

A contribution to the leaf anatomy of some southern African Iphigenieae (Colchicaceae)

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The leaf anatomy of four species in the Colchicaceae is described. Of diagnostic value within the tribe Iphigenieae are included details of wax, cuticle, epidermis, stomata, hypodermis and the vascular bundles. Distribution of these characters isolates *Hexacyrtis* and lends support to the maintenance of *Gloriosa*, *Sandersonia* and *Littonia* as a distinct group. Co-inciding with this grouping, there is an obvious correlation between the habitat and the leaf anatomical details.

Die blaaranatomie van vier Colchicaceae-spesies word beskryf. Besonderhede soos die was, kutikula, epidermis, huidmondjies, hipodermis en vaatbondels is van diagnostiese waarde binne die tribus Iphigenieae. Verspreiding van hierdie kenmerke isoleer *Hexacyrtis* en onderskryf die behoud van *Gloriosa*, *Sandersonia* en *Littonia* as 'n afsonderlike groep. 'n Duidelike korrelasie tussen die habitat en die blaaranatomie kom saam met hierdie groepering na vore.

Keywords: Costal zones, epidermis, intercostal zones, SEM, stomata

Introduction

According to a recent survey of the monocotyledons (Dahlgren, Clifford & Yeo 1985), the tribe Iphigenieae is considered to comprise 6 genera, all of which are represented within the Flora of southern Africa region. In their treatment of Colchicaceae, these workers adopted the taxonomic views expressed mainly by Nordenstam (1982). The African members of two of these genera, *Iphigenia* Kunth and *Ornithoglossum* Salisb., are being examined by Nordenstam; the other 4 genera are being studied by the present author.

Anatomical research in this group by earlier workers appears to have been concentrated on the genus *Gloriosa* L. This could be related to the reported uses of this species either as charms, medicines or as poisons (see Watt & Breyer-Brandwijk 1962). In *Gloriosa*, much reference has been made to the accumulation of toxic compounds in the perennating organs; the anatomy of which has received ample attention (e.g. Mehra & Khoshoo 1951; Burden *et al.* 1955). On the same lines, Breyer-Brandwijk (1934) studied macerated material of the different organs of *G. virescens* Lindl. Leaf-tip tendril anatomy was carried out in all the genera (Arber 1923) with the exception of *Hexacyrtis* Dint. Similar research in *Gloriosa* was published by Kanga & Dastur (1925), and these workers attempted to relate structure to the movement of the tendrils; a phenomenon which also interested Darwin (1906).

The most detailed anatomical study of seedlings and adult plants was undertaken by Queva (1899), who examined and illustrated all the organs of *Gloriosa superba* L. Similar information, although in less detail, was included on *G. virescens* and *Littonia modesta* Hook. Furthermore, the seedling anatomy of *Gloriosa* sp. reported in a survey of monocotyledonous seedlings (Boyd 1932) agrees very much with Queva's earlier observations.

As a preliminary to a much broader study of this tribe, the following southern African species are being examined, the latter two of which are monotypic: *Gloriosa superba* L., *Littonia modesta* Hook., *Sandersonia aurantiaca* Hook. and *Hexacyrtis dickiana* Dint. In this paper the leaf anatomy of the above four species is presented and its usefulness for diagnostic or taxonomic purposes is considered.

Materials and Methods

Leaf material of all the species was obtained mainly from plants in the field. Vouchers of the following gatherings are

housed in the herbarium of the University of Durban-Westville: *G. superba*, Baijnath, s.n., *S. aurantiaca*, Rennie s.n., *L. modesta*, Baijnath, s.n., *H. dickiana*, C.J. & J.D. Ward 148 & 162. Eight samples from a single population of the first two species were studied. For the third species, four samples from one population were examined. Material from a single population of *H. dickiana* collected at different times was studied.

All leaves were examined at a standard level, halfway between the base and the apex. Portions of fresh leaves were fixed in F.A.A. The standard paraffin-wax method was used in the preparation of transverse and longitudinal sections which were stained in safranin and light green. These were supplemented by temporary preparations of hand-cut sections using a razor blade. Leaf scrapes were prepared by the method used at the Jodrell Laboratory (Cutler 1972) for monocotyledons. Scrapes were stained in a mixture of safranin and alcian blue. For macerations, leaf segments were immersed in Jeffrey's fluid, washed and mounted in a mixture of methylene blue and glycerol. The procedure of preparing leaves for SEM was as outlined in Baijnath (1980).

An initial survey indicated that differences between different samples of the same taxon are not marked and, therefore, descriptions and measurements are recorded from a single specimen. Measurements of the length and breadth of epidermal and guard cell pairs in transverse section were obtained from 25 cells and the mean values in these descriptions are in bold type. For epidermal cells that are irregular in shape, values were obtained by measuring in both planes at the approximate centre of each cell. The terminology relating to symmetrical plane shapes is in accordance with that proposed by the Systematic Association for Descriptive Terminology (1962).

Results

The style of presenting anatomical data is in accordance with that used for the 'Anatomy of monocotyledons' series from the Jodrell Laboratory. However, structures that are lacking (e.g. hairs, prickles, tannins and silica) have been excluded from the description.

