Micromorphology of the Labellum and Floral Spur of *Cryptocentrum* Benth. and *Sepalosaccus* Schltr. (Maxillariinae: Orchidaceae)

KEVIN L. DAVIES[1],* and MALGORZATA STPICZYŃSKA[2]

[1]*School of Earth, Ocean and Planetary Sciences, Cardiff University, Main Building, Park Place, Cardiff CF10 3YE, UK and* [2]*Department of Botany, Agricultural University, Akademicka 15, 20-950 Lublin, Poland*

• *Background and Aims* Gross vegetative and floral morphology, as well as modern molecular techniques, indicate that *Cryptocentrum* Benth. and *Sepalosaccus* Schltr. are related to *Maxillaria* Ruiz & Pav. However, they differ from *Maxillaria* in their possession of floral spurs and, in this respect, are atypical of Maxillariinae. The labellar micromorphology of *Maxillaria*, unlike that of the other two genera, has been extensively studied. In the present report, the labellar micromorphology of *Cryptocentrum* and *Sepalosaccus* is compared with that of *Maxillaria* and, for the first time, the micromorphology of the floral spur as found in Maxillariinae is described.
• *Methods* Labella and dissected floral spurs of *Cryptocentrum* and *Sepalosaccus* were examined using light microscopy (LM) and scanning electron microscopy (SEM).
• *Key Results* In each case, the labellum consists of a papillose mid-lobe (epichile), a cymbiform region (hypochile) and, proximally, a spur, which is pronounced in *Cryptocentrum* but short and blunt in *Sepalosaccus*. The inner epidermal surface of the spur of *Cryptocentrum* is glabrous or pubescent, and the bicellular hairs, where present, are unlike any hitherto described for Maxillariinae. Similar but unicellular hairs also occur in the floral spur of *Sepalosaccus*, whereas the glabrous epidermis lining the spur of *C. peruvianum* contains putative nectar pores.
• *Conclusions* The labellar micromorphology of *Cryptocentrum* and *Sepalosaccus* generally resembles that of *Maxillaria*. The floral spur of *Cryptocentrum* displays two types of organization in that the epidermal lining may be glabrous (possibly with nectar pores) or pubescent. This may have taxonomic significance and perhaps reflects physiological differences relating to nectar secretion. The trichomes found within the spurs of *Cryptocentrum* and *Sepalosaccus* more closely resemble the hairs of certain unrelated, nectariferous orchid taxa than those found in the largely nectarless genus *Maxillaria*, and this further supports the case for parallelism.

Key words: Labellum, Maxillariinae, micromorphology, nectar pore, nectary, spur, trichome.

INTRODUCTION

Sub-tribe Maxillariinae, as currently circumscribed, is a Neotropical, species-rich assemblage displaying diverse vegetative morphology and growth patterns, yet retaining a relatively conservative floral morphology (Dressler, 1993; Atwood and Mora de Retana, 1999; Ryan *et al.*, 2000; Whitten *et al.*, 2000; Koehler *et al.*, 2002; Chase *et al.*, 2003; Chase, 2005). It includes Maxillariinae Benth., the former sub-tribes Bifrenariinae Dressler and Lycastinae Schltr., as well as the genus *Xylobium* Lindl. (Davies and Stpiczyńska, 2006, and references therein). Of those genera that constitute Maxillariinae *sensu stricto*, *Cryptocentrum* Benth. is surely one of the most remarkable since it possesses a pronounced sepaline spur. According to Brieger (1977), sepaline spurs also occur in other members of Maxillariinae *sensu stricto*, such as *Anthosiphon* Schltr., *Pseudomaxillaria* Hoehne and *Sepalosaccus* Schltr., but here they are much shorter and often resemble a mentum. As a result, Senghas (1993) states that of the genera that comprise the Maxillariinae, *Cryptocentrum* alone possesses a spur. However, Brieger (1977) states that in these four genera 'the column-foot is not at right angles to the ovary, but curves downward and is more or less parallel to the ovary, while the two lateral sepals are united in their lower part with each other forming the spur, and the

labellum is inserted again at the end of the column-foot with its lower part included within the spur'. Sepaline spurs are not restricted to Maxillariinae and also occur in Spiranthinae Lindl., Glomerinae Schltr., Podochilinae Benth. & Hook. and Comparettiinae Schltr. (Oncidiinae Benth.) (Brieger, 1977).

The genus *Cryptocentrum* was erected to accommodate an Ecuadorian orchid 'in which the very long, slender spur... is closely appressed to the ovary and enclosed with it in the sheathing bract' (Bentham, 1881). This feature, in combination with the absence of pseudobulbs, distinguishes *Cryptocentrum* from other members assigned to Maxillariinae *sensu stricto* and eventually precipitated its removal to a newly established sub-tribe, much nearer to Comparettiinae than to Maxillariinae, namely Cryptocentrinae Garay (Garay, 1958; also cited in Senghas, 1994). Dressler (1961), however, felt that this move was not justified, and Brieger (1977), who had reached the same conclusion, believed that *Cryptocentrum*, *Anthosiphon*, *Sepalosaccus* and *Pseudomaxillaria* represent a generic series best referred to as Cryptocentra.

In *Cryptocentrum*, the floral spur is a double structure comprising a labellar spur formed by the extension of the somewhat straight, lateral lobes of the labellum and sheathed by a second spur formed by fusion of the lateral sepals; the whole partially concealed by a sheathing bract.

