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Comparative vegetative anatomy and systematics of the Oncidiinae (Maxillarieae, Orchidaceae)

WILLIAM LOUIS STERN and BARBARA S. CARLSWARD

Abstract

Subtribe Oncidiinae comprises a vegetatively heterogeneous assemblage of species that has persistently been incapable of organization. Anatomy was considered to be a possible means to resolve the perplexity of relationships amongst the constituent taxa. The consistent occurrence of a foliar hypodermis, homogeneous mesophyll, conical silica bodies in stigmata, and ubiquitous fibre bundles in leaves provides a matrix for linking the taxa, as do the parenchymatous pith and O-thickened endodermal cell walls in roots. However, the strict consensus of the 40 genera studied was completely unresolved, suggesting that vegetative characters alone are insufficient to assess the relationships amongst these taxa, a conclusion also reached for the remainder of Maxillarieae.

Keywords: cladistic analysis; endodermis; hypodermis; stigmata; vegetative anatomy; velamen; water-storage cell

INTRODUCTION

Subtribe Oncidiinae (tribe Maxillarieae) appears to be one of the more intractable groups of Orchidaceae with respect to classification. This has been pointed out by Ayensu & Williams (1972), Chase (1987), Chase & Palmer (1989), Dressler (1993), Williams et al. (2001), Sandoval-Zapotitla & Terrazas (2001), and others. For example, currently about half the species in the subtribe are arranged in two genera: *Oncidium* and *Odontoglossum*. These have traditionally been separated by the angle between the lip and column (the column is parallel with the lip in *Odontoglossum* and at a right angle in *Oncidium*), but this feature varies greatly and does not always define two clear groups (Dressler, 1993). Most studies of orchids have concentrated on floral traits (Chase & Palmer, 1989) to the exclusion of micromorphological and vegetative features, with the exception of Pfitzer's (1882) and his students' contributions to anatomy. For the most part, however, their results have proved to be of little systematic importance, being based on organs and tissues.

We scoured the relevant literature for past anatomical accounts of Oncidiinae. Regrettably, we found no comprehensive reports, and there were few relevant facts referring to definitive structure as they applied to systematics. A few observations, however, appeared to be potentially valuable. Leitgeb (1864) and Groom (1893) noted the occurrence of idioblasts in the outer cortical tissues of roots in *Oncidium* species and in *Rodriquezia secunda* Humb. Bonpl. & Kunth, described as very long, prosenchymatous, thick-walled cells, to which we will refer later. Groom wrote about 'broad prominent bars of lignified membrane in root cortical cells'. Foliar

hypodermal layers in *Oncidium* were reported by Möbius (1887) and Meinecke (1894). Möbius pointed out spirally thickened mesophyll cells. Solereder & Meyer (1930) remarked on the distribution of fibre bundles in the mesophyll of several genera of *Oncidiinae*.

More recently, Ayensu & Williams (1972) considered *Palumbina candida* Rchb.f. (monotypic) and *Odontoglossum* (three species) to be closely related owing to the development and specialization of a uniseriate adaxial hypodermis in both genera; an abaxial hypodermis was absent. Fibre bundles occurred in a single row along both surfaces of the leaf in each genus. They noted that the occurrence of adaxial fibre bundles in *Palumbina* and *Odontoglossum* was unique, because of their absence in other *Oncidiinae* (but see our observations of foliar features). Williams (1974) concentrated on the micromorphology of the *Oncidiinae* and pointed to several anatomical features of leaves he thought to be of putative taxonomic importance, especially in *Oncidium*. The characters chosen involved stomatal position, cuticular structure, hypodermal position and form, vascular bundle construction, spiral thickenings of mesophyll and hypodermal cells, and the formation and location of fibre bundles.

The *Lophiaris* clade (Chase & Palmer, 1992) of *Oncidiinae*, or *Trichocentrum* sensu Williams et al. (2001), includes species of *Oncidium*, *Psychopsis*, *Rossioglossum*, and *Trichocentrum*. Sandoval-Zapotitla & Terrazas (2001) examined the leaf anatomy of these plants to expand the information about leaves, to provide detailed descriptions, and to identify anatomical features of potential taxonomic value. They were able to distinguish two groups: one group in which hypodermis and bulliform cells were absent and secondary thickenings occurred in mesophyll cells, and a second group in which a hypodermis and bulliform cells were present but in which mesophyll cells lacked secondary thickenings. *Trichocentrum* was outstanding because fibre bundles and stegmata bearing silica bodies were absent in leaves.

Vegetatively, *Oncidiinae* are polymorphic, and there is great variation in form amongst the genera and species. For example, plants vary from the pseudobulbless species of *Lockhartia* with slender stems bearing equitant, isobilateral leaves a few centimetres in length, to the variably leafed species of pseudobulbous *Oncidium*. Within *Oncidium* itself, there are species with tough, leathery, conduplicate leaves of more than 60 cm in length (*Oncidium carthaginense* (Jacq.) Sw.), other species with terete longitudinally sulcate leaves of 70 cm in length (*Oncidium stipitatum* Lindl. in Benth.), and still others with linear-ligulate leaves of 60 cm in length (*Oncidium sphacelatum* Lindl.). The overall habit varies from short-lived delicate twig epiphytes, such as *Psychmorchis pusilla* (L.) Dodson & Dressler, to robust long-lived *oncidiums*, such as *O. carthaginense*.

Owing to the difficulty of establishing a stable systematic classification amongst the genera of *Oncidiinae*, an attempt to apply anatomy as a means to examine the relationships was thought to be a potentially fruitful approach, as described in some

cases (Stern et al., 1993; Stern & Judd, 2001, 2002). In other instances, however, the application of anatomy to sort out questions of relationships amongst orchids has proven unproductive (Stern & Morris, 1992; Stern & Whitten, 1999). With these caveats in mind, we attempted to assess anatomical structure as a valuable tool in the systematics of Oncidiinae.

MATERIAL AND METHODS

We had on hand for study 40 of the 77 genera listed for Oncidiinae by Dressler (1993), whose outline we have followed. Species binomials representing these genera are enumerated with their authorities (abbreviated according to Brummitt & Powell, 1992) in Table 1. Unfortunately, we did not always have all parts for examination. However, we believe that we had a representative enough sampling of parts to produce meaningful descriptions for the genera on which our discussion is based. Regrettably, most of our specimens were from nurseries and other horticultural sources and were not associated with voucher material.

