COMPARATIVE ANATOMY OF THE STEM IN THE CARRION FLOWERS

(APOCYNACEAE-ASCLEPIADOIDEAE)

THESIS

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DEDICATION

This thesis is dedicated to my father, the late Donato Katuramu Atwooki, who was my first teacher; and to Rev Isidore Ndagizimana, the sponsor of my studies in the United States of America.

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TABLE OF CONTENTS

Page

LIST OF TABLES

Table **Page**

LIST OF FIGURES

Figure **Page**

ABSTRACT

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The carrion flowers or stapeliads (*Stapelia* and related genera, Apocynaceae) comprise a group of several hundred species of succulent plants native to the Old World, primarily Africa. Despite the size and diversity of the group, surprisingly little is known of the comparative anatomy and morphology of its members. This study documents stem anatomical structure and cuticular characteristics of twenty-eight species representing fourteen genera of stapeliads. Materials were prepared for examination using standard histological techniques. The principal anatomical features examined in stem cross sections were pith radius and cortex thickness and the presence/absence of a thickened

outer epidermal wall, hypodermis, palisade cortex, cortical bundles, collapsible cortex, *and* medullary bundles. Cuticular features examined included epidermal cell wall characteristics, subsidiary cell arrangement, presence/absence of trichomes, papillae, and cuticular striations, and calculation of the stomatal index. Observations showed most species to have distinctive adaptations to the stem succulent habit, including the loss of leaves, development of ribbed stems, production of abundant water storage tissues development of a perennial epidermis, occurrence of stomata in the stem epidermis, and development of columnar cortical cells with numerous chloroplasts and large intercellular spaces. The cortex/pith ratio ranged from 0.4 to 1.7 in all but one species (*Pseudolithos eylensis*), indicating that the cortex contributes a larger storage volume than the pith. The outer epidermal cell walls were thickened in all species. Hypodermis was absent from most species, but present in species of *Duvalia* and in *Stapelia engleriana*. A palisade cortex was present in more than half of the species. Cortical bundles were generally absent, except in the genus *Echidnopsis*. A collapsible cortex was absent in most species, and medullary bundles were seen only in *Caralluma diffusa* and *Duvaliandra dioscoridis*. Epidermal cells were usually hexagonal or pentagonal in shape with straight end walls and were generally not aligned in rows. Subsidiary cell arrangement was varied, with cyclocytic, brachyparacytic, and anomocytic arrangements being most common. The stomatal index ranged from 0.9 to 5.4. Most of these features are common to stem succulent plants in general, although some features characteristic of other stem succulents, most notably the cacti, are generally absent from the stapeliads.

1. INTRODUCTION

The carrion flowers or stapeliads (*Stapelia* and related genera, Apocynaceae) comprise a group of several hundred species of succulent plants native to the Old World primarily Africa (Bruyns 2000, 2005; Mulej and Strilic 2002). Despite the size and diversity of the group, surprisingly little is known of the comparative anatomy and morphology of its members (Mauseth 2004). According to Bruyns (2000), these plants have their origins in northeastern Africa and have spread from there in three main directions. Two of these are recognized as major centers of diversity and they include Southern Africa and Madagascar, the southern center, and Asia, Arabia, India, Burma and Nepal, the northeastern center. The third direction is the spread to West Africa.

Most stapeliads grow best in semi-arid to arid habitats with temperature ranges of 20 to 30°C. Also, most species are considered poor competitors (Bruyns 2005). Generally, carrion flowers require the presence of nurse plants and are usually found growing under the shade of tall grass and shrubs (Mulej and Strilic 2002). Consequently, overcrowding or excessive shade negatively affects their growth (Bruyns 2005).

Although many members of the family Apocynaceae are extremely poisonous, those of the subfamily Asclepiadoideae, which include the stapeliads, are less poisonous. Consequently, some of them are edible (Mulej and Strilic 2002). For instance, in different parts of Southern Africa *Caralluma adscendens* var. *fimbriata* is cultivated and

eaten as a vegetable for its medicinal properties for heart diseases. Also, follicles, flowers and stems of *Baynesia lophophora, Australluma peschii* and some species of *Ophionella, Pectinaria and Tridentea* are consumed All *Hoodia* species are edible and about a hundred years ago *Hoodia officinalis* was imported to the U.S for treatment of hemorrhoids (Brown 1907; Wyk and Gericke 2000). In Southern Africa, *Hoodia pilifera* has been used for the same purpose. Stems of some *Hoodia* species, especially *H gordonii* and *H flava,* have the ability to quench thirst and hunger for long periods. These medicinal properties have not been scientifically proven but this information has led the Council for Scientific and Individual Research of South Africa and various international pharmaceutical firms to a deeper investigation on the plants (Bruyns 2005). The investigation led to the discovery of a glycoside molecule that has been called active principle P57. This extract has been used in the production of a dietary supplement marketed as an appetite suppressant (Wynberg 2004). According to some findings, plants grown in more or less natural conditions usually produce greater quantities of the active principle (Bruyns 2005).

Discovery and classification

Justus Huernius, a traveler from the west, first discovered African stapeliads in 1624 when he noticed the species later identified as *Orbea variegata,* and other western travelers discovered more species in the years that followed. In 1753 the known species of stapeliads were listed in Linnaeus' *Species Plantarum* (Bruyns 2005). In 1783 C. P. Thunberg and Francis Mason started an intensive study on stapeliads. They spent three years studying together and later Mason spent nine years alone, studying and documenting the South African stapeliads (Bruyns 2005). This study led to the

documentation of 41 stapeliad species in Mason's *Stapeliae Novae* Around the same time, Pehr Forsskal, William Roxburgh and Henrietta Clive added more species from Arabia and India. Meanwhile, Mason introduced some of the discovered species into cultivation in Europe (Bruyns 2005).

It has been rather difficult to classify stapeliads into a specific number of genera, and over time scientists have continuously regrouped the plants, leading to the recognition of new genera each time. For instance, White and Sloane (1937) recognized 18 genera, Bruyns (2000) recognized 24 genera, and with the discovery of two more genera the number of recognized genera based on morphological characters increased to 26 (Bruyns 2001). The classification was based on analysis of morphological characters. However, when Meve and Liede (2002) analyzed molecular data, they came out with 34 genera. Despite the efforts made, relationships among many genera remain unresolved (Bruyns 2005). The most recent taxonomic treatment of the group recognizes 31 genera of stapeliads consisting of 326 species. Of these, nineteen genera with 182 species are found in the southern center of diversity. And of the nineteen, fifteen genera with 162 species are endemic to Southern Africa. This constitutes about 92% of all the species found in Southern Africa and the neighboring countries (Bruyns 2005).

Morphology and pollination

Stem Most stapeliads have thick, fleshy, and angled stems that contain a clear bitter tasting sap (Bruyns 2005). The stem surface is usually covered with a thick waxy layer and contains a relatively low number of stomata. With the exception of a few species, the stem is usually slender due to lack of a tough hypodermis and cortical

bundles and the length rarely exceeds 15 cm (Mauseth 2004). In the least derived stapeliads the plants form an upright many-stemmed shrub. Examples are found in some species of *Caralluma* The more derived forms have taken two directions. In the first, the central stem spreads out along the ground to form a clump that roots on the side branches, in the second, the stems become large, robust and free-standing. In the first case, the branch stems may be shorter forming dense mats on the ground as in *Duvalia,* they may retain their length and still form dense mats shooting out roots all along the length of the stem as in *Huernia* and *Stapelianthus,* or they may develop horizontal underground rhizomes that emerge at various places above the ground as in *Tromotriche* Also, there may be a reduction in the number and length of stems in a clump as in the genus *Larryleachia* (Bruyns 2005; Mulej and Strilic 2002).

Leaves· The only species of stapeliad with true leaves is *Frerea indica.* In the rest, the plants have leaf rudiments or leaves are absent. Rudiments, when present, are borne on raised tubercles arranged in rows along the stem in most species. This arrangement gives the stems a thick, angled appearance, one of the distinctive characteristics of stapeliads. Also, the arrangement helps in reducing the surface area of the leaves and increasing the photosynthetic ability of the stem (Bruyns 2005).

In stapeliad species in which the stems have more than four angles, the leaves are arranged in whorls instead of opposite pairs (Bruyns 1988, 1993; Troll 1935). The leaf rudiments in a few genera of the Northern Hemisphere, such as *Caralluma, Echidnopsis* and *Rhytidocaulon*, still show remnants of a midrib and it is possible, although with difficulty, to trace the shape of the leaf blade as either lanceolate, ovate or cordate. However, it is almost impossible to figure out the leaf details for plants in the Southern

Hemisphere. In addition to reduction in size, the leaves of some species are modified into spines, as in *Hoodia* and *Tavaresia.* In some species of *Duvaliandra* and *Notechidnospis* the leaf rudiments have been reduced so much so that not even a trace can be seen (Bruyns 2005). There are cases, particularly in *Tavaresia*, where the modified leaf grows two extensions near the base developing a trifoliate shape, a structure sometimes referred to as a microloma-type leaflet (Bruyns 1999; Bruyns and Linder 1991; Meve and Albers 1990).

Flowers Stapeliad flowers vary greatly in size with the largest being about 40 cm in diameter and the smallest 0.25 cm in the genera *Stapelia* and *Caralluma,* respectively (Barad 1990; Bruyns 2000, 2005). According to studies on flower organization in the carrion flowers, (Bruyns 1988, 1993; Meve 1994, 1997; Wertel 1976), there are two main ways in which the inflorescences may be positioned on the stem. First, plants producing inflorescences near the apex of the stem usually produce them in large numbers and bear small flowers either on the main or the branching stem. Second, plants producing inflorescences near the base of the stem, usually bear one inflorescence per stem and produce large flowers. In the former case the inflorescences are borne on the secondary stem. As in other members of the family, the inflorescences in stapeliads consist of clusters of flowers that open simultaneously (Bruyns 2005).

Usually, the exterior of the flower is dull colored but the interior has attracting colors of differing intensity and patterns. Despite this beauty, the flowers produce a nasty scent similar to that of decomposing flesh,or animal manure. For this reason stapeliads are sometimes referred to as carrion flower plants. This characteristic explains why pollination is mostly by flies or gnats (Barad 1990; Mulej and Strilic 2002). In most

genera flowers last between two and four days, but the time can be as short as eighteen hours in *Piaranthus atrosanguineus* and as long as eight days in *Huernia barbata.* Flowers that seem to be odorless last longer than those with a bad-smell (Bruyns 2005).

A closer examination of the flower shows that all the parts appear in multiples of five and the flower exhibits radial symmetry or actinomorphism (Bruyns 2005; Mulej and Strilic 2002). The greenish, usually lanceolate sepals are easy to locate. The corolla is fleshy and somewhat rigid with short and broad lobes that are usually free at the beginning of the flowering period but later the margins fuse forming a tube (Bruyns 2005). The tube lengths vary depending on the species. The corolla encloses the corona, which is made up of a pair of series of lobes, the outer and inner coronas. The former is opposite the corolla lobes and the later alternates with these lobes. In some species of stapeliads, nectarial cavities, for collecting nectar, develop in the tissues of the outer corona. There is great diversity in the shape and texture of the corolla and the two series of the corona tubes (Bruyns 2005). The filament, in these flowers, has been lost and instead the stamens and corona form a tube around the ovaries termed the gynostegium. Under each inner corona lobe is a rectangular or square shaped anther head which gives rise to two pollinia that contain fused pollen (Mulej and Strilic 2002).

Fruit. An unusual characteristic of the stapeliads is that the fertilized ovaries can take up to four years before they develop into fruit. This is because the seeds are viable for only a short time, and delayed development of fruit ensures germination of seeds takes place at a suitable time and seed dispersal can happen over different seasons. The fruits are a pair of slender horn-like follicles that taper gradually to the tip and bear wind dispersed seeds whose numbers may range from 10 to 700. Irrespective of when the

plants flower, in Southern Africa the fruits ripen at the onset of summer in the months of November and December (Barad 1990; Bruyns 2005).

Pollination Although many asclepiad flowers may be pollinated by insects such as carpenter bees (Wanntorp 1974), honey bees, wasps, butterflies, moths, flies (Kunze and Liede 1991; Liede and Whitehead 1991; Ollerton and Liede 1997), stapeliad flowers are mostly pollinated by flies (Barad 1990; Endress 1994; Leach 1985, 1988; Meve and Liede 1994) especially species of *Calliphora, Musca* and *Sarcophaga* (Bruyns 2000). The insects are attracted to the flower by the bright colors and the nasty smell as they search for nectar. During the feeding process, the insects get stuck in the flower and, in the struggle to get free, pollinators dislodge the whole pollinium that remains attached to the proboscis. On visiting the next flower the pollinium adheres to the gynostegium where pollen grains germinate, grow pollen tubes and complete the process of fertilization (Barad 1990; Bruyns 2005).

General characteristics of succulents

Phylogenetic studies indicate that the succulent stapeliads probably evolved from non-succulent leafy climbers (Von Willert et al. 1992). Consequently morphological and anatomical modifications accompanied this transition in growth habit. A study of anatomical features can offer an understanding of the relationships within different groups. The term succulent describes those plants that store a high percentage of water in their organs. These may be leaves, stems or roots. Therefore plants can be grouped as stem succulents such as *Ferocactus* (Cactaceae), leaf succulents such *Lithops* (Aizoaceae), or root succulents as in *Brachystelma* (Apocynaceae). However, there are other plants with more than one succulent tissue in different organs, for example, *Ceraria*

namaquensis (Portulacaceae). In yet other plants only part of the whole plant remains succulent such as in *Oxalis succulenta* (Oxalidaceae) In such cases it becomes difficult to classify the plant, for various succulent tissues contribute to the utilizable amount of water in the plant (Von Willert et al. 1992). Therefore, the definition of a succulent plant must include presence of at least one living succulent tissue that temporarily stores utilizable water making the plant independent from external supply especially at conditions when soil water becomes unavailable to the plant roots. The cell vacuoles of such plants contain at least 99% of the entire cell's water (Von Willert et al. 1992). More often, just part of the organ may be succulent, for example the leaf epidermis or the cortex of the stem. The type or portion of succulent organ in the plant plays a great role in the plant's physiology and is an important determining factor in the life strategies of succulent plants. For instance, in partial leaf succulent plants, where only one or two leaf tissues are succulent, the non succulent chlorenchyma may photosynthesize and the succulent parenchyma store water. In the all-cell succulents, where the whole leaf apart from the vascular bundles is succulent, the two tissues can perform both functions. Therefore, the partial leaf succulent plant exhibits more task differentiation than the all-cell leaf succulent plant. In a meaningful description of the term succulence, the morphology, anatomy and function of the succulent tissue or organ need to be considered, for the major difference among succulents is in the fraction of utilizable water and not the total amount stored in the plant (Von Willert et al. 1992).

Usually, succulent plants are found in the humid habitats of arid places some of which may sometimes be salty. Storage of utilizable water is a factor that enables succulent plants to live in habitats that endure periodic droughts. The length of time that

the plant can survive depends on the amount of utilizable water present at the onset of the drought. Although succulents are widespread and occur abundantly in humid areas, this does not mean that these plants are adapted to arid zones and drought. For if the drought was to last for very long periods the plants would not survive. Therefore, succulent plants are adapted to periodic droughts that allow time for refilling of water storage tissues (Von Willert et al. 1992).

There are two components of the plant's water content. The first is the proportion of the succulent tissue in the organ and the second is the utilizable water content in the tissue. The absolute water content of a succulent plant varies with the available physiological conditions. Special anatomical features to allow flexibility of succulent tissues must be present in order for the succulent plant to carry out repetitive emptying and refilling of such tissues with utilizable water (Von Willert et al. 1992). Also, there are features that minimize the ability of the plant to lose water. For instance in leaf and stem succulents, epidermal cells may have thickened outer cell walls and/or a thick cuticle. In other plants only part of the leaf is exposed to direct radiation while the other part becomes protected (Von Willert et al. 1992).

In addition to water storage, other adaptations of succulent plants to their habitats include persistence of epidermis in the stem, a reduction in leaf size and large thin-walled cells in the pith and cortex (Mauseth 1999, 2004). With the exception of a few anatomical structures, like the width of the cortex and presence of a collapsible cortex, evolution of some succulent stems shows little difference from that of the non-succulent members of their families. However, this is not the case in the evolution of cacti that show various modifications in stem anatomy (Mauseth 2004). For instance, cacti have

adapted to dry conditions by reducing the presence of vessels, evolving wide-band tracheids and having both Crassulacean Acid Metabolism (CAM) and C_4 metabolism (Laundrum 2002).

Although stapeliads are usually smaller than some succulent plants, such as large members of Euphorbiaceae and Cactaceae, the three groups are similar in some of their growth forms. An example includes growth of prostrate stems (Bruyns 2005). Also, according to Mauseth (2005), a persistent epidermis, a thickened cortex and a palisade cortex are the only three characters that are universally present in stem photosynthetic, stem-succulent plants. The stem epidermis usually contains numerous sunken stomata. According to some plant eco-physiologists this arrangement is not so much to prevent water loss as to increase the rate of carbon dioxide intake and therefore maximize the rate of photosynthesis. The ribbed stem in most succulents allows flexibility of the cortex as it expands and contracts in adjustment for the available water (Gibson 1998).

Previous work on stem anatomy of succulent plants

According to Mauseth (2004), little is known about the anatomy of many stem-photosynthetic succulents other than cacti and agaves. There is also a lack of information concerning their physiology, ecology and survival in their natural habitats (Von Willert et al. 1992). However, Mauseth (2004) documented a study on two groups of photosynthetic succulent stems from eight plant families. The plants were divided into stem succulents that are not significantly photosynthetic and stem succulents that are significantly photosynthetic. Comparison of anatomical stem features of these plants show that there are differences and similarities between the two groups. For instance, many species lack some features considered as adaptations to dry habitats, such as

cortical bundles and a multilayered hypodermis of very thick walled cells, which are usually found in cacti. The three carrion flower plant species, *Hoodia gordonii, H ruschii, and Stapelia grandiflora* have a dense network of medullary bundles, which mainly consist of phloem. *Hoodia* species have no xylem and *S grandiflora* has a few tracheary elements (Mauseth 2004).

In another study on twenty five succulent species from five plant families (Apocynaceae, Asteraceae, Crassulaceae, Euphorbiaceae and Vitaceae), Mauseth showed that many species lack cortical bundles, a multilayered hypodermis of thick-walled cells and deeply sunken stomata. The nine members of the family Apocynaceae have a persistent epidermis of small, flat, thin-walled parenchyma cells that lack tannins or crystal cells and all have an internal phloem. Also, unlike cacti and other desert plants, the species studied lack massive succulent bodies, with their cortex limited to only 0.5 cm in thickness. In addition, guard cells in all species are not sunken (Mauseth 2004).

The purpose of the current study was to investigate stem anatomical features in 28 species representing 14 genera of carrion flowers (Table 1). Results from different species were compared and the findings related to the existing literature on succulent stems.

2. MATERIALS AND METHODS

Fixation: Specimens were obtained from the Biology Department greenhouse at Texas State University-San Marcos. By means of a razor blade a piece of about 3-4 cm was cut from the stem of each species. The piece was further sliced into about 0.3 cm long pieces which were placed into labeled vials containing formalin-acetic acid-alcohol (90:5:5 FAA), and left to stand for 24 hours.

Dehydration: The plant tissues were subjected to graded dehydration by first decanting the fixative and covering them with 50% ethanol and letting the vials stand for 2 hours at room temperature. The procedure was repeated using 70%, 85%, and 95% alcohol solutions. The 95% ethanol was replaced with 100% alcohol dyed with Eosin B and left to stand for 12 hours. The 100% alcohol solution from each vial was decanted and replaced with tertiary–butyl alcohol (TBA). The vials, with their lids still on were placed on top of an oven kept at 45°F and left for two hours. Two more changes of TBA were made leaving the last change for overnight.

Infiltration and Embedding: An amount of liquid paraffin wax equal to the TBA present in each vial was added and the vials, with lids removed, kept in the oven at 45°F overnight. Two more changes of liquid paraffin wax were made. Afterwards, the tissues were embedded in paraffin wax.

Sectioning and mounting: The embedded tissues were mounted onto supporting blocks and by means of a rotary microtome cut into thin sections (8-10 μm). Wax ribbons

containing the tissue sections were floated in 3-4% formalin on dry microscope slides previously subbed with albumin. The slides were placed on a warming table to evaporate the formalin and to allow adherence of tissues to the slides. To ensure complete adherence the slides were be placed in a slide storage box and left on a warming table for 24 hours.

Staining: To remove paraffin wax, the slides were passed through a series consisting of xylene and different concentrations of ethanol (100%, 95%, and 70%) with each lasting 15 min. The tissues were stained in Safranin O for 12-24 hours and later transferred to chromic acid and crystal violet remaining in each solution for 30sec. The slides were washed in water, dehydrated in a graded ethanol series, stained with fast Green and cleared in xylene. The tissues on each slide were mounted by a cover slip secured with Permount. Slides were dried on a warming table and later viewed and photographed with a Nikon Eclipse 50i compound microscope equipped with a Nikon DS Fi1 digital camera system. Observations were recorded in a table.

Preparation of the cuticle. Stem cuticles were prepared by chemical maceration methods where all stem tissues but the cuticle disintegrate. A two centimeter stem cylinder from each of the species was split in half, placed in a beaker and covered with 70% Nitric acid. The set up was left to stand until the color turned pancake brown (usually 30-45 minutes, no more than one hour). The stem material was rinsed one time and the acid was replaced with a 30% chromium trioxide solution. The beakers were covered and left in a fume hood for three days. The cuticle was rinsed until the water remained clear and transferred to vials. Staining was done by adding a drop of Crystal

Violet dissolved in 50:50 water:ethanol and gently tapping the vial for 25 sec. The cuticle was rinsed until water became clear and mounted in glycerin jelly on microscope slides.

Table 1. List of stapeliad specimens used in the present study

Accession No.	Species	Geographic origin
565	*Baynesia lophophora* Bruyns	Namibia
646	*Caralluma diffusa* (Wight) N. E. Br.	India
044	*Caralluma solenophora* Lavranos	Yemen
523	*Duvalia corderoyi* (Hook. F.) N. E. Br.	South Africa
639	*Duvalia modesta* N. E. Br.	South Africa
045	*Duvaliandra dioscoridis* (Lavranos) M. G. Gilbert	Socorsa
315	*Echidnopsis cereiformis* Hook	Ethiopia
562	*Echidnopsis lavraniana* Plowes	Ethiopia
105	*Edithcolea grandis* N. E. Br.	East Africa
051	*Frerea indica* Dalzell	India
728	*Huernia boleana* M. G. Gilbert	Ethiopia
441	*Huernia hislopii* ssp. *robusta* L. C. Leach & Plowes	Zimbabwe
724	*Huernia hystrix* var. *parvula* (L. C. Leach) Bruyns	South Africa
423	*Huernia leachii* Lavranos	Mozambique

Table 1-Continued. List of stapeliad specimens used in the present study.

