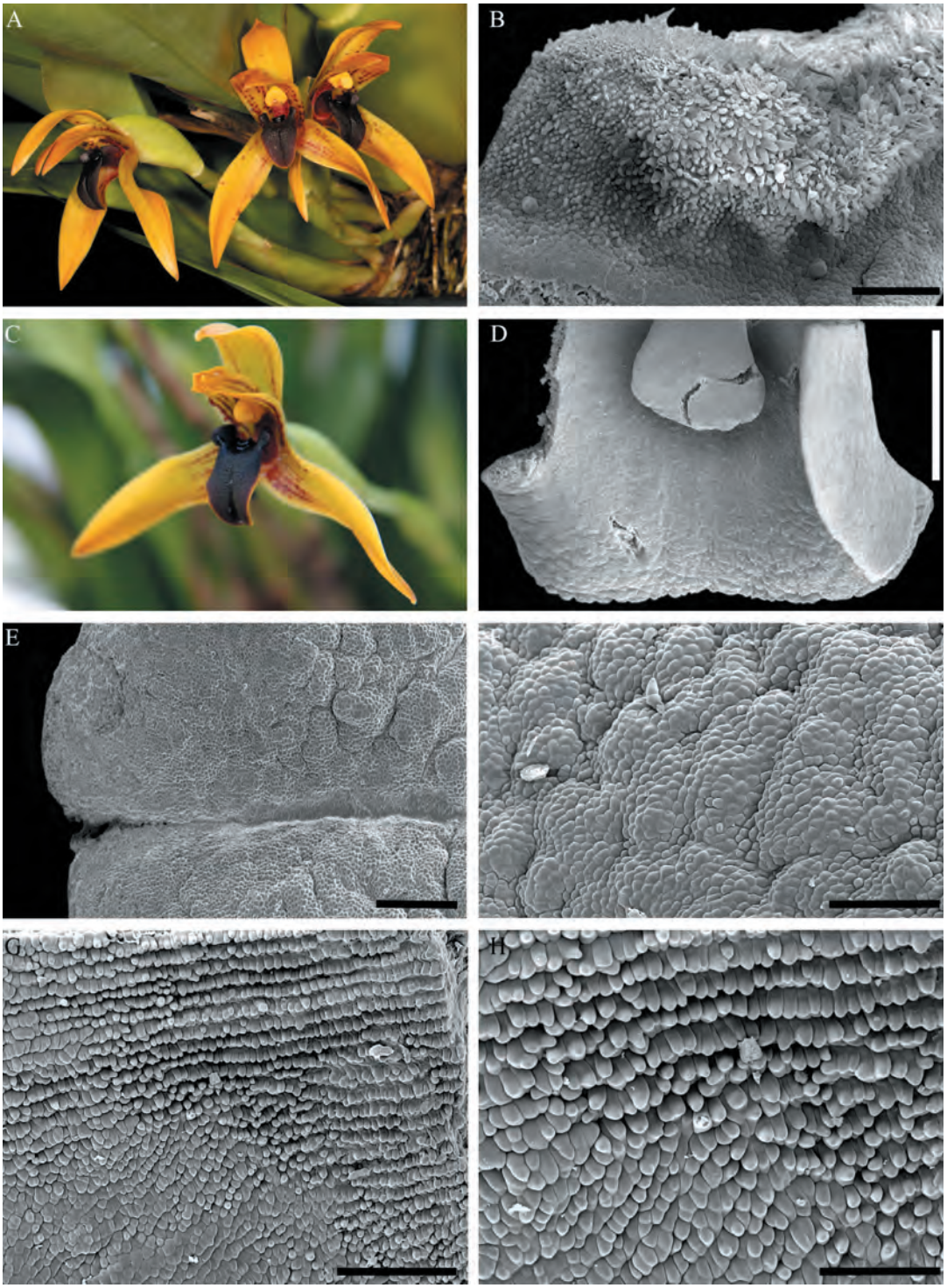

Figure 3. *Maxillaria cucullata* Lindl. (A–B) and *Maxillaria praestans* Rchb.f. (C–H). A – overview of the flowers (Photo credit: John Varigos); B – conical papillae in different stages of development; C – overview of the flower of *Maxillaria* aff. *praestans* (Photo credit: Ross Bayton); D – view of the lip apex and callus; E – lip surface: papillose, folded-rugose near the apex; F – folds consisting of cuboidal cells; G – lip base densely covered with obpyriform to villiform papillae; H – close-up of the lip base densely covered with obpyriform to villiform papillae. Scale bars = 2 mm (D); 500 µm (B, E, G); 200 µm (F); 100 µm (H).

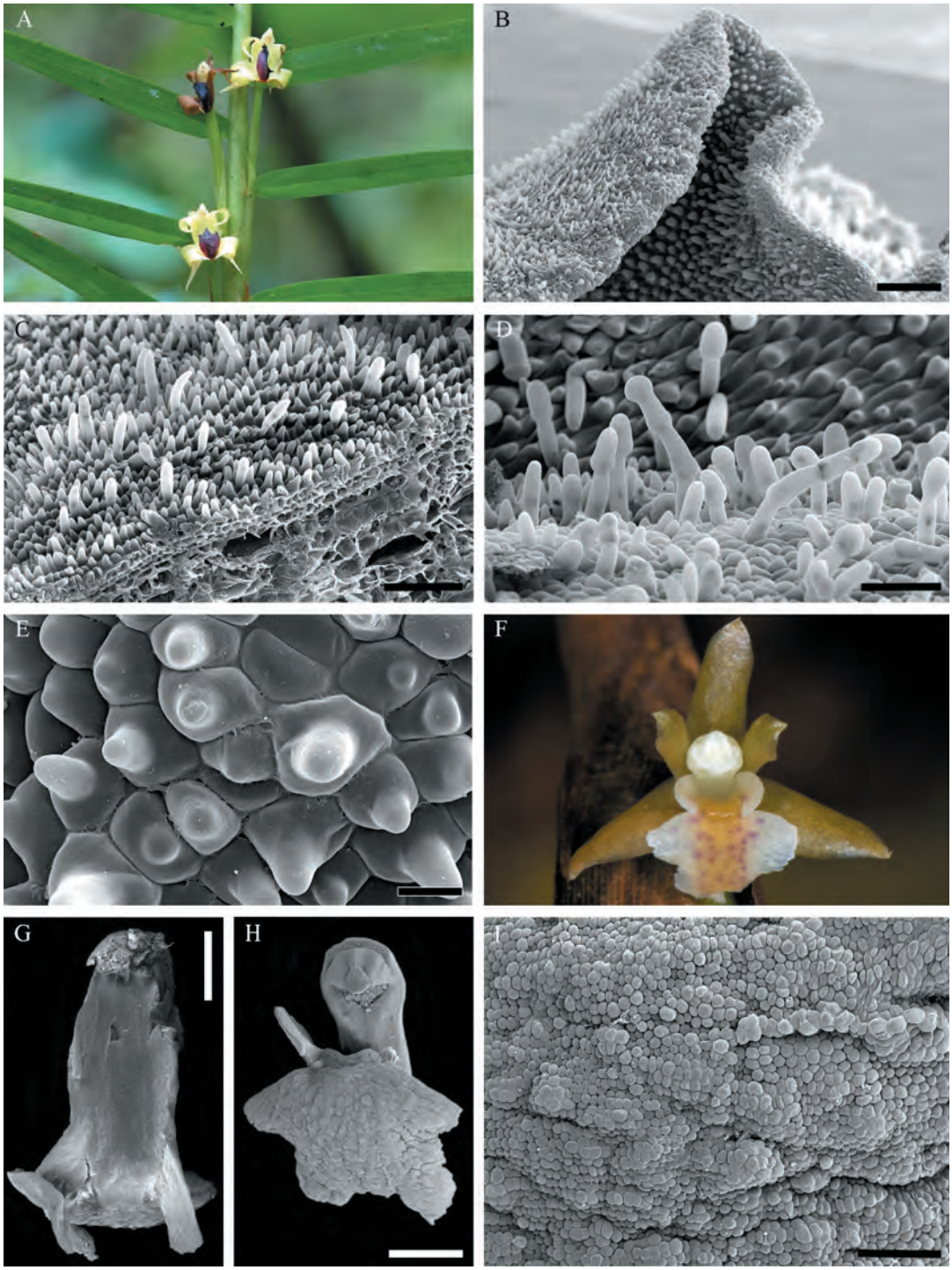

Figure 4. *Maxillaria graminifolia* (Kunth) Rchb. f. (A–E) and *Maxillaria ramosa* Ruiz & Pav. (F–I). A – overview of the flowers (Photo credit: Eric Hunt); B – papillose lip surface, covered with papillae on both adaxial (inner) and abaxial (outer) surfaces; C – various shapes of the papillae: obpyriform, conical and villiform; D – surface of the callus: rather glabrous, with some multicellular, moniliform trichomes; E – papillae covered with residues of secretion of some kind; F – overview of the flower of *Maxillaria* aff. *ramosa* (Photo credit: Eric Hunt); G – view of the lip; H – view of the lip apex and gynostemium; I – close-up of the lip surface, somewhat folded, built by obpyriform papillae. Scale bars = 1 mm (G, H); 200 µm (B, C, I); 100 µm (D); 20 µm (E).