* For correspondence. E-mail kevinldavies@btinternet.com

Senghas (1994) states that a long floral spur is atypical of Maxillariinae *sensu stricto* and differs from the typical floral spur of Orchidaceae (e.g. *Angraecum* Bory) in that, when examined in transverse section, it is attached dorsally to the sepaline spur, yet remains free both laterally and ventrally. Senghas, thus, considered the dorsal surface of the spur homologous with the column-foot and, since a prominent mentum is commonly present in Maxillariinae, that the floral spur of *Cryptocentrum* is derived ontogenetically and possibly phylogenetically from that structure. Similarly, Carnevali (1996, 1999, 2005) proposed that *Cryptocentrum* is closely related to *Anthosiphon* and may have evolved from that genus by elongation of the sepaline spur and proportional reduction of the sepaline cup. The delicate nature of the floral spur, however, makes interpretation of its morphology very difficult (Brieger, 1977). Various earlier attempts are outlined by Brieger (1977) whose interpretation conforms to that of Schlechter (cited in Brieger, 1977). This states that the lateral sepals are connate and form a cup- or funnel-like tube. The lateral sepals are adnate to a long column-foot, the labellum inserted at its end having a long claw which is free from the sepals.

That *Cryptocentrum* and *Maxillaria* Ruiz & Pav. are related is further supported by studies of their respective seeds. Senghas (1993, 1994) claims that although the seeds of *Cryptocentrum* differ from those of *Maxillaria*, they are clearly derived from them.

The genus *Cryptocentrum* is also unusual amongst members of Maxillariinae *sensu stricto* in that, with the exception of two species, namely *C. pseudobulbosum* C. Schweinf. and *C. roseans* (Schltr.) A.D. Hawkes, it lacks pseudobulbs. Instead, it has branched shoots with distichous or spirally arranged, linear leaves. As a result, it was generally considered by Dressler (1961), Brieger (1977) and Carnevali (1996, 1999, 2001, 2005), amongst others, to have a monopodial habit. Senghas (1994), however, argued that the absence of pseudobulbs alone does not necessarily constitute a monopodium and that *Cryptocentrum* is sympodial.

Senghas (1994) recognized some 16 species of *Cryptocentrum* distributed from Costa Rica to Venezuela and south to Peru, whereas Carnevali (2001, 2005), whose infrageneric classification is based upon growth habit, phyllotaxis, foliar anatomy and relative length of the floral bract and spur, lists 17 species for the genus. Of these, only six or so occur in cultivation, and then only infrequently. Consequently, *Cryptocentrum* has seldom been investigated and, with the exception of the authoritative work of Carnevali (1996, 1999, 2001, 2005), information about the genus is scant.

Likewise, according to Senghas (1993), almost no one has had the opportunity to study a living specimen of the related, Costa Rican genus *Sepalosaccus* (Schlechter, 1923). This genus contains only two species (Senghas, 1993) and differs from *Cryptocentrum* in its possession of unifoliate pseudobulbs and its lack of a prominent floral spur. Instead, the lateral sepals are partially fused, forming a globose, saccate perianth, and the labellum is fixed, as in certain species of *Maxillaria* formerly assigned

to *Ornithidium* R. Br. (Brieger, 1977; Senghas, 1993). The labellum is obscurely three-lobed and the side lobes are turned towards the column. It has two longitudinal ridges united by a transverse ridge at their upper end between the margins of the lateral lobes. The foot of the column is relatively long, runs parallel to the ovary and turns sharply upward. The lateral sepals are adnate to the foot and connate, forming a blunt spur (Brieger, 1977). Dressler (1990) grouped *Anthosiphon*, *Chrysocycnis* Linden & Rchb.f., *Cryptocentrum*, *Cyrtidiorchis* Rauschert, *Maxillaria*, *Mormolyca* Fenzl, *Pityphyllum* Schltr., *Scuticaria* Lindl. and *Trigonidium* Lindl. within Maxillariinae. In species of *Maxillaria* formerly assigned to *Ornithidium*, the lip is, to a greater or lesser degree, immovable or fixed as in *Pseudomaxillaria*, and it would seem that *Sepalosaccus* is but one genus within this complex. This view is supported by Brieger (1977) who considered both *Sepalosaccus* and *Pseudomaxillaria* valid genera. Dressler (1993), in a more recent revision, recognized a more broadly defined *Maxillaria* comprising *Camaridium* Lindl., *Heterotaxis* Lindl., *Ornithidium*, *Marsupiaria* Hoehne, *Neourbania* Fawc. & Rendle, *Pseudomaxillaria* and *Sepalosaccus*, as well as seven minor genera, namely *Anthosiphon*, *Chrysocycnis*, *Cryptocentrum*, *Cyrtidiorchis*, *Mormolyca*, *Pityphyllum* and *Trigonidium*. Furthermore, the *Phylogenetics of Maxillariinae (Orchidaceae)* website (http://www.flmnh.ufl.edu/herbarium/max/default.htm) shows that *Sepalosaccus strumatus* (Endres & Rchb.f.) Garay (syn. *S. humilis* Schltr.), referred to as *Maxillaria strumata* (Endres & Rchb.f.) Ames & Correll, is nested within the '*Maxillaria* core'. Conversely, Singer *et al.* (2007) showed that the *Cryptocentrum*/*Anthosiphon* clade is most closely related to the *Maxillaria picta* Hook. alliance, a taxon whose species they assigned to a new genus, *Brasiliorchis* R. Singer, S. Koehler & Carnevali on the basis of 'multiple sequence data and a combination of distinctive vegetative and floral features'. In contrast to *Sepalosaccus*, both these clades fall outside the '*Maxillaria* core'.