Accession No.	Species name	Geographic origin
157	*Huernia occulta* L. C. Leach & Plowes	Zimbabwe
341	*Huernia recondita* M. G. Gilbert	Ethiopia
411	*Lavrania haagnerae* Plowes	Namibia
613	*Piaranthus barrydalensis* Meve	South Africa
057	*Piaranthus comptus* N. E. Br.	South Africa
405	*Piaranthus geminatus* (Masson) N. E. Br.	South Africa
270	*Pseudolithos eylensis* Chiovenda	Somalia
570	*Stapelia cedrimontana* Frandsen	South Africa
172	*Stapelia divaricata* Masson	South Africa
099	*Stapelia engleriana* Schltr.	South Africa
677	*Stapelia paniculata* var. *scitula* (L.C. Leach) Bruyns	South Africa
678	*Stapelia pillansii* var. *pillansii* N. E. Br.	South Africa
495	*Stapelianthus decaryi* Choux	Madgascar
389	*Tavaresia barklyi* N. E. Br	Angola

3. RESULTS

Observations of stem anatomy and cuticular features are summarized in Tables 2 and 3 respectively. Full descriptions of the anatomical characteristics of each species are presented below.

Baynesia lophophora Bruyns (Figures 1-3)

Stem anatomy: Stems four angled, 3.4 mm in diameter; pith radius 0.9 mm; cortex thickness 0.8 mm; cortex:pith ratio 0.9. Epidermal cell length 12-41 μm (average = 23 μm); epidermal cell width 10-37 μm (average = 17 μm). Outer wall of epidermis thickened, hypodermis absent, palisade cortex present, cortical bundles absent, collapsible cortex absent, medullary bundles absent.

Cuticular features: Epidermal cells mostly hexagonal in shape with straight end walls, not aligned in rows. Papillae present, trichomes absent. Cuticular striations present mostly in the cells surrounding the stomatal complex. Stomatal index = 2.3. Subsidiary cell arrangement mostly brachyparacytic with 0-3 rings of encircling cells.

Caralluma diffusa (Wight) N. E. Br. (Figures 4-6)

Stem anatomy: Stems four angled, 2.2 mm in diameter; pith radius 0.7 mm; cortex thickness 0.4 mm; cortex:pith ratio 0.5. Epidermal cell length 21-54 μm (average = 37 μm); epidermal cell width 10-21 μm (average = 15 μm). Outer wall of epidermis

thickened, hypodermis absent, palisade cortex absent, cortical bundles absent, collapsible cortex absent, medullary bundles present, comprised only of phloem.

Cuticular features: Epidermal cells mostly pentagonal in shape with straight end walls, not aligned in rows. Papillae absent, trichomes absent. Cuticular striations present. Stomata not aligned in rows. Stomatal index = 2.1. Subsidiary cell arrangement mostly brachyparacytic with 1-2 rings of encircling cells.

Caralluma solenophora Lavranos (Figures 7-8)

Stem anatomy: Stems four angled, 6.2 mm in diameter; pith radius 1.3 mm; cortex thickness 1.8 mm; cortex:pith ratio 1.4. Epidermal cell length 21-69 μm, (average = 40 μm); epidermal cell width 12-29 μm (average = 20 μm). Outer wall of epidermis thickened, hypodermis absent, palisade cortex present, cortical bundles absent, collapsible cortex present in form of undulate cell walls, medullary bundles absent.

Cuticular features: Epidermal cells mostly pentagonal in shape with straight end walls, not aligned in rows. Papillae present, trichomes absent. Cuticular striations present. Stomata not aligned in rows. Stomatal index = 2.2. Subsidiary cell arrangement mostly brachyparacytic with 1-2 rings of encircling cells.

Duvalia corderoyi (Hook. f.) N. E. Br. (Figures 9-10)

Stem anatomy: Stems five to six angled, 4.2 mm in diameter; pith radius 1.2 mm; cortex thickness 0.9 mm; cortex:pith ratio 0.8. Epidermal cell length 17-69 μm (average = 42 μm); epidermal cell width 22-47 μm (average = 35 μm). Outer wall of epidermis

thickened, hypodermis present, palisade cortex present, cortical bundles absent, collapsible cortex absent, medullary bundles absent.

Cuticular features: Epidermal cells mostly hexagonal in shape with straight end walls, not aligned in rows. Papillae present, trichomes absent. Cuticular striations present but faint. Stomata not aligned in rows. Stomatal index = 3.9. Subsidiary cell arrangement mostly amphicyclocytic.

Duvalia modesta N. E. Br. (Figures 11-13)

Stem anatomy: Stems four angled 1.4 mm in diameter; pith radius 0.4 mm; cortex thickness 0.3 mm; cortex·pith ratio 0.7. Epidermal cell length 13-46 μm (average = 29 μm); epidermal cell width 12-27 μm (average = 19 μm). Outer wall of epidermis thickened, hypodermis present, palisade cortex present, cortical bundles absent, collapsible cortex present in form of undulate cell walls, medullary bundles absent.

Cuticular features: Epidermal cells mostly pentagonal in shape with straight end walls, not aligned in rows. Papillae present, trichomes absent. Cuticular striations present. Stomata not aligned in rows. Stomatal index = 3.0. Subsidiary cell arrangement mostly brachyparacytic with a ring of encircling cells to cyclocytic.

Duvaliandra dioscoridis (Lavranos) M. G. Gilbert (Figures 14-15)

Stem anatomy· Stems four angled, 6.8 mm in diameter; pith radius 2.3 mm; cortex thickness 1.1 mm; cortex:pith ratio 0.5. Epidermal cell length 19-73 μm (average = 44 μm); epidermal cell width 11-28 μm (average = 21 μm). Outer wall of epidermis

thickened, hypodermis absent, palisade cortex absent, cortical bundles absent, collapsible cortex absent, medullary bundles present.

Cuticular features: Epidermal cells mostly hexagonal in shape with straight end walls, not aligned in rows. Papillae present, trichomes absent. Cuticular striations absent. Stomata not aligned in rows. Stomatal index = 1.8. Subsidiary cell arrangement mostly brachyparacytic with a ring of encircling cells to cyclocytic.

Echidnopsis cereiformis Hook. (Figures 16-19)

Stem anatomy: Stems eight angled, 3.0 mm in diameter; pith radius 1.0 mm; cortex thickness 0.5 mm; cortex:pith ratio 0.5. Epidermal cell length 10-41 μm (average = 25 μm); epidermal cell width 7-29 μm (average = 13 μm). Outer wall of epidermis thickened, hypodermis absent, palisade cortex present, cortical bundles present, collapsible cortex present, medullary bundles absent.

Cuticular features: Epidermal cells mostly pentagonal in shape with straight end walls, not aligned in rows. Papillae present, cells with papillae larger and more densely stained than other cells, trichomes absent. Cuticular striations absent. Stomata not aligned in rows. Stomatal index = 1.0. Subsidiary cell arrangement mostly amphicyclocytic.

Echidnopsis lavraniana Plowes (Figures 20-22)

Stem anatomy: Stems eight angled, 4.5 mm in diameter; pith radius 1.5 mm; cortex thickness 0.8 mm; cortex:pith ratio 0.5. Epidermal cell length 14-51 μm (average = 30 μm); epidermal cell width 12-24 μm (average = 21 μm). Outer wall of epidermis thickened, hypodermis absent, palisade cortex present, cortical bundles present,

collapsible cortex absent, medullary bundles absent, laticifers common in much of the cortex.

Cuticular features: Epidermal cells mostly pentagonal in shape with straight end walls, not aligned in rows. Papillae present, trichomes absent. Cuticular striations absent. Stomata not aligned in rows. Stomatal index = 1.0. Subsidiary cell arrangement mostly anomocytic but cells adjacent to guard cells smaller than other cells.

Edithcolea grandis N. E. Br. (Figures 23-24)

Stem anatomy: Stems four angled, 4.6 mm in diameter; pith radius 1.0 mm; cortex thickness 1.3 mm; cortex:pith ratio 1.3. Epidermal cell length 18-37 μm (average = 27 μm); epidermal cell width 13-29 μm (average = 21 μm). Outer wall of epidermis thickened, hypodermis absent, palisade cortex absent, cortical bundles absent, collapsible cortex absent, medullary bundles absent.

Cuticular features: Epidermal cells mostly hexagonal in shape with straight end walls, not aligned in rows. Papillae present, trichomes absent. Cuticular striations present. Stomata not aligned in rows. Stomatal index = 2.7. Subsidiary cell arrangement mostly cyclocytic.

Frerea indica Dalzell (Figures 25-26)

Stem anatomy: Stems almost rounded with a diameter of 4.2 mm; pith radius 1.0 mm; cortex thickness 1.1 mm; cortex:pith ratio 1.1. Epidermal cell length 10-49 μm (average = 26 μm); epidermal cell width 12-33 μm (average = 22 μm). Outer wall of epidermis

thickened, hypodermis absent, palisade cortex present, cortical bundles absent, collapsible cortex absent, medullary bundles absent.

Cuticular features: Epidermal cells mostly pentagonal in shape with straight end walls, aligned in obscure rows. Papillae absent, trichomes absent. Cuticular striations absent. Stomata not aligned in rows. Stomatal index = 1.6. Subsidiary cell arrangement mostly cyclocytic with 2-3 rings of encircling cells.

Huernia boleana M. G. Gilbert (Figures 27-28)

Stem anatomy: Stems four angled, 4.4 mm in diameter; pith radius 1.5 mm; cortex thickness 0.7 mm; cortex:pith ratio 0.4. Epidermal cell length 12-37 μm (average = 23 μm); epidermal cell width 11-20 μm (average = 17 μm). Outer wall of epidermis thickened, hypodermis absent, palisade cortex absent, cortical bundles absent, collapsible cortex absent, pith with collapsible cells, medullary bundles absent.

Cuticular features: Epidermal cells mostly pentagonal in shape with straight end walls, not aligned in rows. Papillae absent, trichomes absent. Cuticular striations present. Stomata not aligned in rows. Stomatal index = 2.2. Subsidiary cell arrangement mostly brachyparacytic with a ring of encircling cells to cyclocytic with 1-3 rings of encircling cells.

Huernia hislopii ssp *robusta* L. C. Leach & Plowes (Figures 29-30)

Stem anatomy: Stems with five to seven wing-like angles, 3.0 mm in diameter; pith radius 0.7 mm; cortex thickness 0.8 mm; cortex:pith ratio 1.1. Epidermal cell length 10-30 μm (average = 22 μm); epidermal cell width 14-30 μm (average = 21 μm). Outer wall

of epidermis thickened, hypodermis absent, palisade cortex absent, cortical bundles absent, collapsible cortex absent, medullary bundles absent.

Cuticular features: Epidermal cells mostly pentagonal in shape with straight end walls, not aligned in rows. Papillae absent, trichomes absent. Cuticular striations absent. Stomata not aligned in rows. Stomatal index = 1.6. Subsidiary cell arrangement mostly weak cyclocytic.

Huernia hystrix var. *parvula* (L.C. Leach) Bruyns (Figures 31-32)

Stem anatomy: Stems five angled, 3.4 mm in diameter; pith radius 1.0 mm; cortex thickness 0.7 mm; cortex:pith ratio 0.7. Epidermal cell length 13-31 μm (average = 21 μm); epidermal cell width 10-25 μm (average = 18 μm). Outer wall of epidermis thickened, hypodermis absent, palisade cortex present, cortical bundles absent, collapsible cortex absent, medullary bundles absent.

Cuticular features: Epidermal cells mostly pentagonal in shape with straight end walls, aligned in obscure rows. Papillae absent, trichomes absent. Cuticular striations present. Stomata not aligned in rows. Stomatal index = 1.5. Subsidiary cell arrangement obscured by striations, but most likely brachyparacytic.

Huernia leachii Lavranos (Figures 33-34)

Stem anatomy: Stems four to five angled 2.6 mm in diameter; pith radius 0.7 mm; cortex thickness 0.6 mm; cortex:pith ratio 0.9. Epidermal cell length 18-62 μm (average = 37 μm); epidermal cell width 13-37 μm (average = 22 μm). Outer wall of epidermis

thickened, hypodermis absent, palisade cortex present, cortical bundles absent, collapsible cortex absent, medullary bundles absent.

Cuticular features: Epidermal cells mostly pentagonal in shape with straight end walls, not aligned in rows. Papillae absent, trichomes absent. Cuticular striations absent. Stomata not aligned in rows. Stomatal index = 1.8. Subsidiary cell arrangement mostly anomocytic.

Huernia occulta L. C. Leach & Plowes (Figures 35-36)

Stem anatomy: Stems four to five angled, 1.6 mm in diameter; pith radius 0.3 mm; cortex thickness 0.5 mm; cortex:pith ratio 1.7. Epidermal cell length 17-45 μm (average = 28 μm); epidermal cell width 10-23 μm (average = 17 μm). Outer wall of epidermis thickened, hypodermis absent, palisade cortex absent, cortical bundles absent, collapsible cortex present in form of slight undulate cell walls, medullary bundles absent.

Cuticular features: Epidermal cells mostly hexagonal in shape with straight end walls, not aligned in rows. Papillae absent, trichomes absent. Cuticular striations absent. Stomata not aligned in rows. Stomatal index = 0.9. Subsidiary cell arrangement mostly brachyparacytic with a ring of encircling cells.

Huernia recondita M. G. Gilbert (Figures 37-38)

Stem anatomy: Stems four angled, 3.4 mm in diameter; pith radius 1.2 mm; cortex thickness 0.5 mm; cortex:pith ratio 0.4. Epidermal cell length 16-47 μm (average = 31 μm); epidermal cell width 9-24 μm (average = 20 μm). Outer wall of epidermis

thickened, hypodermis absent, palisade cortex absent, cortical bundles absent, collapsible cortex present, medullary bundles absent.

Cuticular features: Epidermal cells mostly pentagonal in shape with straight end walls, not aligned in rows. Papillae absent, trichomes absent. Cuticular striations absent, stomata not aligned in rows. Stomatal index = 1.6. Subsidiary cell arrangement mostly brachyparacytic with less than two rings of encircling cells.

Lavrania haagnerae Plowes (Figures 39-40)

Stem anatomy: Stems 10-12 angled, 12.0 mm in diameter; pith radius 3.0 mm; cortex thickness 3.0 mm; cortex:pith ratio 1.00. Epidermal cell length 14-47 μm (average = 26 μm); epidermal cell width 10-32 μm (average = 18 μm). Outer wall of epidermis thickened, hypodermis absent, palisade cortex absent, cortical bundles absent, collapsible cortex present, medullary bundles absent.

Cuticular features: Epidermal cells mostly pentagonal in shape with straight end walls, not aligned in rows. Papillae absent, trichomes absent. Cuticular striations absent. Stomata not aligned in rows. Stomatal index = 3.2. Subsidiary cell arrangement obscured but most likely anomocytic, stomatal apertures occluded.

Piaranthus barrydalensis Meve (Figures 41-43)

Stem anatomy: Stems four angled, 4.0 mm in diameter; pith radius 1.2 mm; cortex thickness 0.8 mm; cortex:pith ratio 0.7. Epidermal cell length 11-50 μm (average = 29 μm); epidermal cell width 14-34 μm (average = 22 μm). Outer wall of epidermis

thickened, hypodermis absent, palisade cortex present, cortical bundles absent, collapsible cortex absent, pith with collapsible cells, medullary bundles absent.

Cuticular features: Epidermal cells mostly pentagonal in shape with straight end walls, not aligned in rows. Papillae present, papillate cells larger and darker staining than other cells, trichomes absent. Cuticular striations absent. Stomata not aligned in rows. Stomatal index = 2.6. Subsidiary cell arrangement mostly amphicyclocytic.

Piaranthus comptus N. E. Br. (Figures 44-45)

Stem anatomy: Stems four angled, 4.2 mm in diameter; pith radius 1.3 mm; cortex thickness 0.8 mm; cortex:pith ratio 0.6. Epidermal cell length 16-42 μm (average = 30 μm); epidermal cell width 16-49 μm (average = 31 μm). Outer wall of epidermis thickened, hypodermis absent, palisade cortex present, cortical bundles absent, collapsible cortex absent, pith with collapsible cell walls, medullary bundles absent.

Cuticular features: Epidermal cells mostly hexagonal in shape with straight end walls, not aligned in rows. Papillae present, trichomes absent. Cuticular striations absent. Stomata not aligned in rows. Stomatal index = 3.7. Subsidiary cell arrangement mostly amphicyclocytic.

Piaranthus geminatus (Masson) N. E. Br. (Figures 46-47)

Stem anatomy: Stems four angled, 3.2 mm in diameter; pith radius 1.1 mm; cortex thickness 0.5 mm; cortex:pith ratio 0.5. Epidermal cell length 13-41 μm (average = 24 μm); epidermal cell width 18-38 μm (average = 28 μm). Outer wall of epidermis thickened, hypodermis absent, palisade cortex present, cortical bundles absent, collapsible cortex present, medullary bundles absent.

Cuticular features: Epidermal cells mostly pentagonal in shape, with straight end walls, not aligned in rows. Papillae absent, trichomes absent. Cuticular striations absent. Stomata not aligned in rows. Stomatal index = 2.0. Subsidiary cell arrangement mostly cyclocytic.

Pseudolithos eylensis Chiovenda (Figures 48-49)

Stem anatomy: Stems somewhat rounded, 40.0 mm in diameter; pith radius 15.0 mm; cortex thickness 5.0 mm; cortex:pith ratio 0.3. Epidermal cell length 12-45 μm (average = 21 μm); epidermal cell width 11-23 μm (average = 17 μm). Outer wall of epidermis thickened, hypodermis absent, palisade cortex present, cortical bundles absent, collapsible cortex absent, medullary bundles absent.

Cuticular features: Epidermal cells mostly hexagonal in shape with straight end walls; not aligned in rows. Papillae present, trichomes absent. Cuticular striations absent. Stomata not aligned in rows. Stomatal index = 5.0. Subsidiary cell arrangement mostly anomocytic, stomatal apertures occluded.

Stapelia cedrimontana Frandsen (Figures 50-51)

Stem anatomy: Stems four angled, 2.6 mm in diameter; pith radius 0.5 mm; cortex thickness 0.8 mm; cortex:pith ratio 1.5. Epidermal cell length 18-63 μm (average = 37 μm); epidermal cell width 12-28 μm (average = 19 μm). Outer wall of epidermis thickened, hypodermis absent, palisade cortex absent, cortical bundles absent, collapsible cortex present in form of undulate cell walls, medullary bundles absent.

Cuticular features: Epidermal cells mostly hexagonal in shape with straight end walls, not aligned in rows. Papillae absent, conical trichomes present, each trichome unicellular, located over the center of an epidermal cell. Cuticular striations absent. Stomata not aligned in rows. Stomatal index = 2.6. Subsidiary cell arrangement mostly anomocytic.

Stapelia divaricata Masson (Figures 52-53)

Stem anatomy: Stems four angled, 4.4 mm in diameter; pith radius 1.5 mm; cortex thickness 0.7 mm; cortex:pith ratio 0.5. Epidermal cell length 19-57 μm (average = 36 μm); epidermal cell width 15-38 μm (average = 23 μm). Outer wall of epidermis thickened, hypodermis absent, palisade cortex present, cortical bundles absent, collapsible cortex absent, medullary bundles absent.

Cuticular features: Epidermal cells mostly hexagonal in shape with straight end walls, not aligned in rows. Papillae present, conical unicellular trichomes present Cuticular striations absent. Stomata not aligned in rows. Stomatal index = 4.3. Subsidiary cell arrangement mostly cylocytic.

Stapelia engleriana L. C. Leach (Figures 54-55)

Stem anatomy: Stems four angled, 4.6 mm in diameter; pith radius 1.5 mm; cortex thickness 0.8 mm; cortex:pith ratio 0.5. Epidermal cell length 15-52 μm (average = 35 μm); epidermal cell width 13-28 μm (average = 20 μm). Outer wall of epidermis thickened, hypodermis present, palisade cortex present, cortical bundles absent, collapsible cortex present in form of undulate cell walls, medullary bundles absent.

Cuticular features: Epidermal cells mostly pentagonal in shape with straight end walls, not aligned in rows. Papillae present, conical unicellular trichomes present. These intergrade with papillae. Cuticular striations absent. Stomata not aligned in rows. Stomatal index = 1.3. Subsidiary cell arrangement mostly cyclocytic.

Stapelia paniculata var *scitula* L. C. Leach (Figures 56-57)

Stem anatomy: Stems four angled, 3.0 mm in diameter; pith radius 0.8 mm; cortex thickness 0.7 mm; cortex:pith ratio 0.9. Epidermal cell length 19-61 μm (average = 38 μm); epidermal cell width 10-25 μm (average = 17 μm). Outer wall of epidermis thickened, hypodermis absent, palisade cortex present, cortical bundles absent, collapsible cortex absent, pith with collapsible cell walls, medullary bundles absent.

Cuticular features: Epidermal cells mostly hexagonal in shape with straight end walls. not aligned in rows. Papillae absent, conical unicellular trichomes present. Cuticular striations present. Stomata not aligned in rows. Stomatal index = 5.4. Subsidiary cell arrangement brachyparacytic and amphibrachyparacytic to laterocytic and more complex patterns.

Stapelia pillansii var *pillansii* N. E. Br. (Figures 58-59)

Stem anatomy: Stems four angled, 2.0 mm in diameter; pith radius 0.6 mm; cortex thickness 0.4 mm; cortex:pith ratio 0.7. Epidermal cell length 17-71 μm (average = 37 μm); epidermal cell width 12-28 μm (average = 19 μm). Outer wall of epidermis thickened, hypodermis absent, palisade cortex present, cortical bundles absent, collapsible cortex absent, pith with collapsible cell walls, medullary bundles absent.

Cuticular features: Epidermal cells mostly hexagonal in shape with straight end walls, not aligned in rows. Papillae absent, conical unicellular trichomes present. Cuticular striations absent. Stomata not aligned in rows. Stomatal index = 1.7. Subsidiary cell arrangement mostly cyclocytic.

Stapelianthus decaryi Choux (Figures 60-61)

Stem anatomy: Stems six to eight angled, 2.8 mm in diameter; pith radius 1.0 mm; cortex thickness 0.4 mm; cortex:pith ratio 0.4. Epidermal cell length 15-52 μm (average = 30 μm); epidermal cell width 12-22 μm (average = 15 μm). Outer wall of epidermis thickened, hypodermis absent, palisade cortex absent, cortical bundles absent, collapsible cortex absent, medullary bundles absent.

Cuticular features: Epidermal cells mostly pentagonal in shape with straight end walls, not aligned in rows. Papillae absent, trichomes absent, Cuticular striations absent. Stomata not aligned in rows. Stomatal index = 1.9. Subsidiary cell arrangement mostly brachyparacytic with a ring of encircling cells to cyclocytic.

Tavaresia barklyi N. E. Br. (Figures 62-63)

Stem anatomy: Stems eight to fourteen angled, 3.6 mm in diameter; pith radius 1.2 mm; cortex thickness 0.6mm; cortex:pith ratio 0.5. Epidermal cell length 16-55 μm (average = 36 μm); epidermal cell width 13-33 μm (average = 22 μm). Outer wall of epidermis thickened, hypodermis absent, palisade cortex present, cortical bundles absent, collapsible cortex present, medullary bundles absent.

Cuticular features: Epidermal cells mostly pentagonal in shape with straight end walls, not aligned in rows. Papillae absent, trichomes absent. Cuticular striations absent. Stomata not aligned in rows. Stomatal index = 3.3. Subsidiary cell arrangement mostly brachyparacytic.

Table 2. Anatomical features of the stems.

