

## Pseudopollen and Food-hair Diversity in *Polystachya* Hook. (Orchidaceae)

K. L. DAVIES<sup>1</sup>, D. L. ROBERTS<sup>2</sup> and M. P. TURNER<sup>3</sup>

<sup>1</sup>Department of Earth Sciences, Cardiff University, PO Box 914, Cardiff CF10 3YE, UK, <sup>2</sup>Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AB, UK and <sup>3</sup>School of Biosciences, Cardiff University, PO Box 915, Cardiff CF10 3TL, UK

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Labellar food-hairs in *Polystachya* Hook. exhibit considerable morphological diversity. The commonest type of trichome is uniseriate, two to four-celled, with a clavate or subclavate terminal cell. This type occurs amongst representatives of most sections examined. Other trichomes are bristle-like with tapering or fusiform terminal cells, whereas representatives of section *Polystachya* have uniseriate, moniliform trichomes that fragment with the formation of rounded or elliptical component cells. Most contain protein and, while some contain starch, lipid is invariably absent. The presence of particular types of labellar trichomes does not coincide with variations in vegetative morphology. Thus, current taxonomic treatment of the genus indicates that trichome types, with perhaps the sole exception of moniliform, pseudopollen-forming hairs found in section *Polystachya* only, have limited taxonomic value. However, the remarkable similarity between pseudopollen-forming hairs of *Polystachya* and those of the Neotropical genus *Maxillaria* in terms of morphology, cellular dimensions and food content indicates that pseudopollen may have arisen several times and evolved in response to similar pollinator pressures.

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**Key words:** Histochemistry, taxonomy, low-vacuum scanning electron microscopy, pollination, trichomes.

### INTRODUCTION

Pseudopollen occurs as a yellow-white farinaceous powder on the labella of certain orchids, such as *Maxillaria*, and is formed by the fragmentation of multicellular trichomes with cells rich in food reserves (Davies *et al.*, 2000). These reserves have variously been described as starch, oil deposits and aleurone grains (van der Pijl and Dodson, 1969). Hitherto, pseudopollen has been reported for relatively few orchid genera, most notably *Polystachya* Hook. (Porsch, 1906; Beck, 1914), *Maxillaria* Ruiz & Pav. (Janse, 1886; Porsch, 1905; van der Pijl and Dodson, 1969; Davies and Winters, 1998; Davies *et al.*, 2000) and certain species of *Eria* Lindl. and *Dendrobium* Sw., such as *E. monostachya*, *E. paniculata* (Beck, 1914) and *D. unicum* (Kjellsson and Rasmussen, 1987). However, detailed studies of pseudopollen have been largely confined to *Maxillaria* (Davies *et al.*, 2000).

Pollinators visit flowers in search of oils, floral fragrances, pollen or floral nectar. Some flowers simulate carrion and attract dipteran pollinators seeking breeding sites. In epidendroid orchids, however, pollen occurs in discrete masses within pollinia and is thus generally inaccessible to visiting insects. Nectar is the most common reward amongst members of the Orchidaceae (van der Pijl and Dodson, 1969; Arditti, 1992; Dressler, 1993). Remarkably, however, nectar is absent from those species that produce pseudopollen (van der Pijl and Dodson, 1969). Thus, potential pollinators are initially attracted to the flower by means of visual or olfactory stimuli (Proctor *et al.*, 1996). On alighting, the insect is enticed further into the flower by a reward of pseudopollen. Even so, approximately

one-third of orchid species have evolved pollination mechanisms whereby the pollinator receives no reward whatsoever (van der Pijl and Dodson, 1969; Ackerman, 1984).

At present, little is known about the pollination and reproductive biology of pseudopollen-producing species of *Polystachya*, *Eria* and *Maxillaria*, although it is likely that all are pollinated by bees (Dodson and Frymire, 1961; Dodson, 1962; Goss, 1977; Dressler, 1993; Pettersson and Nilsson, 1993). Indeed, bees have actually been observed collecting pseudopollen from both *Maxillaria sandariana* and *M. grandiflora* (Dodson and Frymire, 1961; Dodson, 1962). Dressler (1990) suggested that the dominant pollination system in *Polystachya* involves the rewarding of small bees with pseudopollen. A detailed description of the pollination of *Polystachya flavescens* (Lindl.) J.J. Sm. (Goss, 1977) supports this claim in that pseudopollen-producing, moniliform hairs are present, but nectar is lacking. In this species, small female halictid bees (*Dialictus* aff. *creberrimus*) were observed to land on the lateral sepals and labellum. After orientating themselves parallel to the labellar axis, they faced the upturned portion of the mid-lobe and crawled inside the flower, heading towards the base of the labellum. They collected and stored pseudopollen, which extends the entire length of the disc midline, in their scopae. On backing out from the flower, the thorax of the bee maintained contact with the column resulting in the removal and/or deposition of pollinia. In contrast, Pettersson and Nilsson (1993) reported that *Polystachya rosea* Ridl. from Madagascar neither offers a reward of pseudopollen nor mimics any other food plant. Instead, pollination here is solely by means of deception achieved by extensive floral colour polymorphisms and