Table 1. Species of Oncidiinae studied

Taxon	Parts available
<i>Ada ocanensis</i> (Lindl.) N.H. Williams	L, R
<i>Aspasia lunata</i> Lindl.	L, S, R
<i>Bracthia andina</i> Rchb.f.	L, R
<i>Brassia bidens</i> Lindl.	L, S, R
<i>Cischweinfia pusilla</i> (C. Schweinf.) Dressler & N.H. Williams	L, S, R
<i>Cochlioda noezliana</i> Rolfe	L, S, R
<i>Comparettia speciosa</i> Rchb.f.	L, R
<i>Cuitlauzina pendula</i> La Llave & Lex.	L, S, R
<i>Erycina echinata</i> Lindl.	L
<i>Gomesa crispa</i> Klotzsch ex Rchb.	L, S, R
<i>Helcia sanguinolenta</i> Lindl.	L, S, R
<i>Ionopsis utricularioides</i> (Sw.) Lindl.	L
<i>Lemboglossum maculatum</i> (LaLlave & Lex.) Halb.	L, S, R
<i>Leochilus johnstonii</i> Ames & Correll	L, R
<i>Lockhartia lunifera</i> Rchb.f.	L, S
<i>Lockhartia oerstedii</i> Rchb.f.	L, S, R
<i>Macradenia</i> sp.	R
<i>Mesoglossum londesbroughianum</i> (Rchb.f) Halb.	L, S, R
<i>Mesospinidium</i> sp.	L, S, R
<i>Mexicoa ghiesbreghtiana</i> (A.Rich. & Galeotti) Garay	L, S, R
<i>Miltonia bluntii</i> Rchb.f.	L, S, R

<i>Miltoniopsis santanaei</i> Garay & Dunst.	L, S, R
<i>Notylia barkeri</i> Lindl.	L, R
<i>Notylia pentachne</i> Rchb.f.	L, R
<i>Notylia ramonensis</i> Schltr.	L, R
<i>Odontoglossum cordatum</i> Lindl.	L, S, R
<i>Oncidium ampliatum</i> Lindl.	L, R
<i>Oncidium baueri</i> Lindl.	L, S, R
<i>Oncidium boothianum</i> Rchb.f.	L, S, R
<i>Oncidium cebolleta</i> Sw.	R
<i>Oncidium leochilooides</i> Foldats	L, S, R
<i>Oncidium maculatum</i> Lindl.	R
<i>Oncidium microchilum</i> Bateman ex Lindl.	L, R
<i>Oncidium sphacelatum</i> Lindl.	L, S, R
<i>Oncidium stipitatum</i> Lindl. in Benth.	L, R
<i>Oncidium stramineum</i> Bateman ex Lindl.	L, R
<i>Oncidium venustum</i> C. Morren	L, S, R
<i>Osmoglossum pulchellum</i> Schltr.	L, S, R
<i>Otoglossum globuliferum</i> (Kunth) N.H. Williams & M.W. Chase	L, R
<i>Pachyphyllum</i> sp.	L, S, R
<i>Palumbina candida</i> Rchb.f.	L, S, R
<i>Plectrophora</i> sp.	L, R
<i>Psychopsis papilio</i> (Lindl.) H.G. Jones	L, R
<i>Rodriguezia secunda</i> Humb. Bonpl. & Kunth	L, S, R
<i>Rossioglossum grande</i> (Lindl.) Garay & G.C. Kenn.	R
<i>Sigmatostalix radicans</i> Rchb.f.	L, R
<i>Solenidium lunatum</i> Schltr.	S
<i>Symphyglossum sanguineum</i> (Rchb.f.) Schltr.	L, S, R
<i>Tolumnia bahamensis</i> (Nash ex Britt. & Millsp.) Braem	L
<i>Tolumnia tetrapetala</i> (Jacq.) Braem	L, R
<i>Tolumnia variegata</i> (Sw.) Braem	L, R
<i>Trichocentrum albococcineum</i> Lindl.	L, R
<i>Trichopilia marginata</i> Henfr.	L, R
<i>Trizeuxis falcata</i> Lindl.	L
<i>Warmingia</i> sp.	L, S, R

L, leaf; S, stem; R, root.

The methods and descriptive conventions have appeared recently in published papers (Stern & Judd, 2001, 2002; Yukawa & Stern, 2002; Stern, Judd & Carlswald, 2004), and we have followed similar procedures here. As a shorthand in descriptions, instead of ‘periclinally oriented’ and ‘anticlinally oriented’, we have substituted ‘periclinal’ and ‘anticlinal’. Owing to potential confusion, except for *Oncidium*, abbreviated ‘O.’, all generic names have been spelled out.

Plant parts were preserved in FAA (70% ethanol–glacial acetic acid–commercial formalin, 9 : 0.5 : 0.5) and stored in 70% ethanol. Transverse and longitudinal sections of leaves and transverse sections of stems and roots were cut as thinly as

possible with a Reichert sliding microtome, stained in Heidenhain's iron–alum haematoxylin, and counter-stained with safranin. Although tilosomes (Pridgeon, Stern & Benzing, 1983) were seen in roots of some species, we could not characterize them without the use of a scanning electron microscope. Leaf scrapings followed Cutler's method (Cutler, 1978) and were stained with safranin. Sections and scrapings were mounted on glass slides with Canada balsam. Observations were made using a Nikon Optiphot microscope, and photographs were taken with an Olympus BH-2 epifluorescent microscope system and a Pixera 120C digital camera. Measurements of the lengths and widths of ten guard-cell pairs were made, and these are given in Table 2.

Table 2. Stomatal dimensions (μm)

Taxon	Average		Range	
	Length	Width	Length	Width
<i>Ada ocanensis</i>	49	31	42–57	20–42
<i>Aspasia lunata</i>	41	38	37–42	35–42
<i>Brassia bidens</i>	44	30	42–47	27–35
<i>Cischweinfia pusilla</i>	36	26	35–37	22–32
<i>Cochlioda noezliana</i>	34	32	27–37	27–37
<i>Comparettia speciosa</i>	58	46	52–67	42–52
<i>Cuitlauzina pendula</i>	43	42	37–47	35–50
<i>Gomesa crispa</i>	45	33	42–47	30–42
<i>Ionopsis utricularioides</i>	47	31	45–50	27–35
<i>Lemboglossum maculatum</i>	59	51	55–62	47–55
<i>Leochilus johnstonii</i>	40	36	30–45	32–40
<i>Mesoglossum londesbroughianum</i>	37	34	35–40	32–37
<i>Mesospinidium</i> sp.	38	30	37–40	27–32
<i>Mexicoa ghiesbreghtiana</i>	44	30	37–47	27–35
<i>Miltonia*bluntii</i>	41	33	35–45	32–35
<i>Miltoniopsis santanaei</i>	37	27	35–40	17–25
<i>Notylia barkeri</i>	51	45	45–55	42–50
<i>Odontoglossum cordatum</i>	55	51	50–60	42–57
<i>Oncidium ampliatum</i>	46	34	42–50	27–42
<i>Oncidium baueri</i>	39	37	37–40	32–40
<i>Oncidium leochiloides</i>	40	26	37–42	22–27
<i>Oncidium sphacelatum</i>	42	30	37–50	25–32
<i>Osmoglossum pulchellum</i>	36	36	32–40	32–40
<i>Otoglossum globuliferum</i>	42	37	32–47	35–40
<i>Palumbina candida</i>	37	28	30–37	25–32
<i>Psychopsis papilio</i>	63	61	57–65	57–65
<i>Rodriguezia secunda</i>	47	41	42–50	40–42
<i>Symphyglossum sanguineum</i>	41	34	37–42	32–37
<i>Trichocentrum albococcineum</i> adaxial	53	40	47–57	35–47
<i>Trichocentrum albococcineum</i> abaxial	53	38	47–57	30–45
<i>Trichopilia marginata</i>	42	52	37–45	47–57
<i>Warmingia</i> sp.	43	27	40–50	22–37

Nine features of vegetative anatomy and morphology were used to construct a character matrix for cladistic analyses of 40 genera in Oncidiinae (Tables 3 and 4). All characters used were readily divisible into discrete states, and multistate characters were considered to be unordered. Following the molecular analyses of Williams et al. (2001), *Dichaea*, *Pescatorea*, and *Zygopetalum* (*Zygopetalinae*) were used as outgroups. Character states for outgroup genera were taken from Stern et al. (2004). Maximum parsimony analyses were performed using the computer program PAUP* 4.0b10 (Swofford, 1999). Heuristic searches were performed with 1000 random-addition sequence replicates, saving five trees per replicate. For branch-swapping, the tree bisection and reconnection (TBR) algorithm was used, saving multiple trees (MULTREES on). The maximum number of trees saved for all analyses was limited to 20 000. Bootstrap analyses utilized 1000 replicates, with ten random-addition replicates (TBR swapping) per bootstrap replicate.