Species name	Pith radius (mm)	Cortex thickness (mm)	Cortex /pith	Epidermis outer wall thickened	Hypodermis present	Palisade cortex present	Cortical bundles present	Collapsible cortex present	Medullary bundles present
Baynesia lophophora	0.9	0.8	0.9	Yes	No	Yes	No	No	No
Caralluma diffusa	0.7	0.4	0.5	Yes	No	No	No	No	Yes
Caralluma solenophora	1.3	1.8	1.4	Yes	No	Yes	No	UW	No
Duvalia corderoyi	1.2	0.9	0.8	Yes	Yes	Yes	No	No	No
Duvalia modesta	0.4	0.3	0.7	Yes	Yes	Yes	No	UW	No
Duvaliandra dioscoridis	2.3	1.1	0.5	Yes	No	No	No	No	Yes
Echidnopsis cereiformis	1.0	0.5	0.5	Yes	No	Yes	Yes	Yes	No
Echidinopsis lavraniana	1.5	0.8	0.5	Yes	No	Yes	Yes	No	No
Edithcolea grandis	1.0	1.3	1.3	Yes	No	No	No	No	No
Frera indica	1.0	1.1	1.1	Yes	No	Yes	No	No	No

Table 2-Continued. Anatomical features of the stems.

Species name	Pith radius (mm)	Cortex thickness (mm)	Cortex /pith	Epidermis outer wall thickened	Hypodermis present	Palisade cortex present	Cortical bundles present	Collapsible cortex present	Medullary bundles present
Huernia boleana	1.5	0.7	0.4	Yes	No	No	No	Pith	No
Huernia hislopii ssp. *robusta*	0.7	0.8	1.1	Yes	No	No	No	No	No
Huernia hystrix var. *parvula*	1.0	0.7	0.7	Yes	No	Yes	No	No	No
Huernia leachii	0.7	0.6	0.9	Yes	No	Yes	No	No	No
Huernia occulta	0.3	0.5	1.7	Yes	No	No	No	UW	No
Huernia recondita	1.2	0.5	0.4	Yes	No	No	No	Yes	No
Lavrania haagnerae	3.0	3.0	1.0	Yes	No	No	No	Yes	No
Piaranthus barrydalensis	1.2	0.8	0.7	Yes	No	Yes	No	Pith	No
Piaranthus comptus	1.3	0.8	0.6	Yes	No	Yes	No	Pith	No

Table 2-Continued. Anatomical features of the stems.

Species name	Pith radius (mm)	Cortex thickness (mm)	Cortex /pith	Epidermis outer wall thickened	Hypodermis present	Palisade cortex present	Cortical bundles present	Collapsible cortex present	Medullary bundles present
Piaranthus geminatus	1.1	0.5	0.5	Yes	No	Yes	No	Yes	No
Pseudolithos eylensis	15.0	5.0	0.3	Yes	No	Yes	No	No	No
Stapelia cedrimontana	0.5	0.8	1.5	Yes	No	No	No	UW	No
Stapelia divaricata	1.5	0.7	0.5	Yes	No	Yes	No	No	No
Stapelia engleriana	1.5	0.8	0.5	Yes	Yes	Yes	No	UW	No
Stapelia paniculata var. *scitula*	0.8	0.7	0.9	Yes	No	Yes	No	Pith	No
Stapelia pillansii var. *pillansii*	0.6	0.4	0.7	Yes	No	Yes	No	Pith	No
Stapelianthus decaryi	1.0	0.4	0.4	Yes	No	No	No	No	No
Tavaresia barklyi	1.2	0.6	0.5	Yes	No	Yes	No	Yes	No

Table 3. Features of stem cuticle.

Species	Shape of epidermal cell	Epidermal cells in rows	Shape of end wall	Subsidiary cell arrangement	Trichomes /Papillae present	Striations present in cuticle	Stomatal Index
Baynesia lophophora	Hexagonal	No	Straight	Mostly brachyparacytic with 0-3 rings of encircling cells	Papillae	Yes	2.3
Caralluma diffusa	Pentagonal	No	Straight	Mostly brachyparacytic with 1-2 rings of encircling cells	None	Yes	2.1
Caralluma solenopora	Pentagonal	No	Straight	Mostly brachyparacytic with 1-2 rings of encircling cells	Papillae	Yes	2.2
Duvalia corderoyi	Hexagonal	No	Straight	Mostly amphicyclocytic	Papillae	Yes	3.9
Duvalia modesta	Pentagonal	No	Straight	Mostly brachyparacytic with a ring of encircling cells to cyclocytic	Papillae	Yes	3.0
Duvaliandra dioscoridis	Hexagonal	No	Straight	Mostly brachyparacytic with a ring of encircling cells to cyclocytic	Papillae	No	1.8
Echidnopsis cereiformis	Pentagonal	No	Straight	Mostly amphicyclocytic	Papillae	No	1.0

Table 3-Continued. Features of stem cuticle.

Species name	Shape of epidermal cell	Epidermal cells in rows	Shape of end wall	Subsidiary cell arrangement	Trichomes /Papillae present	Striations present in cuticle	Stomatal Index
Echidnopsis lavraniana	Pentagonal	No	Straight	Mostly anomocytic but cells adjacent to guard cells smaller than other cells.	Papillae	No	0.9
Edithcolea grandis	Hexagonal	No	Straight	Mostly brachyparacytic	Papillae	Yes	2.7
Frerea indica	Pentagonal	Yes	Straight	Mostly cyclocytic with 2-3 rings of encircling cells	None	No	1.6
Huernia boleana	Pentagonal	No	Straight	Mostly brachyparacytic with a ring of encircling cells to cyclocytic with 1-3 rings of subsidiary cells	None	Yes	2.2
Huernia hislopii ssp. *robusta*	Pentagonal	No	Straight	Mostly weakly cylocytic	None	No	1.6
Huernia hystrix var. parvula	Pentagonal	Yes	Straight	Obscured by striations but most likely brachyparacytic	None	Yes	1.5
Huernia leachii	Pentagonal	No	Straight	Mostly brachyparacytic	None	No	1.8

Table 3-Continued. Features of stem cuticle.

Species name	Shape of epidermal cell	Epidermal cell in rows	Shape of end wall	Subsidiary cell arrangement	Trichomes /Papillae present	Striations present in cuticle	Stomatal Index
Huernia occulta	Hexagonal	No	Straight	Mostly brachyparacytic with a ring of encircling cells	None	No	0.9
Huernia recondita	Pentagonal	No	Straight	Mostly brachyparacytic with less than two rings of encircling cells	None	No	1.6
Lavrania haagnerae	Pentagonal	No	Straight	Obscured but most likely brachyparacytic with stomatal apertures occluded	None	No	3.2
Piaranthus barrydalensis	Pentagonal	No	Straight	Mostly amphicylocytic	Papillae	No	2.6
Piaranthus comptus	Hexagonal	No	Straight	Mostly amphicylocytic	Papillae	No	3.7
Piaranthus geminatus	Pentagonal	No	Straight	Mostly cyclocytic	None	No	2.0
Pseudolithos eylensis	Hexagonal	No	Straight	Mostly anomocytic	Papillae	No	5.0

Table 3-Continued. Features of stem cuticle.

Species name	Shape of epidermal cell	Epidermal cell in rows	Shape of end wall	Subsidiary cell arrangement	Trichomes /Papillae present	Striations present in cuticle	Stomatal Index
Stapelia cedrimontana	Hexagonal	No	Straight	Mostly anomocytic	Trichomes	No	2.6
Stapelia divaricata	Hexagonal	No	Straight	Mostly cyclocytic	Both	No	4.3
Stapelia engleriana	Pentagonal	No	Straight	Mostly cyclocytic	Both	No	1.3
Stapelia paniculata var. *scitula*	Hexagonal	No	Straight	Brachyparacytic to amphibrachyparacytic to laterocytic and more complex patterns.	Trichome	Yes	5.4
Stapelia pillansii var. *pillansii*	Hexagonal	No	Straight	Mostly cyclocytic	Trichome	No	1.7

Table 3-Continued. Features of stem cuticle.

Species name	Shape of epidermal cell	Epidermal cell in rows	Shape of end wall	Subsidiary cell arrangement	Trichomes /Papillae present	Striations present in cuticle	Stomatal Index
Stapelianthus decaryi	Pentagonal	No	Straight	Mostly brachyparacytic with a ring of encircling cells to to cyclocytic	None	No	1.9
Tavaresia barklyi	Pentagonal	No	Straight	Mostly brachyparacytic	None	No	3.3

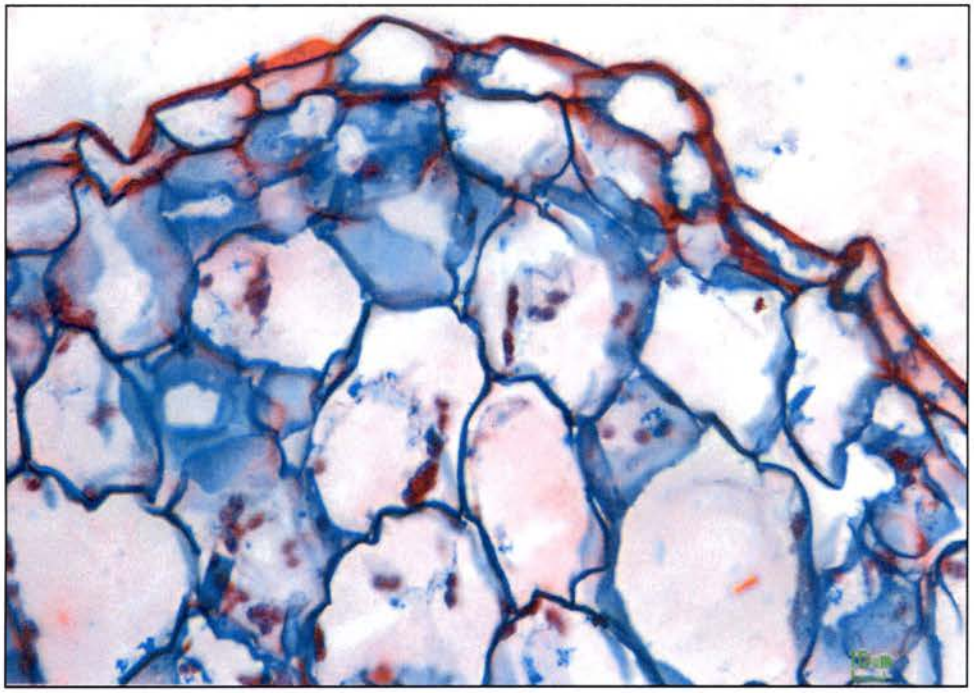

Figure 1. *Baynesia lophophora.* Stem cross section showing thickened epidermal cell walls.

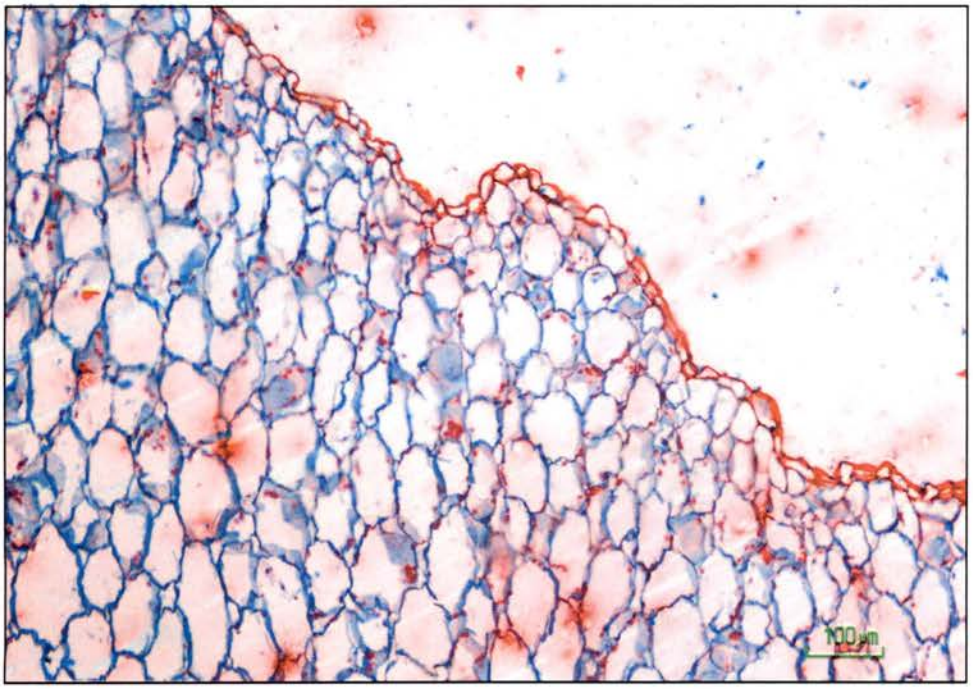

Figure 2. *Baynesia lophophora.* Stem cross section showing columnar cells of palisade cortex.

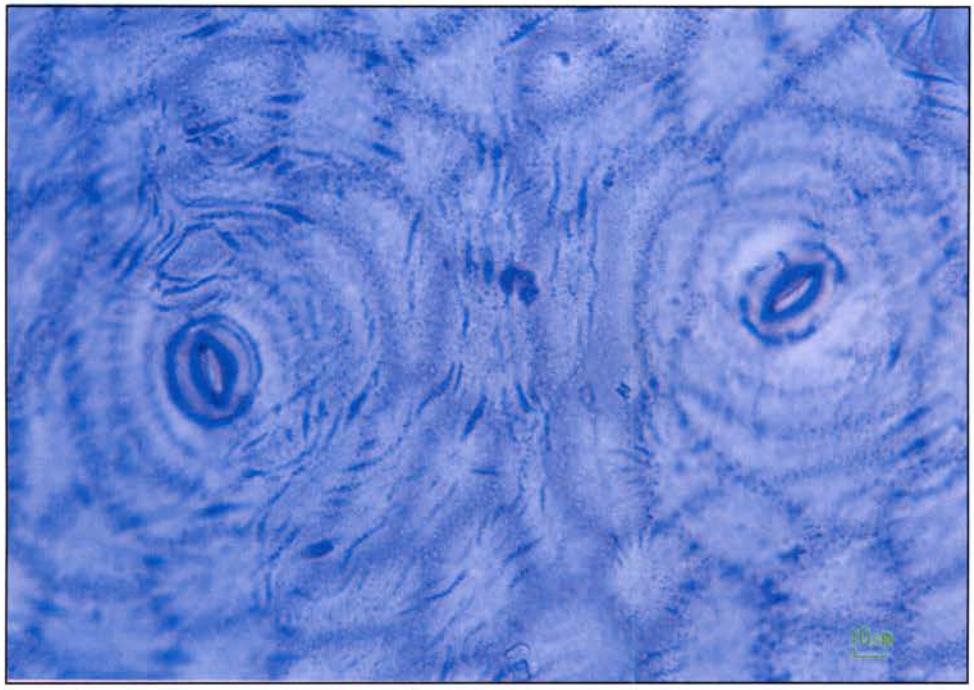

Figure 3. *Baynesia lophophora*. Stem cuticle showing brachyparacytic stomatal complex, hexagonal shape of epidermal cells and cuticular striations.

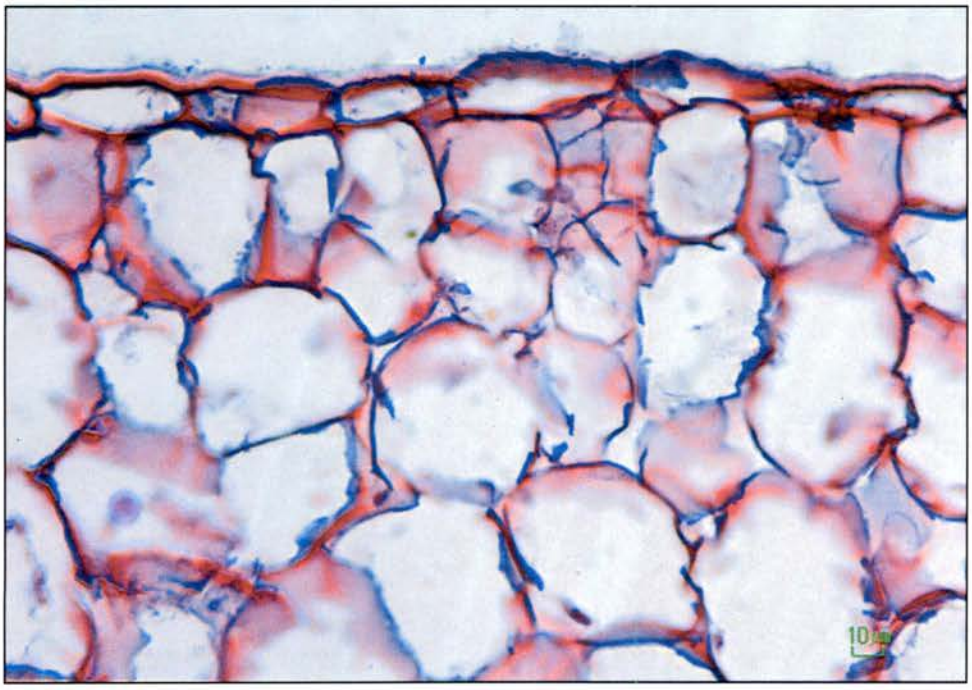

Figure 4. *Caralluma diffusa.* Stem cross section showing thickened epidermal cell walls.

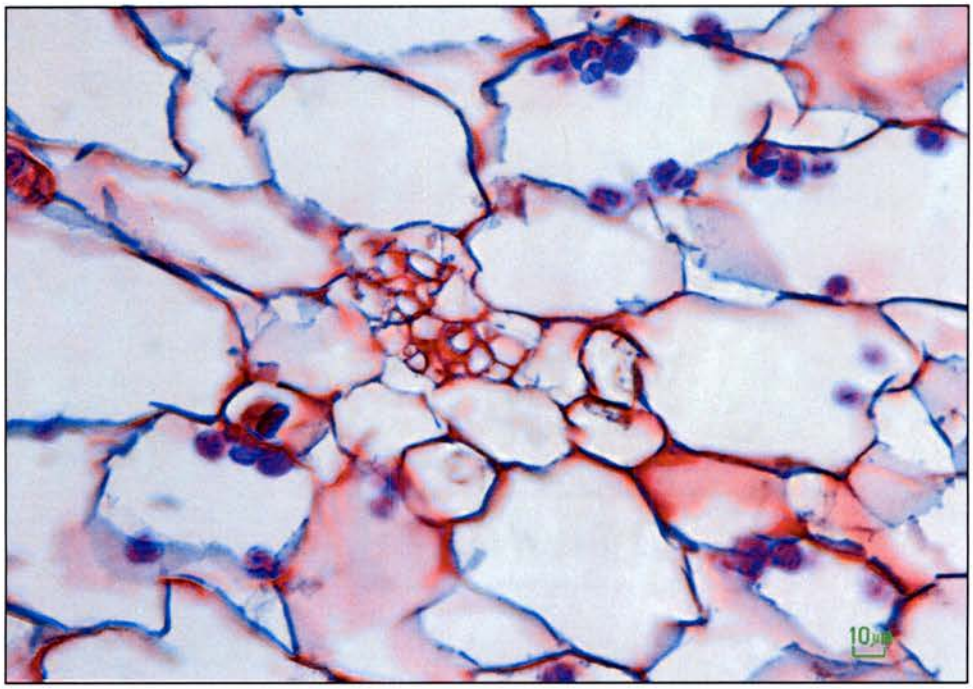

Figure 5. *Caralluma diffusa*. Stem cross section showing medullary bundles.

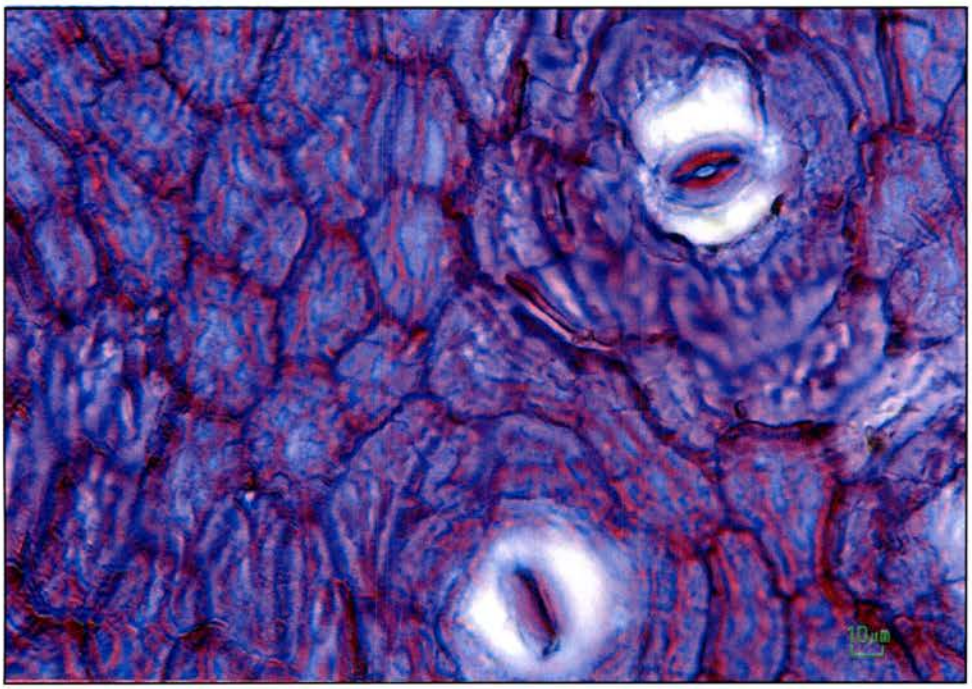

Figure 6. *Caralluma diffusa*. Stem cuticle showing brachyparacytic stomatal complex, cuticular striations and pentagonal epidermal cell shape.

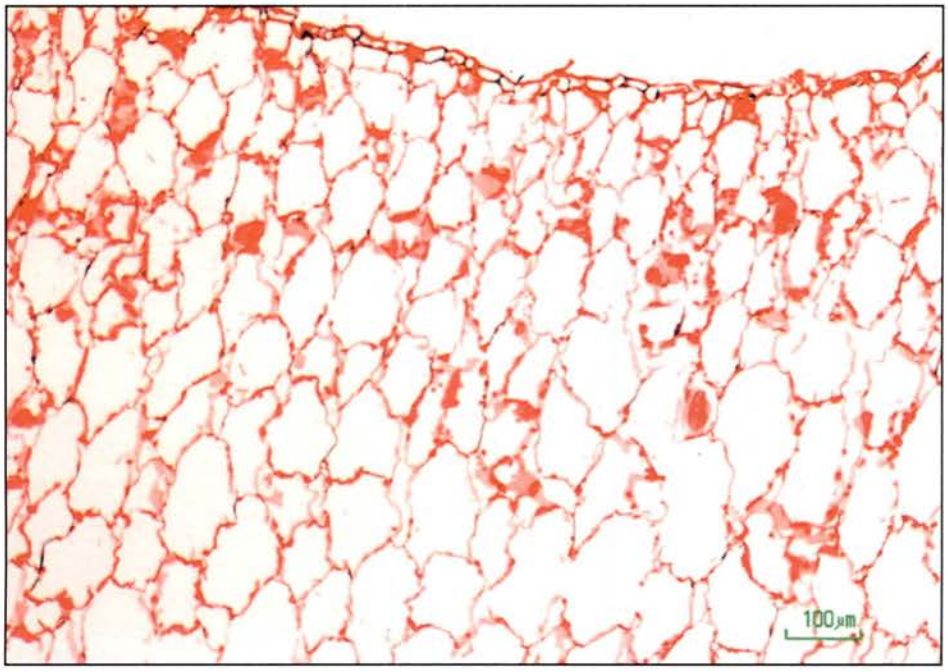

Figure 7. *Caralluma solenophora.* Stem cross section showing thickened outer epidermal cell walls and undulate cell walls of the cortex.