absence of odour, both of which reduce recognition and prevent insects from avoiding flowers that provide no reward. Again, halictid bees (*Lasioglossum emirnense* and *L. nitididorsatum*) are the pollinators. Male bees may use orchid plants as landmarks when seeking mates, thereby contributing to their reproductive success by attracting females to a potential food source and simultaneously benefiting the orchid population.

The occurrence of pseudopollen in *Polystachya*, *Maxillaria* and *Eria* is also noteworthy for the following reason. The greatest diversity of *Polystachya* species occurs in tropical Africa and Madagascar, although a few are pantropical or found in southern Africa, Asia, Australia or Central and South America. *Maxillaria* is a Neotropical genus distributed throughout the American tropics and subtropics, whereas *Eria* is restricted to Asia. Distribution, along with their phylogenetic positions in the Orchidaceae based on DNA sequence data (Cameron *et al.*, 1999), would indicate that the occurrence of pseudopollen is polyphyletic and may have evolved independently on these continents. Comparative studies of pseudopollen would allow us to better understand this process.

Dressler (1990) assigned both Polystachyaeae and Maxillarieae to Vandoideae but placed Eriinae (tribe Epidendreae) in Epidendroideae. Moreover, he believed that 'the Polystachyaeae may be more closely related to the Vandaeae than to the primarily cormous Maxillarieae and Cymbidieae'. In contrast, Cameron *et al.* (1999) considered *Polystachya*, *Maxillaria* and *Eria* to be epidendroid genera. Whereas both Maxillarieae and Podochileae (including *Eria*) are considered monophyletic, the Epidendreae (including *Polystachya*) are grossly polyphyletic (Cameron *et al.*, 1999).

Davies and co-workers (Davies and Winters, 1998; Davies *et al.*, 2000) showed that the exact form of pseudopollen in *Maxillaria* has potential taxonomic value. Pseudopollen in that genus is formed by the fragmentation of multicellular, uniseriate, moniliform trichomes into component cells. Such cells are rounded or lemon-shaped in the *M. grandiflora* complex, whereas in *M. longissima* Lindl. they are fusiform. In those species formerly assigned to *Dicrypta* Lindl., such as *M. violaceopunctata* Rehb.f., cells are often cylindrical (K. L. Davies, unpubl. res.). In contrast, the trichomes of *M. splendens* Poepp. & Endl., *M. ochroleuca* Lodd. ex Lindl. and *M. chlorantha* Lindl., all assigned to the *M. splendens* alliance, are smaller, comprising a few cells only. The food reserve in pseudopollen cells of the *M. grandiflora* complex is largely protein, although starch and lipid may also be present (Davies *et al.*, 2000).

Van der Pijl and Dodson (1969) distinguished between pseudopollen and food-hairs solely on the grounds that food-hairs remain intact in moniliform strings as in *Polystachya luteola* (Beck, 1914) and *P. lineata* (Porsch, 1906), whereas pseudopollen is formed by trichome fragmentation. Most *Polystachya* species are thought to produce pseudopollen (van der Pijl and Dodson, 1969).

The purpose of this paper is to describe the diversity of labellar trichomes found in *Polystachya* and to determine the chemical nature of food reserves they may contain. Comparative studies of pseudopollen from *Polystachya*

species differing in their vegetative morphology would enable assessment of the potential taxonomic value of pseudopollen. Comparisons with *Maxillaria* pseudopollen could provide a useful insight into the evolution of this character on two different continents.

## MATERIALS AND METHODS

The labella of 18 species of *Polystachya* (Table 1), derived from seven different sections (Kraenzlin, 1926; Summerhayes, 1942, 1947; Brenan *et al.*, 1954; Cribb, 1978; Podzorski and Cribb, 1979) were examined. The authorities for plant names follow Brummitt and Powell (1992).

Herbarium specimens were prepared and deposited at the National Museum and Gallery of Wales, Cardiff, UK, under the general accession number NMW. V. 2002. 001.

### Low-vacuum electron microscopy

Labella were removed, attached to aluminium stubs with double-sided, sticky carbon tabs and examined immediately by means of back-scattered electron-imaging using a low-vacuum scanning electron microscope (JSM 5200) in low vacuum mode at an accelerating voltage of 20–25 kV.