Gloriosa superba

Leaf surface

In the light microscope (LM) the following features were observed:

Adaxial surface

Costal zone

Epidermis: 3–6 cells wide, cells 212–337–425 × 27 μm, 6–8 sided, of uniform diameter or tapering very gradually towards the ends, ranging from 7 to 17 times longer than wide. Longitudinal anticlinal walls with some pitting at irregular intervals; walls straight or very slightly sinuous; cross anticlinal walls usually slightly to markedly oblique, cells occasionally tapering to a point. *Papillae*: not seen. *Cuticle*: striae; longitudinal, several, fine, continuous, occasionally oblique; transverse, not seen.

Intercostal zone

Epidermis: 10–18 cells wide, cells 53–115–200 × 40–61–160 μm, 4–7 sided, shapes and orientation very irregular with no distinction between longitudinal and transverse walls, cells ranging from up to 4 times longer than wide to up to twice as wide as long; anticlinal walls with few irregularly spaced pittings, wide V-shape curved. *Papillae*: not seen. *Cuticle*: striae; common, fine, restricted to each cell, randomly oriented but mainly transverse-oblique. *Stomata*: absent.

Abaxial surface

Costal zone

Epidermis: 4–6 cells wide, 213–305–412 × 20–25–27 μm, cells 6–8 sided, almost rectangular; 7–21 times longer than wide. Rest as in adaxial surface.

Intercostal zone

Epidermis: 14–17 cells wide, 53–100–146 × 40–54–67 μm, shapes and orientation somewhat variable, cells ranging from up to 4 times longer than wide to up to 1½ times wider than long. Rest as in adaxial, except stomata present. *Stomata*: superficial, anomocytic, long axes oriented in axial or sometimes oblique-axial direction. Guard cell pair 40 × 27–31–33 μm, outline ranging from broadly elliptical to almost orbicular; poles retuse; polar 'T'-piece represented by short stalk of 'T'.

In the scanning electron microscope (SEM) the following additional features were observed:

Adaxial surface (Figure 1)

Epidermis: outline distinct; well-defined furrows above anticlinal walls in intercostal zones, in addition parallel ridges on either side in costal zones. *Cuticular sculpturing*: micropapillae; usually solitary, randomly distributed in costal zones (arrow); striae; more or less as in LM except more distinct, also evidence of transverse-oblique striae in costal zones. *Wax*: as small amorphous particles of various sizes.

Abaxial surface (Figure 2)

As in adaxial except costae prominent and intercostae with stomata. *Stomata*: superficial, outer stomatal rim raised, few striae encircling outer stomatal rim and merging with adjacent striae.

Leaf transverse section (Figure 9)

Outline: dorsiventrally flattened, almost strap-shaped with prominent midrib bundle; position of main bundle denoted by shallow adaxial V-shaped furrow and well-developed abaxial keel; thickest at midregion and tapering very gradually to the obtuse margins; about 13 mm wide and 0,07 mm thick in the keel region. *Cuticle*: thin (see leaf surface for sculpturing). *Epidermis*: cells on both surfaces opposite larger bundles generally smaller than others; costal cells as wide as tall or slightly taller than wide, intercostal cells as

wide as, or up to twice as wide as tall. Outer walls very slightly convex, very slightly thickened, radial and inner walls thin. *Stomata*: superficial on abaxial surface. *Guard cells*: about ¼ dimensions of adjacent epidermal cells; outer, inner and poral walls somewhat thickened; outer cuticular lip well-developed, inner lip very reduced; substomatal cavity prominent. *Hypodermis*: absent. *Chlorenchyma*: cells in 4–5 layers, lobed, lobes more pronounced on longitudinal walls, keel cells almost circular in transverse section. *Vascular bundles*: 56 in specimen examined, arranged in a single row in chlorenchyma with xylem oriented adaxially; keel bundle largest with medium and small bundles generally alternating, no distinct marginal bundles. *Phloem*: outline of pole indistinct. *Xylem*: in larger bundles generally in a strand consisting of 1–2 fairly wide and 4–6 narrow tracheids. Wide tracheids with spiral thickening, narrow ones with spiral and annular thickening; end walls tapering. *Bundle sheaths*: inner sheath consisting of parenchyma caps at both poles, outline almost semicircular; outer sheath a single layer of wide parenchyma cells. Regions between the xylem and phloem and the sheaths often with narrow thin-walled parenchyma cells. *Crystals*: both druse-like and small prismatic in epidermis and outer chlorenchyma.

Sandersonia aurantiaca

Leaf Surface

In the LM the following features were observed:

Adaxial surface

Costal zone

Epidermis: 3–8 cells wide, cells 160–209–235 × 27 μm, 6–8 sided, often tapering slightly towards the ends, usually almost rectangular, ranging from 5–9 times longer than wide. Longitudinal anticlinal walls straight or very slightly curved; cross anticlinal walls straight, perpendicular, oblique or cells tapering to a point. *Papillae*: absent. *Cuticle*: striae; longitudinal, several, fine, continuous; transverse, obscure.

Intercostal zone

Epidermis: 12–18 cells wide, cells 80–127–160 × 20–27–40 μm, 5–7 sided, almost rectangular or variously shaped, ranging from 2–8 times longer than wide. Longitudinal anticlinal walls straight or slightly sinuous; cross anticlinal walls as in costal region. *Papillae*: absent. *Cuticle*: striae; longitudinal, few, fine; transverse, lacking. *Stomata*: absent.