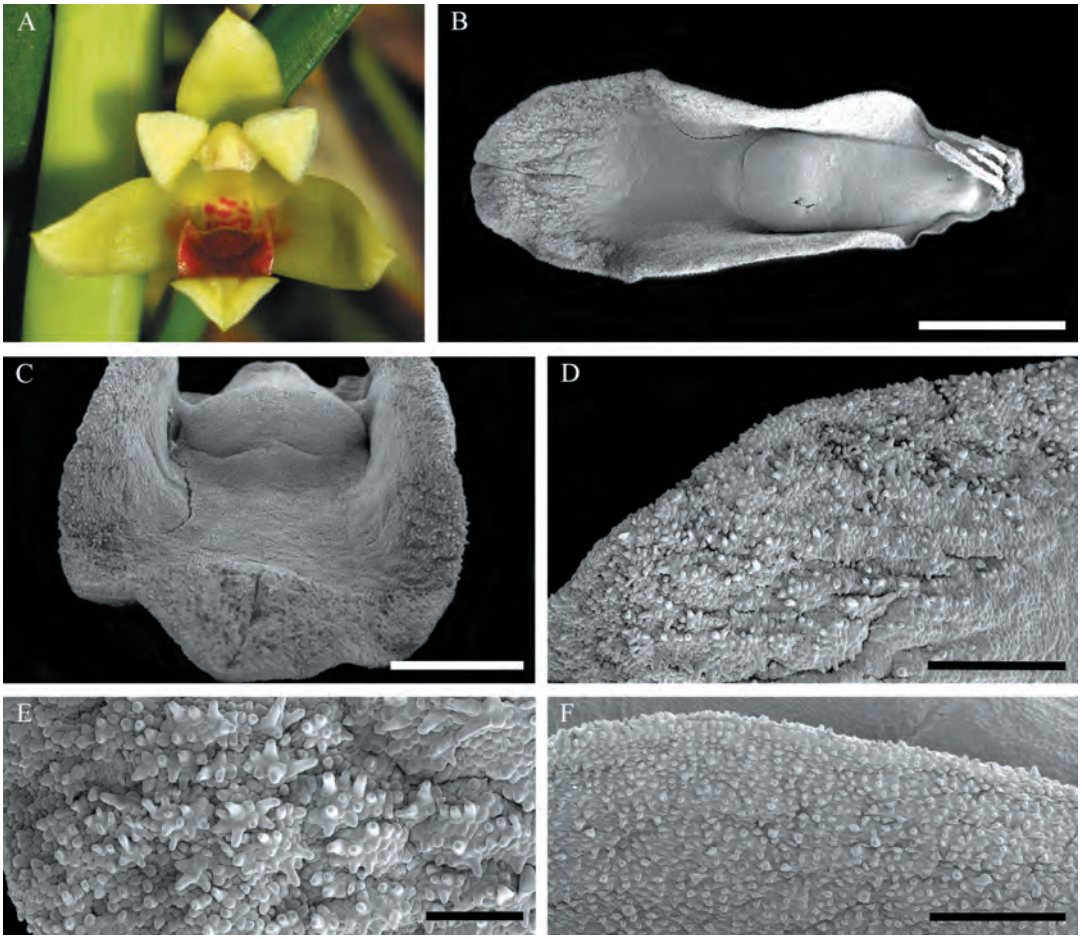

Figure 5. *Maxillaria ponerantha* Rchb. f. A – overview of the flower of *Maxillaria* aff. *ponerantha* (Photo credit: John Varigos); B – view of the lip and callus; C – front view of the glabrous callus and median lip part; D – minutely papillose margins; E – close-up of the lip apex with villiform, conical and sometimes obpyriform papillae at the margins. Folded-rugose surface, some of the papillae occur in aggregations of more than 4 cells, forming three-dimensional star-like clusters; F – outer surface of the lip is covered by conical papillae. Scale bars = 2 mm (B); 1 mm (C); 500 µm (D, F); 200 µm (E).

Maxillaria ramosa Ruiz & Pav., Syst. Veget. Fl. Peruv. Chil. 1: 226. 1798.

The lip of *Maxillaria ramosa* (Fig. 4F) is 3-lobed, elliptic in general outline. It is up to 9 cm long and 6 cm wide. The lateral lobes are erect, obliquely obovate and obtuse-rounded. The middle lobe is oblong-rectangular, obtuse-subtruncate. The callus (Fig. 4F–G) is oblong and extends from the base of the lip to the base of the middle lobe. The lip surface is slightly papillose. It is glabrous, rugose and built by obpyriform papillae in its proximal and median parts (Fig. 4H–I). No presence of any secretory material has been noticed.

Maxillaria section *Erectae* Pfitzer

Maxillaria ponerantha Rchb. f., Bonplandia 2(2): 17. 1854.

The lip of *Maxillaria ponerantha* (Fig. 5A) is unlobed to obscurely 3-lobulate by the suberect-incurved lateral margins and light constriction above the middle of the blade. It is obovate in general outline, obtuse and very shallowly notched at the apex. The callus is low, oblanceolate

and extends from the base of the lip (Fig. 5B) to its middle part. The callus and median lip part are glabrous (Fig. 5B). It is 0.9 cm long and 0.4 cm wide. The margins are minutely papillose (Fig. 5B–E). The shapes of the papillae at the margins are villiform and conical, sometimes obpyriform (Fig. 5E). The surface in this region is folded-rugose and some of the papillae occur in aggregations of more than 4 cells, forming three-dimensional star-like clusters (Fig. 5E). The outer surface of the lip is covered by conical papillae (Fig. 5F). Literature data support, at least partly, the results presented above and according to Davies & Turner (2004), the lip is clothed by conical and villiform papillae.

Maxillaria tenuifolia Lindl., Edwards's Bot. Reg. 23: sub t. 1986. 1837.

Species unplaced in any section proposed by Christenson, but it seems that it belongs to *Maxillaria* section *Erectae* Pfitzer.

The lip of *Maxillaria tenuifolia* (Fig. 6A) is unlobed to obscurely pandurate by way of a slight constriction above the middle. It is elliptic, obtuse, 2–2.3 cm long and 0.7–0.8 cm wide. The callus is broadly oblong and extends from the base of the lip (Fig. 6B) to about ⅓ of its length. The lip surface, including callus (Fig. 6C), is densely papillose (Fig. 6C–E), covered by villiform papillae. The one occurring near the lip center seem to be longer than the one near the sides. The presence of some remnants of secretion has been noticed (Fig. 6D–E). According to Davies & Winters (1998), the lip of *Maxillaria tenuifolia* is heterogeneous. This means that the epidermis is composed by more than one type of cells. Davies & Turner (2004) reported that conical papillae occur on the column and anther cap and the lip surface is covered with villiform papillae, what supports the results presented above. As Davies & Winters (1998) pointed out, the structure of the labellar epidermis is constant regardless of whether the typical red form or yellow one is examined.

Maxillaria section *Multiflorae* Christenson

Maxillaria ochroleuca Lodd. *ex* Lindl., Gen. Sp. Orchid. Pl.: 143. 1832.

The lip of *Maxillaria ochroleuca* (Fig. 6F) is thick and fleshy, narrowly rhomboid-ovate, slightly pubescent above with subcordate base. Near the middle it is deeply 3-lobed. Lateral lobes are large, oblong with rounded apices. Their margins are flat, non-undulate. The terminal lobe is thick, broadly ligulate, with rounded apices. Its margins are undulate and thinly crenulate. The callus is thick, ligulate (Fig. 6G) with shortened apex. It extends from the base to the middle part of the lip. Short, multicellular and uniseriate trichomes are scattered on the lip (Fig. 6H–I). They consist of 3 to 4 cells. The lip surface of *M. ochroleuca* is papillose, densely covered with obpyriform and clavate papillae (Fig. 6H–I). In some places, the surface is somewhat folded-rugose (Fig. 6H). Davies & Turner (2004) and Singer & Koehler (2004) observed on the lip the presence of obpyriform papillae and simple, uniseriate trichomes, consisting of 3–4 cells. According to Davies et al. (2000, 2003b), it is speculated, solely on morphological grounds, that these hairs may become detached or fragmented to form pseudopollen. Indeed, Singer has observed workers of *Trigona* bees collecting these hairs from the tip of the labellum (R.B. Singer pers. comm. in Davies & Turner 2004). He had also reported that they were chewed and stored in a paste-like form on the corbiculae. Furthermore, Singer stated that the bees actually collected papillae rather than hairs as the labellar papillae of the closely related *M. buchtienii* Schltr. are known to contain starch.

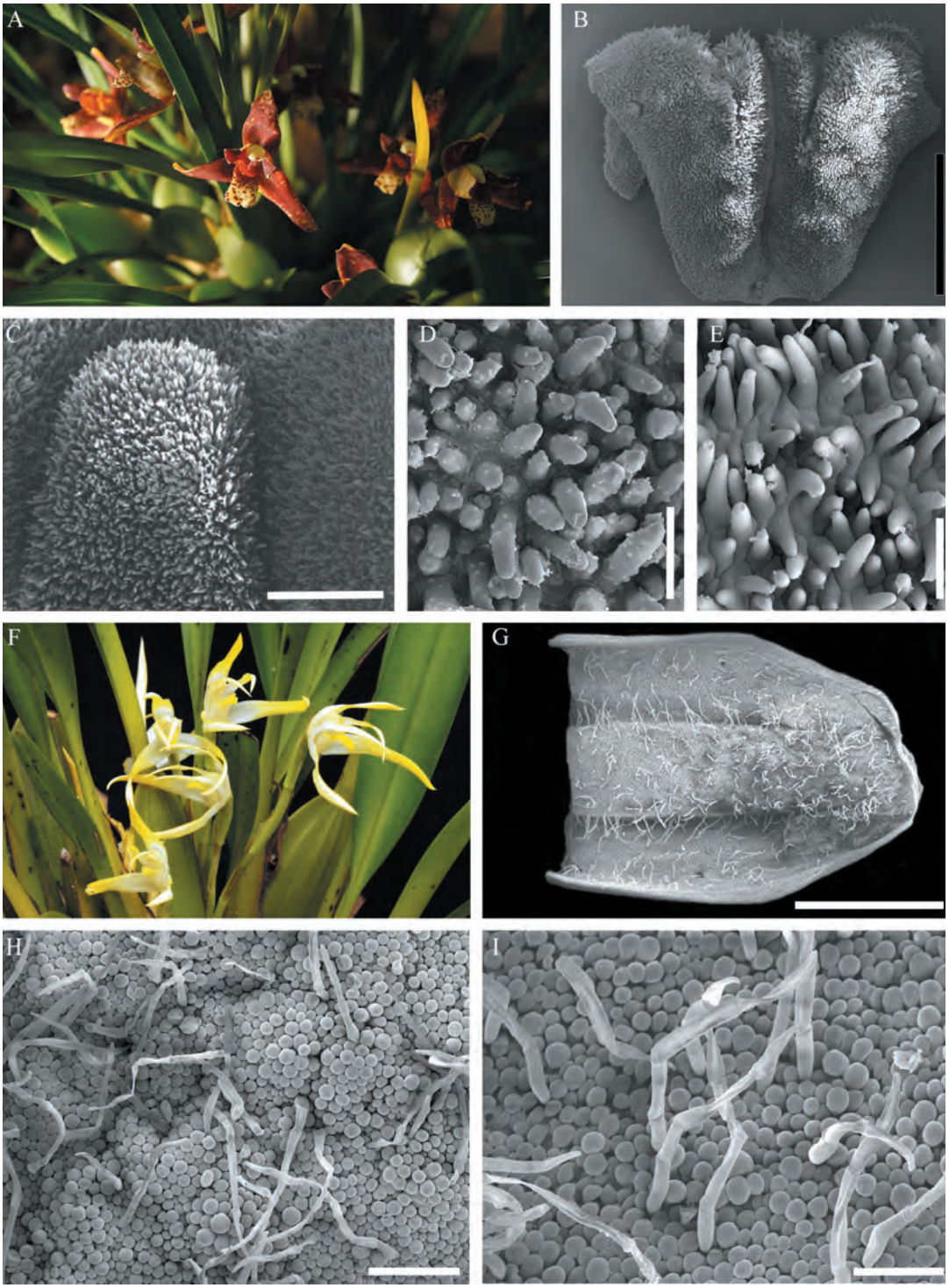

Figure 6. *Maxillaria tenuifolia* Lindl. (A–E) and *Maxillaria ochroleuca* Lodd. ex Lindl. (F–I). A – overview of the flowers; B – overview of the lip apex; C – close-up of the lip and callus surface covered by villiform papillae; D, E – some remnants of secretion visible on papillae; F – overview of the flower (Photo credit: Luiz Filipe Varella); G – view of the lip base and callus with scattered short, multicellular and uniseriate trichomes; H – close-up of papillose lip, densely covered with obpyriform and clavate papillae, in some places somewhat folded-rugose; I – close-up of the trichomes. Scale bars = 2 mm (B, G); 1 mm (C); 200 µm (H); 100 µm (D, E, I).