### Histochemistry

Labellar scrapings were tested for starch using a dilute iodine/potassium iodide (IKI) solution, for lipids using a saturated ethanolic solution of Sudan III and for proteins using a modified xanthoproteic test (Purvis *et al.*, 1964), which involved treating the material with concentrated nitric acid followed by an excess of 10 % (w/v) aqueous potassium hydroxide solution. Blue-black and red reaction products and orange nitroso derivatives demonstrated the presence of starch, lipids and aromatic amino acids, respectively.

## RESULTS

Generally, trichomes in *Polystachya* are uniseriate and two to four-celled with subclavate to clavate terminal cells. Such trichomes occur in *P. cultriformis*, *P. maculata* (section *Cultriformes*) (Fig. 1A and B), *P. caloglossa* and *P. bennettiana* (section *Caulescentes*) (Fig. 1C). Similar structures also occur in *P. campyloglossa*, *P. lawrenceana* (section *Affines*) (Fig. 1D) and *P. eurygnatha* (section *Superpositae*), whereas trichomes virtually identical to those of *P. cultriformis* are found in *P. cf. ottoniana* (section *Humiles*).

Similar trichomes, but with relatively wider subterminal cells, also occur in *P. woosnamii* (section *Polychaete*). However, the possession of simple hairs with clavate tips by species assigned to different sections because of their diverse vegetative morphology would indicate that these hairs are of limited taxonomic value.

Labellar hairs of *P. cultriformis* and *P. piersii* (Fig. 1A) comprise two cells only, a subclavate to clavate terminal

Table 1. Results of histochemical analyses based on light microscopy observations

Species	Section	Accession number	Foods present in trichomes		
			Protein	Starch	Lipid
<i>Polystachya cultriformis</i> (Thouars) Spreng.	Cultriformes Kraenzl.	S19970040	+	±	–
<i>P. cf. cultriformis</i> (Thouars) Spreng.	Cultriformes Kraenzl.	S19990327	+	+	–
<i>P. maculata</i> P.J. Cribb	Cultriformes Kraenzl.	S19950363	±	±	–
<i>P. bennettiana</i> Rchb.f.	Caulescentes Kraenzl.	S19980098	+	–	–
<i>P. caloglossa</i> Rchb.f.	Caulescentes Kraenzl.	S19970040	+	±	–
<i>P. concreta</i> (Jacq.) Garay & H.R. Sweet	<i>Polystachya</i> Rchb.f.	S19960045	+	–	–
<i>P. foliosa</i> (Hook.f.) Rchb.f.	<i>Polystachya</i> Rchb.f.	S19950362	+	+	–
<i>P. tessellata</i> Lindl.	<i>Polystachya</i> Rchb.f.	S19950983	+	+	–
<i>P. elegans</i> Rchb.f.	<i>Polychaete</i> Cribb	S19970041	±	±	–
<i>P. seticaulis</i> Rendle	<i>Polychaete</i> Cribb	*	†	†	†
<i>P. woosnamii</i> Rendle	<i>Polychaete</i> Cribb	*	+	+	–
<i>P. eurygnatha</i> Summerh.	<i>Superpositae</i> Kraenzl.	S19980100	+	±	–
<i>P. spatella</i> Kraenzl.	<i>Superpositae</i> Kraenzl.	S19960046	+	–	–
<i>P. cf. ottoniana</i> Rchb.f.	<i>Humiles</i> Summerh.	S20010097	+	–	–
<i>P. campyloglossa</i> Rolfe	<i>Affines</i> Kraenzl.	S19970039	+	+	–
<i>P. lawrenceana</i> Kraenzl.	<i>Affines</i> Kraenzl.	S19970042	+	+	–
<i>P. pubescens</i> (Lindl.) Rchb.f.	<i>Affines</i> Kraenzl.	S19940364	+	–	–
<i>P. aff. villosa</i> Rolfe	<i>Affines</i> Kraenzl.	S19960049	+	+	–
<i>P. piersii</i> P.J. Cribb	<i>Affines</i> Kraenzl.	S20010545	+	–	–

+ and – indicate presence and absence, respectively, of food substances, whereas ± indicates slight but unconvincing evidence for the presence of a particular food substance based on light microscopy observations.

\*, Specimens lacked an accession number.

†, Insufficient material was available for food tests.

cell and a stalk cell. These cells become detached from the labellum as bicellular units.