Abaxial surface

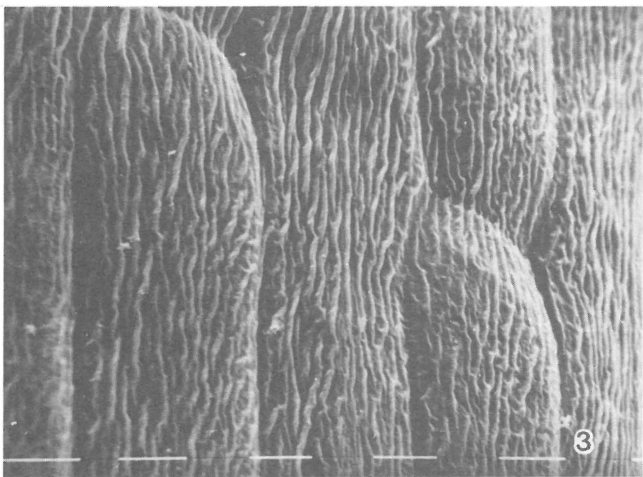
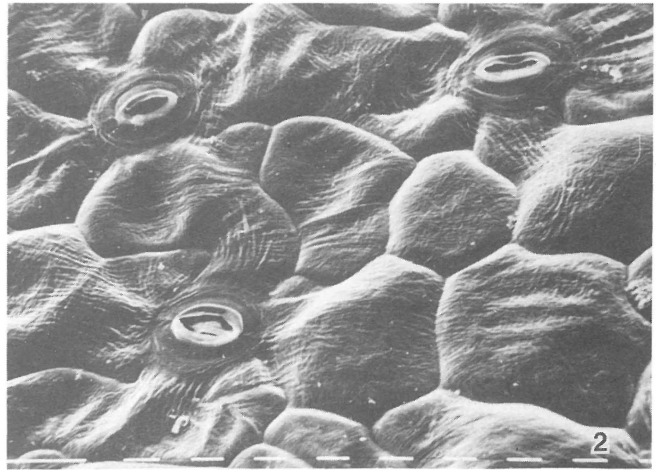
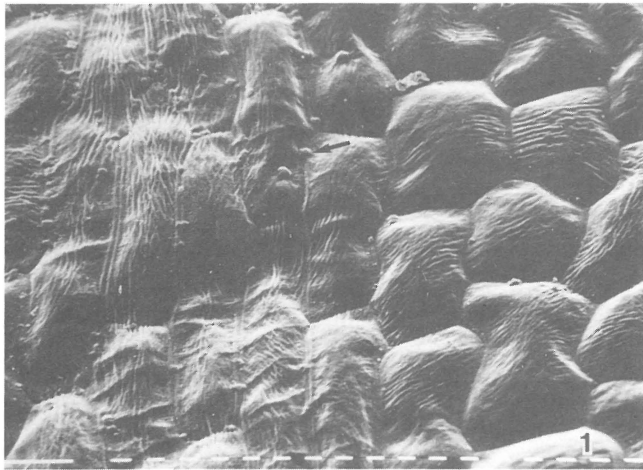
Costal zone

Epidermis: 4–6 cells wide, 133–163–213 × 13 μm, cells 5–8 sided, almost rectangular, ranging from 10–16 times longer than wide. Rest as in adaxial surface except very occasional stomata present (details as in intercostal zone).

Intercostal zone

Epidermis: 12–15 cells wide, 53–119–200 × 27–33–40 μm, 4–8 sided, generally almost rectangular, as wide as, or up to 7 times longer than wide. Rest as in adaxial surface except stomata present. *Stomata*: superficial, anomocytic, longitudinal axes oriented almost regularly in an axial plane. Guard cell pair 40–42–47 × 27–31–40 μm, outline ranging from broadly elliptical to orbicular; poles retuse; polar 'T'-piece absent.

In the SEM the following additional features were observed:



Figures 1–4 Scanning electron micrographs of leaf surfaces of *G. superba* (1 & 2) and *S. aurantiaca* (3 & 4) : 1 & 3, adaxial; 2 & 4, abaxial. Long axis vertical in 1 & 3; horizontal in 2 & 4. Scale bar = 10 μm .

Adaxial surface (Figure 3)

Epidermis: cell outline distinct; distinct furrows above anticlinal walls. *Cuticular sculpturing*: striae; more or less as in LM except more distinct. *Wax*: as amorphous particles of variable sizes.

Abaxial surface (Figure 4)

As in adaxial surface except costal zones prominent and intercostal zones with stomata. *Stomata*: superficial with outer stomatal rim raised. *Cuticle*: striae; few to several in circle on outer stomatal rim, some radiating from the flanks, others continuing longitudinally.

Leaf transverse section (Figures 10, 13 & 15)

Outline: dorsiventrally flattened, almost strap-shaped, single central abaxial rib with 2 parallel ribs on either side. Positions of main bundles denoted by adaxial furrows, most marked in central region; lamina at midregion thickest and tapering very slightly towards the recurved obtuse margins; about 20 mm wide and 0,06 mm thick in the keel region. *Cuticle*: thin (see leaf surface for sculpturing). *Epidermis*: cells on adaxial surface, the margin and keel regions slightly larger than the rest. Cells on both surfaces adjacent to larger bundles regularly smaller than others except those in keel region. Adaxial and abaxial costal cells as wide as high; adaxial intercostal cells twice as wide as high; marginal and keel cells as wide as or half as wide as high; abaxial intercostal cells 2–3 times wider than high. Outer wall slightly convex, slightly thickened; radial and inner walls thin. *Stomata*: superficial, present on abaxial surface.