Table 3. Anatomical characters used in cladistic analyses of Oncidiinae. Plesiomorphic states are listed first (0), followed by unordered apomorphic states (1, 2, 3)

No.	Anatomical character
1	HYPODERMIS present abaxial (0), adaxial (1), ad- and abaxial (2), absent (3)
2	FOLIAR FIBRE BUNDLES absent (0), present (1)
3	MESOPHYLL homogeneous (0), heterogeneous (1)
4	MESOPHYLL WATER-STORAGE CELL WALLS smooth (0), banded (1)
5	STEGMATA in leaves present (0), absent (1)
6	TILSOMES absent (0), present (1)
7	CORTICAL WATER-STORAGE CELL WALLS smooth (0), branched, banded (1)
8	ENDODERMAL CELL WALL THICKENINGS U-thickened (0), Π -thickened (1), O-thickened (2), thin (3)
9	PSEUDOBULBS present (0), absent (1)

Table 4. Character states for taxa used in cladistic analyses of Oncidiinae. *Dichaea*, *Pescatorea*, and *Zygopetalum* (*Zygopetalinae*) were used as outgroups for polarization

Genus	Character								
	1	2	3	4	5	6	7	8	9
<i>Ada</i>	2	1	0	0	0	1	0	2	0
<i>Aspasia</i>	2	1	0	0	0	0	0	0/2	0
<i>Bracthia</i>	2	0	0	0	0	1	0	2	0
<i>Brassia</i>	2	1	0	0	0	0	0	2	0
<i>Cischweinfia</i>	2	1	0	0	0	0	0	2	0
<i>Cochlidia</i>	2	1	0	0	0	0	0	2	0
<i>Comparettia</i>	1	1	0	0	0	0	0	0/2	0
<i>Cuitlauzinia</i>	1	1	1	0	0	1	0	0/3	0
<i>Erycina</i>	2	1	0	1	0	?	?	?	0
<i>Gomesa</i>	2	1	0	0	0	0	0	2	0

<i>Helcia</i>	2	1	0	0	0	0	0	2	0
<i>Ionopsis</i>	2	1	0	0	0	?	?	?	0
<i>Lemboglossum</i>	2	0	0	1	0	0	1	2	0
<i>Leochilus</i>	2	1	0	0	0	0	0	3	0
<i>Lockhartia</i>	1	1	0	1	0	0	0	2	0/1
<i>Macradenia</i>	?	?	?	?	?	0	0	2	0
<i>Mesoglossum</i>	1	1	0	0	0	1	0	2	0
<i>Mesospinidium</i>	1	0	0	1	0	0	1	2	0
<i>Mexicoa</i>	1	1	0	0	0	1	0	2	0
<i>Miltonia</i>	1	1	0	0	0	0	0	3	0
<i>Miltoniopsis</i>	2	1	0	0	0	0	0	2	0
<i>Notylia</i>	?	0/1	0/1	0	0	0	0	2	0
<i>Odontoglossum</i>	2	0	0	0	0	0	0	2	0
<i>Oncidium</i>	1/3	1	0/1	0/1	0	0/1	0/1	0/2/3	0
<i>Osmoglossum</i>	1	1	0	0	0	1	1	0	0
<i>Otoglossum</i>	1	1	0	0	0	0	0	2	0
<i>Pachyphyllum</i>	0	0	?	1	1	0	1	2	1
<i>Palumbina</i>	3	1	0	0	0	0	1	2	0
<i>Plectrophora</i>	0	1	0	1	0	0	0	2	0
<i>Psychopsis</i>	3	1	1	0	0	1	0	2	0
<i>Rodriguezia</i>	2	1	0	0	0	0	0	2	0
<i>Rossioglossum</i>	?	?	?	?	?	0	1	2	0
<i>Sigmatostalix</i>	2	1	0	0	0	0	0	3	0
<i>Symphyglossum</i>	2	1	0	0	0	0	0	2	0
<i>Tolumnia</i>	2	1	0	1	0	0	0/1	2	0/1
<i>Trichocentrum</i>	3	0	0	1	1	0	1	2	0
<i>Trichopilia</i>	1	1	0	0	0	1	0	2	0
<i>Trizeuxis</i>	2	1	0	1	0	?	?	?	0
<i>Warmingia</i>	2	1	0	1	0	0	0	2	0
Functional outgroups									
<i>Dichaea</i>	0	0	0	0	0	0	0	0	1
<i>Pescatoria</i>	0	0	0	0	0	0	0	0	1
<i>Zygopetalum</i>	0	0/1	0	0	0	0	0	0	0

Anatomy

As noted by Stern & Carlswald (2004), there are certain features of orchid anatomy that appear to be more or less consistently structured regardless of the taxonomic affinity of the subject. Amongst these features is the organization of tissues in pseudobulbs (Fig. 1). Regardless of relationship, these consist of ground tissue containing numerous, smaller, thin-walled assimilatory cells, embedded in which are a few, larger, thin-walled, empty, water-storage cells, usually with birefringent cell walls. Collateral vascular bundles are scattered about, seemingly without any particular order. The root cortex is typically three-layered (Fig. 2). The outer and inner cell layers are uniseriate; cells are smaller, angular, and without intercellular spaces. The middle layer cells are larger, rounded, and have triangular intercellular

spaces among them. Raphide-containing idioblasts are a constant feature of parenchyma tissues. Vascular tissues in leaves are organized in collateral bundles with superposed xylem and phloem. In the descriptions that follow, therefore, these structures will not be detailed unless there are unique characteristics of note.

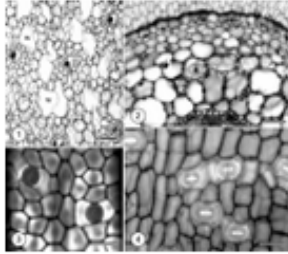


Figure 1–4. Fig. 1. Pseudobulb TS of *Cochlioda noezliana* showing ground tissue with water-storage cells (w), assimilatory cells (a), and scattered vascular bundles. Scale bar = 200 μm . Fig. 2. Root TS of *Osmoglossum pulchellum* showing three-layered cortex. Scale bar = 100 μm . Figs 3, 4. Leaf scrapings. Fig. 3. Tetracytic stomatal organization in *Oncidium venustum*. Scale bar = 50 μm . Fig. 4. C-shaped guard cells (outlined in one pair on upper right side) in *Trichopilia marginata*. Scale bar = 50 μm .