Other types of labellar hairs also occur within the genus. For example, in *P. elegans*, *P. woosnamii* (section *Polychaete*) (Fig. 2A) and *P. spatella* (section *Superpositae*) (Fig. 2B), they are uniseriate and bristle-like, and the component cells are longer than they are wide, with tapering terminal cells. Long, narrow, uniseriate, two to three-celled hairs also occur in *P. pubescens* (section *Affines*), but here the terminal cells are more or less fusiform (Fig. 2E), whereas *P. aff. villosa* (section *Affines*) has simple, unicellular, clavate hairs (Fig. 2C and D).

Finally, all representatives of section *Polystachya* examined were found to possess multicellular, uniseriate, moniliform trichomes that fragment to form unicellular units (Figs 2F and 3A–D). Their component cells are typically rounded, ellipsoid or lemon-shaped with polar papillae (Fig. 3B), and are remarkably similar to those found in members of the *M. grandiflora* complex (Davies *et al.*, 2000).

Labella of representatives of all sections examined were papillose. Papillae were often obpyriform to shortly conical (Figs 2A–C, F and 3D), but in *P. woosnamii* marginal papillae tended to be longer and villiform.

Labellar parenchyma of a number of species (e.g. *P. bennettiana*, *P. cf. ottoniana*, *P. woosnamii*) contained numerous spherical idioblasts with raphides.

Histochemical analyses revealed that the trichomes of most of the species examined, regardless of section and vegetative morphology, stained positively for aromatic amino acids. Conversely, lipids were invariably absent, and starch was often (but not always) detectable

(Table 1). In *P. foliosa*, starch was observed within numerous small plastids, whereas in certain other species (e.g. *P. pubescens*) starch was absent from the trichomes although present in other labellar epidermal cells. Frequently, these labellar cells were also rich in protein as was the mucilage secreted upon the labellum (e.g. *P. campyloglossa*).

## DISCUSSION

*Polystachya* Hook. is a large and complex genus of over 200 species. Although some species occur in Madagascar, Asia, Australia and Central and South America, most are confined to Africa. No satisfactory infrageneric classification currently exists, but Kraenzlin (1926) divided the genus on morphological grounds into 12 sections that have generally been adopted by later authors (e.g. la Croix *et al.*, 1983, 1991). Since then, a further five sections have been added (Summerhayes, 1942, 1947; Brenan *et al.*, 1954; Cribb, 1978; Podzorski and Cribb, 1979). Seven of these sections are represented in the present paper. They are distinguished as follows:

### *Section Cultriformes Kraenzl.*

Pseudobulbs terete, conical or ovoid, bilaterally compressed, usually single-noded with one terminal, erect or suberect, linear, oblong or obovate leaf. Inflorescence apical, racemose to paniculate with few to many, medium to large, fleshy flowers that are resupinate or not. Lip three-lobed.