Guard cells: $\frac{1}{3}$ dimensions of adjacent epidermal cells with outer, inner and poral walls slightly thickened; outer cuticular lip prominent, inner lip poorly developed; substomatal cavity prominent. *Hypodermis*: absent. *Chlorenchyma*: cells in 4–6 layers, only lobed types present, lobes generally wide and short; cells slightly elongated in transverse section, 2–5 times longer than wide in longitudinal section, keel cells rounded. *Vascular bundles*: 59 in specimen examined, arranged in a single row in chlorenchyma with xylem oriented adaxially; keel bundles largest, rest of bundles medium and small, no distinct marginal bundle present. *Phloem*: poles of large bundles almost circular in outline. Sieve tubes quite narrow, 5–6 sided, companion cells about $\frac{1}{4}$ width of sieve tubes. *Xylem*: pole composed of a strand of 3–4 rather wide and 2–4 narrow tracheids in keel bundles; in smaller bundles 2–5 medium and/or small tracheids present. Wall thickening spiral and annular; end walls tapering. *Bundle sheaths*: inner sheath consisting of a well-developed sclerenchyma fibre cap at xylem pole with semi-circular outline in keel bundles and few-celled in other bundles, inner sheath towards phloem pole of compact polygonal parenchyma cells; outer bundle sheath parenchymatous. Fibres elongate, thick-walled with simple pits; end walls pointed. *Crystals*: small solitary prisms in epidermis and chlorenchyma, occasionally large druses seen in longitudinal section of chlorenchyma.

Littonia modesta

Leaf surface

In the LM the following features were observed:

Adaxial surface

Costal zone

Epidermis: 7–9 cells wide, $240\text{--}287\text{--}360 \times 13\text{--}15\text{--}20 \mu\text{m}$, cells 5–8 sided, almost rectangular, ranging from 12–18 times longer than wide. Longitudinal anticlinal walls wide U-shaped; cross anticlinal walls straight, perpendicular, oblique or cells tapering to a point. *Papillae*: not seen. *Cuticle*: striae; longitudinal, several, fine, continuous; transverse, not seen.

Intercostal zone

Epidermis: 12–27 cells wide; cells $80\text{--}131\text{--}226 \times 13\text{--}22\text{--}33 \mu\text{m}$, cells 4–7 sided, shapes and orientation very irregular with no distinction between longitudinal and transverse walls, 2–17 times longer than wide; anticlinal walls wide U-shape curved. *Papillae*: not seen. *Cuticle*: striae; not seen. *Stomata*: absent.

Abaxial surface

Costal zone

Epidermis: 3–7 cells wide; cells $239\text{--}395\text{--}612 \times 13 \mu\text{m}$, cells 5–8 sided, almost rectangular, ranging from 18–47 times longer than wide. Rest as in adaxial surface except very occasionally stomata present (details as in intercostal zone).

Intercostal zone

Epidermis: 12–17 cells wide; cells $40\text{--}102\text{--}160 \times 13\text{--}24\text{--}40 \mu\text{m}$, cells 4–8 sided, shapes and orientation somewhat vari-

able, as wide as, or up to 13 times longer than wide. Rest as in adaxial surface except stomata present. *Stomata*: superficial, anomocytic, long axes oriented in an axial or oblique axial direction. Guard cell pair $37\text{--}39\text{--}47 \times 27\text{--}29\text{--}33 \mu\text{m}$, outlines ranging from broadly elliptical to almost orbicular; poles retuse; polar 'T'-piece not seen.

In the SEM the following additional features were observed:

Adaxial surface (Figure 5)