Leaf

Surface: Hairs absent throughout. Stomata abaxial, except abaxial and adaxial in *O. microchilum*, *O. stramineum*, *O. venustum*, *Trichocentrum albococcineum*, and probably other species not studied here. Stomata appear on all exposed surfaces of isobilateral leaves in *Lockhartia*, *Notylia ramonense*, *O. stipitatum*, *Plectrophora* sp., and *Trizeuxis falcata*. Exposed surfaces constitute the abaxial epidermis; vestiges of the adaxial epidermis sometimes appear on the surface where the leaf attaches to the stem. The stomatal apparatus is basically tetracytic (Fig. 3) in all taxa, although on some surfaces there are divisions of subsidiary cells that distort a sharp tetracytic organization. Guard cells are typically reniform and stomata are parallel to the long axis of the guard cells. In *Trichopilia marginata*, guard cells are C-shaped and the stomata extend on both sides into the coves of the two facing Cs (Fig. 4). Average stomatal lengths (Table 2) range from 34 μm in *Cochlioda noezliana* to 63 μm in *Psychopsis papilio*, and widths from 26 μm in *Cischweinfia pusilla* and *O. leochiloides* to 61 μm in *Psychopsis papilio*. Epidermal cells are polygonal on both surfaces; walls are straight-sided or curvilinear.

Section: Cuticle smooth, grooved in *Psychopsis papilio*, papillate in *Trichocentrum albococcineum*; up to 25 μm thick in *O. microchilum*, generally less than 2.5–5.0 μm thick, thinner on the abaxial than adaxial surface. Epidermal cells variable, mostly periclinal and isodiametric; adaxial cells larger than abaxial cells. Stomata (Table 5) usually superficial, sunken in *Cochlioda noezliana*, *Cuitlauzina pendula*, *Odontoglossum cordatum*, *O. stramineum*, and *Notylia barkeri*; slightly sunken in *Aspasia lunata*, *Brachtia andina*, *Comparettia speciosa*, *Gomesa crispa*, *Lemboglossum maculatum*, *O. ampliatum*, *O. leochiloides*, *O. microchilum*, *O. venustum*, *Trizeuxis falcata*, and *Warmingia* sp. Substomatal chambers are mostly very small to moderate compared with the adjacent mesophyll cells, small to large in *O. venustum*, moderate to large in *Miltoniopsis santanaei*, and large in *O. microchilum*, *O. stipitatum*, and *Psychopsis papilio*. Stomatal ledges are often poorly defined in sections; outer ledges mostly small to large in *Ada ocanensis*, *Brassia bidens*, *Cochlioda noezliana*, *O. microchilum*, and *O. venustum*; outer ledges are sometimes accompanied by over-arching cuticular ‘horns’; inner ledges vestigial to

apiculate. Rows of fibre bundles (Table 5) are generally present abaxially but rarely adaxially; absent in *Bractia andina*, *Ionopsis utricularioides*, *Mesospinidium* sp., *Osmoglossum pulchellum*, *Pachyphyllum* sp., and *Trichocentrum albococcineum*. Hypodermis (Fig. 5, Table 5) uniseriate adaxially in most species studied, except *Pachyphyllum* sp. and *Plectrophora* sp.; uniseriate abaxially in many species, absent in some; absent from both surfaces in *O. microchilum*, *O. stipitatum*, *O. stramineum*, *Palumbina candida*, *Psychopsis papillo*, and *Trichocentrum albococcineum*. Cell walls sometimes with birefringent thickenings. Mesophyll (Table 5) cells thin-walled, predominantly homogeneous, heterogeneous in *Cuitlautzinia pendula* (Fig. 6), *Notylia barkeri*, *O. ampliatus*, *O. microchilum*, and *Psychopsis papilio*. Vascular bundles collateral in a single series; biseriate to triseriate in *Ionopsis utricularioides* and *O. microchilum*. Sclerenchyma variable, usually present adjacent to the xylem and phloem in larger bundles; in smaller bundles of different species sclerenchyma sometimes predominates at the xylem pole, sometimes at the phloem pole; in *Ionopsis utricularioides*, larger vascular bundles have sclerenchyma on the xylem side only; in *Notylia ramonense*, *O. stipitatum*, *Pachyphyllum* sp., *Tolumnia bahamense*, and *Trizeuxis falcata*, sclerenchyma is present on the phloem side only; smallest bundles often lack sclerenchyma completely. Stegmata (Table 5) with conical, rough-surfaced silica bodies occur along vascular bundle and fibre bundle sclerenchyma, except there are none along fibre bundles of *Miltoniopsis santanaei*; absent in *Trichocentrum albococcineum* and *Pachyphyllum* sp. Bundle sheaths are variable, sometimes discontinuous, ill-defined, or absent; cells are thin-walled and chlorenchymatous; in *Cochlioda noeziiana*, both thin-walled and thick-walled cells occur in the same sheath; in *Ionopsis utricularioides*, bundle sheath cells radiate from the vascular bundle (Fig. 7).

Table 5A. Selected foliar features: stomata, hypodermis, and fibre bundles

Taxon	Stomata		Hypodermis		Fibre bundles		
	Superficial	Sunken	Adaxial	Abaxial	Adaxial	Abaxial	Mid-mesophyll
<i>Ada ocanensis</i>	+		+1	+1	-	+1	-
<i>Aspasia lunata</i>		+	+1	+1	-	+1	-
<i>Bractia andina</i>		+	+1	+1	-	-	-
<i>Brassia bidens</i>	+		+1	+1	-	+1	+
<i>Cischweinfia pusilla</i>	+		+1	+1	-	+1	+
<i>Cochlioda noeziiana</i>		+	+1	+1	-	+2,3	-
<i>Comparettia speciosa</i>		+	+1	-	-	+1	-
<i>Cuitlautzinia pendula</i>		+	+3,4	-	-	+1	-
<i>Erycina echinata</i>	+		+1	+1	-	-	+
<i>Gomesa crispa</i>		+	+1	+1	-	+2	-
<i>Helcia sanguinolenta</i>	+		+1	+1	-	+1	-
<i>Ionopsis utricularioides</i>	+		+2,3	+1	-	+1	-

<i>Lemboglossum maculatum</i>		+	+1	+1	-	-	-
<i>Leochilus johnstonii</i>	+		+1	+1	-	+1	-
<i>Lockhartia lunifera</i>	?	?	+1	-	-	+1	-
<i>Mesoglossum londesbroughianum</i>	+		+1	-	-	+1	-
<i>Mesospinidium</i> sp.	+		+1	-	-	-	-
<i>Mexicoa ghiesbreghtiana</i>	+		+1	-	-	+2	-
<i>Miltonia</i> × <i>bluntii</i>		+	+1,2	-	-	+2	-
<i>Miltoniopsis santanaei</i>		+	+2,3	+1	-	+1	+
<i>Notylia barkeri</i>		+	+1	-	-	-	+3
<i>Notylia ramonensis</i>	+		?	+1	-	-	-
<i>Odontoglossum cordatum</i>		+	+1,2	+1	-	-	-
<i>Oncidium ampliatum</i>		+	+2	-	+1	-	+
<i>Oncidium boothianum</i>	+		+1	-	+1	+1	-
<i>Oncidium leochiloides</i>		+	+1	-	-	+1	+
<i>Oncidium microchilum</i>		+	-	-	-	+2	+
<i>Oncidium sphacelatum</i>	+		+2	-	+	-	+
<i>Oncidium stipitatum</i>	+		-	-	-	+	-
<i>Oncidium stramineum</i>		+	-	-	+1	+1	-
<i>Oncidium venustum</i>		+	+1	-	-	+	-
<i>Osmoglossum pulchellum</i>	+?		+	-	+1	+1	+
<i>Otoglossum globuliferum</i>	?	?	+1,2	-	-	+1	-
<i>Pachyphyllum</i> sp.	?	?	-	+1	-	-	-
<i>Palumbina candida</i>	?	?	-	-	+1	+1	-
<i>Plectrophora</i> sp.	+		-	+1	-	+2	+
<i>Psychopsis papilio</i>	+		-	-	-	+2	+
<i>Rodriguezia secunda</i>	+		+1	+1	-	+1	-
<i>Sigmatostalix radicans</i>	+		+1	+1	-	+1	-
<i>Symphyglossum sanguineum</i>	?	?	+1	+1	-	+2	-
<i>Tolumnia bahamensis</i>	+		+1	+1	-	+1	-
<i>Trichocentrum albococcineum</i>	+		-	-	-	-	-
<i>Trichopilia marginata</i>	+		+1	-	-	+1	+1
<i>Trizeuxis falcata</i>		+	+1	+1	-	+1	-
<i>Warmingia</i> sp.		+	+1	+1	-	-	+