Stern *et al.* (2004) have shown that Maxillariinae and Lycastinae can be distinguished on anatomical grounds from other sub-tribes of Maxillarieae (*sans* Oncidiinae) in that they possess tilosomes, foliar glands and foliar fibre bundles. These features were also found to be present in *Cryptocentrum*. Unfortunately, insufficient material precluded the investigators from determining whether all these characters are present in any one of the species of *Cryptocentrum* studied.

Modern molecular data have generally supported the inclusion of *Cryptocentrum* and *Sepalosaccus* in Maxillariinae. For example, the cladistic parsimony analyses of *rbcL* nucleotide sequences have vindicated the placement of *Cryptocentrum* within Maxillariinae (including Bifrenariinae but excluding Lycastinae) (Cameron *et al.*, 1999). Whitten *et al.* (2000), who investigated the monophyly of Maxillariinae using parsimony analyses of combined nuclear ribosomal and plastid DNA sequence data of internal transcribed spacer (ITS) 1 and 2, *matK*, the *trnL* intron and the *trnL–F* intergenic spacer, showed that Maxillariinae *sensu lato* is strongly supported by SW

bootstrap analysis and contains several strongly supported clades including Maxillariinae *sensu stricto* containing *Maxillaria*, *Trigonidium* and *Cryptocentrum*. Dathe and Dietrich (2006) investigated the phylogenetic relationships of Maxillariinae *sensu stricto* using maximum parsimony and Bayesian analyses of nuclear ribosomal ITS1 and ITS2 DNA sequences. Their results showed that Maxillariinae is monophyletic but that *Maxillaria*, in its current, narrower circumscription, is paraphyletic with the currently accepted *Chrysocycnis*, *Cryptocentrum*, *Mormolyca* and *Trigonidium*, as well as the former segregates *Camaridium*, *Heterotaxis*, *Marsupiaria*, *Neourbania*, *Ornithidium* and *Pseudomaxillaria*, nested within it. Since then, Whitten *et al.* (in prep.), by means of combined molecular data, have shown that *Maxillaria sensu stricto* and *Camaridium* are distinct clades and that *Sepalosaccus* is embedded within *Camaridium*.

Recently, the labellar micromorphology of Maxillariinae *sensu stricto* and Bifrenariinae has been extensively studied (Davies and Winters, 1998; Davies *et al.*, 2000, 2003*a*, *b*; Davies and Turner, 2004*a*; Davies and Stpiczyńska, 2006). The present report compares the labellar micromorphology of the seldom encountered and enigmatic genera *Cryptocentrum* and *Sepalosaccus* with other members of Maxillariinae *sensu lato* as part of an ongoing programme to characterize the micromorphological features of this sub-tribe. The authors had also intended to compare the floral micromorphology of other related genera such as *Anthosiphon*, *Pityphyllum*, *Chrysocycnis* and *Cyrtidiorchis*. Unfortunately, this proved impossible owing to a lack of suitable fresh and spirit-preserved material.

MATERIALS AND METHODS

Spirit-preserved material of four species of *Cryptocentrum* and one species of *Sepalosaccus* was obtained from the Royal Botanic Garden, Kew, UK (Table 1). Their accession numbers are prefixed 'K'. The names by which these specimens were originally collected have been retained, but recent changes in nomenclature have been noted. The authorities for plant names follow Brummit and Powell (1992). Preserved material, whilst at R.B.G. Kew, was stored in Kew mix [53 % ethanol (industrial methylated spirit), 37 % water, 5 % formaldehyde solution, 5 % glycerol]. However, it was transferred to, and kept in, Copenhagen mix [70 % ethanol (industrial methylated spirit), 28 % water, 2 % glycerol] for the duration of this study.

Following preliminary examination by means of light microscopy, labella and dissected floral spurs were prepared for scanning electron microscopy (Stpiczyńska *et al.*, 2004; Davies and Turner, 2004*b*) and examined by means of a TESLA BS-300 at an accelerating voltage of 20–25 kV.

The floral spurs of a number of unrelated orchid taxa were obtained from Swansea Botanical Complex, UK (accession numbers prefixed 'S') and compared with the above.