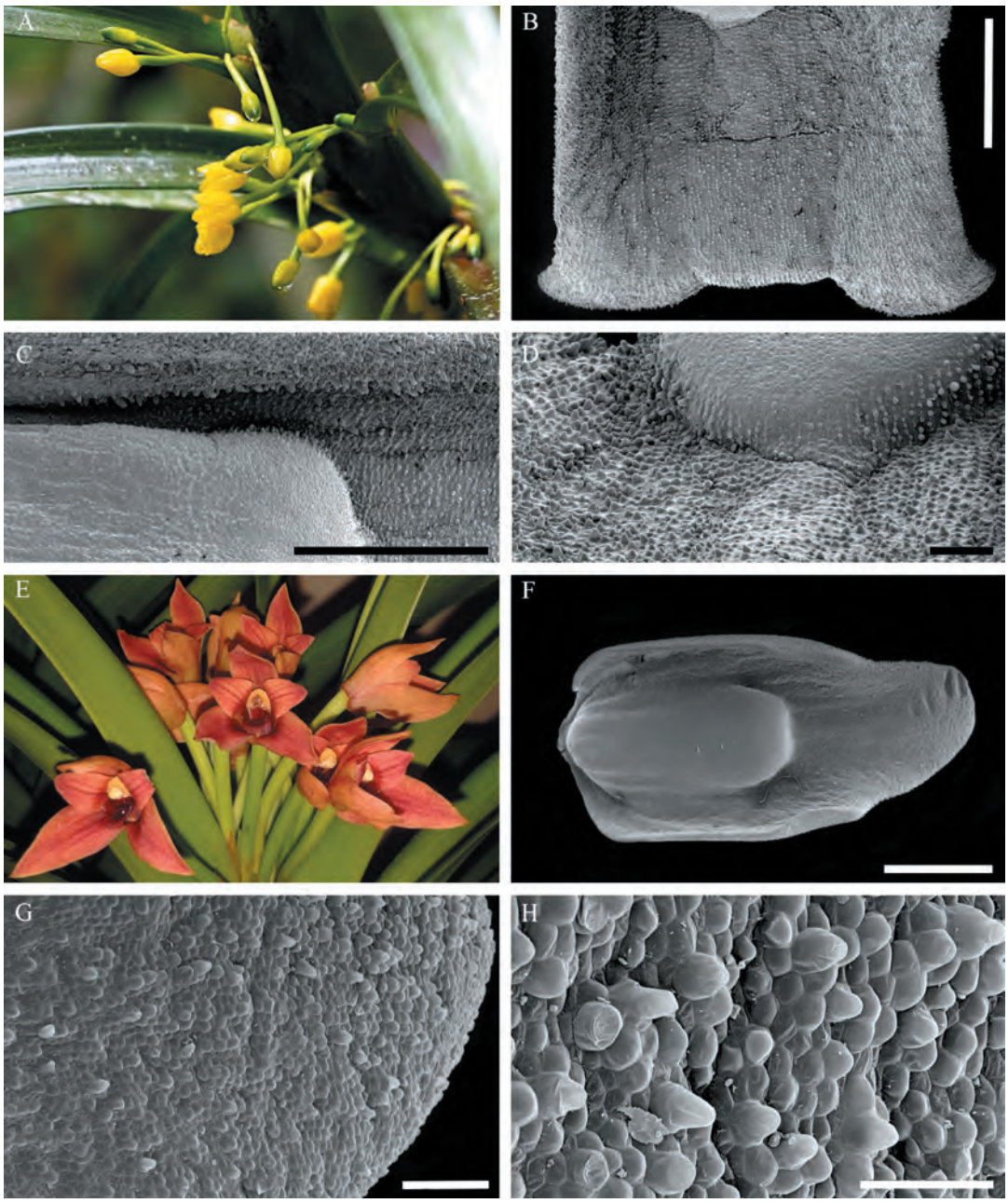

Figure 7. *Maxillaria aurea* (Poepp. & Endl.) L.O. Williams (A–D) and *Maxillaria purpureolabia* D.E. Bennett & Christenson (E–H). A – overview of the flowers (Photo credit: Kurt Buzard); B – general view of the lip apex; C – papillose lip surface: obpyriform (mainly in proximal part) to conical and villiform papillae; D – obpyriform papillae on the lip surface; E – overview of the flower; F – overview of the lip; G – slightly papillose lip surface; H – lip apex covered with obpyriform and conical papillae. Scale bars = 2 mm (F); 1 mm (B, C); 200 µm (D, G); 100 µm (H).

Maxillaria section *Ornithidium* (Salisb.) Christenson

Maxillaria aurea (Poepp. & Endl.) L.O. Williams, Caldasia 1(3): 14. 1941.

The lip of *Maxillaria aurea* (Fig. 7A) is rigid, fleshy, with the margins of the upper part incurved and wavy giving the appearance of being lobed. It is 0.8–1.1 cm long and 0.5–0.6 cm wide, when

extended. The median smooth callus expands on the basal half of the lip length and is oblong-ligulate in general outline (Fig. 7C). The labellum surface is papillose (Fig. 7B–D). Obpyriform (mainly in proximal part) to conical and villiform (on margins in lateral parts) papillae have been observed. They are found at both lateral and middle lobes of the lip. Papillae are obpyriform in general outline (Fig. 7C–D). No presence of wax or other secretion could be found.

Maxillaria purpureolabia D.E. Benn. & Christenson, Ic. Orchid. Peruv.: pl. 702. 2001.

The lip of *Maxillaria purpureolabia* (Fig. 7E) is obscurely 3-lobed, elliptic in general outline and it is about 0.9 cm long and 0.6 cm wide. The lateral lobes are erect, obliquely oblanceolate and obtuse. The middle lobe is broadly ovate and obtuse. The callus (Fig. 7F) is oblong-ellipsoid, obtuse-truncate and extends from the base of the lip to about its middle. The lip surface is slightly papillose (Fig. 7G–H). The lip apex is covered with obpyriform and conical papillae (Fig. 7H). The papillae seem to occur on both top and bottom side of the lip.

Maxillaria section *Repentes* Pfitzer

Maxillaria marginata Fenzl, Fl. Serres Jard. Europe 10: 112. 1854–1855.

Maxillaria marginata (Fig. 8A) has a 3-lobed lip, elliptic in general outline and it is up to 1.6 cm long and 0.9 cm wide. The lateral lobes are obliquely obovate and obtuse-rounded. The middle lobe is oblong-elliptic, obtuse-rounded. The callus (Fig. 8B) is oblong, obtuse-rounded and extends from the base of the lip to its middle part, below the base of the middle lobe. The lip surface is papillose, covered with obpyriform papillae and 3-celled trichomes with clavate terminal cells (Fig. 8C–D). Residues of some kind of secretion have been observed on the apex of the lip (Fig. 8D). Workers of *Trigona* sp. (Apidae: Meliponini) have been observed during the pollination of the flowers of this species (Singer & Koehler 2004). Singer & Koehler (2004) reported that there is no evidence for the presence of trichomes or any food rewards in the flowers of *M. marginata*, what has been clearly undermined by our results.

Maxillaria picta Hook., Bot. Mag. 59: t. 3154. 1832.

Maxillaria picta (Fig. 8E) has a 3-lobed lip, broadly elliptic in general outline. It is 1.7 cm long and 1 cm wide. The lateral lobes are erect-incurved, transversely elliptic and obtuse-rounded. The middle lobe is elliptic-ovate, obtuse-rounded and slightly crenulated. The lip surface, including the callus, is papillose. It is densely covered by clavate, conical and villiform papillae (Fig. 8F–H). The lower part of the callus is almost glabrous with villiform papillae occurring occasionally (Fig. 8G). Its middle part is densely covered by conical and clavate papillae, with strongly rounded tips, scattered between them. Some trichomes, probably consisting of 2 or more cells, with globose or elliptic top cells have been observed (Fig. 8H). The flowers of *M. picta* are strongly scented, emitting honey-like fragrance. According to Singer & Cocucci (1999), they do not produce nectar or any other reward. Davies & Winters (1998) reported that its lip is lacking trichomes, but is heavily clothed with villiform papillae. *M. picta* is pollinated by the stingless bee *Trigona spinipes* (Singer & Cocucci 1999). It is suspected that the papillae produce an intoxicating fragrance which facilitates pollination by partially anaesthetizing the insect (Davies & Turner 2004). According to Flach et al. (2004) and Singer et al. (2006), it is composed mostly of linalool, phenylacetaldehyde and b-ocimene. Davies & Stpiczyńska (2012) investigated the anatomy of the resin-secreting and putative resin-mimic species including *M. picta*. Their research revealed that the conical, villiform or subclavate epidermal papillae, located on the adaxial labellar