Table 5B. Selected foliar features: mesophyll and stigmata

Taxon	Mesophyll			Stigmata		
	Homogeneous	Heterogeneous	Water-storage cell banding	Vascular bundles		Fibre bundles
				Xylem	Phloem	
<i>Ada ocanensis</i>	+		-	+	+	+
<i>Aspasia lunata</i>	+		-	+	+	+
<i>Bracthia andina</i>	+		-	+	+	-
<i>Brassia bidens</i>	+		-	+	+	+
<i>Cischweinfia pusilla</i>	+		-	+	+	+

<i>Cochlioda noezliana</i>	+		-	+	+	+
<i>Comparettia speciosa</i>	+		-	+	+	+
<i>Cuitlauzina pendula</i>		+	-	+	+	+
<i>Erycina echinata</i>	+		+	+	+	+
<i>Gomesa crispera</i>	+		-	+	+	+
<i>Helcia sanguinolenta</i>	+		-	+	+	+
<i>Ionopsis utricularioides</i>	+		-	+	+	+
<i>Lemboglossum maculatum</i>	+		+	+	+	-
<i>Leochilus johnstonii</i>	+		-	+	+	+
<i>Lockhartia lunifera</i>	+		+	+	+	+
<i>Mesoglossum londesbroughianum</i>	+		-	+	+	+
<i>Mesospinidium</i> sp.	+		+	+	+	-
<i>Mexicoa ghiesbreghtiana</i>	+		-	+	+	+
<i>Miltonia</i> × <i>bluntii</i>	+		-	+	+	+
<i>Miltoniopsis santanaei</i>	+		-	+	+	-
<i>Notylia barkeri</i>		+	-	+	+	+
<i>Notylia ramonensis</i>	?		-	-	+	+
<i>Odontoglossum cordatum</i>	+		-	+	+	-
<i>Oncidium ampliatum</i>		+	-	+	+	+
<i>Oncidium boothianum</i>	+		-	+	+	+
<i>Oncidium leochiloides</i>	+		-	+	+	+
<i>Oncidium microchilum</i>		+	+	+	+	+
<i>Oncidium sphacelatum</i>	+		-	+	+	+
<i>Oncidium stipitatum</i>	+		+	-	+	+
<i>Oncidium stramineum</i>	+		+	+	+	+
<i>Oncidium venustum</i>	+		-	+	-	+
<i>Osmoglossum pulchellum</i>	+		-	+	+	+
<i>Otoglossum globuliferum</i>	+		-	+	+	?
<i>Pachyphyllum</i> sp.	?	?	+	-	-	-
<i>Palumbina candida</i>	+		-	+	+	+
<i>Plectrophora</i> sp.	+		+	+	+	+
<i>Psychopsis papilio</i>		+	-	+	+	+
<i>Rodriguezia secunda</i>	+		-	+	+	+
<i>Sigmatostalix radicans</i>	+		-	+	+	+
<i>Symphyglossum sanguineum</i>	+		-	+	+	+
<i>Tolumnia bahamensis</i>	+		+	-	+	+
<i>Trichocentrum albococcineum</i>	+		+	-	-	-
<i>Trichopilia marginata</i>	+		-	+	+	+
<i>Trizeuxis falcata</i>	+		+	+	+	+
<i>Warmingia</i> sp.	+		+	+	+	+

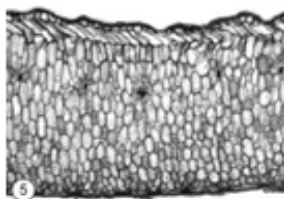


Figure 5–6. Leaf TS. Fig. 5. Adaxial, uniseriate hypodermis in *Rodriguezia secunda*. Scale bar = 200 μ m. Fig. 6. Heterogeneous mesophyll in *Cuitlauzina pendula*. Scale bar = 100 μ m.

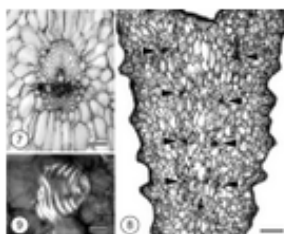
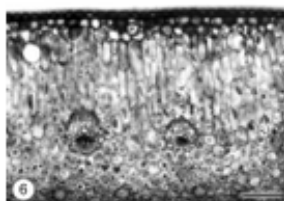
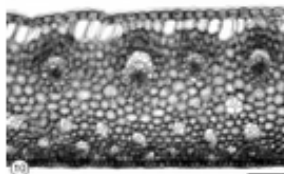


Figure 7–10. Leaf TS. Fig. 7. Bundle sheath cells radiating from the vascular bundle in *Ionopsis utricularioides*. Scale bar = 100 μ m. Fig. 8. Isobilateral leaf of *Tolumnia velutina* with vascular bundles (arrowheads) occurring in pairs. Scale bar = 200 μ m. Fig. 9. Polarized, banded thickenings of a water-storage cell in *Oncidium microchilum*. Scale bar = 50 μ m. Fig. 10. Three-layered mesophyll in *Cochlioda noezliana*. Scale bar = 100 μ m.



Miscellaneous observations: Triangular intercellular spaces are ubiquitous in the mesophyll. Crystalliferous, circular (TS), raphide-containing cells occur throughout the mesophyll. Cruciate starch grains are deposited in cells of the mesophyll in some cases. In isobilateral leaves, vascular bundles occur in opposite pairs (Fig. 8). A midvein bundle is often distinguishable. Variably shaped primary pit fields characterize mesophyll cells. Water-storage cells angular with wavy-margined birefringent walls occur in the mesophyll of some species. These cells may have banded or spirally-thickened walls (Fig. 9, Table 5). The mesophyll in *Cochlioda noezliana* is three-layered, consisting of an adaxial and abaxial band of tightly compressed smaller cells between which is a band of larger, rounded to almost circular cells (Fig. 10). The hypodermis may consist exclusively of parenchyma cells, some of which may be assimilatory and others which may store water, or alternating series of parenchyma and thick-walled sclerenchyma cells. Sclerenchyma alternates with parenchyma cells in *Cochlioda noezliana* (Fig. 10), *Erycina echinata*, *Ionopsis utricularioides*, *O. leucochilum*, *O. sphacelatum*, *Rodriguezia secunda*, *Symphyglossum sanguineum*, and *Tolumnia bahamense*. Parenchyma cells are adaxial to vascular bundles between which are rows of sclerenchyma cells. Cell wall banding or spiral thickenings occur in hypodermal water-storage cells in *Lemboglossum maculatum*, *Notylia barkeri*, *Notylia ramonense*, *Odontoglossum cordatum*, and *Rodriguezia secunda*. Epidermal, hypodermal, and mesophyll cells adaxial to the midrib are often different from

surrounding cells. Cells are often inflated, anticlinal, or bulliform. They take part in the unfolding of conduplicate leaves during vernation, as discussed by Löv (1926). It is doubtful whether any systematic importance can be attached to their structure and position, which appear to be related solely to mechanical functions.