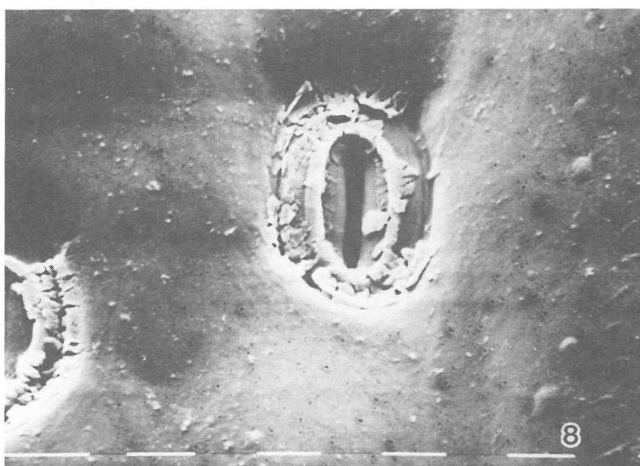
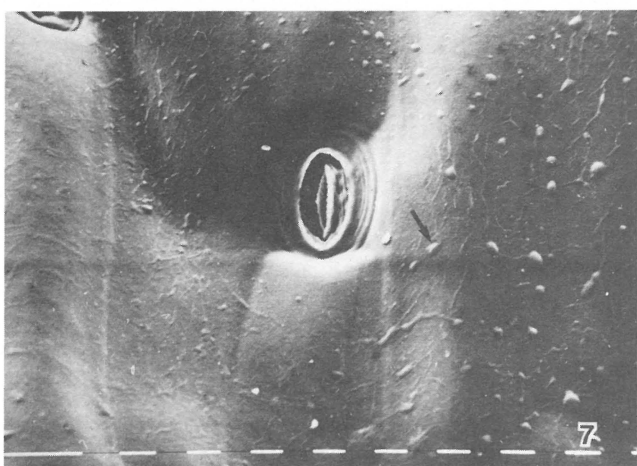
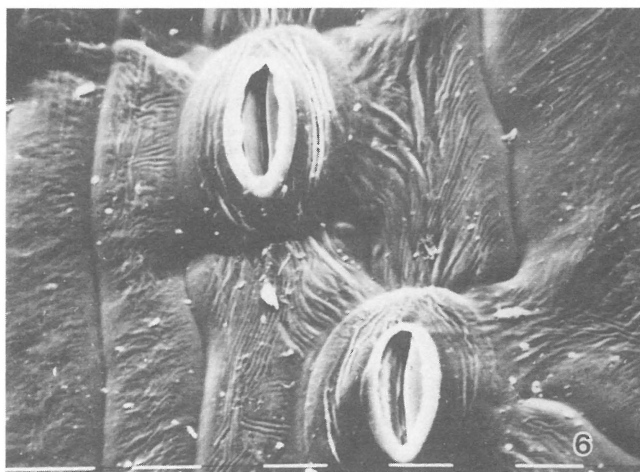
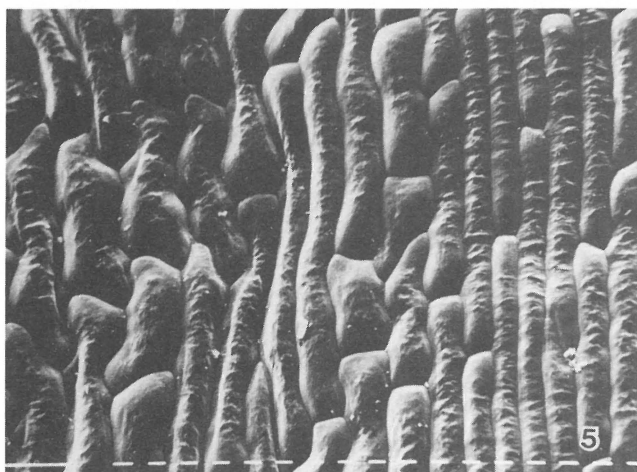
Epidermis: cell outline distinct; distinct furrows above anticlinal cell walls. *Cuticular sculpturing*: micropapillae; 1–few, often joined together; striae; more or less as in LM except more distinct, also some evidence of transverse striae. *Wax*: small, amorphous bodies of various sizes.

Abaxial surface (Figure 6)

As in adaxial except costal zones prominent and intercostal zones with stomata. *Stomata*: superficial, outer stomatal rim raised; few striae on flanks of outer stomatal rim, continuing longitudinally.

Leaf transverse section (Figure 11)

Outline: dorsiventrally flattened, broadly V-shaped, with prominent keel, thickest at mid-position, tapering very gradually to the rounded margins, about 15,4 mm wide and 0,09 mm thick in keel region. *Cuticle*: thin (for sculpturing see leaf surface). *Epidermis*: cells opposite larger bundles generally smaller than others on both surfaces; all cells as wide as tall except those in mid-adaxial region twice as tall



Figures 5–8 Scanning electron micrographs of leaf surfaces of *L. modesta* (5 & 6) and *H. dickiana* (7 & 8); 5 & 7, adaxial; 6 & 8, abaxial. Long axis vertical in all. Scale bar = 10 μm .

as wide. Outer walls slightly thickened on both surfaces, thickening marked in marginal and keel regions; other walls thin. *Stomata*: superficial, on abaxial surface. *Guard cells*: about $\frac{1}{3}$ dimensions of adjacent epidermal cells with outer, inner and poral walls slightly thickened, outer cuticular lips prominent, inner lip very reduced; substomatal cavity large. *Hypodermis*: absent. *Chlorenchyma*: cells in 6–7 layers, in transverse section almost rounded with short lobes and small intercellular air spaces, in longitudinal section cells elongated in longitudinal plane, up to 4 times longer than wide, lobes and intercellular air spaces pronounced. *Vascular bundles*: 30 in specimen examined, in a single row in chlorenchyma with xylem oriented adaxially, keel bundle largest with medium and small generally alternating, no distinct marginal bundle present. *Phloem*: pole outline in larger bundles almost triangular. *Xylem*: in larger bundles consisting of 2–3 wide and 3–5 narrow tracheids with scalariform and annular thickening; end walls tapering. *Bundle sheaths*: inner sheath of few-celled parenchyma cap at phloem pole and well-formed sclerenchyma cap at xylem pole; outer sheath of single layer of wide parenchyma cells. Regions between xylem and phloem and sheath cells with thin-walled narrow parenchyma cells. Sclerenchyma fibres elongated in longitudinal section, thick-walled with primary pits; end walls pointed. *Crystals*: small solitary prisms sparse in epidermis and chlorenchyma, rarely druses in chlorenchyma.