RESULTS

The labella of all four species of *Cryptocentrum* studied are obscurely tri-lobed and comprise three distinct regions: a linguiform mid-lobe (epichile), a cymbiform region (hypochile) formed by the upturned margins of the lateral lobes of the labellum and, proximally, a tubular spur (Fig. 1A). Three prominent veins run the length of the labellum, but only the central vein extends almost to the tip of the mid-lobe. The mid-lobe is papillose (Figs 1B and 2A), the papillae being obpyriform (Figs 1C and 2B), whereas the cymbiform region is usually glabrous, and in some species, such as *C. standleyi*, composed of thin-walled cells that are longer than wide (Fig. 1D). In others, such as *C. gracillimum* (Fig. 2C) and *C. calcaratum*, these cells are more or less isodiametric. In the latter species, the cymbiform region becomes increasingly pubescent proximally (Figs 3B, C). Similarly, epidermal cells lining the spur may be elongate (Figs 1E and 3E, F) or isodiametric (Fig. 2D). In *C. standleyi* and *C. peruvianum*, the epidermis lining the spur is glabrous (Fig. 1E), whereas that of *C. gracillimum* (Fig. 2D) and *C. calcaratum* (Figs 3E, F) is pubescent. Although hairs, at low magnifications, appear unicellular, they are in fact bicellular, comprising a short basal cell and a longer, gradually tapering, terminal cell (Figs 2D, E and 3A–F). In *C. calcaratum*, trichomes, whether within the spur or upon the proximal surface of the cymbiform region, have very similar features (Fig. 3A–F). The spur of *C. peruvianum*, however, lacks trichomes, but elliptic perforations in the epidermis lining the spur were occasionally observed (Fig. 1F), measuring approx. $31·3 \times 5·0 \ \mu m$.

In many ways, the labellum of *Sepalosaccus* resembles that of *Cryptocentrum*. The mid-lobe of the labellum,

TABLE 1. *Taxa examined and their provenance*

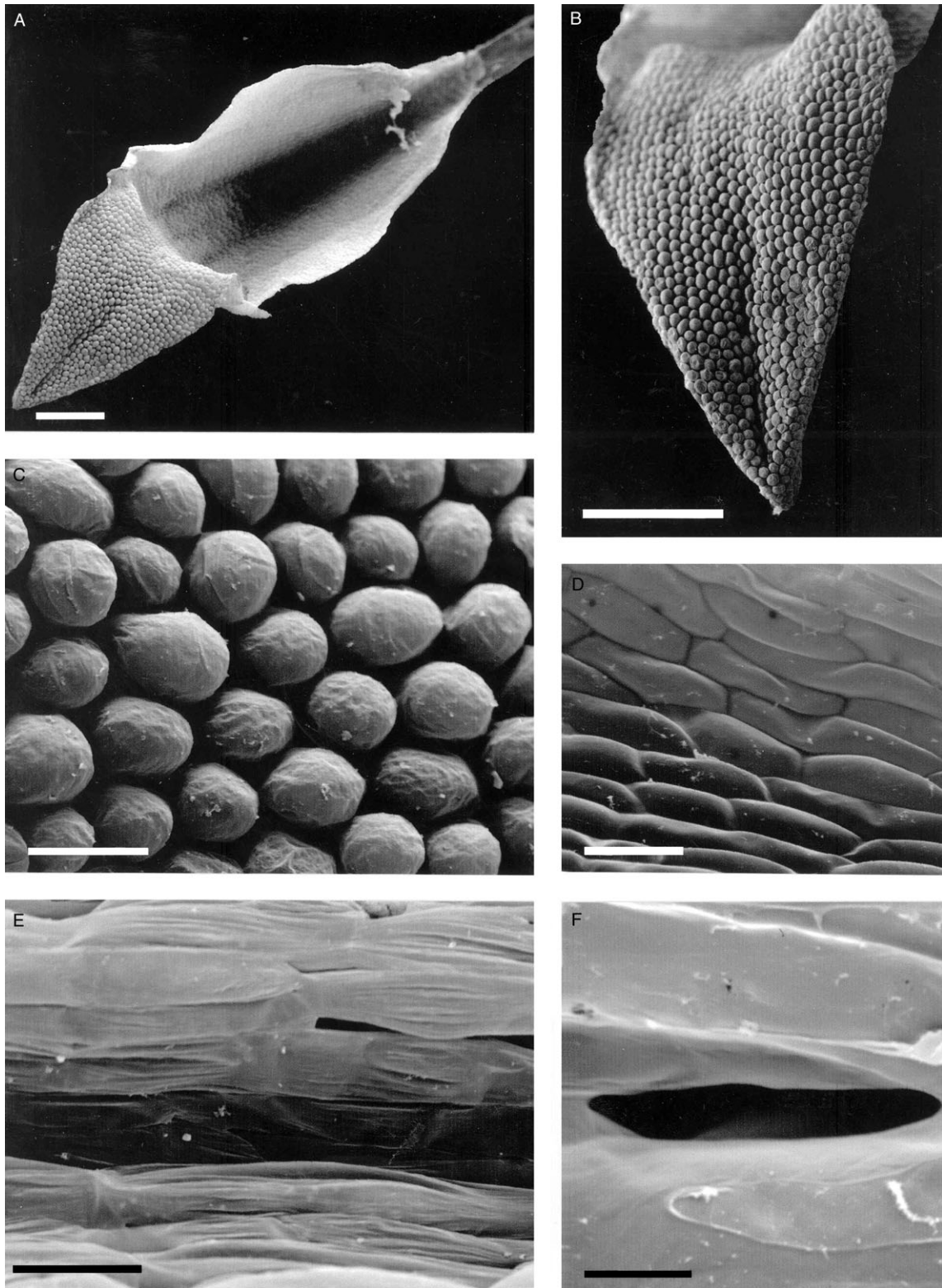| Taxon	Accession no.	Collector	Collector no.	Provenance	Date	Taxonomic notes
Cryptocentrum calcaratum (Schltr.) Schltr.	K13598			Costa Rica		
C. gracillimum Ames & C. Schweinf.	K37139	Dunsterville		Venezuela		
C. peruvianum (Cogn.) C. Schweinf.	K48260	H. Pfennig	1558	Ecuador	1984	
C. standleyi Ames	K48525			Panama		
Sepalosaccus humilis Schltr.	K12636	L.H. Lankester		Costa Rica	1935	syn. *Maxillaria strumata* (Endres & Rchb.f.) Ames & Correll, syn. *Sepalosaccus strumatus* (Endres & Rchb.f.) Garay