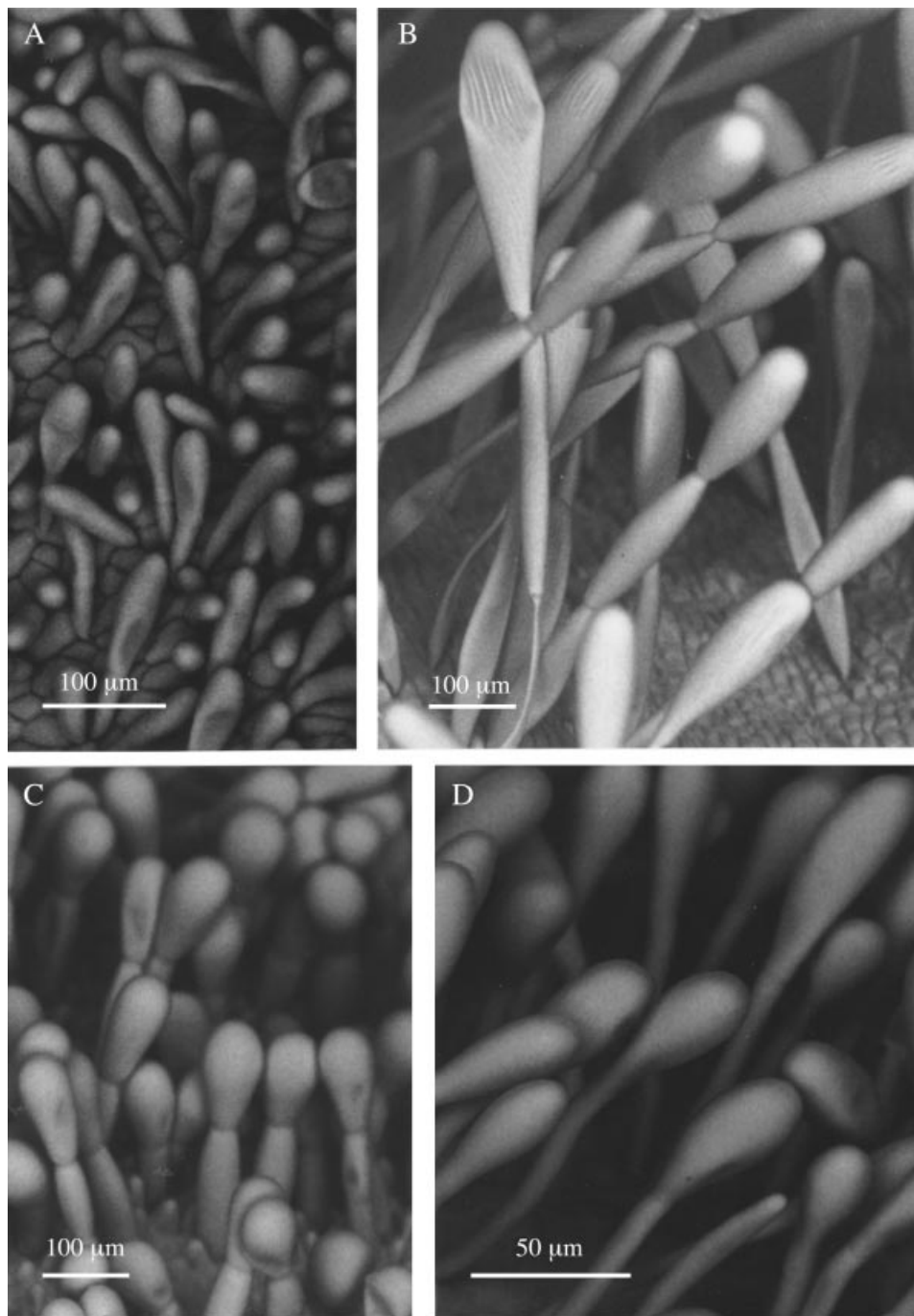


FIG. 1. Low-vacuum scanning electron micrographs of *Polystachya* labella showing a variety of uniseriate, two to four-celled trichomes with subclavate to clavate terminal cells. A, Bicellular trichomes of *P. cultriformis* (section *Cultriformes*) comprising a clavate terminal cell and stalk cell. B, Three to four-celled trichomes of *P. maculata* (section *Cultriformes*), of distinctly articulate appearance. C and D, Bicellular, uniseriate trichomes of *P. caloglossa* (section *Caulescentes*) (C) and *P. campyloglossa* (section *Affines*) (D) comprising clavate terminal cell with wide or narrow stalk cell, respectively.

#### *Section Caulescentes Kraenzl.*

Stems cylindrical and cane-like, not swollen to form pseudobulbs. Leafy in upper part but lower parts covered with leaf sheaths. Inflorescence racemose or paniculate and many-flowered. Flowers small to medium. Lip three-lobed.

#### *Section Polystachya Kraenzl.*

Pseudobulbs well-developed but often obscure and covered by leaf bases. Leaves oblanceolate to obovate and deciduous. Inflorescence racemose or paniculate and many-flowered. Flowers small to medium, fleshy, glabrous or