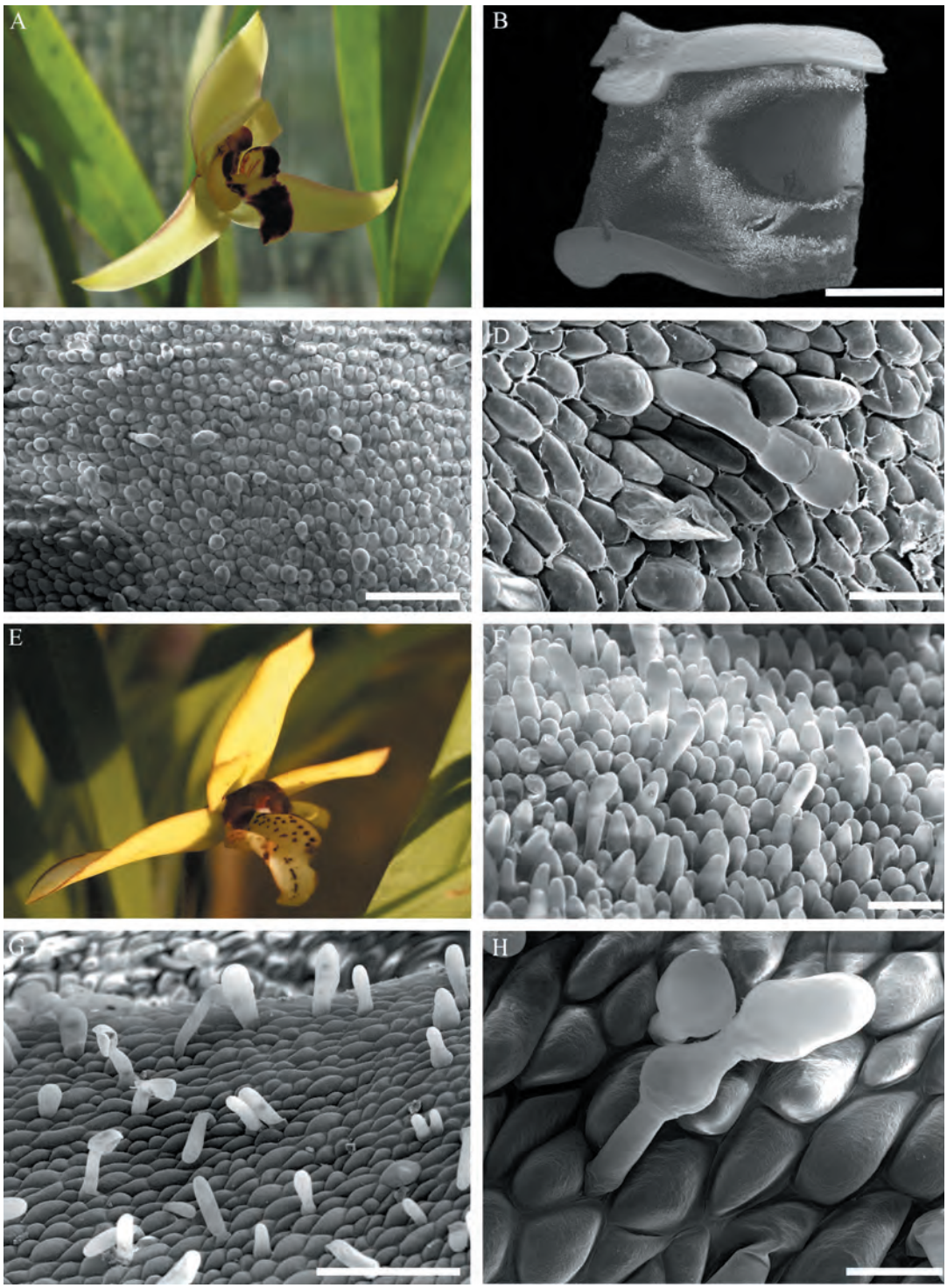

Figure 8. *Maxillaria marginata* Fenzl. (A–D) and *Maxillaria picta* Hook. (E–H). A – overview of the flower; B – overview of the medial part of the lip; C – obpyriform papillae and 3-celled trichomes with clavate terminal cells; D – close-up of the 3-celled trichome with clavate terminal cell and residues of some kind of secretion; E – overview of the flower of *Maxillaria* aff. *picta*; F – lip surface densely covered by clavate, conical and villiform papillae; G – lower part of the callus: almost glabrous with villiform papillae occurring occasionally; H – trichomes consisting of at least two cells, with globose or elliptic top cell. Scale bars = 2 mm (B–D); 200 µm (G); 100 µm (F); 50 µm (H).

surface, function as secretory tissue. What is more, the presence of the labellar secretion has been demonstrated based on combined light, scanning and transmission electron microscopy and histochemistry results. It is thought to be the fragrance residues.

Maxillaria cf. *mosenii* Kraenzl., Konigl. Svenska Vet. Acad., n.s. 46(10): 73, t. 11, f. 6. 1911.

Species unplaced in any of the sections proposed by Christenson, but it seems that it belongs to the section *Repentes* Christenson.

The lip of *Maxillaria mosenii* (Fig. 9F) is obovate to oblanceolate, obscurely 3-lobed and about 1.9 cm long and 1 cm wide. The middle lobe is orbicular with rounded apex, which can be retuse. The callus is oblong, 4.5–9.7 mm long and extends slightly above the ⅓ of the lip length. The adaxial (inner) surface of the lip base (Fig. 9G) and callus (Fig. 9H) of *Maxillaria* cf. *mosenii* is glabrous. The surface towards the margins is rugose and at the margins densely covered with conical papillae, which are gathered in three-dimensional clusters (Fig. 9H–I), resembling somewhat a sea anemone. As Davies et al. (2004) reported, *M. mosenii* Kraenzl. has conical labellar papillae and no presence of trichomes has been demonstrated. According to the authors, *M. mosenii* Kraenzl. var. *hatschbachii* (Schltr.) Hoehne possesses conical papillae on the column, anther cap as well as on the lip. The papillae contain proteins, but neither lipids nor starch.

Maxillaria section *Rufescens* Christenson

Maxillaria rufescens Lindl., Edwards's Bot. Reg. 21: sub. t. 1802.

The lip of *Maxillaria rufescens* (Fig. 9A) is 3-lobed, elliptic-ovate in general outline. It is 1.7 cm long and 1.3 cm wide. The lateral lobes are erect-incurved, obliquely ovate, acute and about half of the lip length. The middle lobe is rectangular, rounded-truncate. The callus (Fig. 9B) is oblong and extends from the base of the lip to below the base of the middle lobe. The lip surface is papillose, covered with clavate papillae on the callus and near the central part of the middle lobe (Fig. 9C) and on the whole surface with obpyriform papillae (Fig. 9D–E). The remnants of secreted material have been observed (Fig. 9C). This observations are strongly supported by already published data. According to Davies & Turner (2004), the shape of labellar papillae can be clavate or obpyriform, they contain protein, lipids and starch. The presence of the latter one is common among other members of this alliance. The labellar surface is generally clothed with obpyriform papillae. Those located towards the center of the lip are clavate and much larger by distended apices (Davies & Turner 2004). They stated that these papillae at the center of the lip often contain more starch than the others. It is thought that the papillae produce an intoxicating fragrance which can partially anaesthetize the insect and thus facilitates pollination. Van der Pijl & Dodson (1969) reported the vanillin production in *M. rufescens*. They pointed also to another theory: even in species, which at first sight seem to be rewardless, food substances may be present, but located within papillae and are only accessible to gnawing insects. However, there is no direct evidence for this. This could be the case in *M. rufescens* where, according to Porsch (1905), the unicellular 'hairs' have delicate walls and contain aleurone grains and oil droplets. According to Davies & Turner (2004), no presence of trichomes has been observed. An opposite observation was made by Singer & Koehler (2004). Researchers observed clusters of tightly packed, short to long, unicellular, claviform, yellowish trichomes on the lip surface, mainly in the middle lobe region. Research conducted by Flach et al. (2004) supported this observation and revealed that *M. rufescens* produce some reward (trichomes) for its pollinators.

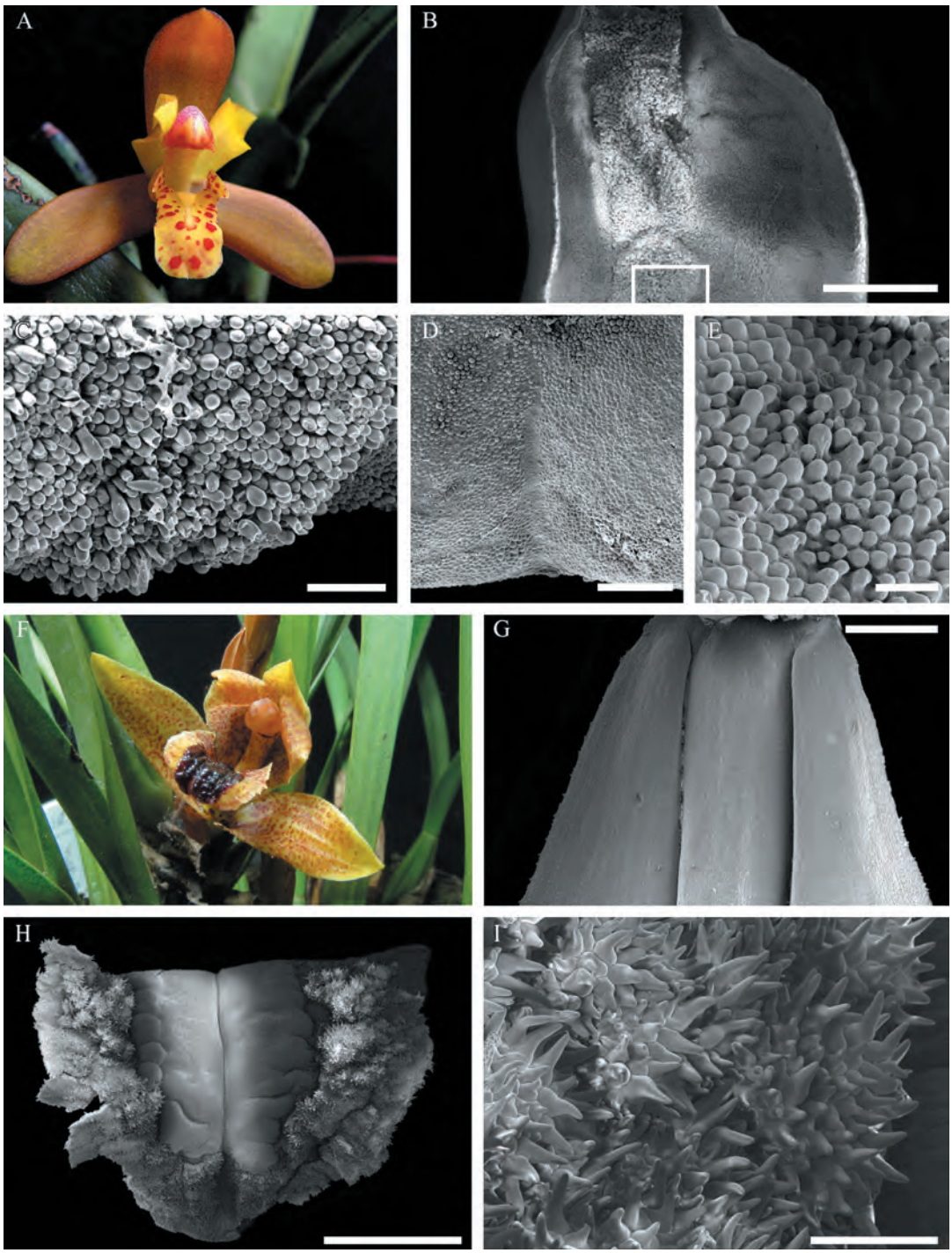

Figure 9. *Maxillaria rufescens* Lindl. (A–E) and *Maxillaria mosenii* Kraenzl. (F–I). A – overview of the flower (Photo credit: Eddie Thalen); B – view of the lip base; C – papillose lip surface, covered with clavate papillae on the callus and near the central part of the middle lobe with visible remnants of secreted material; D – close-up of the callus: visible remnants of secreted material and clavate papillae; E – lip surface covered with obpyriform papillae; F – overview of the flower (Photo credit: Luis Renato); G – glabrous adaxial (inner) surface of the lip base and callus; H – adaxial (inner) surface of the lip apex and callus: rugose towards the margins and at the margins densely covered with conical papillae, gathered in three-dimensional clusters; I – close-up of conical papillae, gathered in three-dimensional clusters. Scale bars = 2 mm (B, C, H); 1 mm (G); 500 µm (D); 200 µm (I); 100 µm (E).