Stem

Hairs and stomata absent. Cuticle smooth, 2.5 µm thick in *Gomesa crispa*, *Mesospinidium* sp., and *Miltonia bluntii* to 37 µm thick in *Cochlioda noezliana* and *O. boothianum*. Epidermal cells mostly periclinal, few isodiametric; tiny, bead-like in *Pachyphyllum* sp. Epidermal cell walls usually thin or thickened internally in *Osmoglossum pulchellum*, and thickened overall in *Cuitlauzina pendula*, almost to the exclusion of the cell cavity (Fig. 11). Cortex present in pseudobulbs of *Aspasia lunata* and *Brassia bidens*, also in the rhizomes of *Aspasia lunata*, *Gomesa crispa*, *O. baueri*, and *Warmingia* sp., and in stems of *Lockhartia lunifera*. All other material lacks a distinct cortex. Endodermis and pericycle are absent throughout, except for a one- to three-layered endodermis of O-thickened, oval cells surrounding the ground tissue of the rhizome in *Gomesa crispa*. Ground tissue in pseudobulbs is similar throughout and consists of smaller, variably shaped, rounded, assimilatory cells, some of which may contain cruciate starch grains, and fewer, larger, wavy-margined, more or less angular, empty water-storage cells embedded among the assimilatory cells; there are small triangular intercellular spaces scattered about. The cell walls of water-storage cells in *Lemboglossum maculatum*, *Mesoglossum londesbroughianum*, *Mexicoa ghiesbreghtiana*, and *Odontoglossum cordatum* (Fig. 12) are banded or spirally thickened. Vascular bundles in pseudobulbs collateral, scattered, numerous; sclerenchyma surrounds entire bundle in *O. baueri*. Sclerenchyma occurs only at the phloem pole in *Aspasia lunata*, *Cochlioda noezliana*, *Cuitlauzina pendula*, *Mesoglossum londesbroughianum*, *Mexicoa ghiesbreghtiana*, *Miltonia bluntii*, *O. boothianum*, *O. leucochilum*, *O. sphacelatum*, *Pachyphyllum* sp., and *Symphyglossum sanguineum*; at both poles of larger bundles of *Brassia bidens*, *Cischweinfia pusilla*, *Gomesa crispa*, *Helcia sanguinolenta*, *Lemboglossum maculatum*, *Mesospinidium* sp., *Milioniopsis santanaei*, *Odontoglossum cordatum*, *O. venustum*, *Palumbina candida*, *Plectrophora* sp., and *Rodriguezia secunda*. Phloem lacunae occur in *Cischweinfia pusilla*, *Cochlioda noezliana*, *Mesospinidium* sp., and *Osmoglossum pulchellum*. Stegmata contain conical, rough-surfaced silica bodies associated with phloem sclerenchyma in all species; with phloem and xylem sclerenchyma in larger bundles in *Brassia bidens*, *Cischweinfia pusilla*, *Gomesa crispa*, *Lemboglossum maculatum*, *Milioniopsis santanaei*, and *Rodriguezia secunda*; absent in *Pachyphyllum* sp. and *O. baueri*.

Root

Velamen mostly four to seven cells wide, ranging from two cells in *Macradenia* sp. to 16 cells in *Mesoglossum* sp. Cell walls thin, but with thickenings at cell wall junctures in *Macradenia* sp. and *O. venustum* (Fig. 13). Epivelamen and endovelamen cell orientation variable (Table 6); endovelamen cells often of two

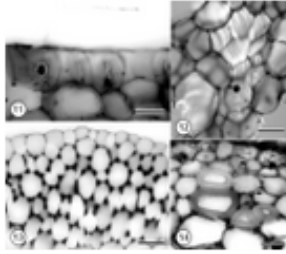


Figure 11–14. Figs 11, 12. Pseudobulb TS. Fig. 11. Epidermal cells of *Cuitlauzina pendula* with thickened walls. Scale bar = 30 μm . Fig. 12. Water-storage cells with banded thickenings in *Odontoglossum cordatum*. Scale bar = 100 μm . Figs 13, 14. Root TS. Fig. 13. Velamen cells with thickenings at cell wall junctures in *Oncidium venustum*. Scale bar = 50 μm . Fig. 14. Angular idioblasts with thickened cell walls within the outer cortex of *Osmoglossum pulchellum*. Scale bar = 50 μm .

distinct orientations (Table 6). Cell wall thickenings mostly tenuous, spiral and looped, thickish in *Bracthia andina*, *O. cebolleta*, and *O. leucochilum*. Unicellular hairs absent, except in *Helcia sanguinolenta*. Cells often infested with hyphae. Tilosomes present or absent (Table 6). Exodermal cell wall thickenings variable (Table 6), most often thin-walled. Passage cells intermittent, thin-walled with large nuclei. Cortex three to five cells wide in *Comparettia speciosa* and *Sigmatostalix radicans* to more than 20 cells wide in *Macradenia* sp.; cells thin-walled, those of the outer and inner layers often angular, isodiametric, smaller than middle layer cells and lacking intercellular spaces. The middle layer of root cortices in almost all species examined consists of two kinds of cells: typical, thin-walled, more or less circular parenchyma cells, embedded in the outer layers of which are angular idioblasts, sometimes with greatly thickened cell walls that refract polarized light (Figs 2, 14). These cells may occur singly or clustered in small groups; they are empty, lacking both nucleus and cytoplasm. Triangular intercellular spaces occur among the circular parenchyma cells. Cells infested with living hyphae and dead hyphal masses. Chloroplasts present in *O. maculatum*. Angular water-storage cells with birefringent cell walls occur among the parenchyma cells of the middle layer. Broad branched bands and thin scalariform thickenings occur in water-storage cells of the cortex in some species (Fig. 2, Table 6). Endodermal and Pericyclic cells are variously orientated and their cell walls differently thickened (Table 6). Most are isodiametric with 0-thickened cell walls. Vascular cylinder 5-arch in *Leochilus johnstonii* to 27-arch in *Bracthia andina* (Table 6). The number of xylem poles appears to be related to the diameter of the root, narrower roots having fewer xylem poles than wider roots. Vascular tissue embedded in thick- or thin-walled sclerenchyma; in parenchyma in *Sigmatostalix radicans*. Pith cells mostly thin-walled, parenchymatous, circular to oval, with triangular intercellular spaces; cell walls thick to somewhat thickened, angular, lacking intercellular spaces in *Cischweinfia pusilla*, *Comparettia speciosa*, *Leochilus johnstonii*, *Lockhartia oerstedii*, *Mexicoa ghiesbreghtiana*, *Notylia ramonense* (Fig. 15), *O. maculatum*, *Plectrophora* sp., *Psychopsis papilio*, *Tolumnia tetrapetala*, *Trichocentrum albococcineum*, and *Trichopilia marginata*.