Hexacyrtis dickiana

Leaf surface

In the LM the following features were observed:

Adaxial surface

Costal zone

Epidermis: 4–8 cells wide, $346\text{--}524\text{--}692 \times 20\text{--}22\text{--}30 \mu\text{m}$, cells 5–8 sided, almost of uniform diameter or tapering slightly towards the ends; ranging from 10–35 times longer than wide. Longitudinal anticlinal walls almost straight with very occasional pitting; cross anticlinal walls perpendicular, oblique or cells tapering to a point. *Papillae*: not seen. *Cuticle*: striae; not seen.

Intercostal zone

Epidermis: 7–17 cells wide; $53\text{--}170\text{--}293 \times 50\text{--}60\text{--}80 \mu\text{m}$, cells 4–10 sided, almost rectangular to polygonal, generally widest at mid-point, ranging from as wide as long to up to 7 times longer than wide. Longitudinal anticlinal walls rarely pitted, slightly curved; cross anticlinal walls almost perpendicular. *Papillae*: absent. *Cuticle*: striae; not seen. *Stomata*: as in abaxial surface.

Abaxial surface

Costal zone

Epidermis: 4–9 cells wide; $306\text{--}487\text{--}692 \times 20\text{--}24\text{--}30 \mu\text{m}$, cells 5–8 sided, almost rectangular, as wide as or up to 7 times longer than wide. Rest as in adaxial surface.

Intercostal zone

Epidermis: 15–18 cells wide; $52\text{--}187\text{--}293 \times 48\text{--}57\text{--}67 \mu\text{m}$, cells 4–8 sided. Rest as in adaxial surface except stomata present. *Stomata*: abundant, thus reducing numbers of cross anticlinal walls, sunken, anomocytic, longitudinal axes oriented in an axial plane. Guard cell pair $33\text{--}40\text{--}47 \times 33\text{--}36\text{--}40 \mu\text{m}$, rotund to orbicular; poles retuse; polar 'T'-piece represented by a short stalk of the 'T'.

In the SEM the following additional features were observed:

Adaxial surface (Figure 7)

Epidermis: cell outlines distinct, slight depressions flanked by narrow raised ridges above anticlinal walls. *Papillae*: probably absent (papilla-like artefacts probably through beam damage—arrowed). *Cuticular sculpturing*: striae; absent. *Stomata*: sunken, suprastomatal cavity almost square in outline; outer stomatal rim flanked by 2–4 cuticular striae, the outermost quite prominent; inner-stomatal rim sometimes visible. *Wax*: forming a prominent covering with the exception of the stomatal pore.

Abaxial surface (Figure 8)

As in adaxial surface, except stomatal region with flaking wax. Here, also, beam damage is obvious.

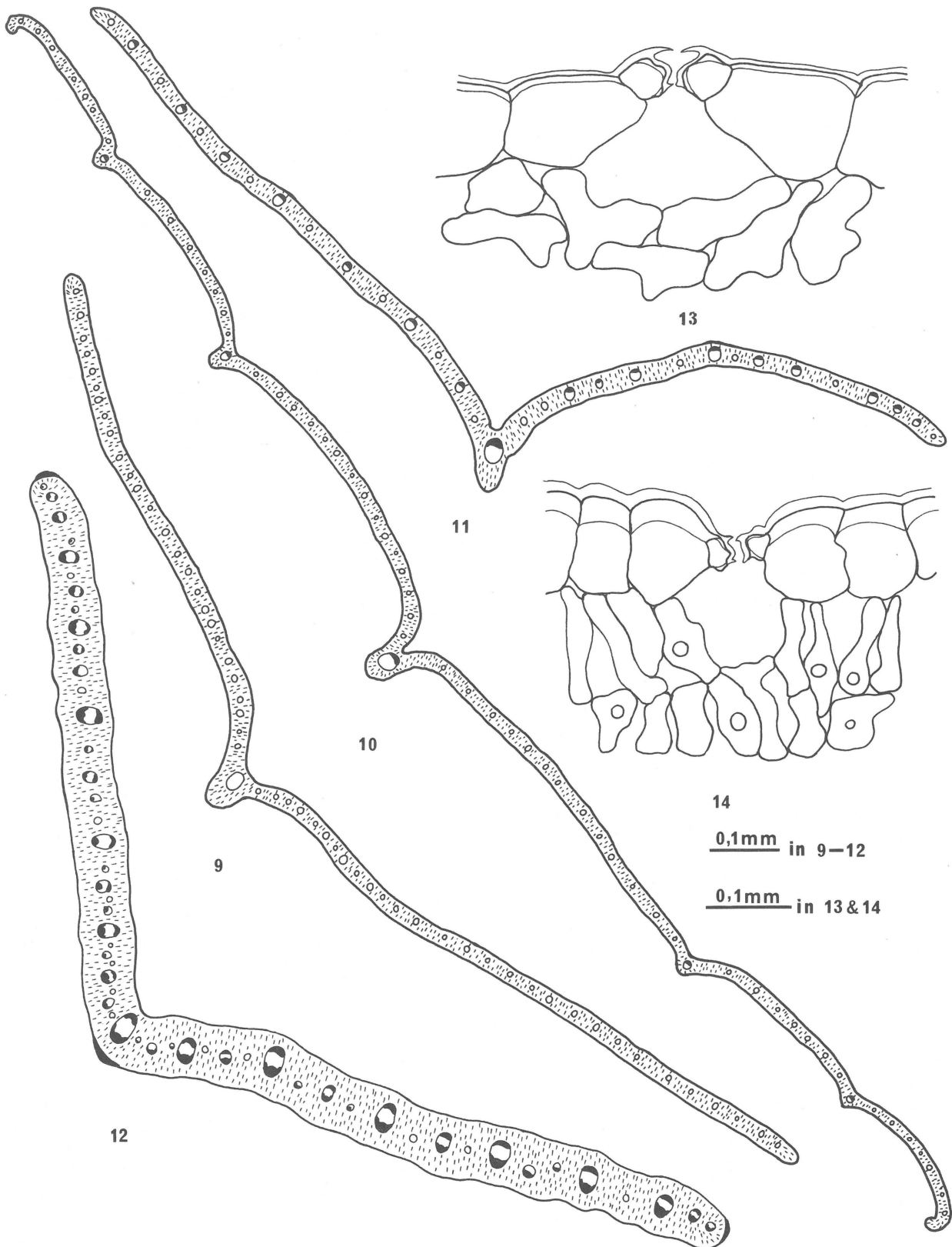
Leaf transverse section (Figures 12, 14 & 16)