Maxillara section *Urceolatae* Christenson

Maxillaria vitelliniflora Barb. Rodr., Gen. Sp. Orchid. Nov. 1: 121. 1877.

The lip of *Maxillaria vitelliniflora* (Fig. 10A) is unlobed, broadly oblong in general outline, arching with shallowly suberect lateral margins, obtuse with minute apical notch. It is 0.7 cm long and 0.3 cm wide. The callus is an indistinct central thickened pad (Fig. 10B). The apex of the lip is covered with obpyriform papillae (Fig. 10C). The lip surface is partly papillose. Its margins are clothed with conical and villiform papillae (Fig. 10D). The basal and median part is completely devoid of them. No presence of secretion or any other kind of reward has been observed. Available literature data seem to support presented results. According to Davies & Turner (2004), conical and obpyriform papillae occur on the column and anther cap and the lip is covered with conical papillae. As Singer & Koehler (2004) reported, the flowers of this species are rewardless, what is upheld by the results presented above.

Maxillaria section *Trigonae* Christenson

Maxillaria pterocarpa Barb. Rodr., Gen. Sp. Orchid. Nov. 2: 204. 1882.

Species unplaced in any of the sections proposed by Christenson, but it seems to belong to *Maxillaria* section *Trigonae* Christenson.

The lip of *Maxillaria pterocarpa* (Fig. 10E) is obscurely 3-lobed, elliptic in general outline, up to 0.6 cm long and 0.3 cm wide, with incurved sides. The middle lobe is broadly ovate to suborbicular, acute, minutely warty with the warts arranged in rows. The callus is oblong, somewhat dilated towards the apex, obtuse-rounded. It extends from the base of the lip to beyond its middle, reaches about ⅔ of the lip length. The lip surface is papillose near the apex and margins (Fig. 10F–H), but the median part is glabrous. The shape of papillae is villiform. The ones near the edge of the lip are sometimes fused together in pairs (Fig. 10H). The remnants of secretion are visible on the papillae (Fig 10G).

'Grandiflora Complex'

Maxillaria molitor Rchb. f., Gard. Chron. ser. 3, 2: 242. 1887.

Species unplaced in any of the sections proposed by Christenson (2013), but it seems that it belongs to the 'Grandiflora Complex'.

The lip of *Maxillaria molitor* (Fig. 11A) is unlobed, but appears to be 3-lobed due to the folding. It is elliptic in general outline and up to 2.1 cm long and 1.5 cm wide. The lateral margins are suberect. The middle lobe is elliptic, obtuse, concave with undulate margins. The callus is broadly oblong and extends from the base of the lip to its middle part. Both lip surfaces are papillose. The abaxial (outer) surface is densely covered by elliptical and villiform papillae, sometimes dichotomously divided (Fig. 11B). The adaxial (inner) surface at the base is formed by parallel arranged conical papillae with striated cuticle (Fig. 11C–D). The callus is covered by obpyriform to globose papillae (Fig. 11G). Abundant masses of pseudopollen have been observed on the adaxial surface of both middle (including callus) and lateral lobes (Fig. 11B, C, E–H). Pseudopollen grains are lemon-shaped, attached together in moniliform chains, with distended cuticle and remnants of secreted material (Fig. 11G). In the transverse section large cells, most probably idioblasts, were noticed under the single layer of epidermis (Fig. 11F). According to

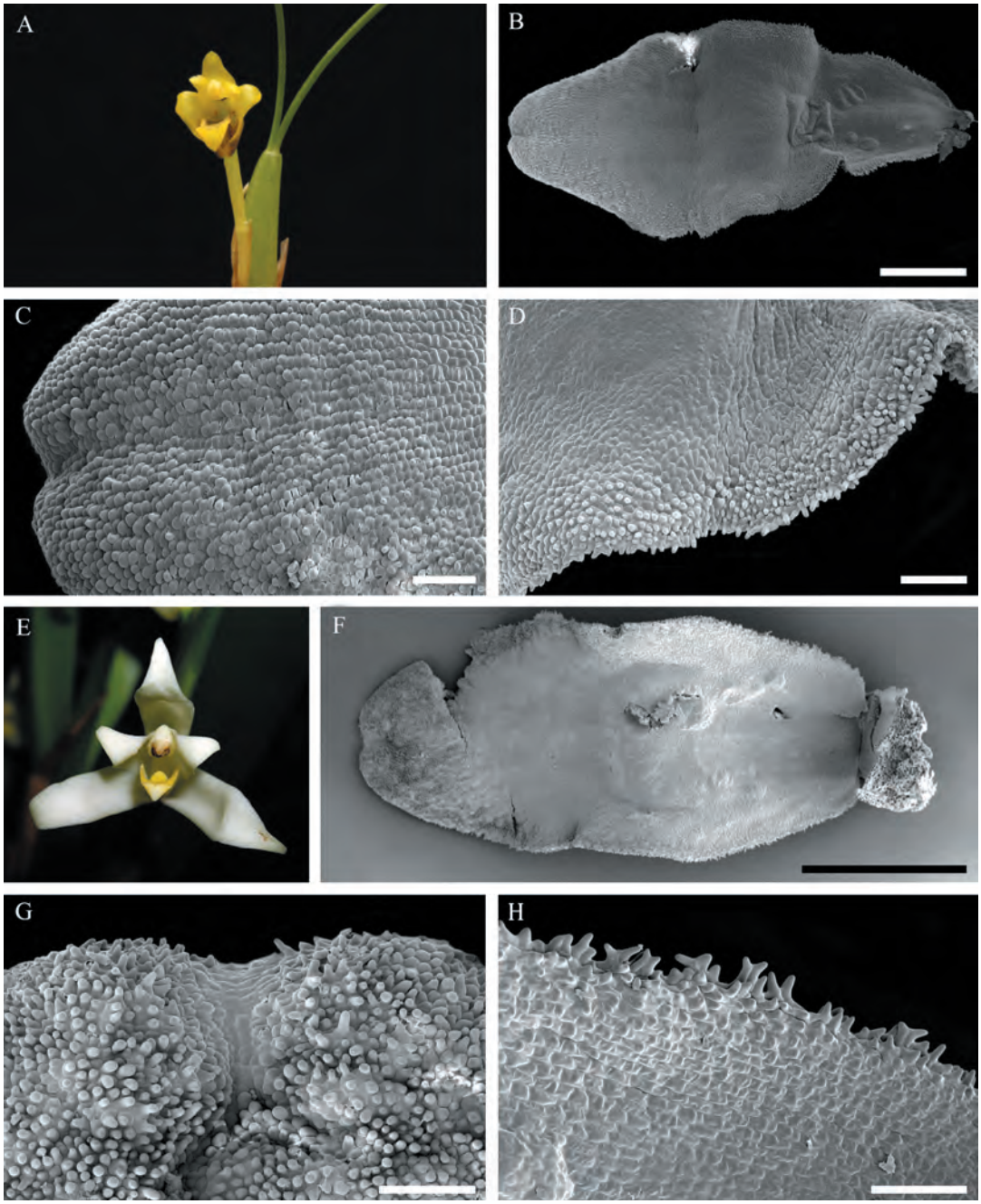

Figure 10. *Maxillaria vitelliniflora* Barb. Rodr. (A–D) and *Maxillaria pterocarpa* Barb. Rodr. (E–H). A – overview of the flower (Photo credit: Luiz Filipe Varella); B – view of the lip; C – view of the lip apex covered with obpyriform papillae; D – lip margins clothed with conical and villiform papillae; E – overview of the flower (Photo credit: John Varigos); F – view of the lip; G – view of the lip apex with visible remnants of secretion on the papillae; H – villiform papillae at the lip apex near the edge of the lip, sometimes fused together in pairs. Scale bars = 2 mm (F); 1 mm (B); 200 µm (C, D, G, H).

Davies & Turner (2004), on the lip surface of *M. molitor* obpyriform papillae and moniliform trichomes are present. Furthermore, they pointed that wherever pseudopollen-forming trichomes occur, labellar papillae tend to be obpyriform. The component cells of the pseudopollen are

lemon-shaped and squat in appearance with distinct polar papillae. Pseudopollen contains protein and starch, but no lipid (Davies et al. 2000).

Maxillaria striata Rolfe, Orchid Rev. 1: 265. 1893.

Species unplaced in any section proposed by Christenson (2013), according to him it belongs to the 'Grandiflora Complex'.

The lip of *Maxillaria striata* (Fig. 12A) is obscurely 3-lobed, elliptic, acute to obtuse. It is about 3.5–4 cm long. The lateral lobes are suberect. The middle lobe has undulate margins. The callus is oblong and extends to ⅔ of the lip length. The lip surface is papillose. The base and the sides of the lip are covered with conical and villiform papillae arranged in rows (Fig. 12B). The lip surface is covered by obpyriform (Fig. 12C) and conical papillae (Fig. 12D). Towards the median part, grains of pseudopollen (Fig. 12E–F) occur more abundantly, reaching a peak in the middle part of the middle lobe. It appears, that pseudopollen is formed from obpyriform papillae. Indeed, some researchers connect the presence of the latter one with the occurrence of pseudopollen. Almost all papillae and pseudopollen grains are covered with residues of secretion of some kind (Fig. 12D–F). Results presented above are supported by already published literature data. Davies & Turner (2004) reported that on the lip surface of *Maxillaria striata* villiform papillae occur. According to Davies et al. (2000), its pseudopollen contain protein, but no starch. In their opinion, based on light microscopy observations, there is slight, but unconvincing evidence for the presence of lipids.