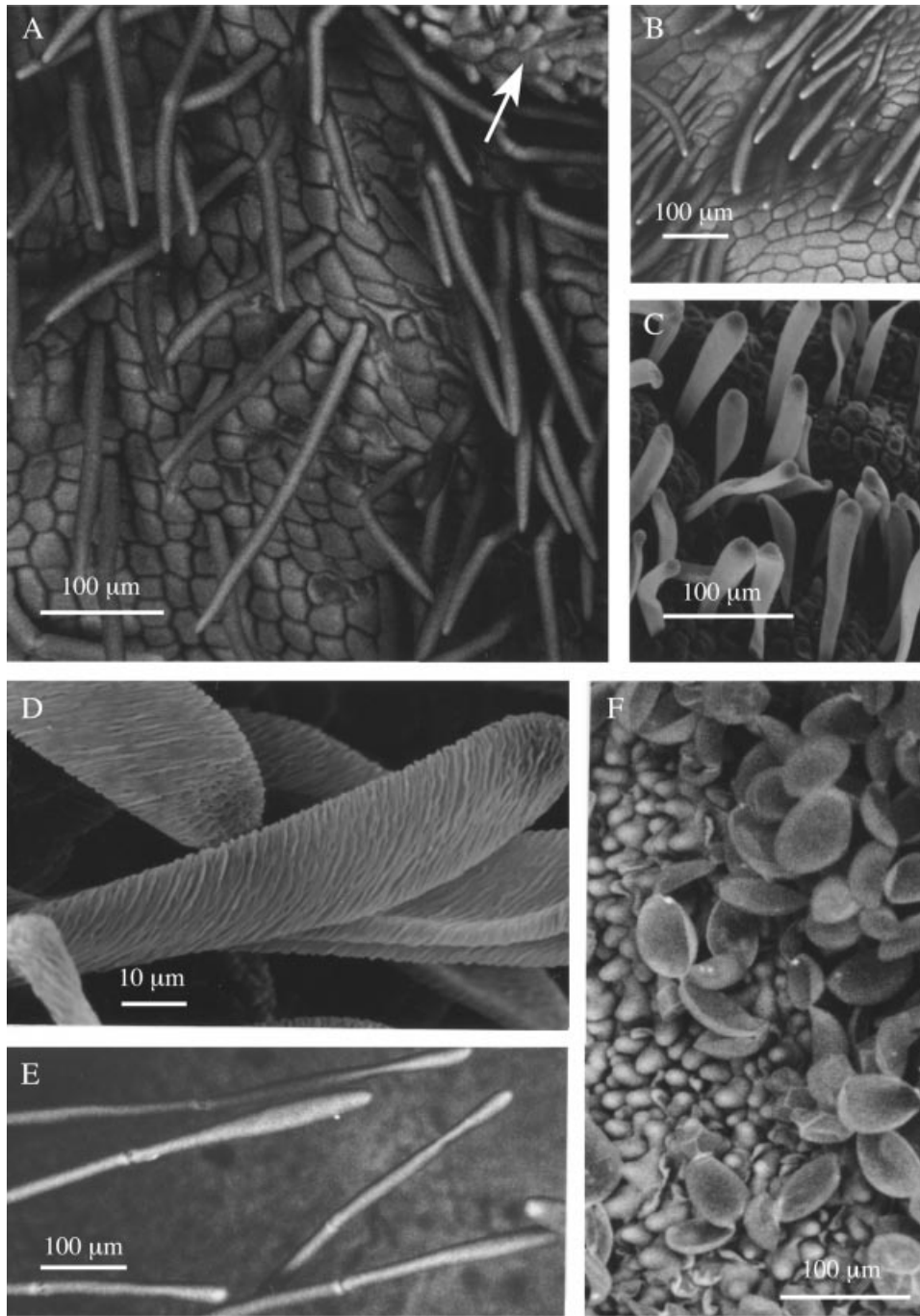


FIG. 2. A and B, Uniseriate, bristle-like trichomes of *P. elegans* (section *Polychaete*) (A) and *P. spatella* (section *Superpositae*) (B). Note conical papillae (arrow) and tapering terminal cells of trichomes. C and D, Simple, unicellular labellar trichomes of *P. aff. villosa* (section *Affines*). E, Narrow, uniseriate trichomes of *P. pubescens* (section *Affines*). F, Moniliform trichomes of *P. tessellata* (section *Polystachya*) with rounded component cells that become detached forming pseudopollen. Note also the shortly conical papillae with rounded apices.

hairy. Lip variously trilobed, ecallose, with an obscure central callus or more or less densely farinaceous.

#### *Section Polychaete P.J. Cribb*

Pseudobulbs well-developed, conical to subcylindrical with several linear to lanceolate leaves. Inflorescence erect,

densely many-flowered. Flowers small and glabrous with setiform bracts larger than the flowers. Lip three-lobed.

#### *Section Superpositae Kraenzl.*

Pseudobulbs superposed, cylindrical or fusiform with several nodes from which new growths arise, sometimes forming long chains. Leaves terminal on new pseudobulbs.