FIG. 1. *Cryptocentrum standleyi* (accession no. K48525). (A) Labellum showing papillose, linguiform mid-lobe, cymbiform median region and part of a spur arising proximally. Scale bar = 500 μm. (B) Detail of a papillose mid-lobe. Scale bar = 500 μm. (C) Detail of obpyriform papillae of the mid-lobe. Scale bar = 50 μm. (D) Detail of glabrous, cymbiform region of the labellum with rectangular epidermal cells. Scale bar = 50 μm. (E, F) *Cryptocentrum peruvianum* (accession no. K48260). (E) Glabrous, internal surface of spur. Scale bar = 50 μm. (F) Detail of a putative nectar pore. Scale bar = 10 μm.
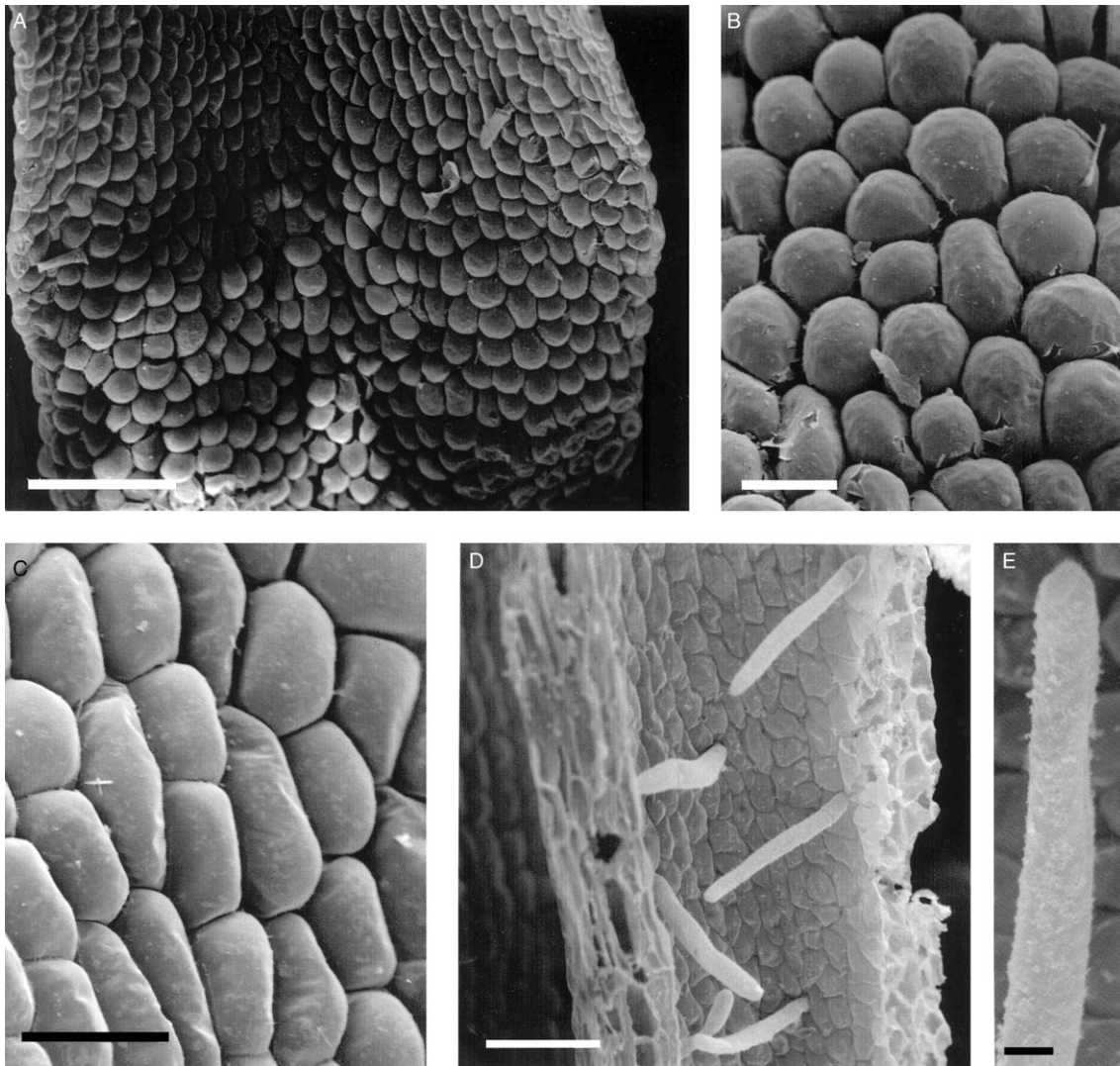
Fɪɢ. 2. *Cryptocentrum gracillimum* (accession no. K37139). (A) Papillose, mid-lobe of labellum similar to that of *C. standleyi*. Scale bar = 200 μm. (B) Detail of obpyriform, mid-lobe papillae. Scale bar = 50 μm. (C) Detail of glabrous, cymbiform region of labellum with isodiametric to rectangular epidermal cells. Scale bar = 50 μm. (D) Internal surface of a spur with bicellular trichomes. Scale bar = 100 μm. (E) Detail of a single spur trichome. Scale bar = 10 μm.

