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

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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 Maxillariae Benth., the former sub-tribes Bifenariinae Dressler and Lycastinae Schltr., as well as the genus Xylolobium 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 Comparettiiinae 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.

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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, Chrysoycnys Lindl. & Rchb.f., Cryptocentrum, Cyrtidiorchis Rauschert, Maxillaria, Mormolyca Fenzl., Pitypsyllum 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, Marsuparia Hoehne, Neourbania Fawc. & Rendle, Pseudomaxillaria and Sepalosaccus, as well as seven minor genera, namely Anthosiphon, Chrysoycnys, Cryptocentrum, Cyrtidiorchis, Mormolyca, Pitypsyllum 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 pelta 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 Oncidinae) in that they possess tisolesomes, 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 Bifrenariniinae 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 *Chrysocorys*, *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 Bifrenarinae has been extensively studied (Davies and Winters, 1998; Davies et al., 2000, 2003a, b; Davies and Turner, 2004a; 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*, *Chrysocorys* 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 [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, 2004b) and examined by means of a TESLA BS-300 at an accelerating voltage of 20–25 kV.

**RESULTS**

The labella of all four species of *Cryptocentrum* studied are obviously 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), whereas the spur may be elongate (Figs 1E and 3E, F) or isodiametric (Fig. 2D). In *C. standleyi* and *C. calcaratum*, the epidermis lining the spur is pubescent (Fig. 1E), whereas that of *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 × 5.0 m.

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

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<th>Taxon</th>
<th>Accession no.</th>
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<th>Provenance</th>
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<th>Taxonomic notes</th>
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<td>K37139</td>
<td>Dunsterville</td>
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<td><em>C. Schweinf.</em></td>
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<td><em>C. peruvianum</em> (Cogn.) Sch.</td>
<td>K48260</td>
<td>H. Pfennig</td>
<td>1558</td>
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<td>1984</td>
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<td><em>C. standleyi</em> Ames</td>
<td>K48525</td>
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Table 1. Taxa examined and their provenance.
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.
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, 2003a, 2004; Singer and Sazima, 1999; Stpiczyńska and Matusiewicz, 2001). Some flowers, such as those of

FIG. 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.
**Fig. 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.
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, 1997, 2000, 2003).

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. geminianum Hook.f. (S1997002), Mystacidium brayboniae Summerh. (S19960027) (K.L. Davies, unpublished data), Aeranthes arachnites (Thouars) Lindl., A. grandiflora Lindl. (Roberts, 2001), Platanthera bifolia (L.) Rich. (Stpiczynska, 1997), P. chlorantha (Custer) Rchb. (Stpiczynska, 2003a, 2004) and Gymnadenia conopsea (L.) R. Br. (Stpiczynska and Matusiewicz, 2001). These hairs are unicellular and, especially in the case of P. bifolia (Stpiczynska, 1997), resemble to varying degrees the spur trichomes of Cryptocentrum spp. However, the spur hairs of A. geminianum, unlike those of Cryptocentrum, have wide bases and longitudinal, cuticular striations. Hairs can significantly enlarge the surface area for nectar secretion and nectar resorption (Stpiczynska 2003a, b, 2004; Nepi and Stpiczynska, 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 (Stpiczynska, 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, 2003a, b; Davies and Turner, 2004a; Davies and Stpiczynska, 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. (Serrvetta et al., 1994; Ascensao 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 Eugresia 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 Stpiczynska, 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. Klashova 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* (Stpiczyn'ska and Matusiewicz, 2001). Conical, conopsea-like similar to those lining the floral spur of *Cryptocentrum*. 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* (Poeppl. & 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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**LITERATURE CITED**