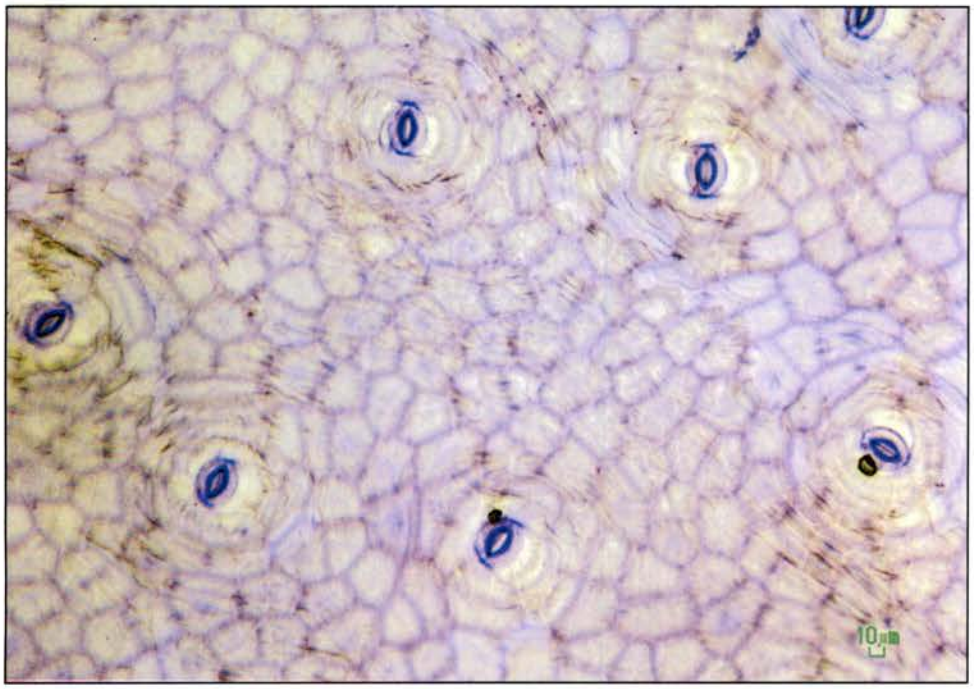

Figure 8. *Caralluma solenophora.* Stem cuticle showing brachy-paracytic stomatal complex,pentagonal epidermal cell shape and locations of papillae.

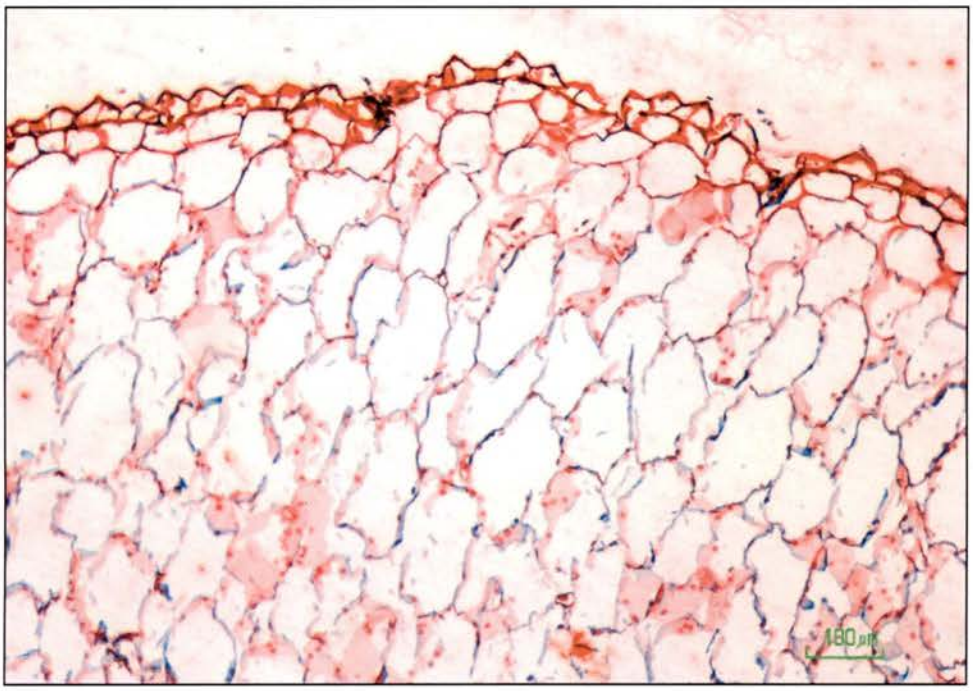

Figure 9. *Duvalia corderoyi.* Stem cross section showing thickened outer epidermal cell walls, papillate epidermis and hypodermis.

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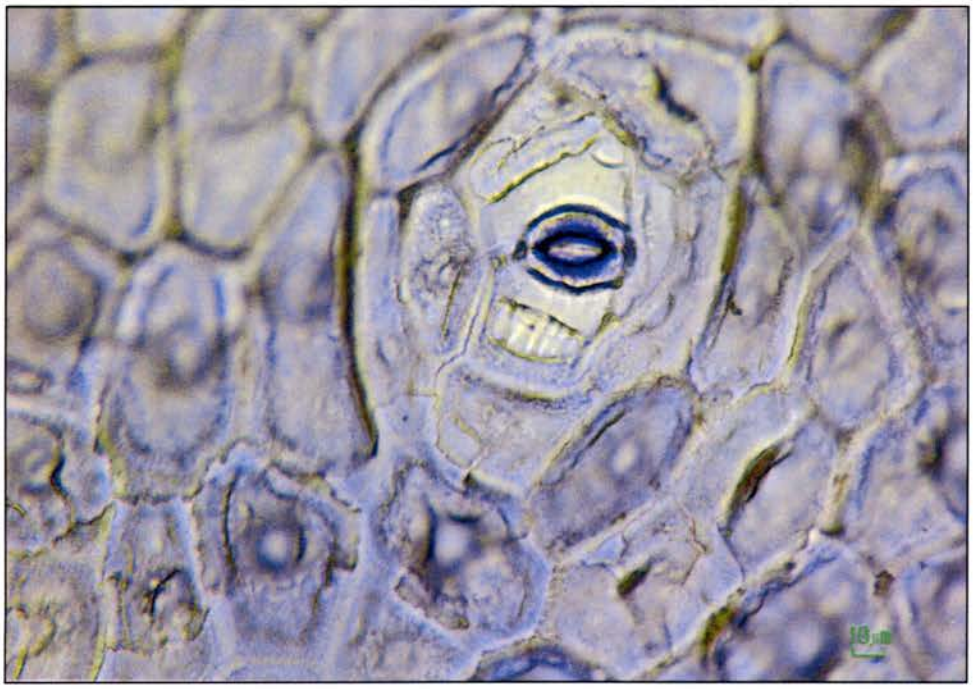

Figure 10. *Duvalia corderoyi*. Stem cuticle showing amphicyclocytic stomatal complex, hexagonal epidermal cell shape and locations of papillae.

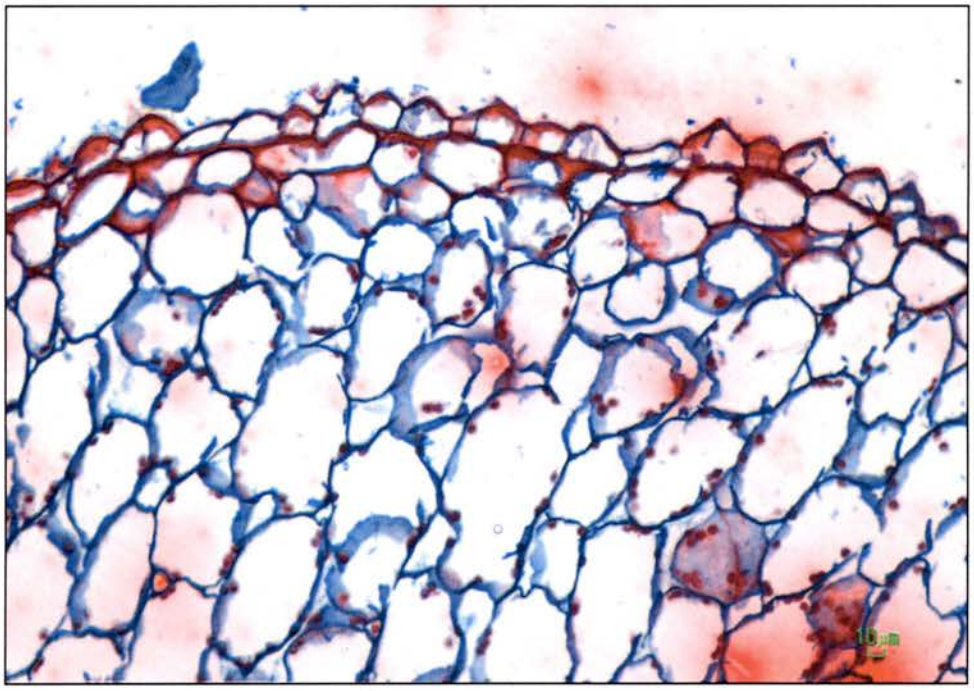

Figure 11. *Duvalia modesta*. Stem cross section showing papillate epidermis with thickened walls and hypodermis.

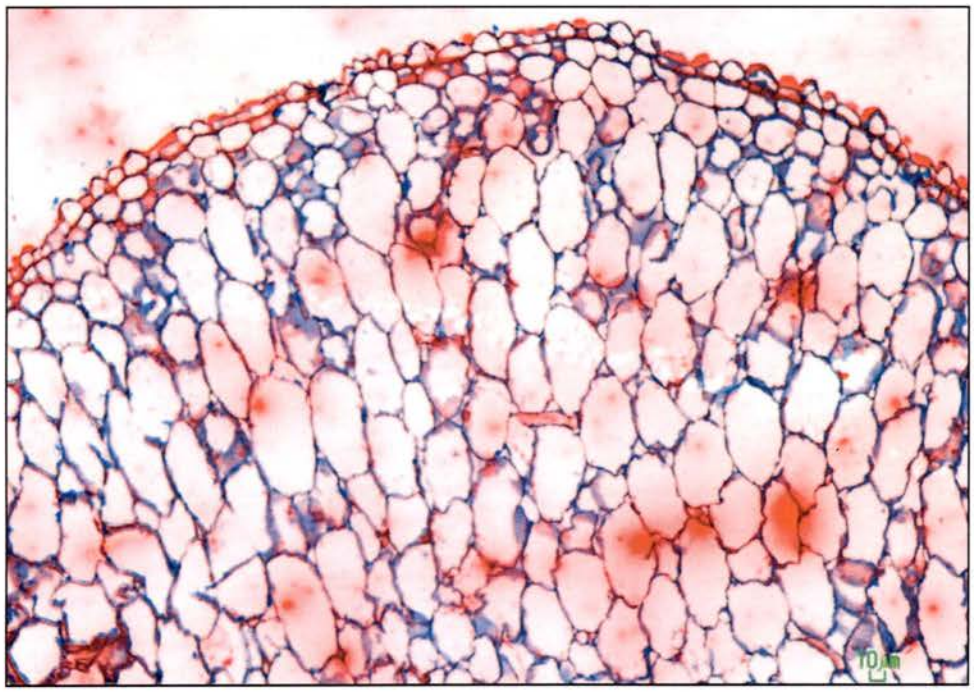

Figure 12. *Duvalia modesta.* Stem cross section showing palisade cortex.

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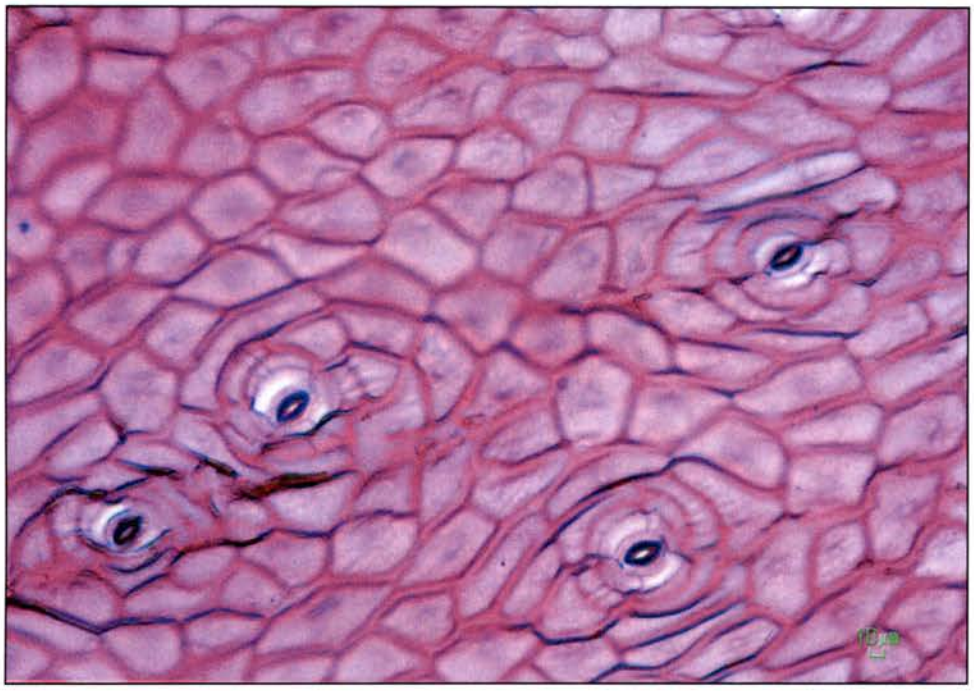

Figure 13. *Duvalia modesta.* Stem cuticle showing pentagonal epidermal cell shape, cuticular striations and locations of papillae.

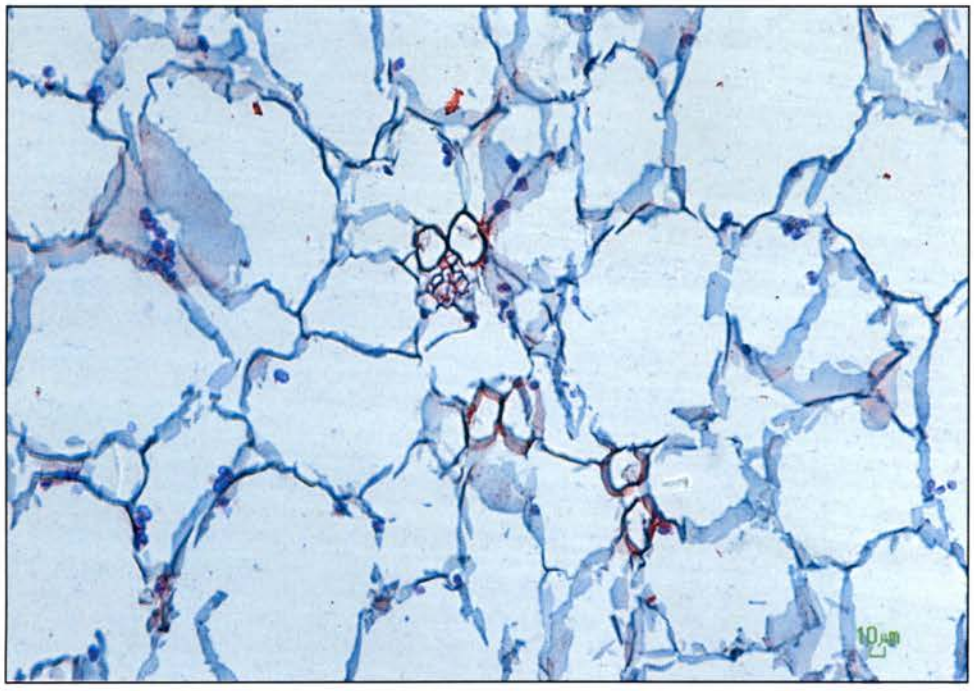

Figure 14. *Duvaliandra dioscoridis.* Stem cross section showing medullary bundles.

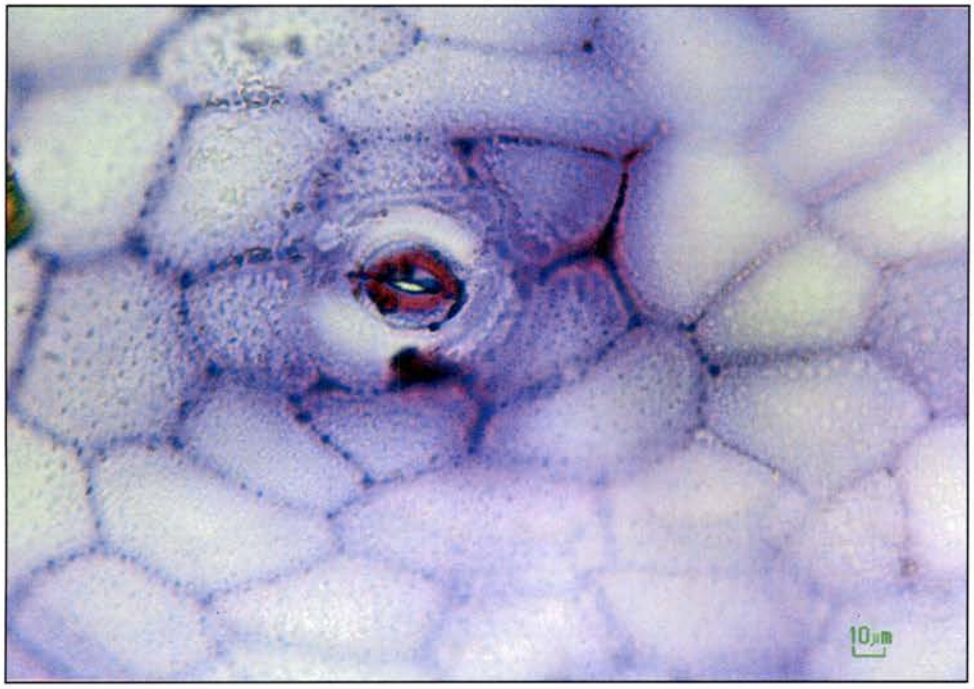

Figure 15. *Duvaliandra dioscoridis*. Stem cuticle showing brachyparacytic stomatal complex and hexagonal epidermal cell shape.

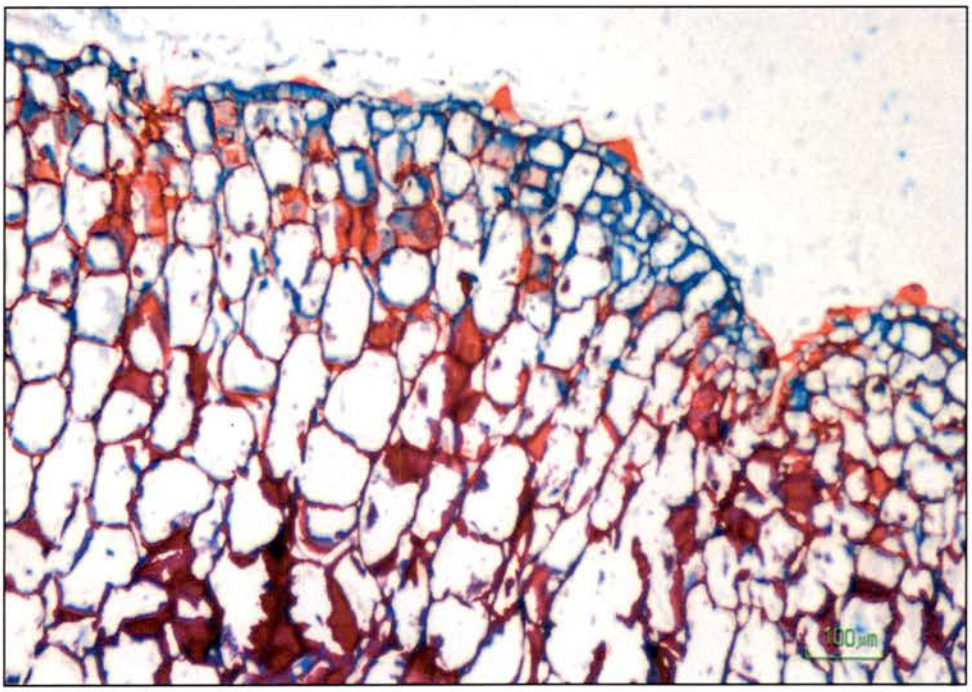

Figure 16. *Echidnopsis cereiformis* Stem cross section showing papillate epidermis and palisade cortex.

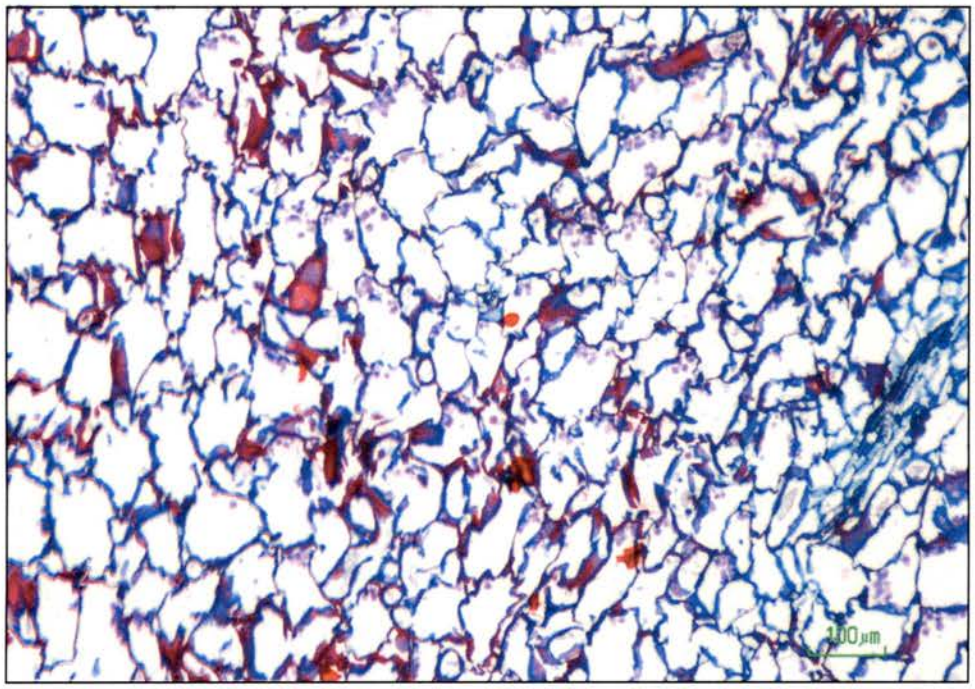

Figure 17. *Echidnopsis cereiformis*. Stem cross section showing collapsible cortex.