although more rounded than that of *Cryptocentrum*, is again papillose, and the papillae, like those of *Cryptocentrum*, are obpyriform (Fig. 4A). Marginally, the mid-lobe bears nipple-like, conical papillae. The upturned margins of the lateral lobes of the labellum, as in *Cryptocentrum*, form a cymbiform region which is composed of thin-walled, more or less isodiametric cells. Proximally, the labellum forms a blunt spur whose cells are isodiametric and shortly papillose (Fig. 4B). Unicellular trichomes arise from these papillae.

DISCUSSION

Cryptocentrum is atypical for Maxillariinae in its possession of a floral spur. Spur length is usually correlated with that of the proboscis of the insect pollinator (Johnson, 1997, 2006; Nilsson, 1998, and references

therein; Benitez-Vieyra *et al.*, 2006). Thus, the relatively long spur of *Cryptocentrum*, together with flower coloration and sweet nocturnal scent (Carnevali, 1999, 2001), is probably an adaptation for moth pollination (Dressler, 1990; Carnevali, 2005), unlike most species of *Maxillaria* which are thought to be pollinated by Meliponini (stingless bees) (Singer and Cocucci, 1999; Roubik, 2000). The floral spur of *Cryptocentrum* is a double structure consisting of a labellar spur enclosed within an outer, sepaline spur, and is reported to contain nectar at its extreme tip (Carnevali, 2005). Floral spurs also occur in a number of unrelated genera native to other continents. They arise from the proximal part of the labellum and are formed by the partial fusion of the lateral sepals (Figueiredo and Pais, 1992; Galetto *et al.*, 1997; Stpiczyńska, 1997, 2003*a*, 2004; Singer and Sazima, 1999; Stpiczyńska and Matusiewicz, 2001). Some flowers, such as those of
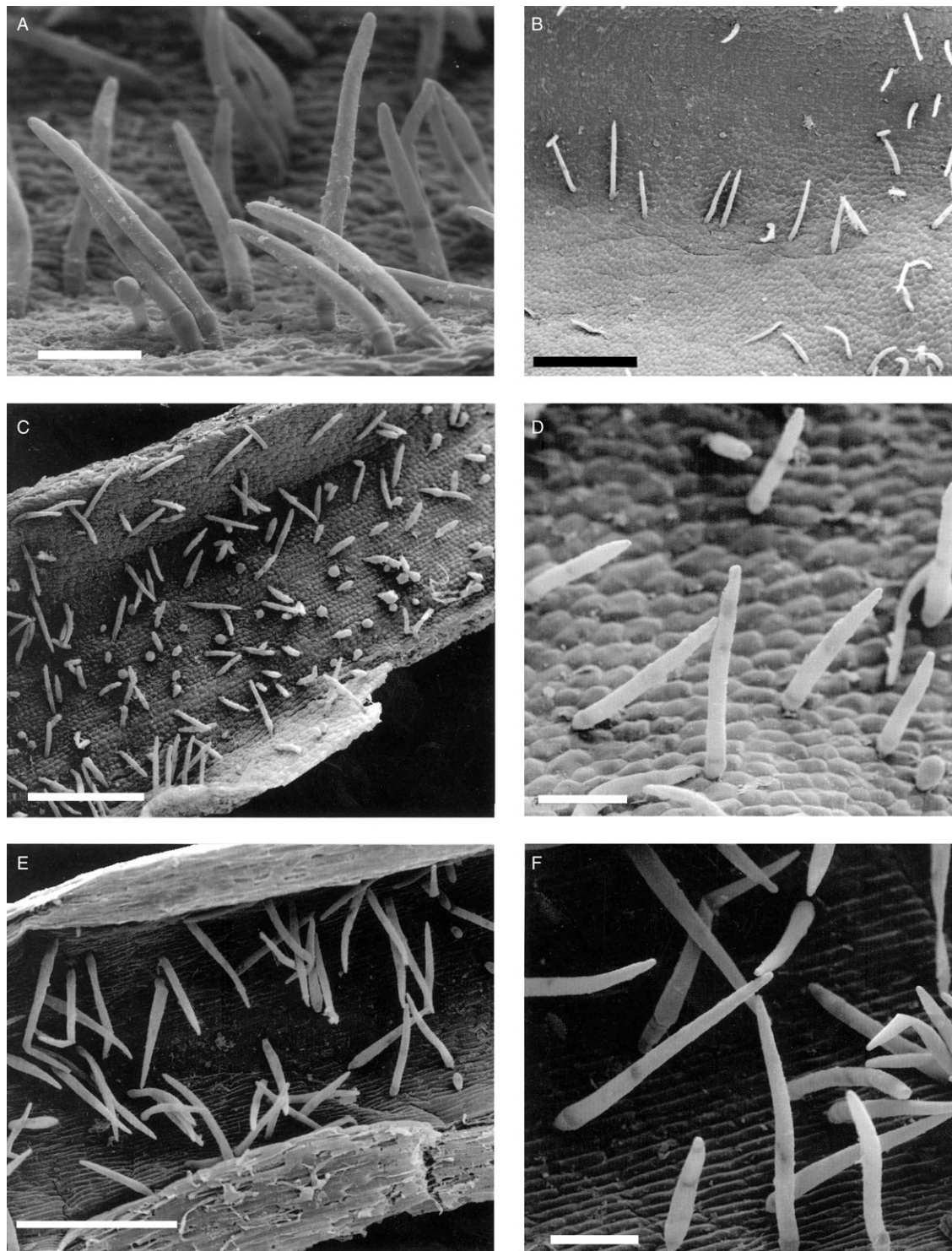
Fɪɢ. 3. *Cryptocentrum calcaratum* (accession no. K13598). (A) Bicellular hairs of *C. calcaratum* comprising a basal cell and a longer, tapering terminal cell with rounded tip. Scale bar = 100 μm. (B) Pubescent, proximal part of cymbiform region of labellum with isodiametric, epidermal cells. Scale bar = 500 μm. (C) Increasingly pubescent region of labellum close to the origin of the spur. Note that isodiametric, epidermal cells are still present here. Scale bar = 500 μm. (D) Detail of trichomes from the proximal part of the cymbiform region of a labellum. Scale bar = 100 μm. (E) Pubescent, internal surface of a spur. Note the elongate epidermal cells. Scale bar = 500 μm. (F) Detail of the internal surface of a spur showing trichomes and elongate epidermal cells. Scale bar = 100 μm.
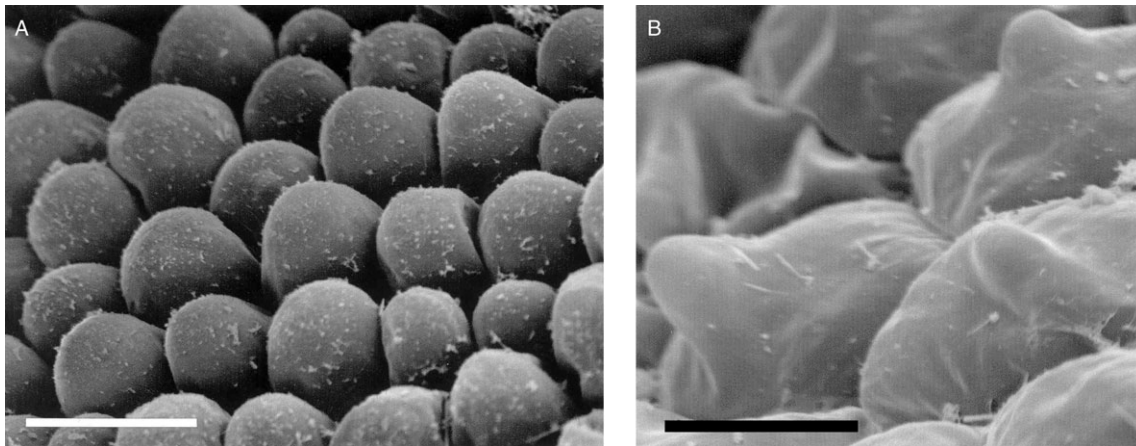
FIG. 4. *Sepalosaccus humilis* (accession no. K12636). (A) Detail of papillose mid-lobe of labellum. Scale bar = 50 μm. (B) Detail of the proximal region of a labellum showing short papillae which develop into unicellular trichomes. Scale bar = 50 μm.