Outline: dorsiventrally flattened, slightly undulate with convex areas tending to co-incide with positions of large and medium sized bundles, shallow V-shaped, tapering very slightly to a rounded margin, about 14,1 mm wide and 0,09 mm thick in the keel region. *Cuticle*: thick, almost twice as thick as the other three species (for sculpturing see leaf surface). *Epidermis*: cells opposite larger bundles regularly smaller than others, all cells slightly taller than wide. Outer walls slightly convex, markedly thickened, other walls thin except in marginal and keel cells where all walls thickened. *Stomata*: sunken, present on both surfaces. *Guard cells*: about $\frac{1}{3}$ the dimensions of adjacent epidermal cells with outer, inner and poral walls thickened; outer and inner cuticular lips present; substomatal cavity well-developed. *Hypodermis*: cells thick-walled, consisting of 2–3 rows in marginal and keel regions. *Chlorenchyma*: cells in 13–16 layers, clearly radiating from around each vascular bundle; outermost cells transversely elongated, small lobed, 3–5 times higher than wide; innermost cells with pronounced lobes and large intercellular air spaces. *Vascular bundles*: 54 in specimen examined, in a single row in chlorenchyma with xylem oriented adaxially; generally large and medium sized bundles separated by small ones; no definite marginal bundle. *Phloem*: outline of poles of larger bundles triangular. *Xylem*: in larger bundles as a radial elongate strand, consisting of 3–7 very wide and 2–5 medium to narrow width tracheids with mainly spiral or occasionally annular thickening; end walls tapering. *Bundle sheaths*: inner sheath of well-developed sclerenchyma fibre caps at both poles, outlines almost semi-circular; outer sheath of single layer of parenchyma cells. Regions between xylem and phloem and sheath cells with thin-walled parenchyma. Sclerenchyma fibres in longitudinal section very elongate, thick-walled with simple pits; end walls blunt or pointed. *Crystals*: druse-like, numerous in costal epidermis; small prisms sparse in chlorenchyma.

Discussion and Conclusions

This preliminary investigation of the leaf anatomy of four members of the tribe Iphigenieae has revealed some characters which may be of possible diagnostic value. These attributes include: the degree of development of the wax layer, cuticle and outer epidermal wall; the distribution and position of stomata; the presence or absence of a hypodermis; and the composition and distribution of vascular bundles.

Unlike the other three species, *H. dickiana* is characterized by a very distinctive and prominent layer of wax which completely masks the cuticular details. In this species, also, the cuticle is well-developed and the outer