Table 6A. Selected root features: velamen, tilosomes, and exodermal, endodermal, and pericycle wall thickening/shape

Taxon	Velamen		Tilosomes	Exodermal wall thickening	Endodermal wall thickening/ shape	Pericycle wall thickening/ shape
	Epi	Endo				
<i>Ada ocanensis</i>	peri	anti	+	O	O/iso	O/iso
<i>Aspasia lunata</i>	peri/iso	iso→anti	–	thin	u,O/iso,anti	O/iso
<i>Bracthia andina</i>	peri	iso→anti	+	O	O/iso	O/iso
<i>Brassia bidens</i>	peri/iso	iso→anti	–	O	O/iso	O/iso
<i>Cischweinfia pusilla</i>	peri/iso	iso→anti	–	thin	O/iso	O/iso
<i>Cochlioda noezliana</i>	iso	iso→anti	–	thin	O/iso	O/iso
<i>Comparettia speciosa</i>	peri/iso	iso	–	thin	u,O/iso	O/iso
<i>Cuitlauzina pendula</i>	peri/iso	iso→anti	+	O	u,thin/peri	O,peri/iso
<i>Gomesa crispa</i>	iso	iso	–	O	O/iso	O/iso
<i>Helcia sanguinolenta</i>	peri/iso	iso→anti	–	O	O/iso	O/iso
<i>Lemboglossum maculatum</i>	iso	iso→anti	–	O	O/iso	O/iso
<i>Leochilus johnstonii</i>	peri/iso	iso	–	thin	thin,iso/anti	thin,iso/anti
<i>Lockhartia oerstedii</i>	iso	iso→anti	–	u	O/iso	O/iso
<i>Macradenia</i> sp.	anti	anti	–	∩	O/iso	thin,iso/peri
<i>Mesoglossum londesbroughianum</i>	peri/iso	iso→anti	+	O	O/iso	O/iso
<i>Mesospinidium</i> sp.	peri	iso→anti	–	thin	O/iso	O/iso
<i>Mexicoa ghiesbreghtiana</i>	anti/iso	iso	+	O	O,iso/anti	O/iso
<i>Miltonia×bluntii</i>	iso	iso→anti	–	thin	thin/iso	thin/iso
<i>Miltoniopsis santanaei</i>	iso	anti	–	O	O/peri	O/iso
<i>Notylia barkeri</i>	iso	iso	–	O	O/anti	O/iso
<i>Notylia ramonensis</i>	peri/iso	iso	–	O	O/iso	O/iso
<i>Odontoglossum cordatum</i>	peri/iso	iso→anti	–	thin	O/iso	O/iso
<i>Oncidium ampliatum</i>	peri/iso	anti	+	thin	u/iso	O/iso
<i>Oncidium baueri</i>	iso	iso→anti	+	thin	O/iso→anti	O/iso
<i>Oncidium boothianum</i>	iso	anti	–	thin	O/iso	thin/iso
<i>Oncidium cebolleta</i>	iso	iso→anti	–	thin	O/iso	O/iso
<i>Oncidium leochiloides</i>	iso	anti	–	thin	O/iso→anti	O/iso
<i>Oncidium maculatum</i>	iso	iso	–	O	O/anti	O/iso
<i>Oncidium microchilum</i>	anti	anti→iso	+	∩	O/iso	O/iso
<i>Oncidium sphacelatum</i>	peri	anti	+	thin	O/anti	O/iso
<i>Oncidium stipitatum</i>	anti	iso	–	thin	O/anti	O/iso
<i>Oncidium stramineum</i>	anti/peri/iso	anti→iso	–	thin	O/iso	O/iso
<i>Oncidium venustum</i>	iso	iso	–	thin	thin/iso	thin/iso→peri
<i>Osmoglossum pulchellum</i>	iso	iso→anti	+	∩	u/iso	O/iso
<i>Otoglossum globuliferum</i>	iso	anti	–	thin	O/iso	O/iso
<i>Pachyphyllum</i> sp.	iso	anti	–	thin	O/iso	O/iso

<i>Palumbina candida</i>	iso/peri	iso→anti	–	thin	O/iso	O/iso
<i>Plectrophora</i> sp.	iso	iso/anti/irr	–	O	O/iso,anti	O/iso
<i>Psychopsis papilio</i>	anti	iso/anti	+	O	O/iso	O/iso
<i>Rodriguezia secunda</i>	anti	iso	–	O	O/anti	O/iso
<i>Rossioglossum grande</i>	anti/iso	anti/iso	–	∩	O/iso	O/iso
<i>Sigmatostalix radicans</i>	anti	anti/iso	–	thin	thin/iso,anti	thin/iso
<i>Symphyglossum sanguineum</i>	anti/iso	anti/iso	–	O	O/anti	O/iso
<i>Tolumnia tetrapetala</i>	peri/iso	iso	–	thin	O/iso	O/peri
<i>Tolumnia variegata</i>	anti	iso/peri	–	thin	O/iso	absent
<i>Trichocentrum albococcineum</i>	iso	iso	–	O	O/iso	O/iso
<i>Trichopilia marginata</i>	peri	anti/iso	+	thin	O/iso,peri	O/iso
<i>Warmingia</i> sp.	iso	iso→anti	–	thin	O/iso	O/iso

Epi, epivelamen; endo, endovelamen; anti, anticlinal; iso, isodiametric; peri, periclinal; O, O-thickened; u, u-thickened; ∩, ∩-thickened; *Vascular cylinder destroyed.

Table 6B. Selected root features: pith, cortical cell wall bands, and xylem arching

Taxon	Pith				Cortical cell wall bands	Xylem archy
	Parenchyma	Sclerenchyma	Cells circular	Cells angular		
<i>Ada ocanensis</i>	+		+		–	18
<i>Aspasia lunata</i>	+		+		–	15
<i>Bractia andina</i>	+		+		–	27
<i>Brassia bidens</i>	+		+		–	26
<i>Cischweinfia pusilla</i>		±		+	–	9
<i>Cochlioda noeztiana</i>	+		+		–	12
<i>Comparettia speciosa</i>		+		+	–	6
<i>Cuitlauzina pendula</i>	+		+		–	13
<i>Gomesa crispa</i>	+		+		–	20
<i>Helcia sanguinolenta</i>	+		+		–	14
<i>Lemboglossum maculatum</i>	+		+		+	18
<i>Leochilus johnstonii</i>	+		+		–	5
<i>Lockhartia oerstedii</i>		+		+	–	6
<i>Macradenia</i> sp.	+		+		–	12
<i>Mesoglossum londesbroughianum</i>	+		+		–	21
<i>Mesospinidium</i> sp.	+		+		+	10
<i>Mexicoa ghiesbreghtiana</i>		+		+	–	9
<i>Miltonia×bluntii</i>	+		+	→+	–	14
<i>Miltoniopsis santanaei</i>	+		+		–	15
<i>Notylia barkeri</i>	+		+		–	10
<i>Notylia ramonensis</i>		+		+	–	4