Discussion

The results of labellar micromorphology studies of *Maxillaria reichenheimiana, M. cucullata, M. ponerantha, M. tenuifolia, M. ochroleuca, M. marginata*, *M. picta*, *M. rufescens*, *M. mosenii, M. vitelliniflora, M. molitor* and *M. striata* generally confirm those previously obtained by Davies and co-workers (Davies & Winters 1998; Davies et al. 2000; Davies et al. 2003a,b; Davies & Turner 2004; Davies & Stpiczyńska 2012) or Singer and co-workers (Singer & Cocucci 1999; Flach et al. 2004; Singer & Koehler 2004).

Comparison within the sections

Section *Aggregatae* Pfitzer. Up to date, 4 more representatives of section *Aggregatae* have been examined. *Maxillaria robusta* and *M. parkeri* according to Singer & Koehler (2004) offer no reward to their pollinators. *Maxillaria* cf. *setigera* possesses conical papillae and simple 2–3-celled trichomes at the column, the same type of papillae occurs at the anther cap and obpyriform papillae with moniliform 2–3-celled trichomes at the lip surface have been observed (Davies & Turner 2004). According to the same authors, both labellar papillae and trichomes contain starch and protein, but no lipids. Davies & Winters (1998) stated that *Maxillaria triloris* has trichomes and papillae with pointed tips and they concentrate at the lip margins, those structures presented therein on the figures 10–11 strongly resemble the ones observed in *M. callichroma* in our research. Later, Davies & Turner (2004) examined another specimen of *Maxillaria,* this time identified as cf. *triloris*. They have observed obpyriform papillae on the lip surface and simple 2–3-celled trichomes. This resemblance between all three specimens of *M. callichroma*, *M. triloris* and *M.* cf. *triloris* may lead to the conclusion that either both species are extremely similar in respect of their micromorphology or some misidentification has been made, what is

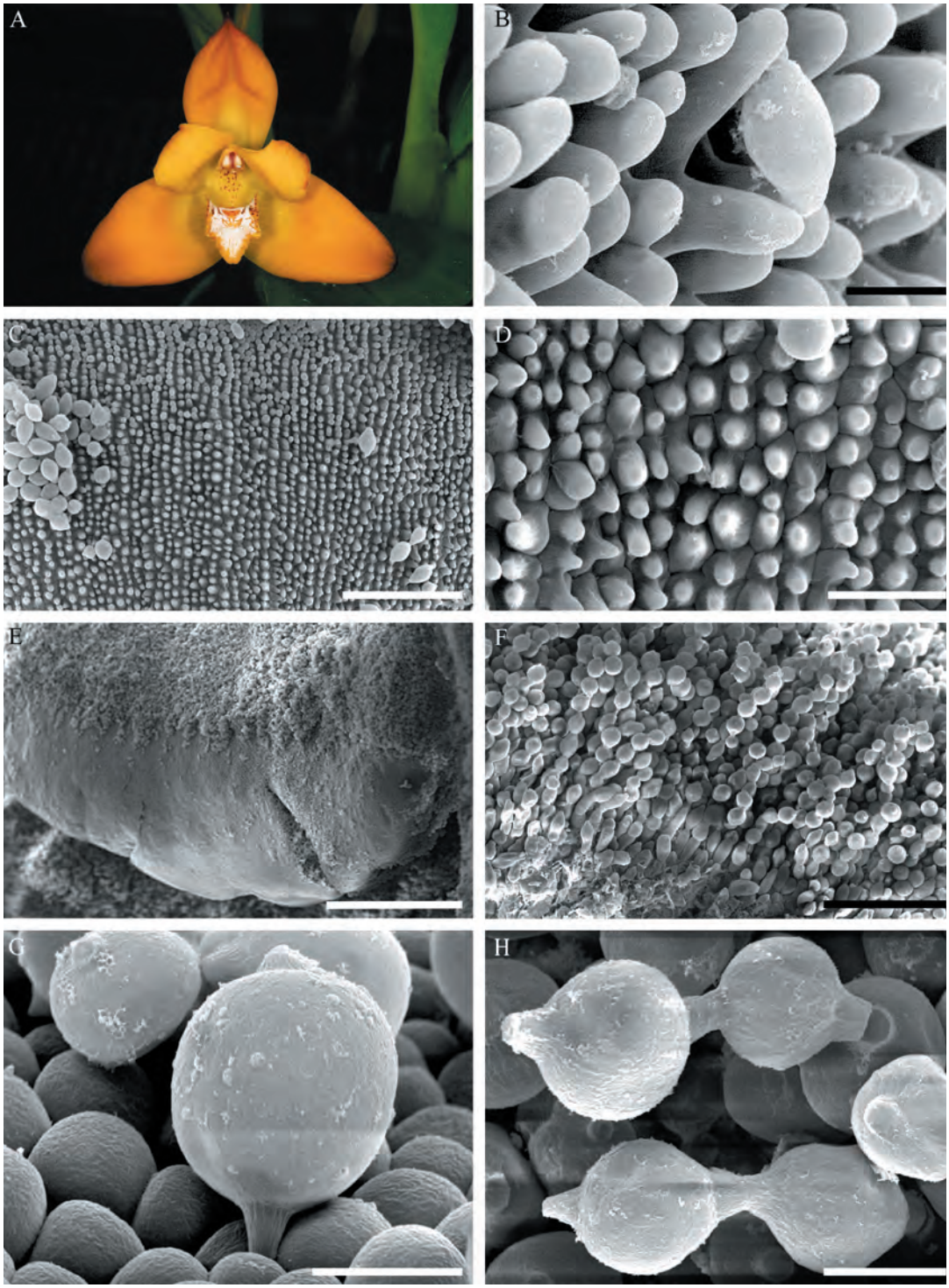

Figure 11. *Maxillaria molitor* Rchb. f. A – overview of the flower (Photo credit: Eric Hunt); B – villiform papillae, sometimes dichotomous, with pseudopollen grain; C – adaxial (inner) surface at the base is formed by parallel arranged conical papillae; D – close-up of the adaxial (inner) surface at the base with parallel arranged conical papillae with striated cuticle; E – masses of pseudopollen; F – lemon-shaped pseudopollen grains, attached together in moniliform chains; G – lemon-shaped pseudopollen grains with distended cuticle and remnants of secreted material; H – pseudopollen grains. Scale bars = 1 mm (E); 200 µm (C, F); 50 µm (D); 20 µm (B, G, H).

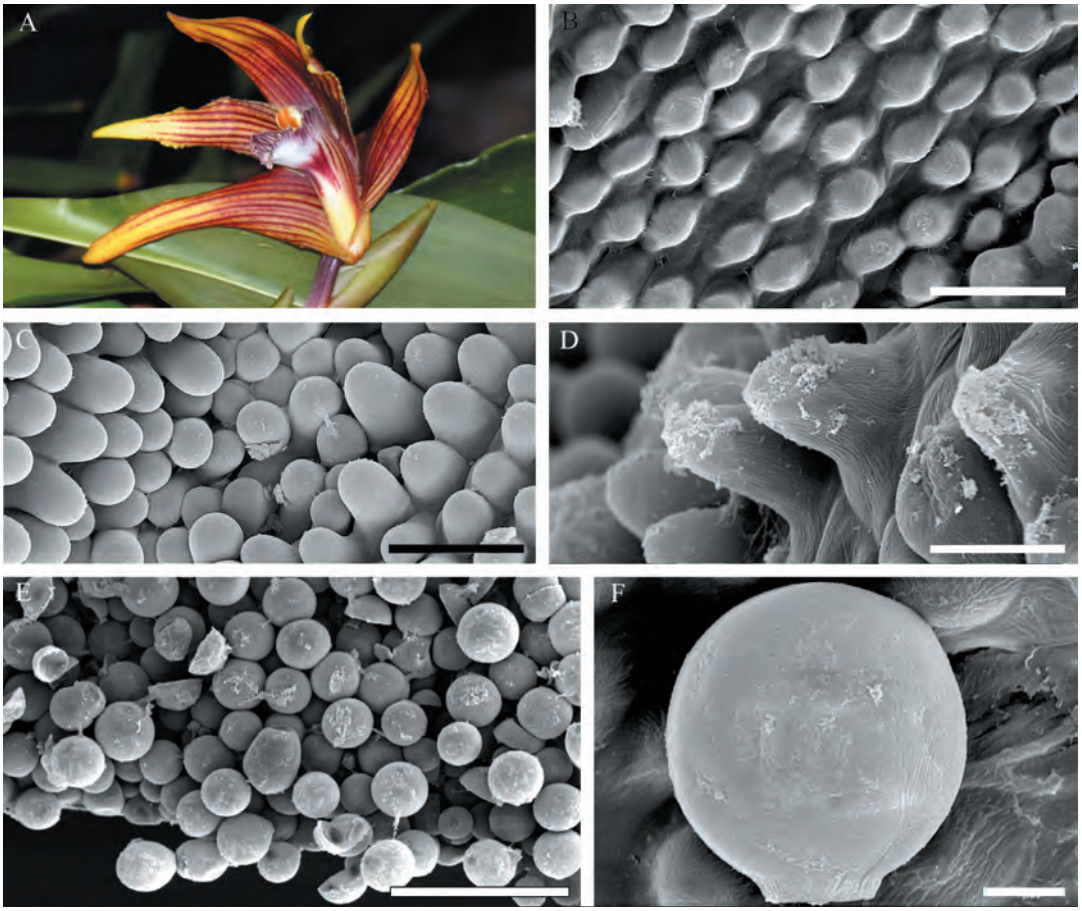

Figure 12. *Maxillaria striata* Rolfe. A – overview of the flower; B – conical papillae arranged in rows; C – obpyriform papillae arranged in rows; D – papillae covered with residues of some kind of secretion; E – masses of pseudopollen, visible residues of some kind of secretion; F – single grain of pseudopollen. Scale bars = 200 µm (E); 50 µm (B, C); 20 µm (D); 10 µm (F).

quite common in this group. It seems that the presence of obpyriform papillae and trichomes is conservative, but not a unique character of this section.