Satyrium hallackii Bolus ssp. *hallackii*, have two spurs (Johnson, 1997). However, the possession of a floral spur does not necessarily indicate that a flower produces nectar (Roy and Widmer, 1999) since flowers of some rewardless orchids mimic unrelated species that have nectar-laden flowers. For example, *Disa ferruginea* (Thunb.) Sw. mimics *Tritoniopsis triticea* (Burm. F.) Goldbl. (Iridaceae) and *Kniphofia uvaria* (L.) Hook. (Asphodelaceae) (Johnson, 1994).

The epidermis lining the floral spur of orchids may be glabrous as in *Thunia* × *veitchiana* [*T. alba* (Lindl.) Rchb.f. × *T. bensoniae* Hook.f.] (S00004322) and *Cribbia* cf. *confusa* P.J. Cribb (S19970064), but is frequently pubescent as in *Angraecum scottianum* Rchb.f. (S19950021), *A. germinyanum* Hook.f. (S1997002), *Mystacidium braybonae* Summerh. (S19960027) (K.L. Davies, unpublished data), *Aeranthes arachnites* (Thouars) Lindl., *A. grandiflora* Lindl. (Roberts, 2001), *Platanthera bifolia* (L.) Rich. (Stpiczyńska, 1997), *P. chlorantha* (Custer) Rchb. (Stpiczyńska, 2003*a*, 2004) and *Gymnadenia conopsea* (L.) R. Br. (Stpiczyńska and Matusiewicz, 2001). These hairs are unicellular and, especially in the case of *P. bifolia* (Stpiczyńska, 1997), resemble to varying degrees the spur trichomes of *Cryptocentrum* spp. However, the spur hairs of *A. germinyanum*, unlike those of *Cryptocentrum*, have wide bases and longitudinal, cuticular striations. Hairs can significantly enlarge the surface area for nectar secretion and nectar resorption (Stpiczyńska 2003*a*, *b*, 2004; Nepi and Stpiczyńska, 2007), thereby enabling the conservation of valuable material and energy resources. The resemblance of the spur trichomes of the Neotropical genus *Cryptocentrum* to those of the unrelated and largely European *P. bifolia* (Stpiczyńska, 1997), as well as other unrelated orchid species native to other continents, is perhaps indicative of parallelism, especially since such hairs have not been described for the closely related genera *Maxillaria* and *Mormolyca* (Maxillariinae) (Davies and Winters, 1998; Davies *et al.* 2000, 2003*a*, *b*; Davies and Turner, 2004*a*; Davies and Stpiczyńska, 2006). Indeed, it has been estimated that only some 8 % of *Maxillaria* spp. produce