<i>Odontoglossum cordatum</i>	+	+	–	18	
<i>Oncidium ampliatum</i>	+	+	–	10	
<i>Oncidium baueri</i>	+	+	?	?	
<i>Oncidium boothianum</i>	+	+	–	8	
<i>Oncidium cebolleta</i>	+	+	–	8	
<i>Oncidium leochilooides</i>	+	+	–	13	
<i>Oncidium maculatum</i>		+	+	–	7
<i>Oncidium microchilum</i>	+	+	+	18	
<i>Oncidium sphacelatum</i>	+	+	–	7	
<i>Oncidium stipitatum</i>	+	+	–	7	
<i>Oncidium stramineum</i>	+	+	+	14	
<i>Oncidium venustum</i>	+	+	–	10	
<i>Osmoglossum pulchellum</i>	+	+	+	11	
<i>Otoglossum globuliferum</i>	+	+	–	13	
<i>Pachyphyllum</i> sp.	+	+	+	15	
<i>Palumbina candida</i>	+	+	+	10	
<i>Plectrophora</i> sp.		+	+	–	10
<i>Psychopsis papilio</i>		+	+	–	7
<i>Rodriguezia secunda</i>	+	+	–	12	
<i>Rossiglossum grande</i>	+	+	+	+	9
<i>Sigmatostalix radicans</i>	+	+	–	*	
<i>Symphyglossum sanguineum</i>	+	+	–	12	
<i>Tolumnia tetrapetala</i>		+	+	–	7
<i>Tolumnia variegata</i>		absent		+	*
<i>Trichocentrum albococcineum</i>	+	+	+	8	
<i>Trichopilia marginata</i>		+	+	–	7
<i>Warmingia</i> sp.		+	+	–	7

Epi, epivelamen; endo, endovelamen; anti, anticlinal; iso, isodiametric; peri, periclinal; O, O-thickened; u, u-thickened; Π, Π-thickened; *Vascular cylinder destroyed.

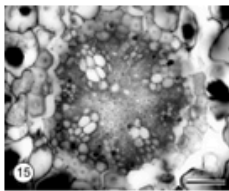


Figure 15. Root TS showing thick-walled cells in the pith of *Notylia ramonensis*. Scale bar = 50 μm.

RESULTS AND DISCUSSION

Anatomy

There is considerable anatomical homogeneity amongst the genera surveyed despite the great diversity of vegetative features (Chase & Palmer, 1989; Dressler, 1993). In leaves, a hypodermis (Table 5) occurs in almost all taxa and is entirely

lacking only in *O. microchilum*, *O. stipitatum*, *O. stramineum*, *Palumbina candida*, *Plectrophora* sp., and *Trichocentrum albococcineum*. Fibre bundles (Table 5) are ubiquitous in leaves of *Oncidiinae* and are absent only in *Brachtia andina*, *Lemboglossum maculatum*, *Mesospinidium* sp., *Odontoglossum cordatum*, *Pachyphyllum* sp., and *Trichocentrum albococcineum*. Mesophyll (Table 5) is homogeneous overall and is heterogeneous only in *Cuitlauzina pendula*, *Notylia barkeri*, *O. ampliatus*, *O. microchilum*, and *Psychopsis papilio*. Stegmata (Table 5) with conical silica bodies occur with phloem sclerenchyma in all genera and in association with xylem sclerenchyma of all taxa except *Notylia ramonense*, *O. stipitatum*, and *Tolumnia bahamense*. Stegmata occur along the fibre bundles in leaves of all species, except for *Brachtia andina*, *Lemboglossum maculatum*, *Mesospinidium* sp., *Miltoniopsis santanaei*, and *Odontoglossum cordatum*. Stegmata are totally absent in *Pachyphyllum* sp. and *Trichocentrum albococcineum*.

Root anatomy (Table 6) is more heterogeneous than leaf anatomy. Nevertheless, there are trends towards homogeneity in certain features. Thin- and thick-walled exodermal cells are almost equally present. Two-thirds of endodermal cells are isodiametric and well over half have O-thickened cell walls. The great majority of pericyclic cells are isodiametric with O-thickened cell walls. Pith is basically parenchymatous with circular cells and triangular intercellular spaces. The majority of cortical cells lack secondary cell wall banding. Tulosomes are absent in three-quarters of species examined. Vascular tissue is surrounded by sclerenchyma, except for a single species.

Bentham (1883) established the subtribe *Oncidiinae* (as ‘*Oncidieae*’) with seven subgroups (called series), and included the genera *Zygostates*, *Ornithocephalus*, *Phymatidium*, and *Chyrtoglossa* in series five. These genera are considered in subtribe *Ornithocephalinae* by Dressler (1993) and Toscano de Brito (1998). However, Williams et al. (2001), based on molecular studies involving four gene regions, support the inclusion of these genera and *Telipogon* in *Oncidiinae*. If we examine the foliar anatomy of components of *Ornithocephalinae*, we find that fibre bundles are absent, there are no hypodermises, and stegmata are lacking, except in *Chyrtoglossa* and *Phymatidium falcifolium*. These features appear to support Toscano de Brito’s (2001) *Ornithocephalinae*, and are in distinct contrast to the leaf anatomy of *Oncidiinae* described here, where the presence of fibre bundles, hypodermis, and stegmata is almost constant in the studied taxa.

Chase & Palmer (1989) reviewed the chloroplast DNA systematics of lilioid monocots and especially of the vegetatively modified *Oncidiinae*. These plants are represented by the so-called mule-ear-leafed and rat-tail-leafed *oncidiums* and associated genera, amongst which is *Trichocentrum*. Evidence is provided to show that vegetatively modified members form a monophyletic unit, exclusive of *Trichocentrum*, which is hypothesized to be a closely related derivative of the larger vegetatively modified lineage. Anatomically, *Trichocentrum* presents a unique picture amongst the genera: it lacks fibre bundles, hypodermises, and stegmata in the amphistomatal leaves.

The function of the angular, thick-walled cells that occur in the outer regions of the root cortex is uncertain. They resemble similar cells in structure and position described for other Maxillarieae by Stern et al. (2004). As in that paper, we hesitate here to call them water-storage cells for lack of evidence and because of their thick, presumably inflexible, cell walls. However, they may impart stability to the otherwise thin-walled cortical tissues. That they occur throughout the tribe Maxillarieae may indicate a synapomorphy for the entire group.

Cladistics

Heuristic analyses of 40 genera using nine vegetative anatomical and morphological characters (Tables 3 and 4) produced 1444 equally parsimonious trees with $L = 27$, consistency index (CI) = 0.44, retention index (RI) = 0.73, and rescaled consistency index (RC) = 0.32. The strict consensus of these genera was completely unresolved, suggesting that vegetative characters alone are insufficient to assess the relationships amongst the genera of Oncidiinae. This was also found to be the case for the rest of the Maxillarieae (Stern et al., 2004). The bootstrap analyses showed weak support (60%) for the subtribe; members of Oncidiinae were united by the presence of an adaxial and abaxial hypodermis and O-thickened endodermal cell walls.

Although the strict consensus was totally unresolved, the strict majority consensus revealed several relationships: *Cuitlouzina* + *Osmoglossum* (found in 59% of the 1444 trees); *Lemboglossum* + *Mesospinidium* + *Pachyphyllum* + *Trichocentrum* (found in 55% of the 1444 trees); *Pachyphyllum* + *Trichocentrum* (found in 87% of the 1444 trees); and *Leochilus* + *Sigmatostalix* (found in 70% of the 1444 trees). The only clade that agrees with the molecular data of Oncidiinae (Williams, Whitten & Chase, 1999) is *Cuitlouzina* + *Osmoglossum*, which is supported by the presence of U-thickened endodermal cell walls.

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