Section *Arachnites* Christenson. So far, eight other species from relatively large section *Arachnites* have been examined. *M. buchtienii* possesses conical papillae at the column and anther cap and obpyriform papillae as well as 3–4-celled trichomes on the lip surface (Davies & Turner 2004). According to the same authors, labellar papillae contain protein and starch, but no lipids, these substances are absent in trichomes. According to Davies et al. (2013), spherical or obpyriform epidermal papillae are confined to the distal part of the labellum and the callus in this species, and the uniseriate trichomes found on the lateral parts of the labellum are composed of three to four elongate cells only. In *M. fractiflexa*, conical papillae have been observed at the column and anther cap, additionally villiform and 3–4-celled trichomes on the lip. *M. lepidota* Lindl. possesses obpyriform papillae with glands and 2–3-celled trichomes on the lip surface, similar structures occur in *M.* cf. *arachnites* (Davies & Turner 2004). The authors stated that in the first species labellar papillae, as previously described by Davies & Winters (1998), become modified into unicellular, spherical glands. They observed that those are more abundant on the ventral

surface of the labellum than the dorsal. According to them, around the anther and stigmatic surface, papillae may become enlarged or swollen and appear to contain a thin layer of peripheral cytoplasm and a large vacuole with watery cell sap that occupies most of the cell. In many species (e.g. *M. lindleyana* Schltr., another member of the section) many of these conical papillae are replaced by villiform papillae, some of which are curved like a scythe (Davies & Turner 2004). In the later paper, Davies et al. (2013) stateed, that in *M. lepidota* pseudopollen is present on the adaxial and abaxial surfaces of the lip and is formed by the fragmentation of uniseriate, moniliform trichomes, the four to six component cells of these trichomes are interspersed amongst typical labellar obpyriform papillae, between which occur enlarged, secretory, unicellular, obpyriform to spherical glands. *M. lindleyana* has conical papillae at the column and the anther cap, additionally obpyriform ones occur on the lip surface as well. As mentioned before, many of these conical papillae are replaced by villiform papillae (Davies & Turner 2004). Singer & Koehler (2004) report clusters of trichomes for this species, but this may be as well misnaming of villiform papillae found by Davies & Turner (l.c.). *M. longissima* has obpyriform papillae and moniliform trichomes at the lip surface, they contain protein and lipids, but no starch (Davies & Turner 2004). The same authors stated that solely on morphological grounds, these trichomes might be pseudopollen-forming labellar hairs (Davies & Winters 1998; Davies et al. 2000, 2003a,b) with the fusiform component cells. *Maxillaria pseudoreichenheimiana* has conical and villiform papillae at the column, obpyriform and villiform ones at the anther cap and obpyriform ones on the lip surface as well as bicellular trichomes (Davies & Turner 2004). Morphologically, these resemble the food hairs described by Davies et al. (2002) for certain species of *Polystachya*. Papillae and trichomes contain protein and the latter one probably also lipids. Singer & Koehler (2004) stated that *M. bradei*, another member of the section, possess trichomes. It seems that the presence of the trichomes and obpyriform papillae is quite constant in this section, the same as in section *Aggregatae*.

Section *Cucullatae* Christenson. Until now, two more species of section *Cucullatae* have been examined, *M. hematoglossa* and *M. lexarzana*. The first one possesses conical papillae at the column surface, conical and obpyriform ones at the anther cap, and its lip is completely devoid of any papilla (Davies & Turner 2004). The same authors observed conical papillae only at the anther cap of *M. lexarzana*. Davies & Turner (2004) pointed out that in *M. meleagris* Lindl., which is thought to be closely related to the members of discussed section, the labellum is papillose, covered with the conical papillae with pointed tips. We have obviously observed conical papillae on the lip surface in our research, which may lead to the conclusion that some identification errors might have occurred. Indeed, members of this group are often misidentified and this may cause problems with correct taxonomic identification. In fact, there was a time when nearly all of the species in the section were included in the highly variable *M. cucullata* (Christenson 2013). However, *M. cucullata* can be easily distinguished from similar species by almost wholly unmarked sepals and petals and this fits the description of the flower used in our research. Thus, to resolve this problem, further investigations are needed. In general and according to Davies & Turner (2004), glabrous labella completely devoid of papillae were found in *M. cucullata, M. hematoglossa* and *M. lexarzana*. In *M. praestans*, a species included by Christenson to discussed section, we observed that the lip base is densely covered with obpyriform to villiform papillae. It is therefore possible that a glabrous lip surface is neither a conservative feature nor characteristic of this section.

Section *Erectae* Pfitzer. Only two other members of section *Erectae* have been investigated. In *Maxillaria procurrens* Lindl. conical papillae have been observed on the lip surface (Davies & Turner 2004). *Maxillaria variabilis* has villiform and conical papillae at the column and lip surface and conical ones at the anther cap (Davies & Winters 1998; Davies & Turner 2004; Davies et al. 2012). Conical papillae are most common, thus they are not of taxonomic importance. It is worth to mention that species of the discussed section investigated by us have a more diverse labellar epidermis because we observed, for instance, also villiform and obpyriform papillae.

Section *Multiflorae* Christenson. So far, only two members of section *Multiflorae* have been examined, *M. chlorantha* and *M. splendens*. According to Davies & Turner (2004), members of the *M. splendens* alliance have labella with uniseriate, relatively few-celled hairs (3–4) as well as obpyriform papillae, and it has been speculated that these hairs may become detached or fragment to form pseudopollen (Davies et al. 2000, 2003a,b). Histochemical analysis, however, failed to demonstrate the presence of protein, starch or lipids within such hairs in *M. buchtienii*. Nevertheless, identical hairs occur in *M. ochroleuca* (Davies et al. 2000). The presence of obpyriform papillae and multicellular trichomes seem to be a constant feature for the members of this section, since they have been observed also in *M. ochroleuca* (Davies & Turner 2004).

Section *Ornithidium* (Salisb.) Christenson. Only one other species of section *Ornithidium* has been examined to date. In *M. coccinea*, conical papillae have been observed at the anther cap and lip surface, although even papillose labella may have some glabrous regions (Davies & Turner 2004). Furthermore, nectar production has also been demonstrated for this species (Stpiczyńska et al. 2004).

Section *Repentes* Pfitzer. Eight other species of section *Repentes* have been examined. According to Singer & Koehler (2004), *M. barbosae* Loefgr. ex Porto, *M. chrysantha* Barb. Rodr., *M. consanguinea* Klotzsch, *M. gracilis* Lodd., *M. kautskyi* Pabst, *M. phoenicanthera* Barb. Rodr., *M. porphyrostele* Rchb. f., *M. ubatubana* Hoehne possess neither papillae nor trichomes. Davies & Turner (2004) reported that in *M. chrysantha* conical papillae occur at the column and anther cap. The same authors stated that the labellar epidermis of *M. chrysantha* produces wax upon its surface and this protects the plant from desiccation. According to Davies et al. (2012), flowers of both *M. picta* and *M. porphyrostele* are highly fragrant, and the callus epidermis consists mainly of cuboidal cells. Although SEM and TEM analyses of both species revealed small quantities of epidermal secretion, this, unlike other secretions, was barely visible using fluorescence microscopy and may have represented fragrance residues (i.e. that component of the fragrance that remains after the more volatile constituents have vaporized), especially as parenchyma cells of *M. porphyrostele* contained droplets of presumed terpenoids, as well as cuticular pores, similar to those found in osmophores of *Restrepia* Kunth and *Scaphosepalum* Pfitzer (Pridgeon & Stern 1983, 1985), were occasionally observed (Davies et al. 2012). Davies & Turner (2004) have also examined a specimen identified as *M.* cf. *gracilis*. They observed conical papillae at the column, anther cap and lip. At the latter one occurred also obpyriform papillae and simple, 3–4-celled trichomes. In the specimen of *M. marginata* used in our research, the lip surface was papillose, covered with obpyriform papillae and 3-celled trichomes with clavate terminal cells. We have also observed residues of some kind of secretion on the apex of the lip. Singer & Koehler (2004) reported that there is no evidence for the presence of trichomes or any food rewards in the flowers of *M. marginata*, what clearly has been undermined by our results. This may indicate

that some identification error might have occurred. Davies & Winters (1998) reported that the lip of *M. picta* is lacking trichomes, but it is heavily clothed with villiform papillae. Davies & Stpiczyńska (2012) revealed that the conical, villiform or subclavate epidermal papillae located on the adaxial labellar surface function as secretory tissue. As our research support the result obtained by them in the case of papillae, it does not support it in case of the trichomes, since we have observed some. This may be caused either by the limited number of these, as in the sample examined by Davies & Winters (1998) they might be skipped, or by the incompatibility of the naming used.

In our research, the adaxial (inner) surface of the lip base and callus of *Maxillaria* cf. *mosenii* is glabrous. The surface towards the margins is rugose and at the margins densely covered with conical papillae, which are gathered in the three-dimensional clusters, resembling somewhat a sea anemone. As Davies et al. (2004) reported, *M. mosenii* Kraenzl. has conical labellar papillae and no presence of trichomes has been found. According to the authors, *M. mosenii* Kraenzl. var. *hatschbachii* (Schltr.) Hoehne possesses conical papillae at the column, anther cap as well as on the lip. The papillae contain proteins, but neither lipids nor starch.

Section *Rufescens* Christenson. Until now, six other species of section *Rufescens* have been examined. Wherever pseudopollen-forming trichomes occur, labellar papillae tend to be obpyriform (Davies & Turner 2004). However, this type of papilla may occur in the absence of pseudopollen hairs as in *M. rufescens* Lindl., *M. acutifolia* Lindl., *M. tenuibulba* E.A. Christenson and *M. moralesii* Carnevali & Atwood, all members of discussed section (Davies & Turner 2004). As Davies & Turner (2004) reported, the apices of these, in particular the larger, central papillae, are greatly distended and the papillae obtain a clavate profile, except *M. hedwigae* Hamer & Dodson, where the papillae tend to be somewhat fusiform or villiform. Moreover, the labella of *M. acutifolia* and *M. tenuibulba* produce a lipoidal secretion much like that found in the *M. acuminata* alliance and some members of the *M. discolor* alliance (Davies et al. 2003a,b). In *M. acutifolia*, labellar papillae are conical or obpyriform (Davies & Turner 2004), with secretory, unicellular, clavate papillae and hairs located centrally. The latter are coated in secreted material (Davies et al. 2012). According to Davies & Turner (2004), *M. hedwigae* Hamer & Dodson possesses fusiform and villiform papillae on the lip surface, *M. moralesii* Carnevali & Atwood conical, obpyriform and clavate ones and *M. tenuibulba* E.A. Christenson obpyriform ones at the column and anther cap and conical, obpyriform and clavate papillae on the lip. Davies et al. (2012) also mentioned the presence of labellar hairs and a detached cuticle on the papillae, but cuticular pores were absent. In *M. chacoensis*, the epidermal papillae were clavate or villiform and the surface secretion scant (Davies et al. 2012). According to the same authors, in *M. richii*, the adaxial, secretory epidermis comprised unicellular, secretory, villiform or clavate papillae or trichomes copiously coated (more so than in *M. acutifolia*) with secretion. The presence of obpyriform papillae seem to be constant, but again, it is not a unique feature of this section.