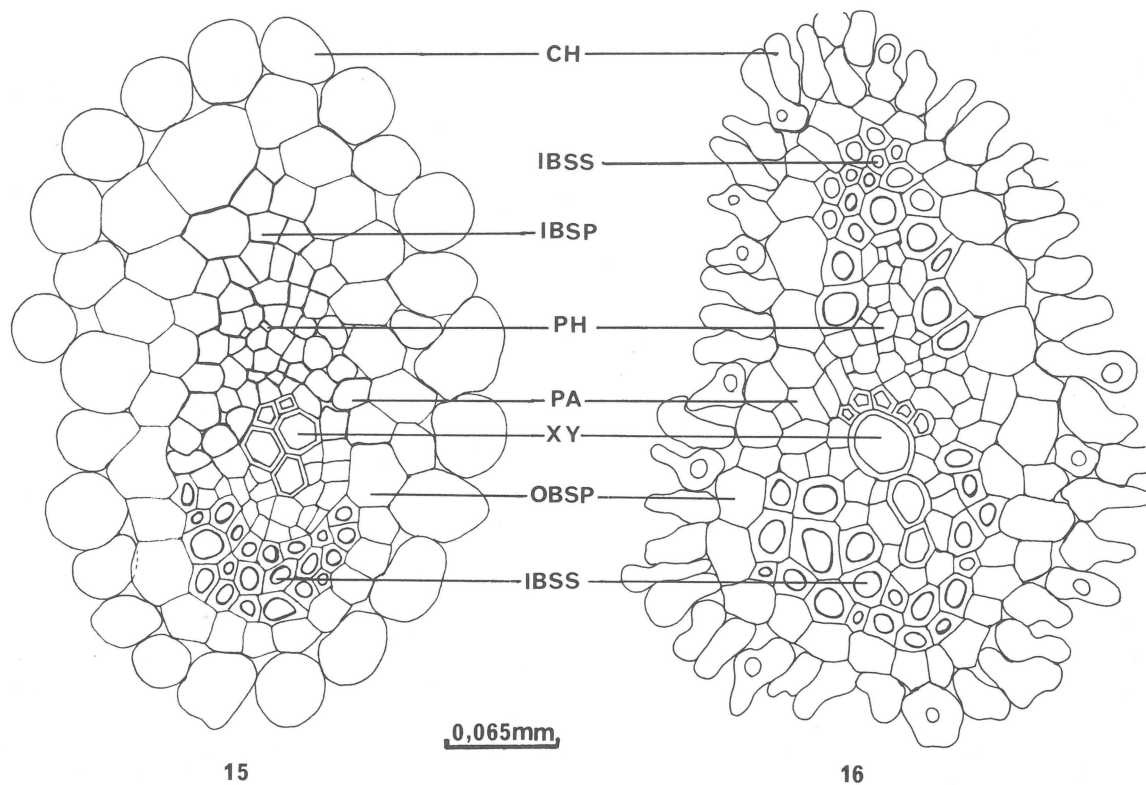
Figures 9-14 Transverse sections of leaves illustrating distribution of tissues (9-12) and details of abaxial stomata (13 & 14) in *G. superba* (9), *S. aurantiaca* (10 & 13), *L. modesta* (11) and *H. dickiana* (12 & 14). Note: stipple = chlorenchyma, black = sclerenchyma.

epidermal wall is over twice as wide as that of the other three species. In *G. superba*, *S. aurantiaca* and *L. modesta*, stomata are superficial and occur only on the abaxial surface, whereas in *H. dickiana*, the leaves are amphistomatic and the stomata sunken.

A two- to three-cell layered hypodermis of thickened cells is located at the keel and margins of the leaves only in *H. dickiana*. The keel bundle in all the leaves with the exception of *H. dickiana* is characteristically larger and more

prominent than the other bundles. Unlike the other species, in *H. dickiana* most of the vascular bundles have a well-developed inner sclerenchymatous bundle sheath at both the xylem and phloem poles.

An evaluation of the above sets of distinctive characters tends to keep *H. dickiana* separate from the other three species. It is interesting that for the species examined, there appears to be an obvious correlation between the leaf anatomical characters and the growth forms and possibly also



Figures 15 & 16 Details of main keel bundle as seen in transverse leaf sections of *S. aurantiaca* (15) and *H. dickiana* (16). CH = chlorenchyma, IBSP = inner bundle sheath parenchyma, IBSS = inner bundle sheath sclerenchyma, OBSP = outer bundle sheath parenchyma, PA = parenchyma, PH = phloem, XY = xylem.

the habitats of the species. Some of the anatomical features in *H. dickiana* are usually found in xerophytes and this tends to be in accordance with the dry sandy habitats in the Namib Desert. During the vegetative period, these plants are acaulescent with well-developed basal leaves. Leaves are also borne on the flowering stalk, but these characteristically decrease in size from the base to the apex.

The anatomical features of the other three species are more characteristic of mesophytic plants. These three species occur in partly or wholly shaded localities but are often found in full sun twining and climbing on other vegetation. The rainfall in these areas is sufficient to maintain active growth through the whole life cycle. Furthermore, *S. aurantiaca* inhabits very cool shaded moist streambanks.

Unlike *Sandersonia* and *Hexacyrtis* which are monotypic, *Gloriosa* and *Littonia* consist of several species. From a comparison of the growth forms of the latter two, it emerges that other species of these genera endemic to areas in and around Somalia are much smaller plants. Also, some of these, especially in the genus *Littonia*, bear hairy leaves. It seems quite obvious that a fuller understanding of the relationships and evolutionary trends within these groups would depend on a wider investigation of all the species.

In a study of the vegetative morphology of Liliiflorae with reticulate and parallel-veined leaves, Conover (1983) included the genera *Gloriosa*, *Sandersonia* and *Littonia*. Of particular interest to the present study is the section dealing with leaf anatomy of 39 genera. Although Conover gave a broad survey, it must be emphasized that some of the conclusions could be very misleading. A feature that is very marked in the above three species and has been overlooked, is the distinct structural differences between the costal and the intercostal zones. Furthermore, the conclusion in reference to the stomata of these genera as being 'oriented strictly parallel to the leaf axis' is quite incorrect especially in *G. superba*. Perhaps the attribute concerning the number of contact cells associated with the stomata as

being four or more in the parallel-leafed species, would be a more realistic view.

The genus *Hexacyrtis* shares many morphological similarities with *Ornithoglossum* as has already been recorded by Nordenstam (1982). However, decisions concerning how closely these two genera may be related would need to await the accumulation of data from other fields including leaf anatomy. Nevertheless, on the basis of morphology and leaf anatomy, *Hexacyrtis* could undoubtedly be maintained separately from the other three genera. This may eventually lend support to the earlier decisions on tribal limits proposed by Buxbaum (1936), who maintained *Gloriosa*, *Sandersonia* and *Littonia* in a separate tribe, Gloriosieae.

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