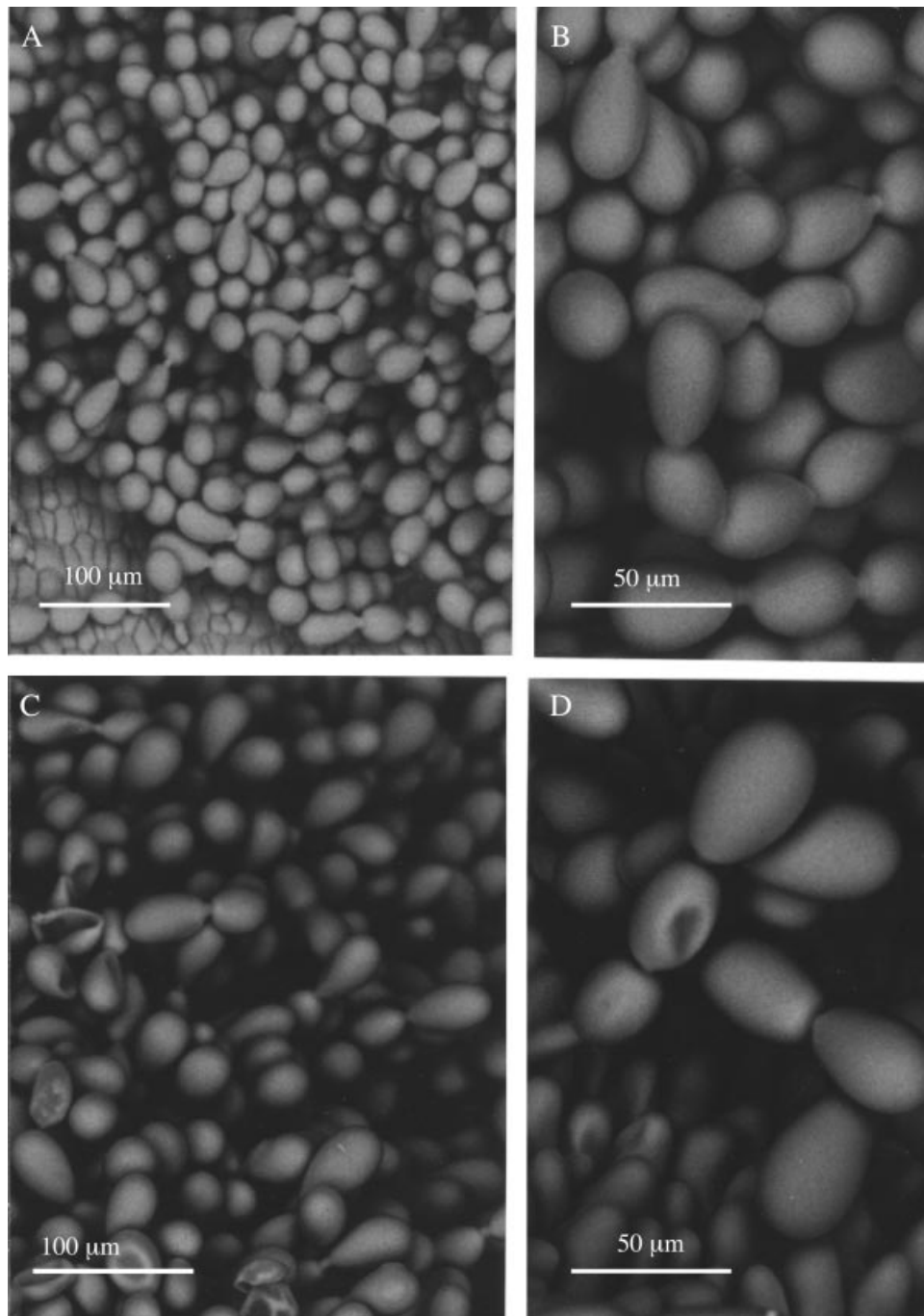


FIG. 3. Uniseriate, moniliform, pseudopollen-producing trichomes common in section *Polystachya*. A, Moniliform trichomes of *P. foliosa*. B, Detail of A showing ellipsoid component cells with apical papillae. C and D, Similar studies of *P. concreta*. Note also the obpyriform labellar papillae.

Inflorescence racemose or paniculate, several to many-flowered. Flowers small to medium, glabrous or hairy. Lip three-lobed.

*Section Humiles Summerh.*

Plants dwarf with well-developed, clustered, two to three-leaved pseudobulbs. Leaves subapical. Inflorescence one to few-flowered with relatively large, glabrous or sparsely

hairy flowers that are often yellowish or yellowish green, and turn black on pressing. Mentum prominent. Floral bracts slender and inconspicuous. Lip three-lobed.

*Section Affines Kraenzl.*

A large and confusing section. Pseudobulbs clustered, ovoid to conical, erect or bilaterally compressed and adpressed to substratum; two-leaved at apex. Leaves

lanceolate or elliptic and usually present at flowering. Flowers, bracts and peduncle pubescent. Inflorescence usually densely flowered, erect or arcuate with few to many, medium to large, white, green, yellow, orange or pink flowers with fleshy, strongly recurved and trilobed labella, often with a glabrous to clavately hairy callus between the side lobes. Labella are impossible to flatten without breaking. Mentum obscure to prominent.