Section *Urceolatae* Christenson. To date, four other members have been of the section *Urceolatae*. According to Singer & Koehler (2004), *M. acicularis* Herb. ex Lindl and *M. juergensii* Schltr. possess neither papillae nor trichomes. In *M. seidelii* Pabst, conical and obpyriform papillae occur at the column, conical, obpyriform and villiform ones at the anther cap and conical ones on the lip (Davies & Turner 2004). In *M. vernicosa* Barb. Rodr., conical papillae occur at the column, anther cap and lip surface (Davies & Turner 2004). In *M. vitelliniflora*, the apex of the lip is covered with obpyriform papillae. The lip surface is partly papillose. Its margins are

clothed with conical and villiform papillae. Available literature data seem to support the obtained results. According to Davies & Turner (2004), conical and obpyriform papillae occur on the column and anther cap and the lip is covered with conical papillae. As Singer & Koehler (2004) reported, the flowers of this species are rewardless, what is upheld by the results presented above. Conical papillae are most common. The glabrous lip is not common but still not unique to this section.

'Grandiflora Complex'. So far, nine members of the informal complex 'Grandiflora' have been studied. *M. elegantula* Rolfe possesses conical and villiform papillae at the column, obpyriform papillae and moniliform trichomes on the lip (Davies & Turner 2004). *M. fucata* Rchb. f. has obpyriform papillae and moniliform trichomes on the lip surface, which consist of fusiform component cells (Davies & Turner 2004). In general, the lip surface is largely papillose and trichomes are scanty (Davies et al. 2000). In *M. huebschii*, the uniseriate, moniliform trichomes also occur mainly on the adaxial surface of the lip and are composed of up to seven, spherical, component cells. Those towards the base of the trichome, however, are elliptical or lemon-shaped (Davies et al. 2013). In *M. grandis*, pseudopollen is distributed predominantly on the adaxial surface of the labellum, but some pseudopollen is also present on the abaxial surface (Davies et al. 2013). According to Davies et al. (2013), it is formed by fragmentation of hairs arising from the papillose epidermis. According to the same authors, both moniliform trichomes and individual component cells or chains of cells are called pseudopollen when they become detached from the labellum and form farina. Each uniseriate, pseudopollen-forming, moniliform trichome usually consists of five to seven spherical component cells. In *M. roseola*, pseudopollen-forming, moniliform trichomes arise as tufts from the adaxial, papillose, labellar epidermis, which consists of rounded to obpyriform papillae. The basal cells of each trichome are elongate, whereas those towards the trichome apex are more or less spherical. In *M. irrorata* Rchb. f., conical papillae have been observed at the column and anther cap, at the surface of the latter also villiform, on the lip obpyriform papillae and moniliform trichomes were found (Davies & Turner 2004). In *M. johniana* Kraenzl., *M.* cf. *lehmanii* Rchb. f. and *M. sanderiana* Rchb. f., obpyriform and moniliform trichomes were observed on the lip, according to the same authors. It is clearly shown that the presence of obpyriform and moniliform trichomes is typical of members of the 'Grandiflora Complex'. The presence of this particular type of the papillae is not surprising, since wherever pseudopollen-forming trichomes occur, labellar papillae tend to be obpyriform (Davies & Turner 2004). In our research, we have found other additional features such as secretion, conical and villiform papillae (in both *M. striata* and *M. molitor*) and elliptical papillae (in *M. molitor*).

Conclusion

Glabrous labella are not common in *Maxillaria* and tend to occur mainly in species assigned to the *M. cucullata* alliance (Davies & Turner 2004). As Davies & Turner (2004) reported, the upper surface of the lip of *M. chartacifolia* Ames & C. Schweinf. is glabrous, whereas the lower is papillose and covered with obpyriform papillae. In members of the *M. rufescens* alliance, the obpyriform papillae have been found on the labellar surface, whereas those towards the center of the lip are clavate and much larger with distended apices (Davies & Turner 2004). As Davies & Turner (2004) predicted, multiseriate trichomes, which have been known so far only in *M. camaridii* Rchb. f. and *M. pulchra* (Schltr.) L.O. Williams ex Correll, might be more

important as taxonomic characters. In recent years, Davies has become less convinced that the multiseriate 'hairs' of *M. camaridii* are trichomes, but merely projections from the labellar surface, which migth be the reason why they bear papillae (K.L. Davies, pers. comm. 2016).

Species examined in this study have been classified in 11 formal sections and one complex. In all taxa, the presence of the papillae of various shapes has been demonstrated (Table 2). The most common shape of the papillae is obpyriform and those have been noticed on the labellar surface of 15 species including *M. callichroma* and *M. luteoalba* (both from sect. *Aggregatae* Pfitzer), *M. reichenheimiana* (sect. *Arachnites* Christenson), *M. praestans* (sect. *Cucullatae* Christenson), *M. graminifolia* and *M. ramosa* (both placed in sect. *Ebulbes* Pfitzer), *M. ponerantha* (sect. *Erectae* Pfitzer), *M. molitor* (probably sect. *Maxillaria* Ruiz & Pav.), *M. ochroleuca* (sect. *Multiflorae* Christenson), *M. aurea* and *M. purpureolabia* (both placed in sect. *Ornithidium* (Salisb.) Christenson), *M. marginata* (sect. *Repentes* Pfitzer), *M. rufescens* (sect. *Rufescens* Christenson), *M. vitelliniflora* (sect. *Urceolatae* Christenson) and *M. striata* ('Grandiflora Complex'). Conical papillae have been found on the lip surface of 10 species: *Maxillaria cucullata* (sect. *Cucullatae*), *M. graminifolia* (sect. *Ebulbes*), *M. ponerantha* (sect. *Erectae*), *M. molitor* (probably sect. *Maxillaria*), *M. aurea* and *M. purpureolabia* (both placed in sect. *Ornithidium*), *M. picta* and *M.* cf. *mosenii* (both from sect. *Repentes*), *M. vitelliniflora* (classified most probably in section *Urceolatae* Christenson) and *M. striata* ('Grandiflora Complex'). Villiform papillae were observed also in 10 species: *M. praestans* (sect. *Cucullatae*), *M. graminifolia* (sect. *Ebulbes*), *M. ponerantha* and *M. tenuifolia* (both most probably from sect. *Erectae*), *M. molitor* (probably sect. *Maxillaria*), *M. aurea* (sect. *Ornithidium*), *M. picta* (sect. *Repentes*), *M. vitelliniflora* (sect. *Urceolatae*), *M. pterocarpa* (probably sect. *Trigonae* Christenson), *M. striata* ('Grandiflora Complex'). Clavate papillae have been noted on the lip of only 4 species: *Maxillaria callichroma* (sect. *Aggregatae*), *M. ochroleuca* (sect. *Multiflorae*), *M. picta* (sect. *Repentes*), *M. rufescens* (sect. *Rufescens*). Elliptical papillae occurred in one single species, *M. striata* ('Grandiflora Complex'). Trichomes seem to be limited to the species from 5 sections: *M. callichroma* and *M. luteoalba* (sect. *Aggregatae*), *M. reichenheimiana* (sect. *Arachnites*), *M. graminifolia* (sect. *Ebulbes*), *M. ochroleuca* (sect. *Multiflorae*), *M. marginata* and *M. picta* (sect. *Repentes*). Reward in the form of pseudopollen has been recorded in *M. molitor* and *M. striata* (both from 'Grandiflora Complex'). Residues of some kind of secretion we observed on the lip surface of *M. callichroma* (sect. *Aggregatae*), *M. graminifolia* (sect. *Ebulbes*), *M. tenuifolia* (probably sect. *Erectae*), *M. molitor* (probably sect. *Maxillaria*), *M. marginata* (sect. *Repentes*), *M. pterocarpa* (probably sect. *Trigonae*) and *M. striata* ('Grandiflora Complex'). Papillae occurred also on the outer surface of the lip of *M. graminifolia* (sect. *Ebulbes*), *M. molitor* (probably sect. *Maxillaria*), *M. aurea* and *M. purpureolabia* (both placed in sect. *Ornithidium*) and *M. striata* ('Grandiflora Complex').

The papillae of *Maxillaria* are highly adaptable and fulfil a variety of functions (Davies & Turner 2004). They play a role as attractants and guides for visiting insects using a combination of visual, olfactory and tactile cues. Since some of them are rich in aromatic amino acids, they can provide rewards in the form of nectar or a viscid wax-like material or may be a part of protection from desiccation and herbivorous insects. The exact function of the papillae in a particular species can only be established for certain by observing how pollinators respond to them in the field (Davies & Turner 2004). Until such data will be collected, morphological studies can only provide partial answers.

Table 2. Summary of structures occurring on labellar epidermises of examined species. *Species unplaced in any known section by Christenson (2002, 2013)

	Papillae on the bottom side	Pseudopollen	Secretion on the inner surface	Trichomes (inner surface)	Papillae (inner surface)				
					Conical	Clavate	Obpyriform	Elliptical	Villiform
Section *Aggregatae*									
Maxillaria callichroma			×	×		×	×		
Maxillaria luteoalba				×			×		
Maxillaria cf. *setigera**		×		×			×		
Maxillaria cf. *triloris**				×			×		
Section *Arachnites*									
Maxillaria reichenheimiana				×			×		
Maxillaria buchtienii				×	×		×		
Maxillaria fractiflexa				×	×				×
Maxillaria lepidota				×			×		
Maxillaria lindleyana					×		×		×
Maxillaria longissima				×			×		
Maxillaria pseudoreichenheimiana				×			×		
Section *Cucullatae*									
Maxillaria cucullata					×				
Maxillaria praestans							×		×
Section *Ebulbes*									
Maxillaria graminifolia	×		×	×	×		×		×
Maxillaria ramosa							×		
Section *Erectae*									
Maxillaria ponerantha					×		×		×
*Maxillaria tenuifolia**			×						×
Maxillaria procurrens					×				
Section *Multiflorae*									
Maxillaria ochroleuca				×		×	×		
Section *Ornithidium*									
Maxillaria aurea	×				×		×		×
Maxillaria purpureolabia	×				×		×		
Section *Repentes*									
Maxillaria marginata			×	×			×		
Maxillaria picta				×	×	×			×
Maxillaria cf. *mosenii**					×				
Section *Rufescens*									
Maxillaria rufescens						×	×		
Section *Urceolatae*									
Maxillaria vitelliniflora					×		×		×
Section *Trigonae*									
*Maxillaria pterocarpa**			×						×
'Grandiflora Complex'									
*Maxillaria striata**	×	×	×		×		×		×
*Maxillaria molitor**	×	×	×		×		×	×	×

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