nectar (Davies *et al.*, 2005), and trichomes in this genus tend to be multicellular. The presence of bicellular hairs in *Anthosiphon* would support the proposal that it is nested within *Cryptocentrum* (Singer *et al.*, 2007) but, unfortunately, specimens of *Anthosiphon* were not available for study. Unicellular hairs, however, occur in *Mormolyca*. These are much longer than wide, with narrow points of insertion and pointed tips, much like those of *Ophrys* L. (Servettaz *et al.*, 1994; Ascensão *et al.*, 2005), and this may be due to the fact that pseudocopulation occurs in both genera (Singer *et al.*, 2004; Flach *et al.*, 2006). Trichomes similar to those found in *Cryptocentrum* and *Sepalosaccus* do not occur in *Bifrenaria*, *Rudolfiella*, *Teuscheria* or *Xylobium* (genera formerly assigned to Bifrenariinae but currently assigned to Maxillariinae *sensu lato*). Nevertheless, the genus *Bifrenaria*, which is nectarless and is pollinated by *Eufriesia violacea* (Euglossini) and *Bombus brasiliensis* (Bombini) (Singer and Koehler, 2004), has unicellular, labellar hairs, and certain species of *Xylobium*, a genus pollinated by Meliponini, have bicellular trichomes (Davies and Stpiczyńska, 2006). In both cases, however, these hairs differ in their relative proportions from those found in *Cryptocentrum* and *Sepalosaccus*.

The spurs of certain species of *Cryptocentrum*, such as *C. standleyi* and *C. peruvianum*, lack hairs. Instead, elliptical perforations were found on the inner epidermal surface of the spur of *C. peruvianum*, and these resemble the nectar pores found in *Chamaecytisus ruthenicus* A. Klaskova and *Retama monosperma* (L.) Boiss. (Fabaceae: Genistinae) (Vogel, 1997). The nectar pores of *Chamaecytisus* are non-stomatal in origin and are thought to arise from an initially intact epidermis by the selective dissolution of epidermal cells. Moreover, they have similar dimensions to the putative nectar pores of *C. peruvianum*. Senghas (1994) and Carnevali (2001, 2005) placed *C. peruvianum* and *C. standleyi*, together with *C. flavum* Schltr., in a separate sub-genus (*Caulescentes* K. Senghas) since they differ from other species of *Cryptocentrum* in that they display polystichous phyllotaxis and relatively short floral bracts. Thus, the absence or presence of hairs within the floral

spur of *Cryptocentrum* may be taxonomically significant and requires further investigation.

The labellum of *Sepalosaccus strumatus* (syn. *S. humilis*) resembles that of *Cryptocentrum.* Hairs occur within the short, blunt spur of this species, and although these are unicellular, they otherwise resemble spur hairs of *Cryptocentrum.* They are derived from small, conical papillae similar to those lining the floral spur of *Gymnadenia conopsea* (Stpiczyńska and Matusiewicz, 2001). Conical, floral papillae are ubiquitous amongst angiosperms (Kay *et al.*, 1981), including the genus *Maxillaria* (Davies and Turner, 2004*a*). Even so, the presence of unicellular hairs in *Sepalosaccus* is atypical of Maxillariinae *sensu stricto*. Their presence within the short, blunt spur and their similarity to those found within the spurs of unrelated, nectariferous orchids supports the possibility that nectar occurs in this species and also parallelism. Indeed, on the basis of phylogenetic analyses [*Phylogenetics of Maxillariinae (Orchidaceae)* website], *S. strumatus* (listed as *M. strumata*) is thought to be closely related to other nectariferous species of *Maxillaria* such as *M. parviflora* (Poepp. & Endl.) Garay, although there nectar occurs in a shallow depression of the lip (Singer and Koehler, 2004). Moreover, combined molecular data indicate that *Sepalosaccus* is embedded within *Camaridium*, a taxon that contains several nectariferous species (Whitten *et al.*, in prep.). However, Stern *et al.* (2004) and Dathe and Dietrich (2006) concur with Benzing (1986) that, owing to convergence, anatomical characters alone, and in particular those related to pollination, are of limited use in determining relationships within Maxillariinae.

Finally, the relative rarity of *Cryptocentrum* and *Sepalosaccus* spp. in European collections precluded examination of live flowers and, until this is done, neither the presence and composition of nectar nor the role of spur hairs and putative nectar pores in its secretion can be established. However, it is significant that the flowers of nectarless members of Maxillariinae *sensu stricto*, whose micromorphology otherwise resembles that of *Cryptocentrum* and *Sepalosaccus*, lack such hairs, even though they are present in unrelated, nectariferous species. On the basis of this evidence, it is speculated that representatives of both genera produce nectar and that spur hairs are modified for this purpose.

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