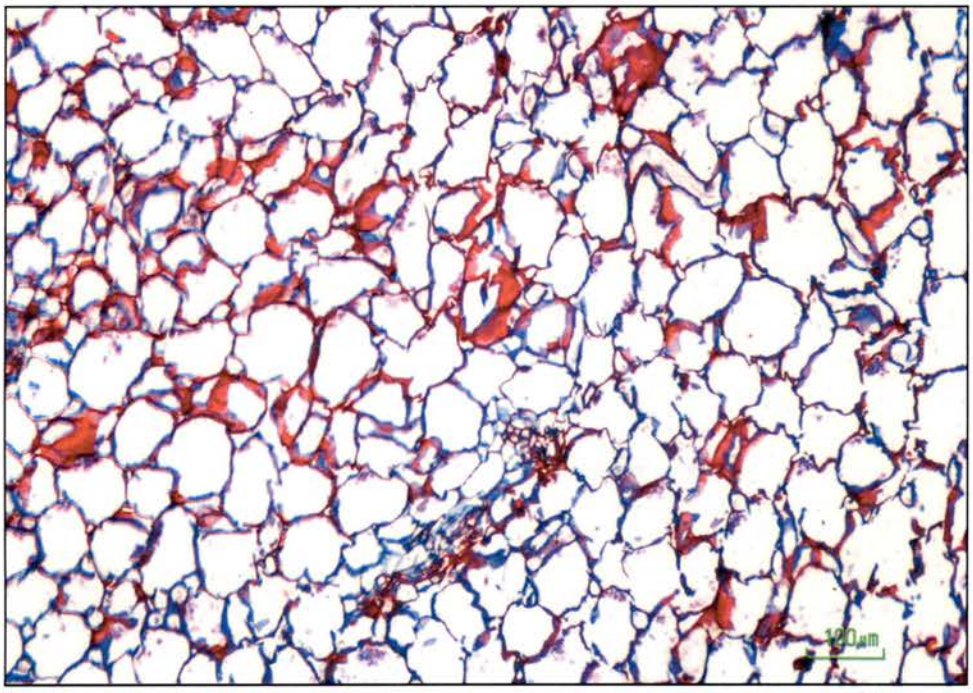

Figure 18. *Echidnopsis cereiformis.* Stem cross section showing cortical bundles.

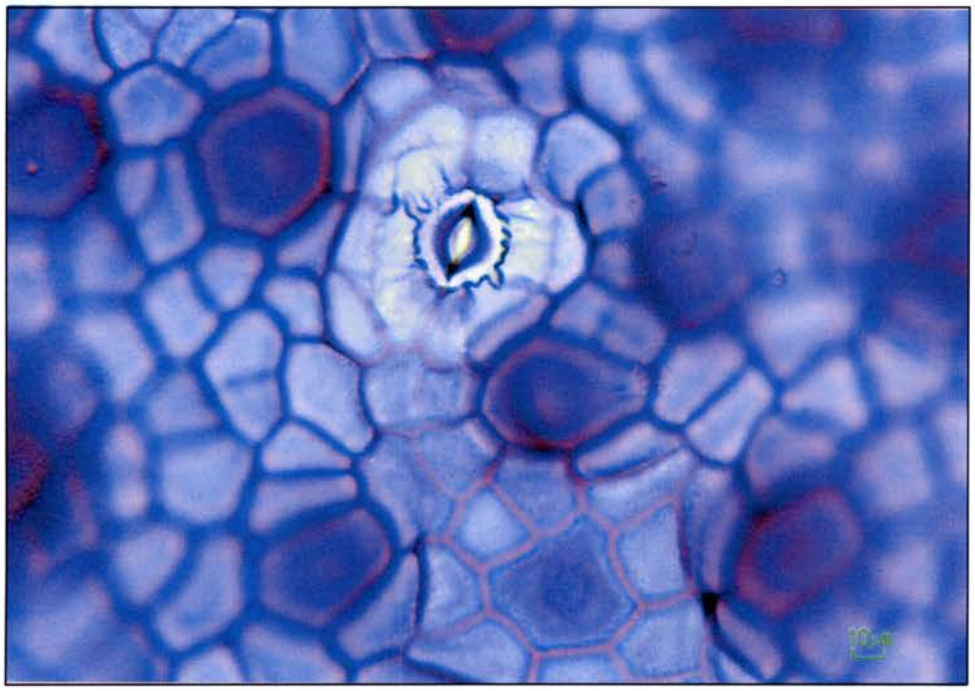

Figure 19. *Echidnopsis cereiformis.* Stem cuticle showing amphicyclocytic stomatal complex, pentagonal epidermal cell shape and locations of papillae.

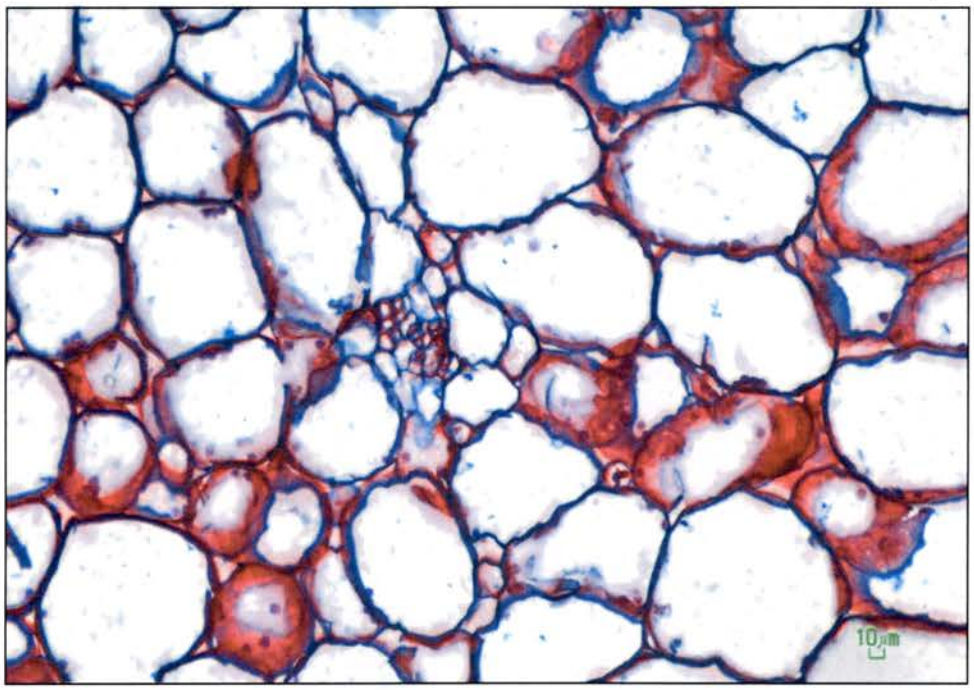

Figure 20. *Echidnopsis lavraniana.* Stem cross section showing cortical bundles.

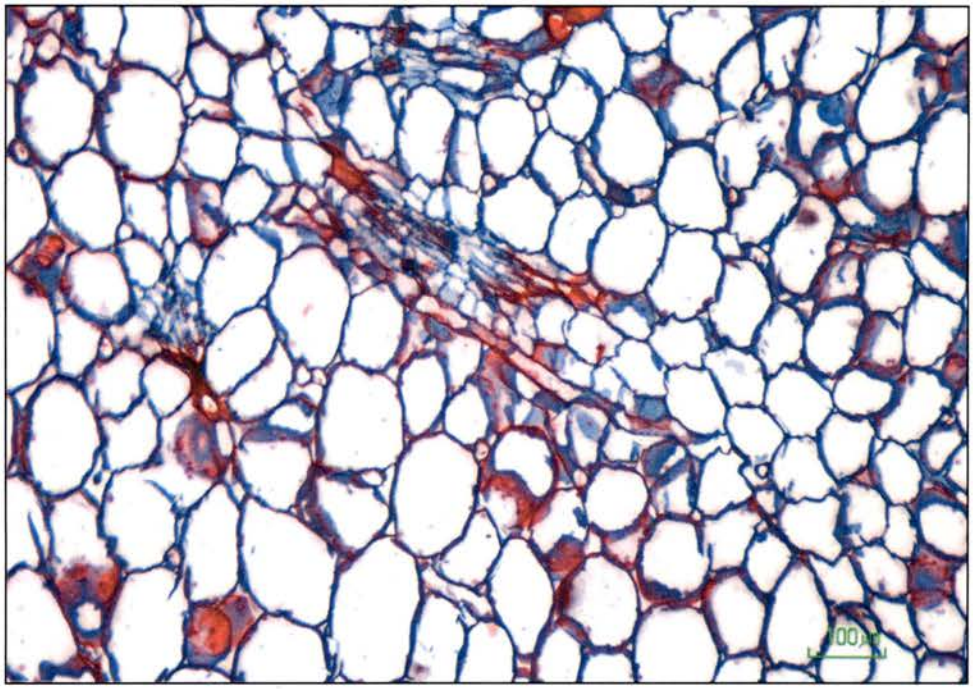

Figure 21. *Echidnopsis lavraniana.* Stem cross section showing laticifers.

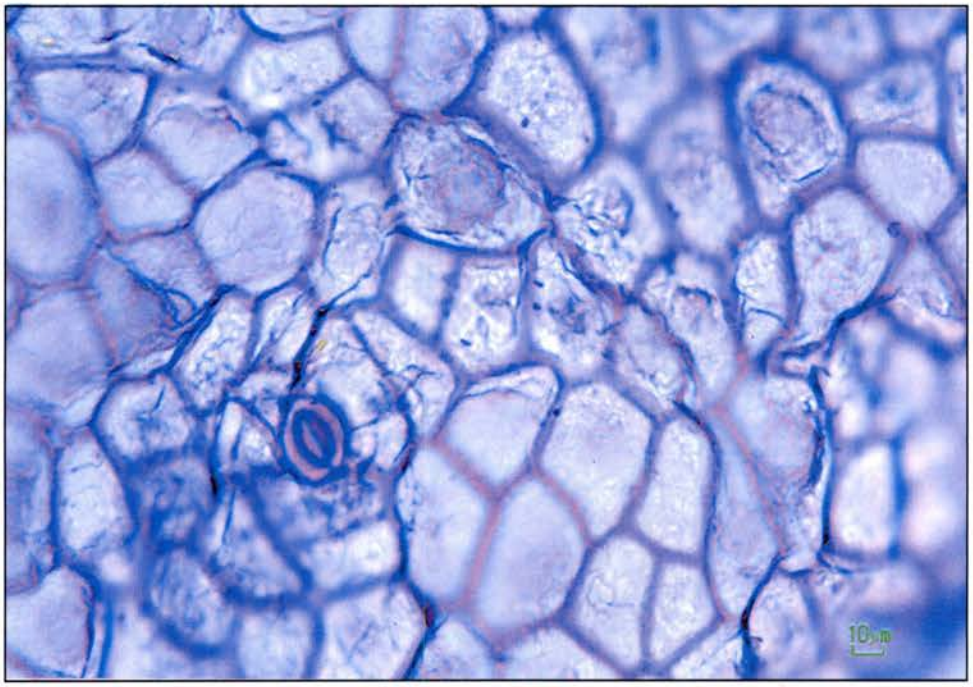

Figure 22. *Echidnopis lavraniana.* Stem cuticle showing anomocytic stomatal complex, and pentagonal epidermal cell shape.

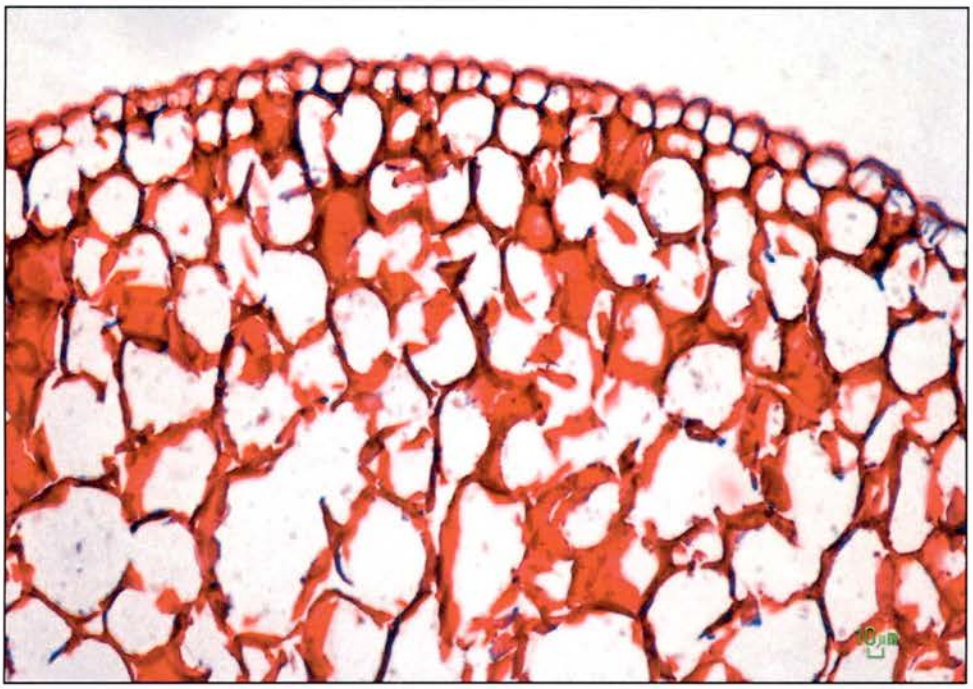

Figure 23. *Edithcolea grandis.* Stem cross section showing thickened outer epidermal cell walls.

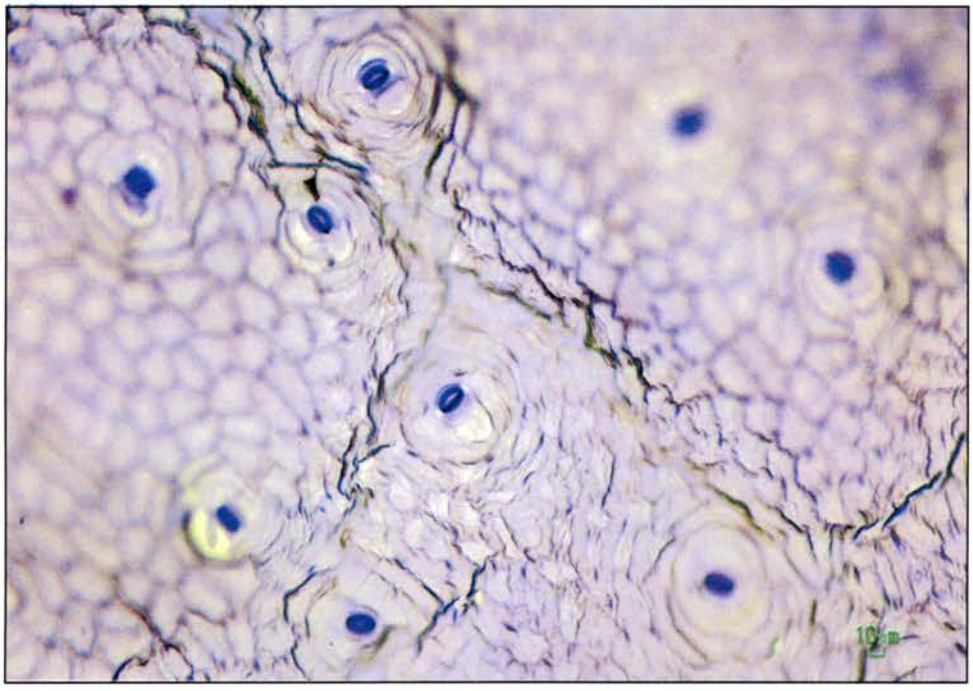

Figure 24. *Edithcolea grandis.* Stem cuticle showing cyclocytic and brachyparacytic stomatal complexes, and hexagonal epidermal cell shape.

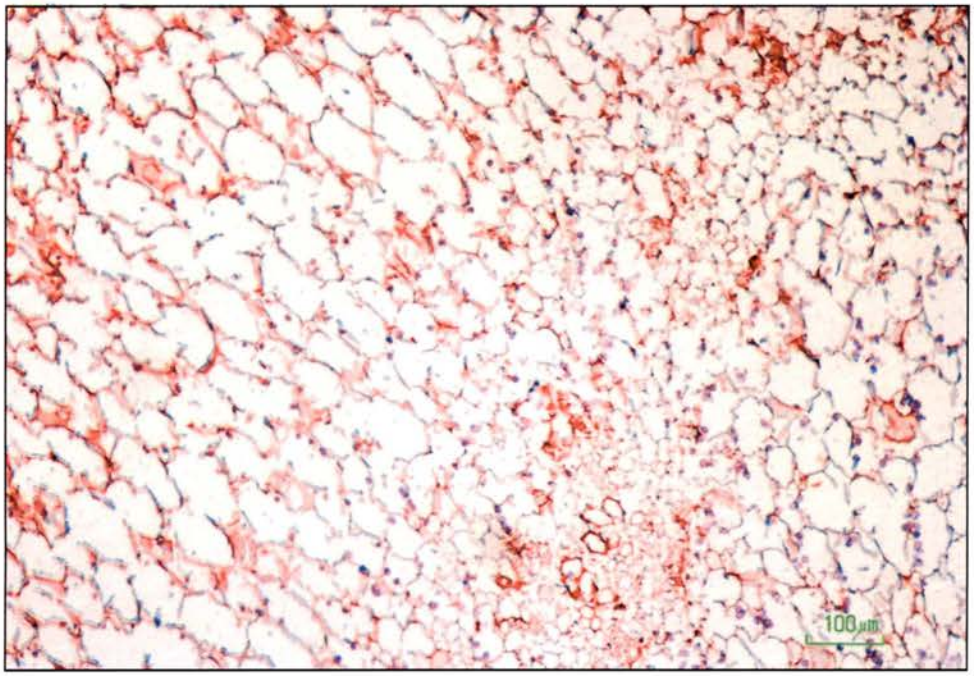

Figure 25. *Frerea indica.* Stem cross section showing chloroplasts in the palisade cortex.

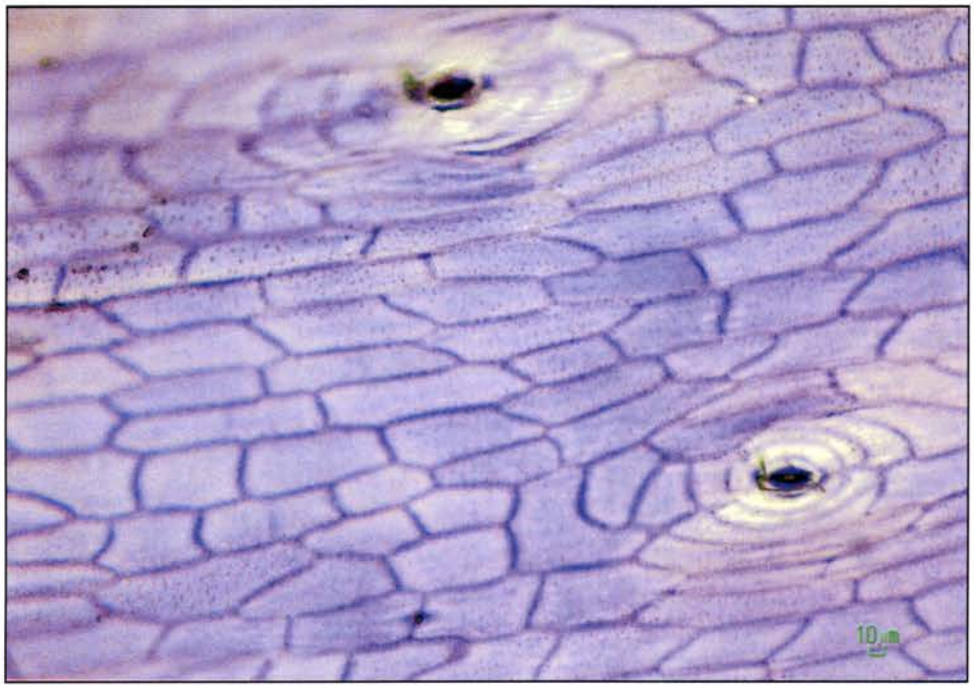

Figure 26. *Frerea indica.* Stem cuticle showing brachyparacytic and cyclocytic stomatal complexes and pentagonal epidermal cell shape.

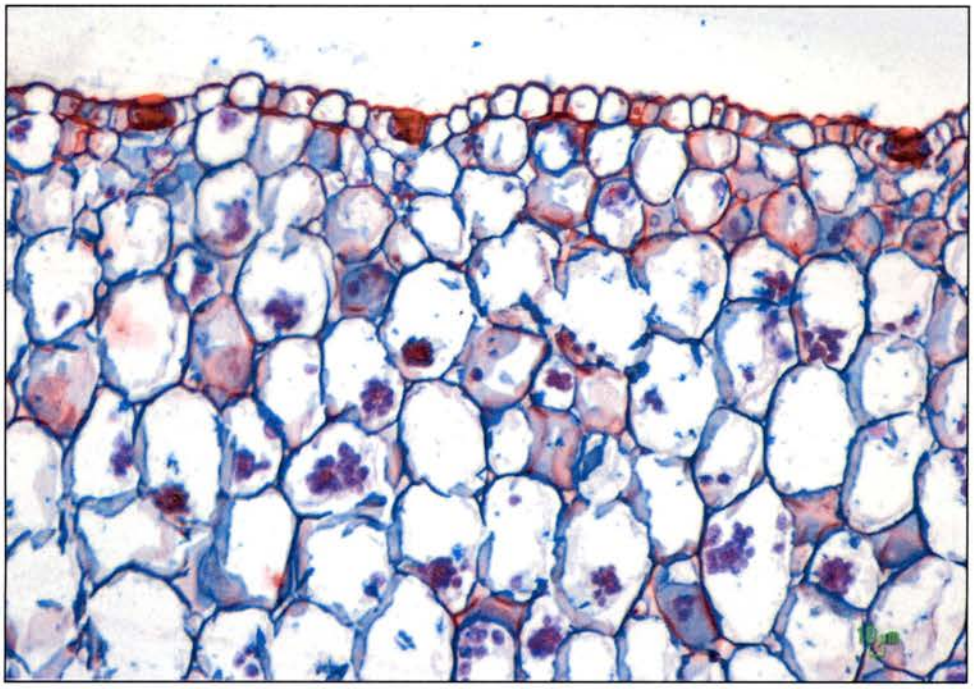

Figure 27. *Huernia boleana.* Stem cross section showing convex outer epidermal cell walls.