Despite enormous diversity in the form of food-hairs within any given section of the genus, at least one representative of all sections examined, except section *Polystachya*, possesses uniseriate, two to four-celled trichomes with subclavate to clavate terminal cells. This was by far the commonest type of labellar hair observed. Moreover, in *P. cultriformis* and *P. piersii*, the two-celled food-hairs become detached at their bases, forming bicellular units which may function as pseudopollen. In some ways, these trichomes resemble the small, sparse, few-celled hairs found on the labella of species of the *Maxillaria splendens* alliance. The current taxonomic treatment of *Polystachya* would indicate that, owing to their ubiquity, the taxonomic value of clavate hairs is limited in that their presence does not generally coincide perfectly with other characters related to vegetative morphology. Nevertheless, all species of section *Polystachya* studied were united in their possession of pseudopollen. However, the term 'pseudopollen' has often been misapplied (Davies and Winters, 1998; Davies *et al.*, 2000). Contrary to previous reports, where it had obviously been used in a general sense to include food-hairs also (e.g. van der Pijl and Dodson, 1969), true pseudopollen appears to be produced in relatively few species of *Polystachya*. Those species that produce pseudopollen are all confined to section *Polystachya*. True pseudopollen is formed by the fragmentation of uniseriate, moniliform trichomes into rounded, elliptic or lemon-shaped individual component cells and these are thus distinguished from other types of food-hairs that consist of relatively few cells and become detached as a unit from the labellum.

However, the pseudopollen of *Dendrobium unicum* Seidenf. is different and consists of 3–12-celled trichomes comprising a stalk cell and a spherical, multicellular 'head' (Kjellsson and Rasmussen, 1987). These fragment forming unicellular or four-celled units or granulae which are collected by insects. To date, there is no evidence that the cells contain elevated levels of food substances but Kjellsson and Rasmussen (1987) argue that the granulae may act as 'deceptive pollen dummies' even if food reserves are absent.

In *Polystachya*, the process of pseudopollen formation, the morphology of pseudopollen-producing trichomes and their component cells, and the dimensions of the latter (despite the much smaller flowers of *Polystachya* species), are remarkably similar to those observed for the *M. grandiflora* complex (Davies *et al.*, 2000). Furthermore, histochemistry revealed that the main food substance found in both genera (as well as other types of food-hairs in *Polystachya*) is protein, whereas lipid tends to be absent. Although starch is generally present in *Maxillaria*, this is not always the case in *Polystachya*. However, when starch

was observed in *Polystachya* (e.g. in *P. foliosa*), it occurred in small plastids, not unlike the amyloplasts described for the pseudopollen of *Maxillaria*. Moreover, in *Maxillaria*, each pseudopollen component cell contains a single protein body that occupies most of the cell (Davies *et al.*, 2000). Protein in the pseudopollen of *Polystachya* species, however, is distributed throughout the cytoplasm, and the relative intensity of the xanthoproteic reaction would indicate that aromatic amino acids are usually present at lower concentrations than in *Maxillaria*.

In view of the striking similarity between the pseudopollen of species of African *Polystachya* and Central American *Maxillaria*, and the fact that both genera are bee-pollinated (Dodson and Frymire, 1961; Dodson, 1962, Dressler, 1993), it would appear that this character is polyphyletic (Cameron *et al.*, 1999) and that it evolved independently but in a similar manner on both continents. Some species, such as *P. concreta*, are found in both Africa and the tropical Americas, and a more detailed comparative study of pseudopollen, using plants obtained from both sources, may shed further light on how the evolution of this character occurred.

Davies *et al.* (2000) have shown that several different types of pseudopollen-producing trichomes exist in *Maxillaria* and that other labellar features such as trichomes, papillae, etc. show great diversity (Davies and Winters, 1998). Similar trichome diversity occurs in *Polystachya*. At present, it is impossible to tell whether pseudopollen-forming hairs are derived from simple clavate hairs in *Polystachya*. However, the recent discovery of trichomes intermediate between simple, uniseriate, multicellular hairs and moniliform, pseudopollen-producing hairs in certain species of *Maxillaria* (K. L. Davies, unpubl. res.) would indicate that pseudopollen developed in that genus as trichomes became more elaborate.

As in *Maxillaria*, a paucity of recorded field observations makes it impossible to determine the efficiency of pseudopollen in attracting insects and to assess whether different types of food hairs attract specific pollinators. However, the occurrence of starch, in conjunction with protein, in a relatively large percentage of species would perhaps attract a greater variety of potential pollinators than if the food hairs contained protein alone. Finally, the formation of pseudopollen and food hairs represents a major stride in the evolution and diversification of the genus. However, until more field studies involving the pollination biology of *Polystachya* are undertaken, the full significance of such diverse and complex labellar structures continues to elude us, especially when one considers the great variety of reproductive strategies found within the genus (Goss, 1977; Pettersson and Nilsson, 1993).

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