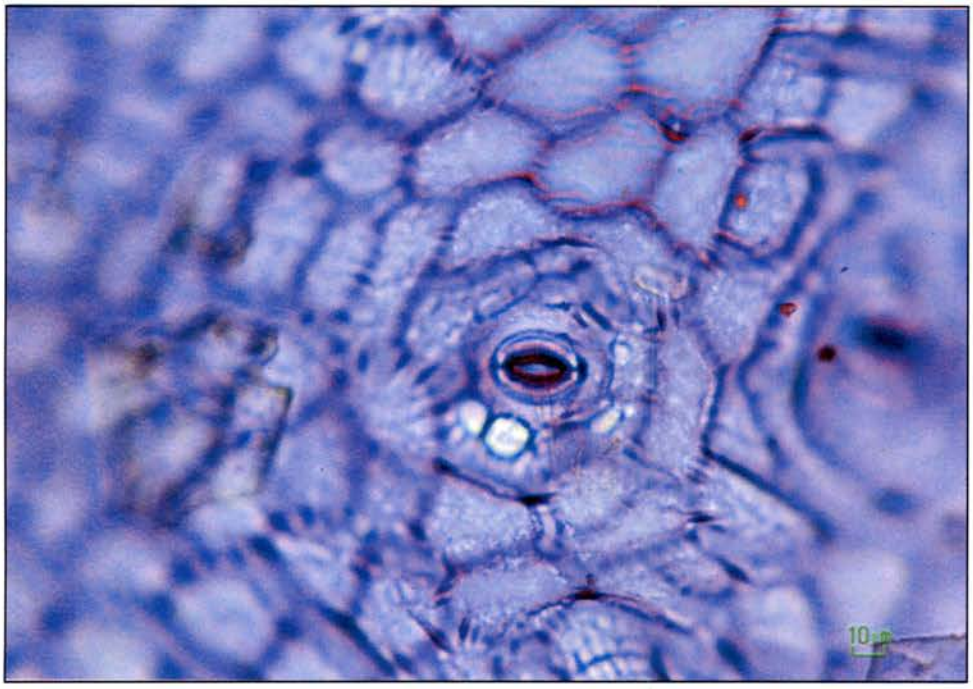

Figure 28. *Huernia boleana.* Stem cuticle showing cyclocytic stomatal complex, cuticular striations, and pentagonal epidermal cells.

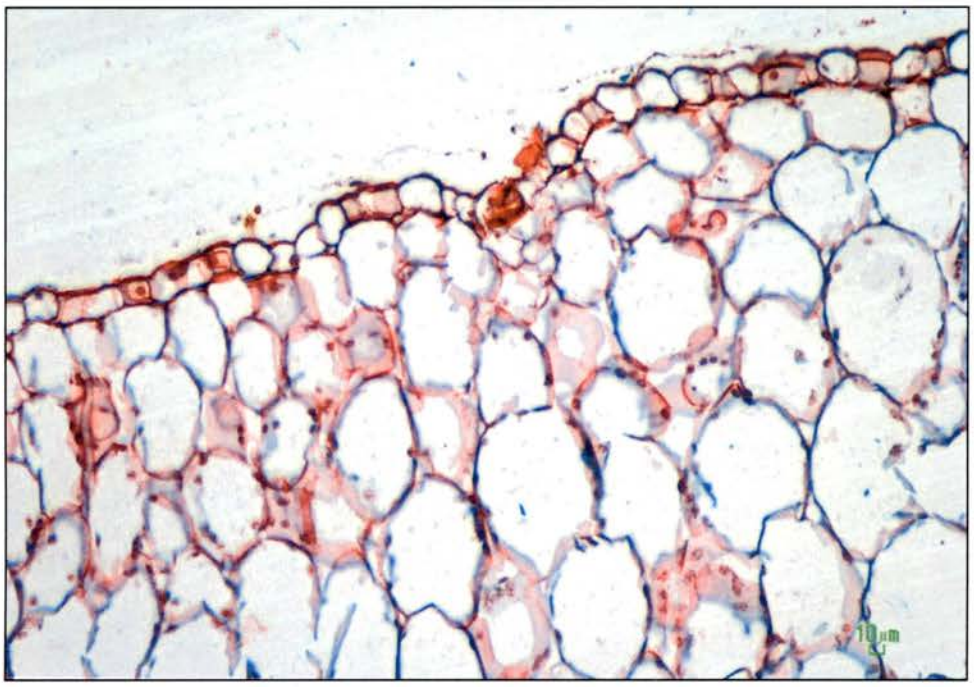

Figure 29. *Huernia hislopii* ssp. *robusta.* Stem cross section showing thickened outer epidermal cell walls and stoma.

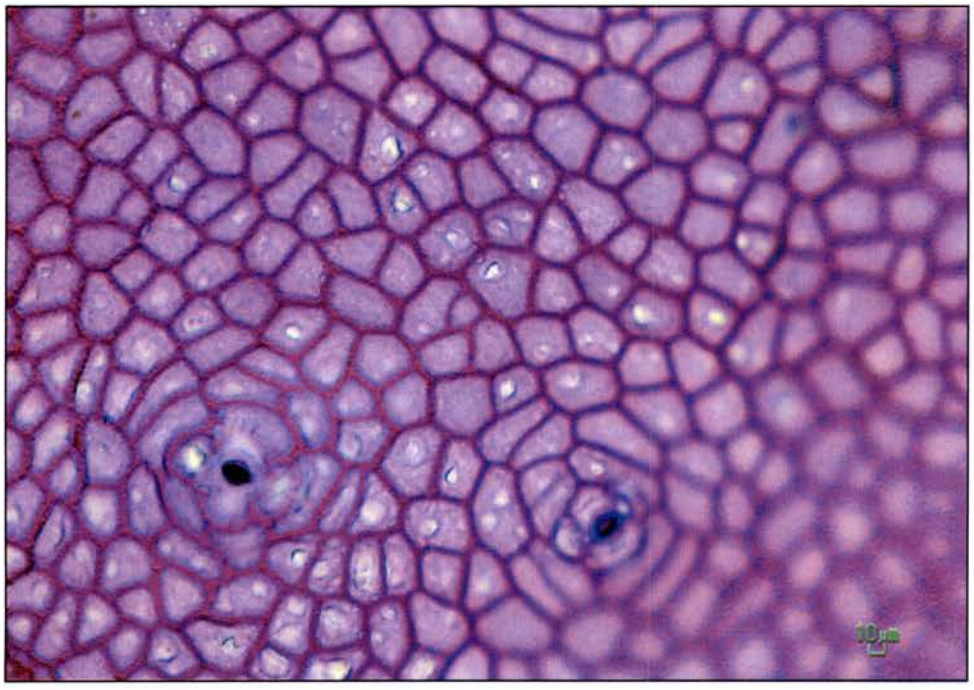

Figure 30. *Huernia hislopii* ssp. *robusta.* Stem cuticle showing cyclocytic stomatal complex and pentagonal epidermal cell shape.

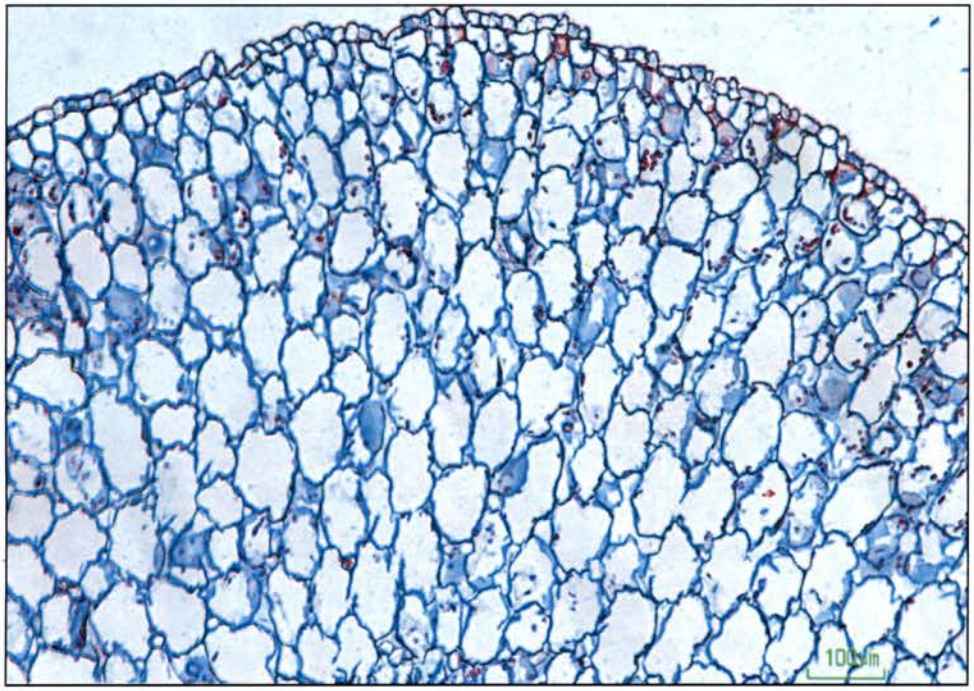

Figure 31. *Huernia hystrix* var. *parvula.* Stem cross section showing palisade cortex.

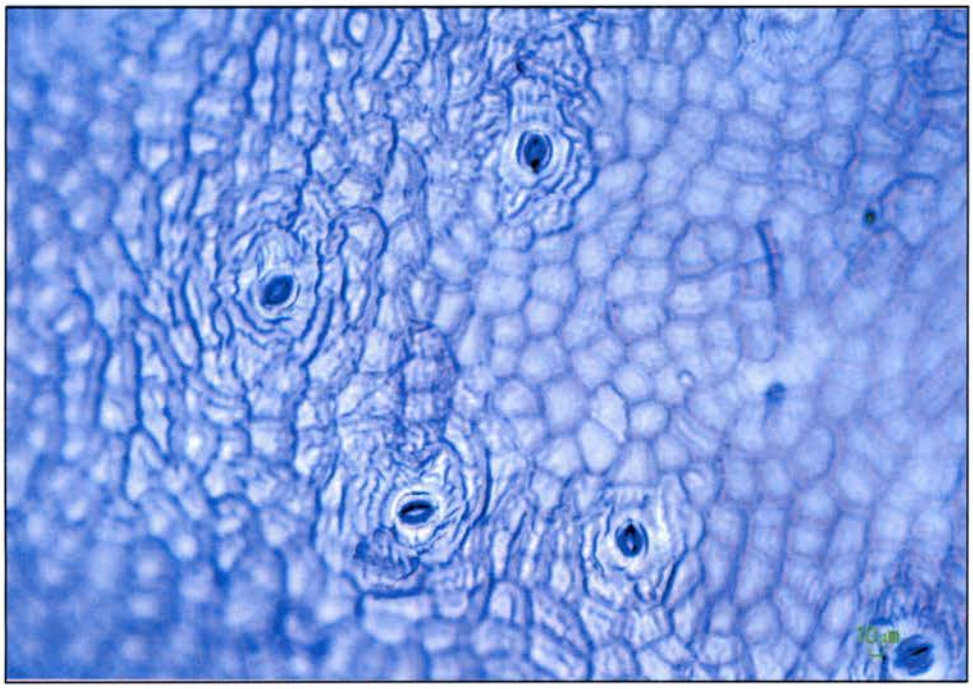

Figure 32. *Huernia hystrix* var. *parvula.* Stem cuticle showing pentagonal epidermal cells arranged in obscure rows, cuticular striations and brachyparacytic stomatal complex.

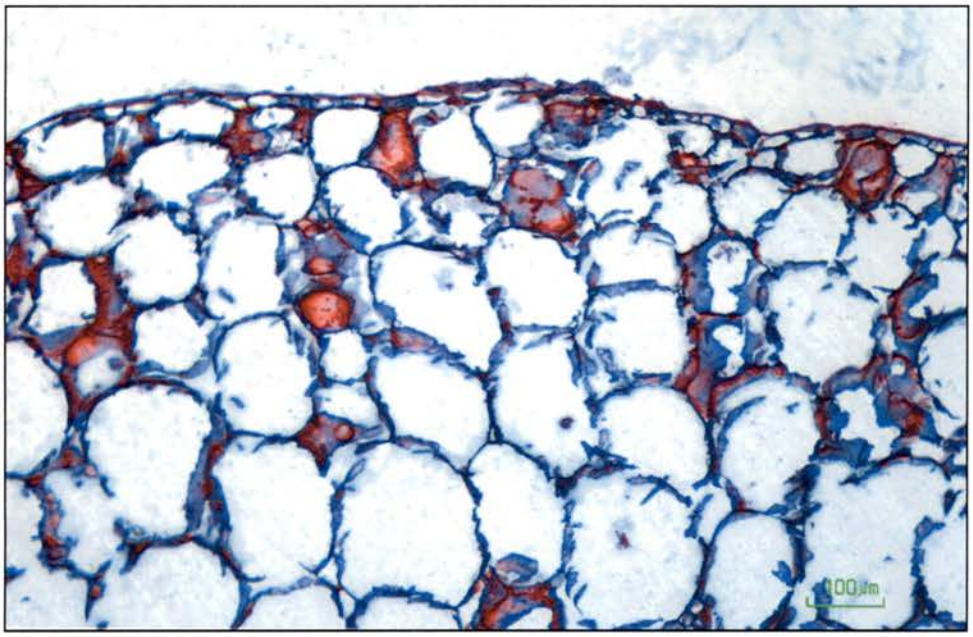

Figure 33. *Huernia leachii.* Stem cross section showing palisade cortex.

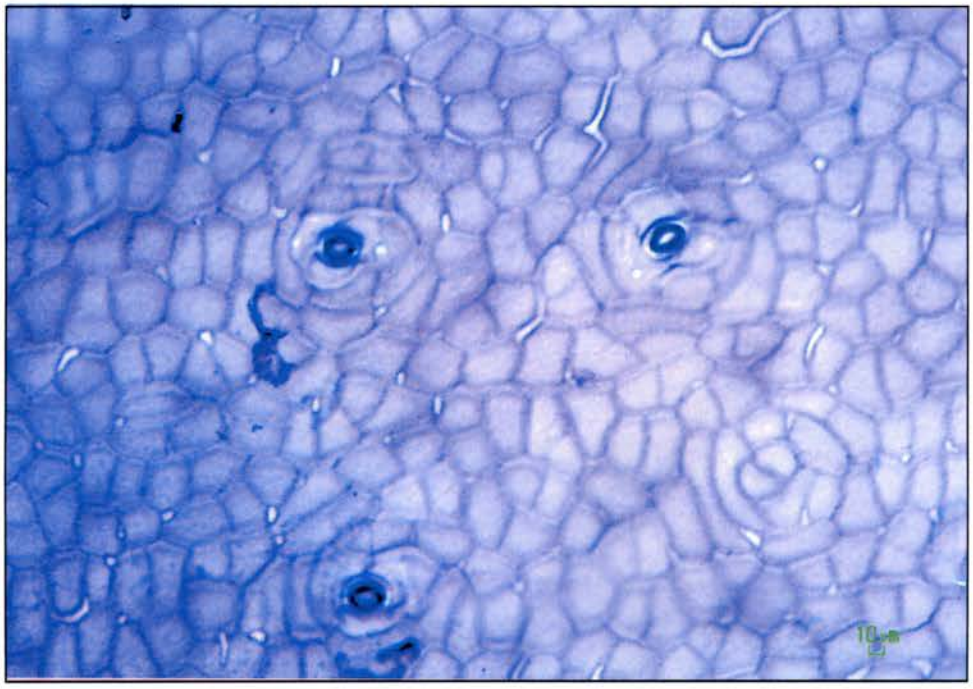

Figure 34. *Huernia leachii.* Stem cuticle showing pentagonal epidermal cell shape and brachyparacytic stomatal complex.

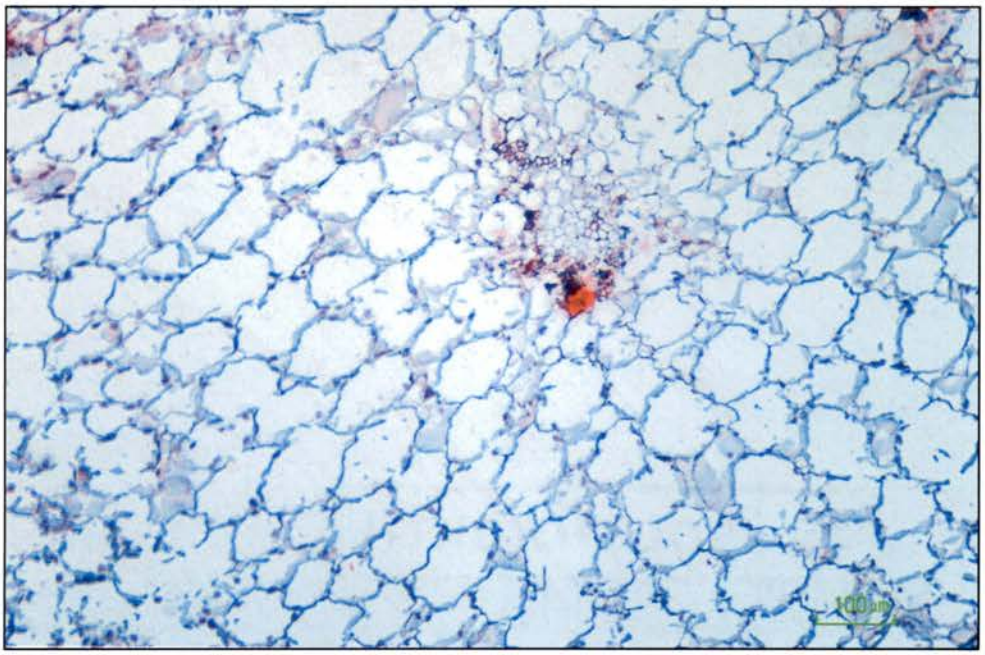

Figure 35. *Huernia occulta.* Stem cross section showing collapsible cortex. exhibted by undulate cell walls.

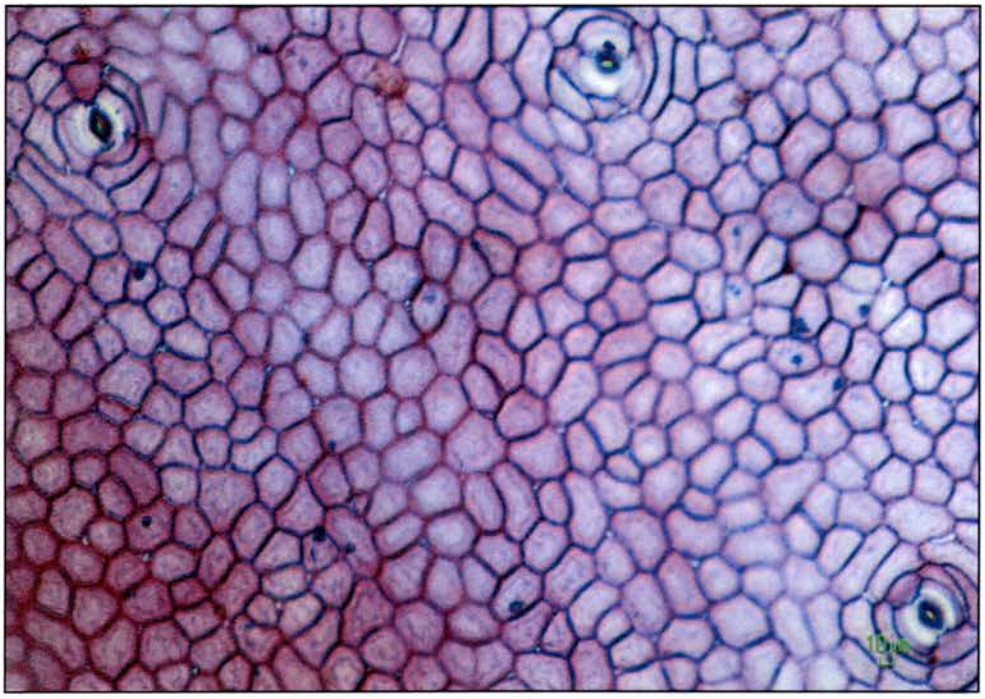

Figure 36. *Huernia occulta*. Stem cuticle showing hexagonal epidermal cell shape and brachyparacytic stomatal complex.

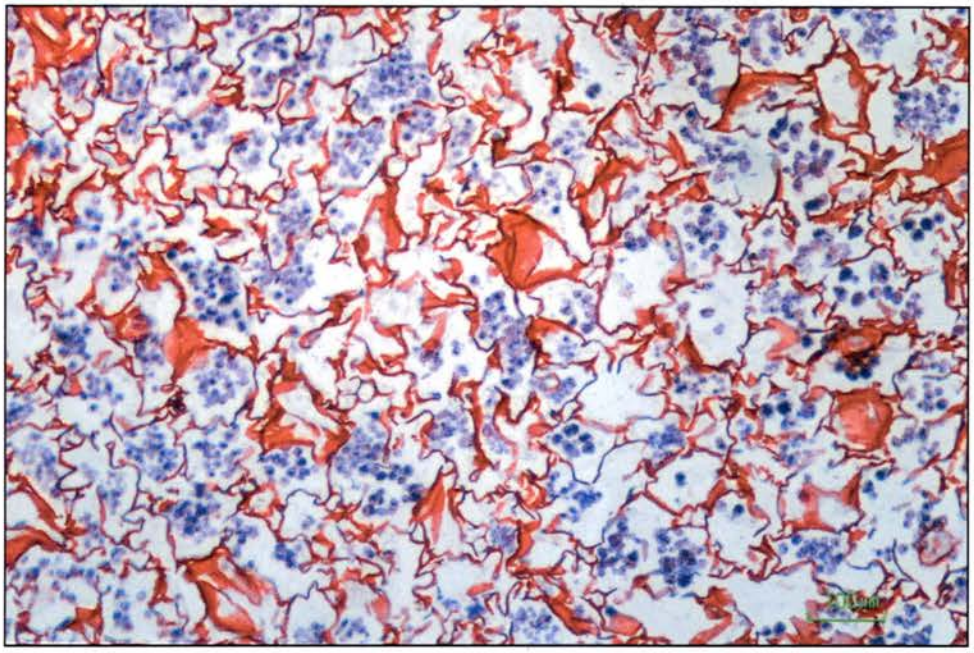

Figure 37. *Huernia recondita*. Stem cross section showing collapsible cortex and collapsible pith.

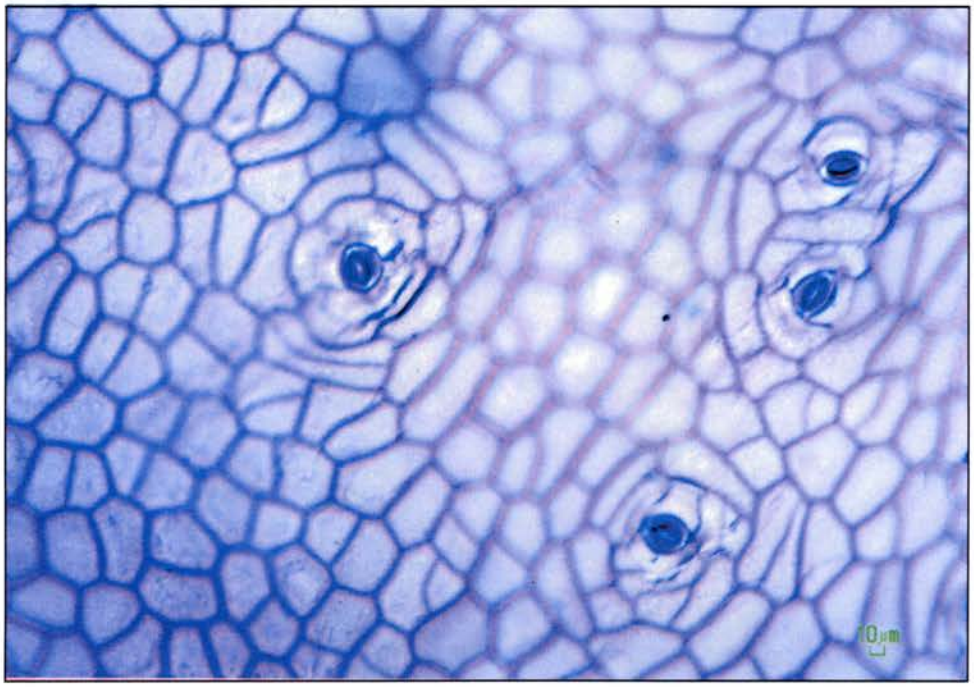

Figure 38. *Huernia recondita*. Stem cuticle showing pentagonal epidermal cell shape and brachyparacytic stomatal complex.

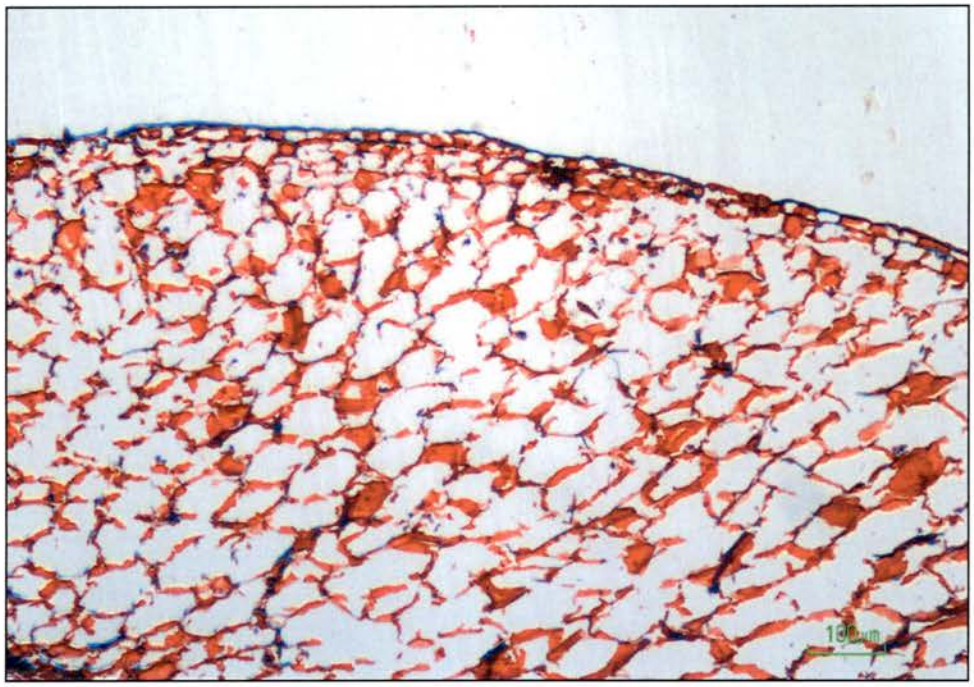

Figure 39. *Lavrania haagnerae.* Stem cross section showing collapsible cortex.

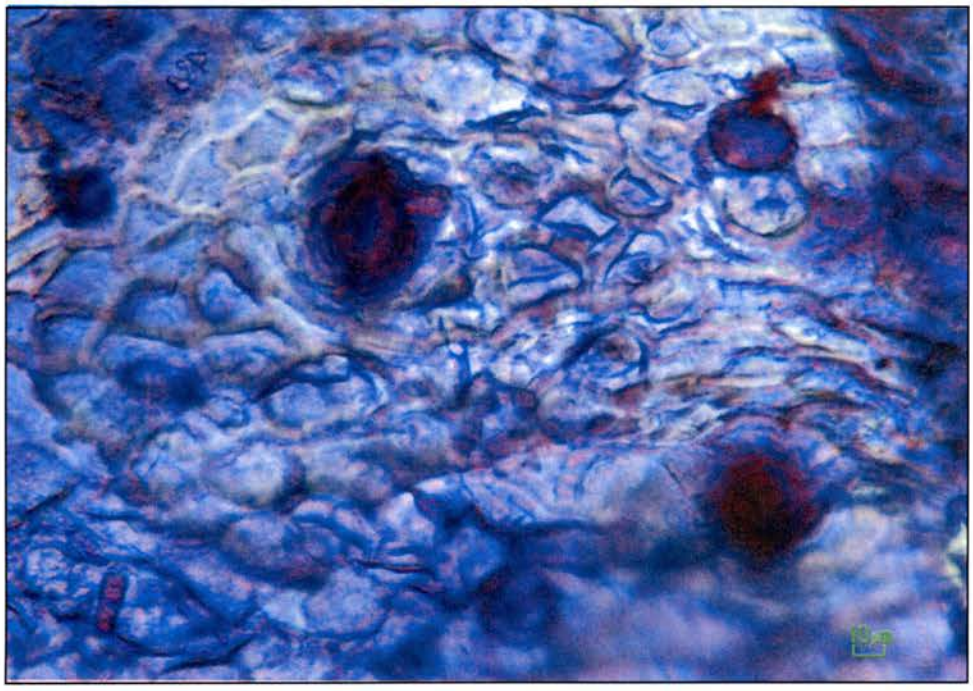

Figure 40. *Lavrania haagnereae.* Stem cuticle showing stomatal apertures occluded.

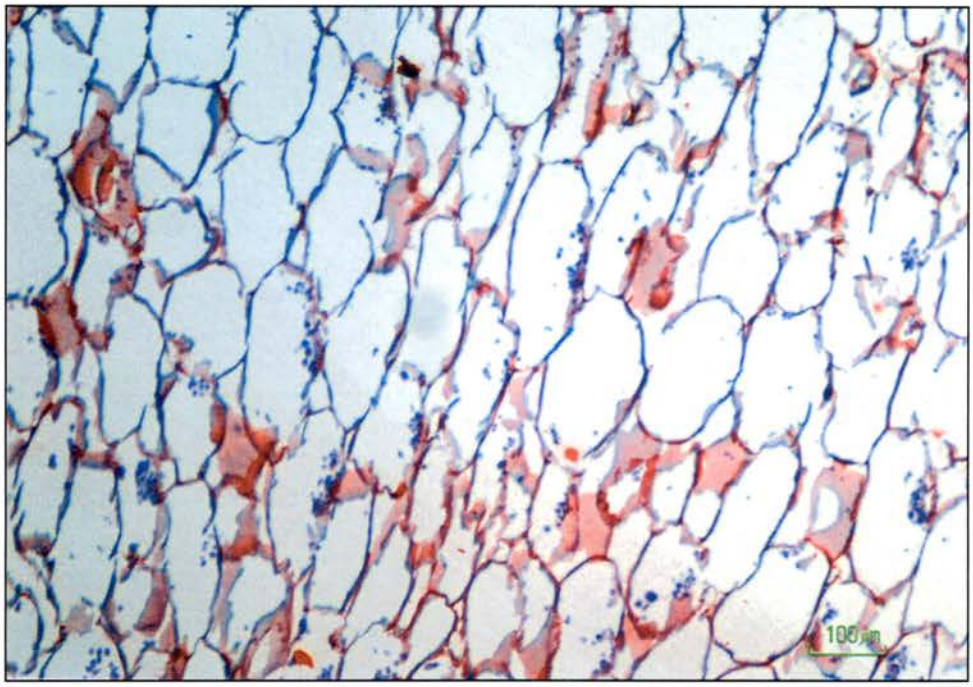

Figure 41. *Piaranthus barrydalensis.* Stem cross section showing palisade cortex.

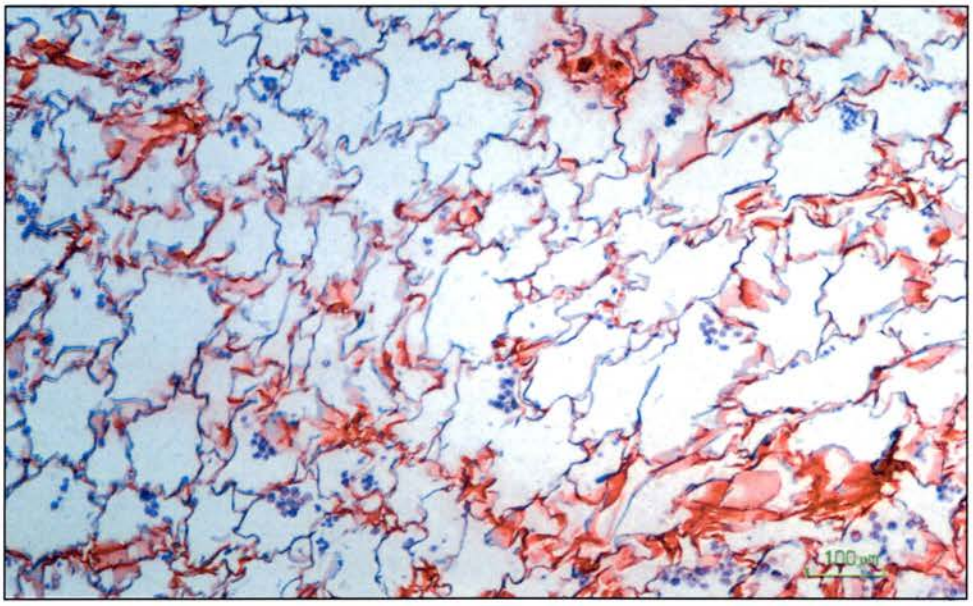

Figure 42. *Piaranthus barrydalensis.* Stem cross section showing collapsible pith.

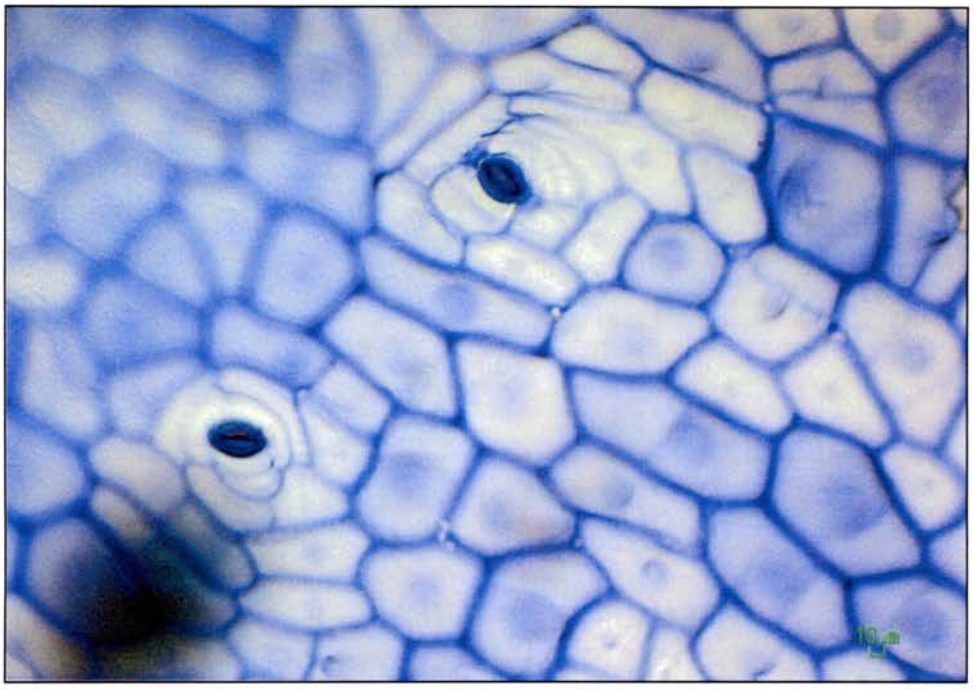

Figure 43. *Piaranthus barrydalensis*. Stem cuticle showing pentagonal epidermal cell shape, amphicyclocytic stomatal complex and locations of papillae.

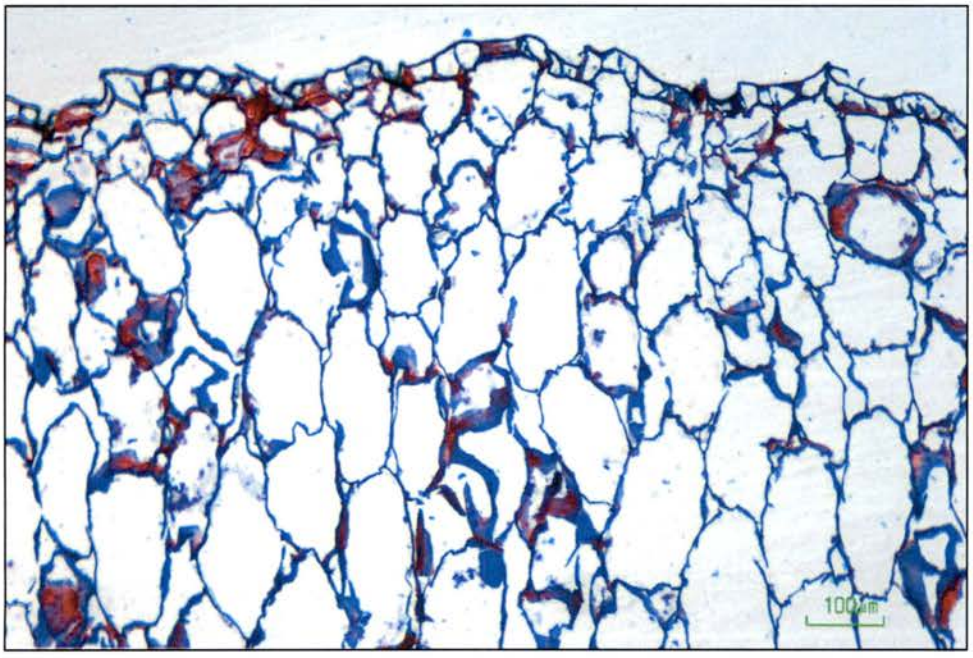

Figure 44. *Piaranthus comptus.* Stem cross section showing palisade cortex.

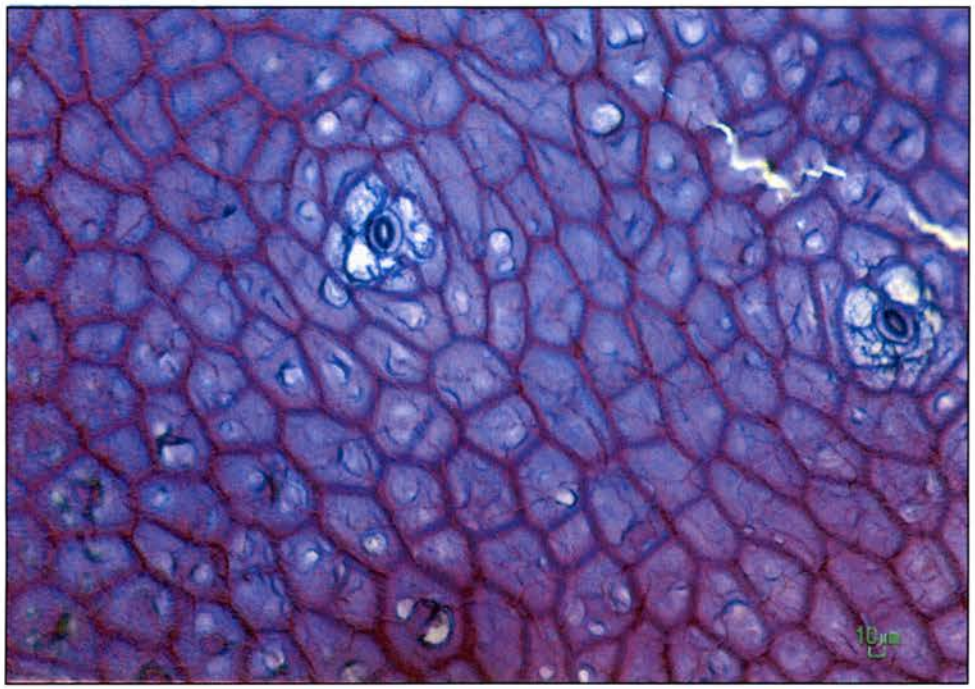

Figure 45. *Piaranthus comptus.* Stem cuticle showing hexagonal epidermal cell shape, amphicyclocytic stomatal complex and locations of papillae.

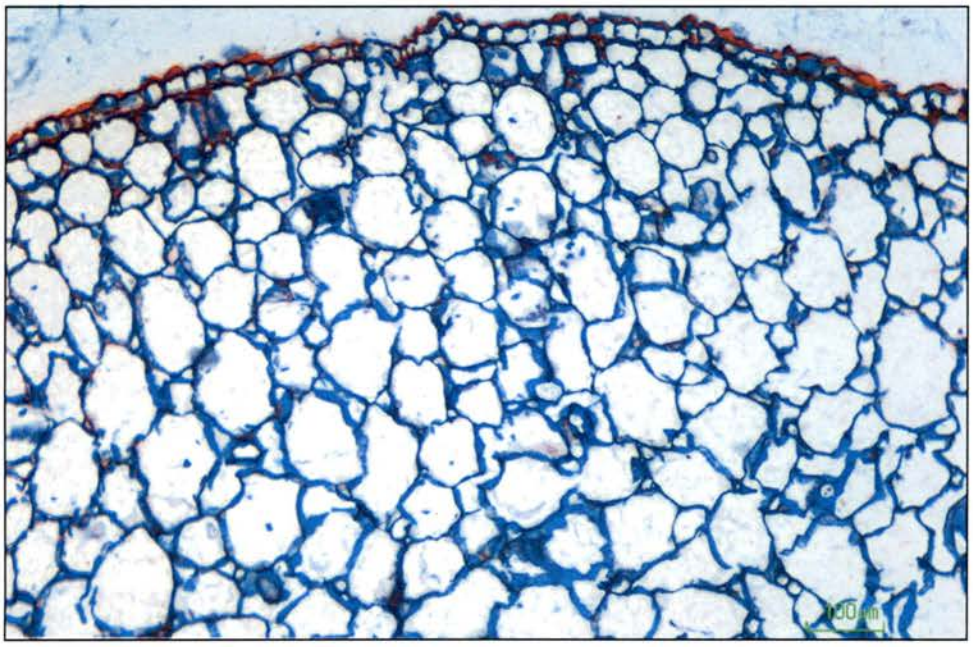

Figure 46. *Piaranthus geminatus.* Stem cross section showing collapsible cortex.

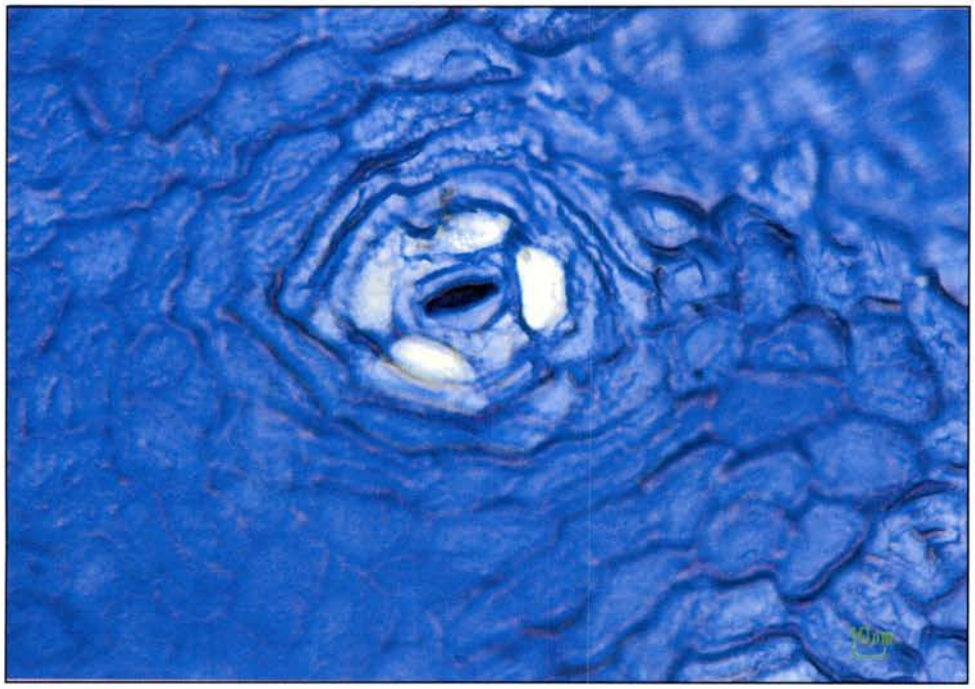

Figure 47. *Piaranthus geminatus* Stem cuticle showing pentagonal epidermal cell shape and cyclocytic stomatal complex.

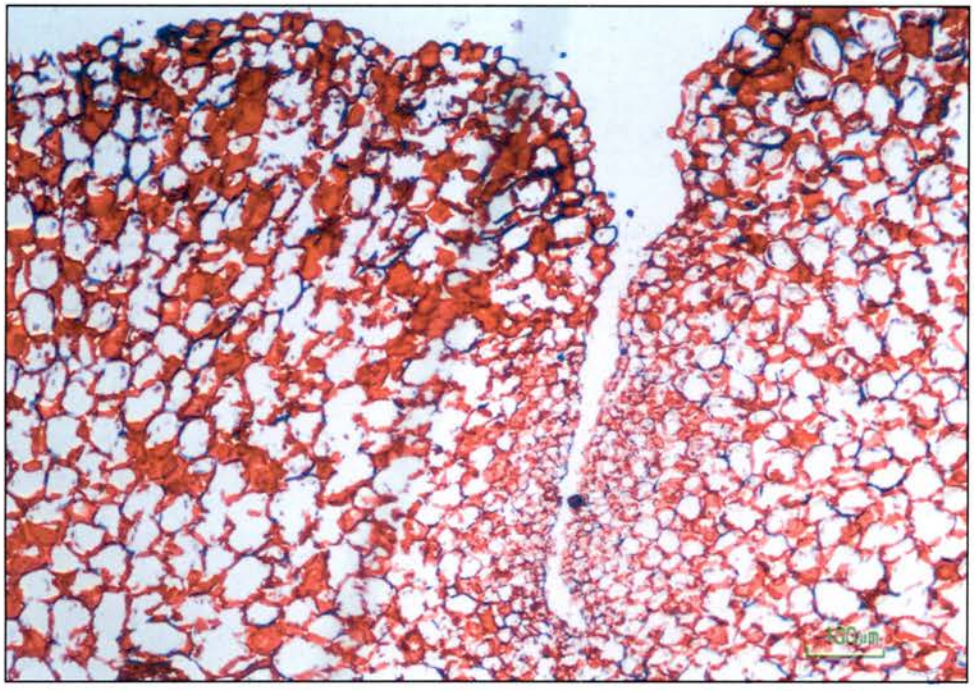

Figure 48. *Pseudolithos eylensis.* Stem cross section showing ridges.

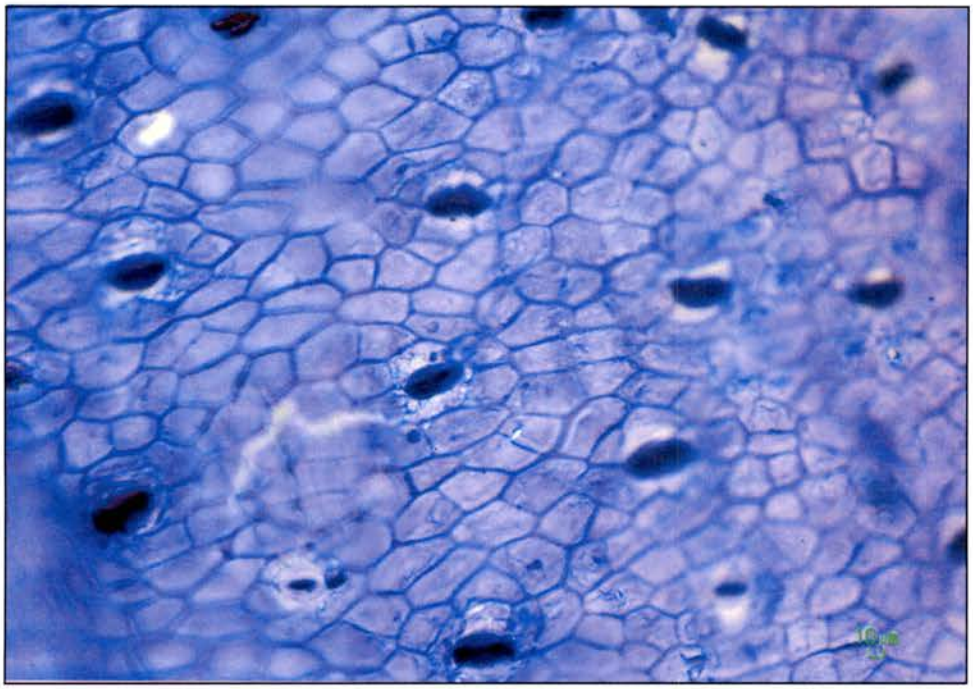

Figure 49. *Pseudolithos eylensis.* Stem cuticle showing hexagonal epidermal cell shape, anomocytic stomatal complex with stomatal apertures occluded and locations of papillae.

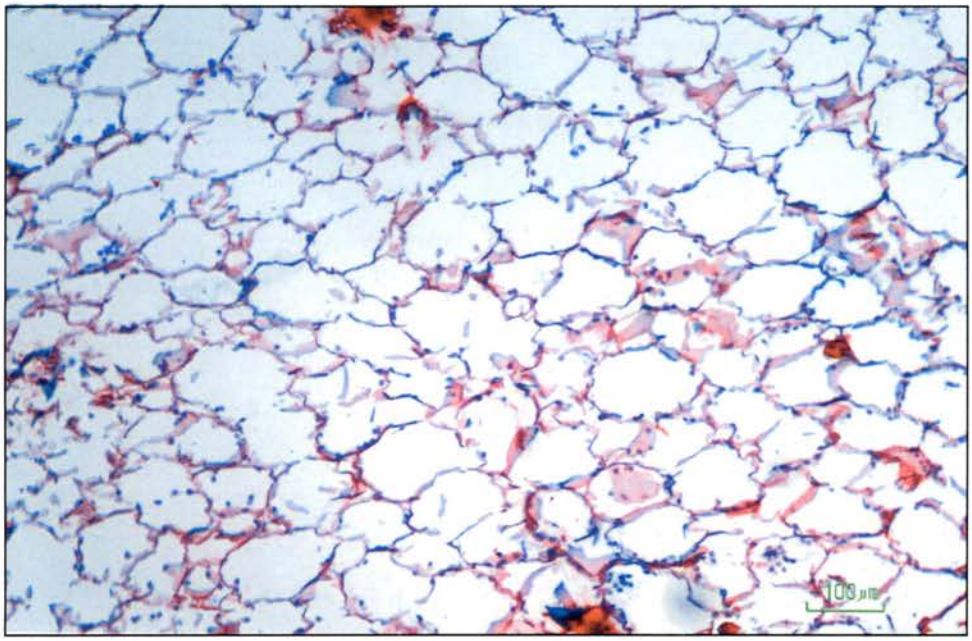

Figure 50. *Stapelia cedrimontana.* Stem cross section showing collapsible cortex exhibited by presence of undulate cell walls.

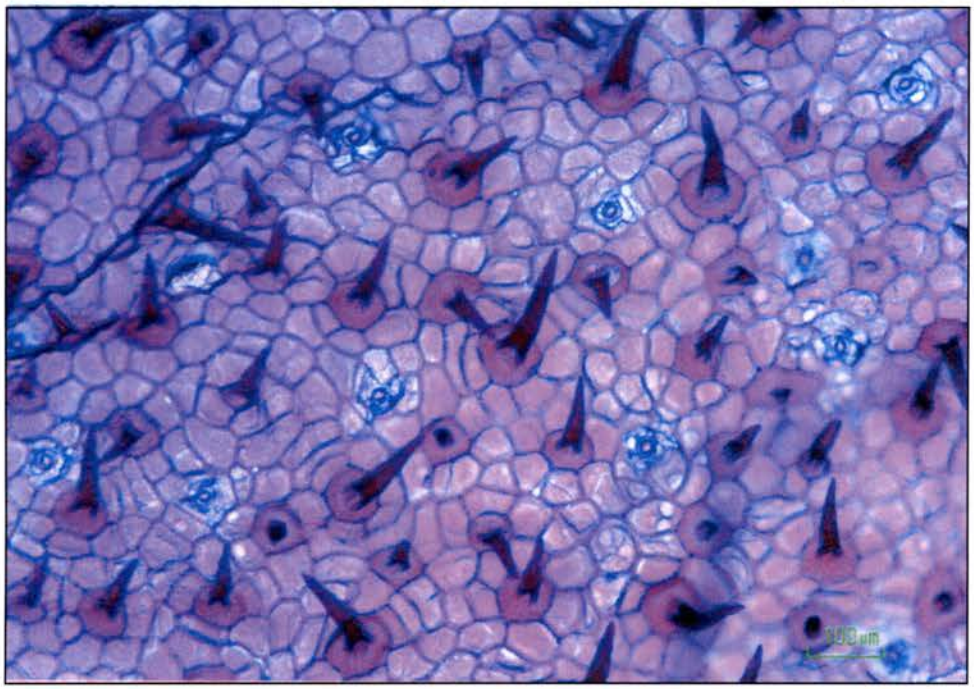

Figure 51. *Stapelia cedrimontana.* Stem cuticle showing hexagonal epidemal cell shape, anomocytic stomatal complex and conical unicellular trichomes.

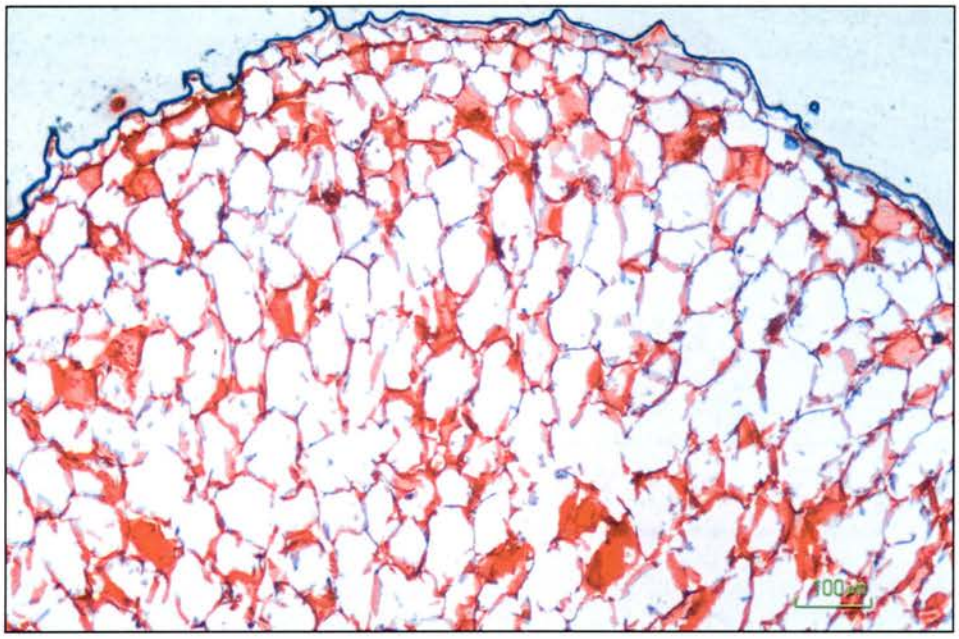

Figure 52. *Stapelia divaricata*. Stem cross section showing palisade cortex and papillate epidermis.

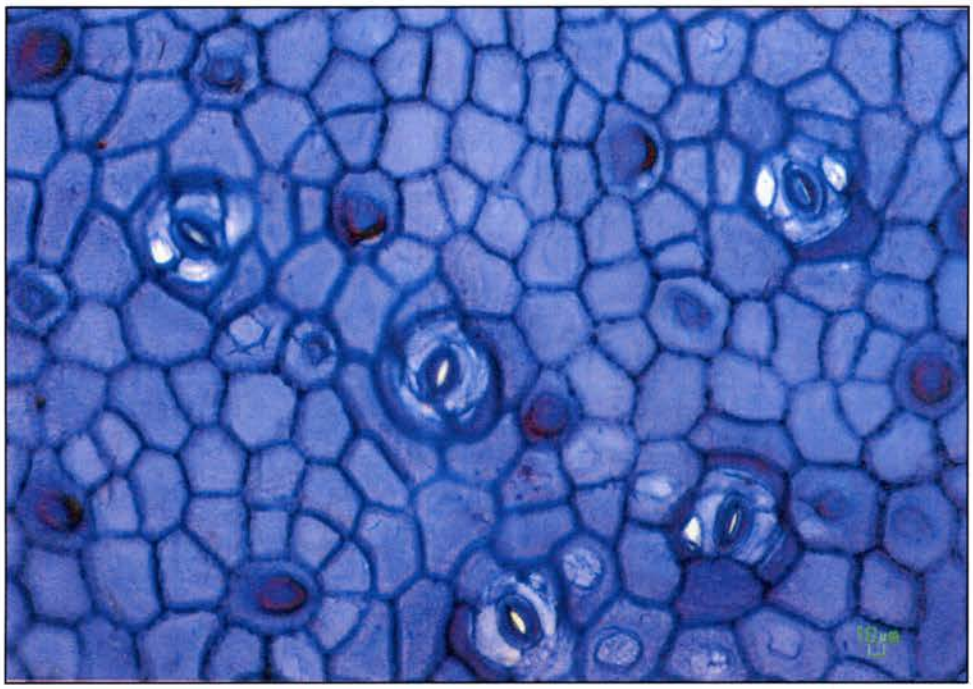

Figure 53. *Stapelia divaricata.* Stem cuticle showing epidermal cell shape, location of trichomes and cyclocytic stomatal complex.

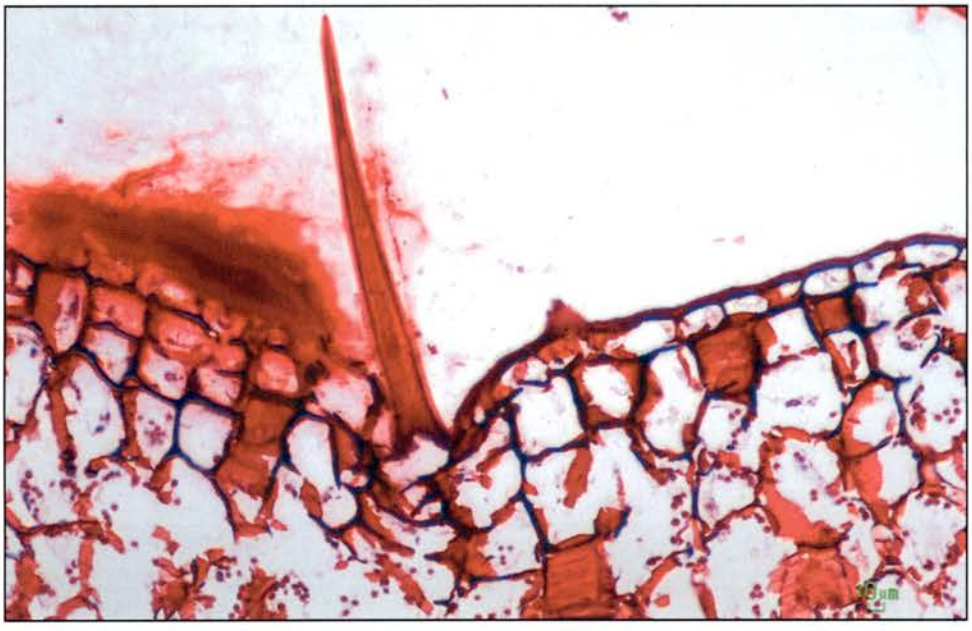

Figure 54. *Stapelia engleriana.* Stem cross section showing thickened outer epidermal cell walls, hypodermis, palisade cortex and conical unicellular trichome.

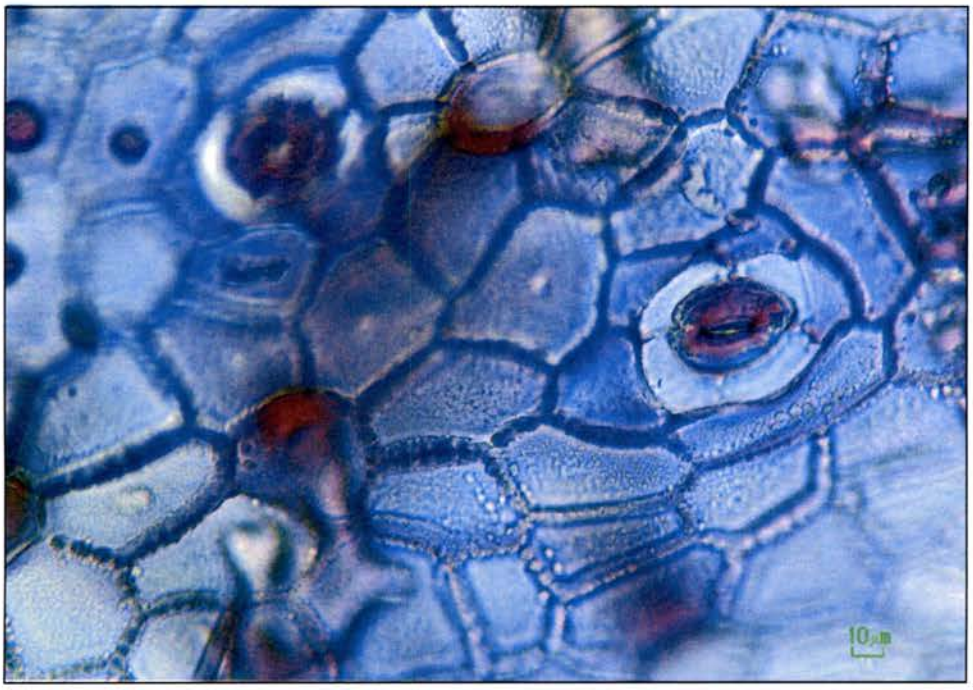

Figure 55. *Stapelia engleriana*. Stem cuticle showing pentagonal epidermal cell shape locations of trichomes and cyclocytic stomatal complex.

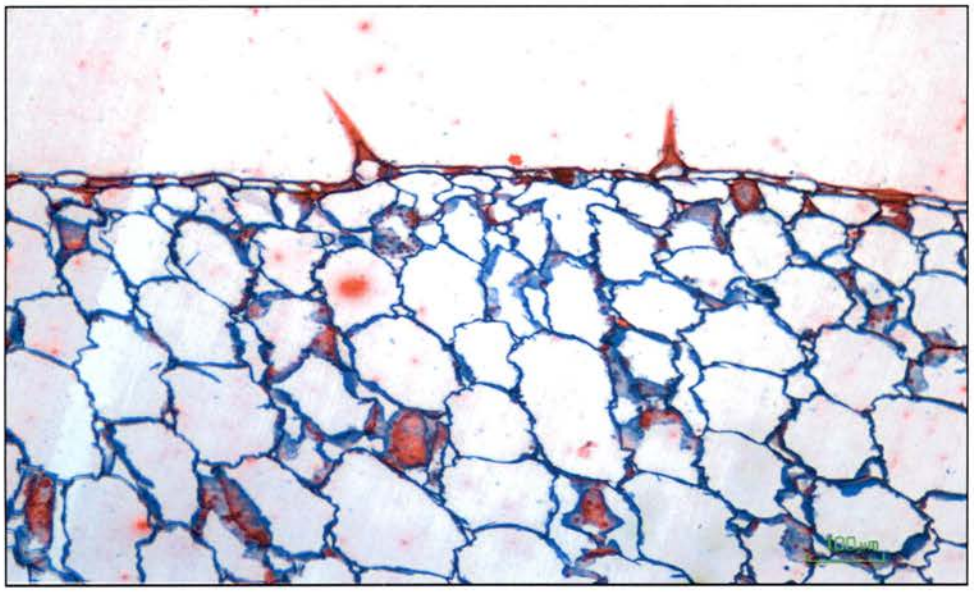

Figure 56. *Stapelia paniculata.* Stem cross section showing palisade cortex, and conical unicellular trichomes.

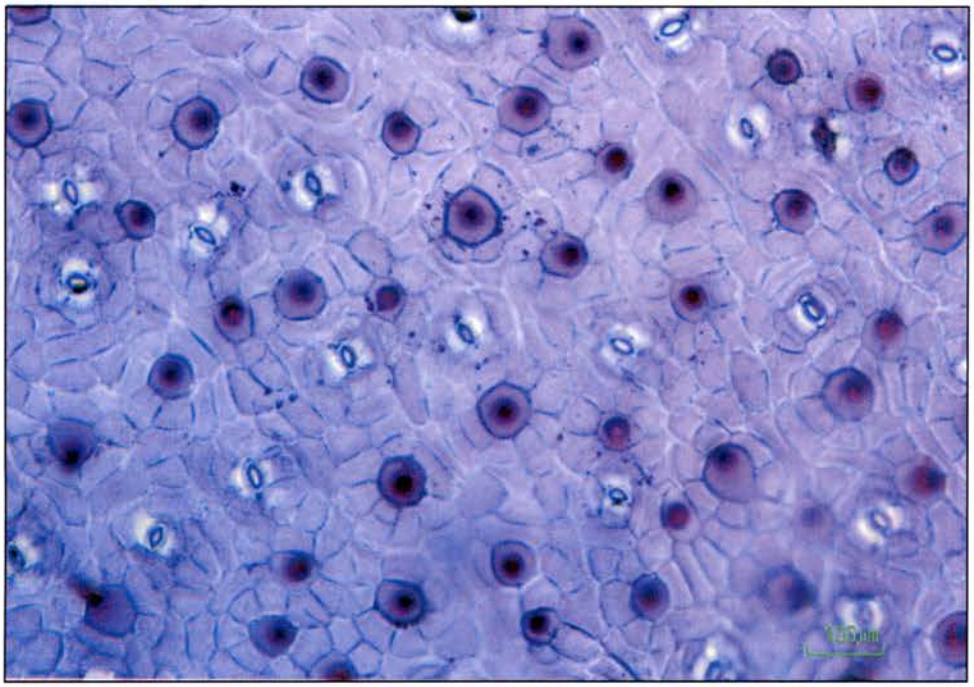

Figure 57. *Stapelia paniculata.* Stem cuticle showing hexagonal cell shape, cuticular striations and brachyparacitic stomatal complex.

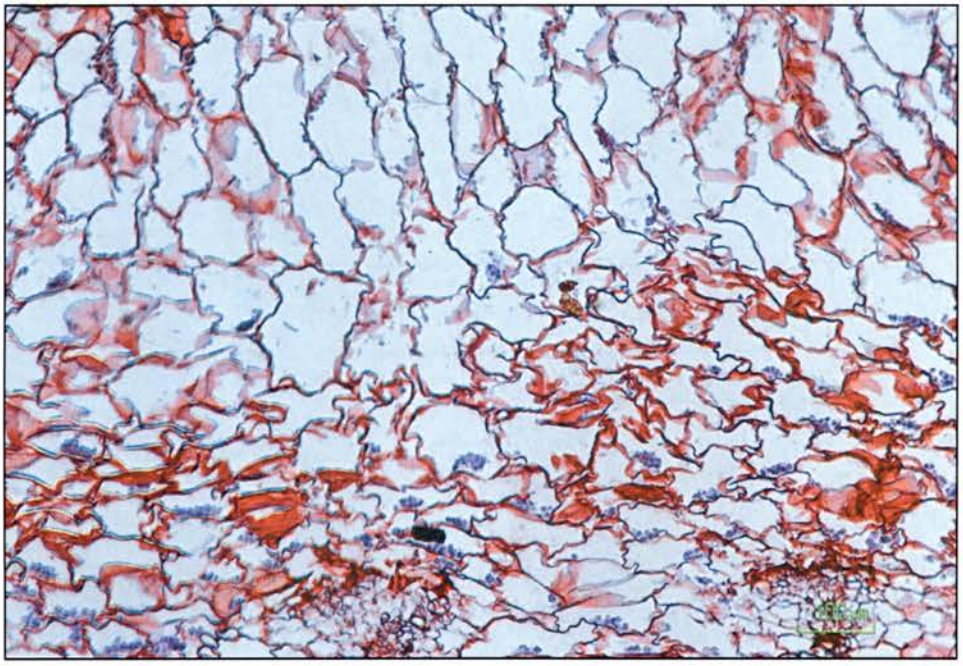

Figure 58. *Stapelia pillansii* var. *pillansii*. Stem cross section showing palisade cortex and collapsible pith.

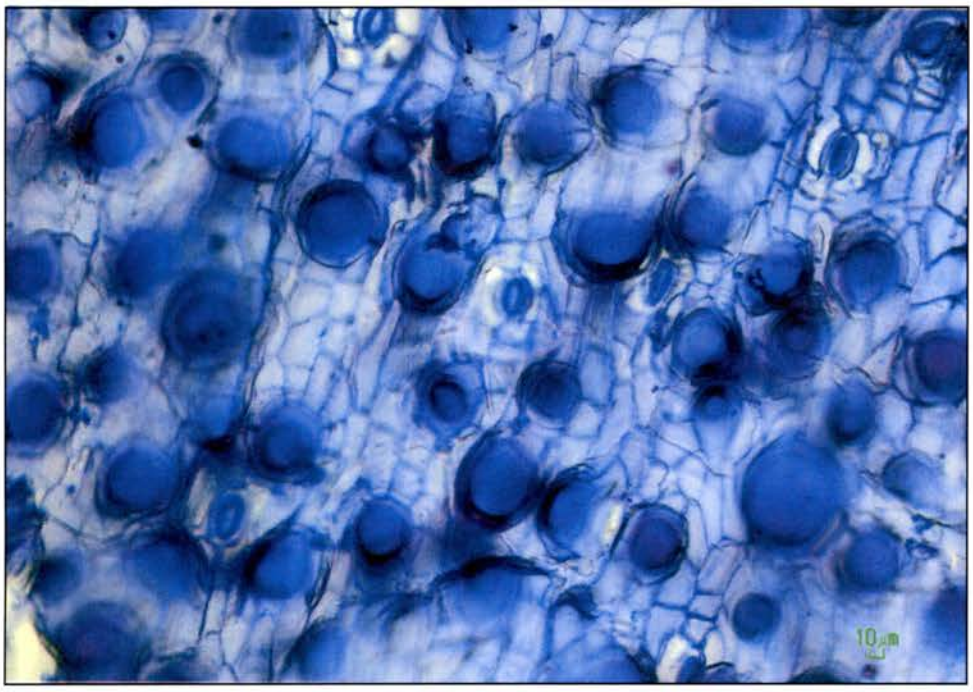

Figure 59. *Stapelia pillansii* var. *pillansii*. Stem cuticle showing hexagonal epidermal cell shape, locations of trichomes and cyclocytic stomatal complex.

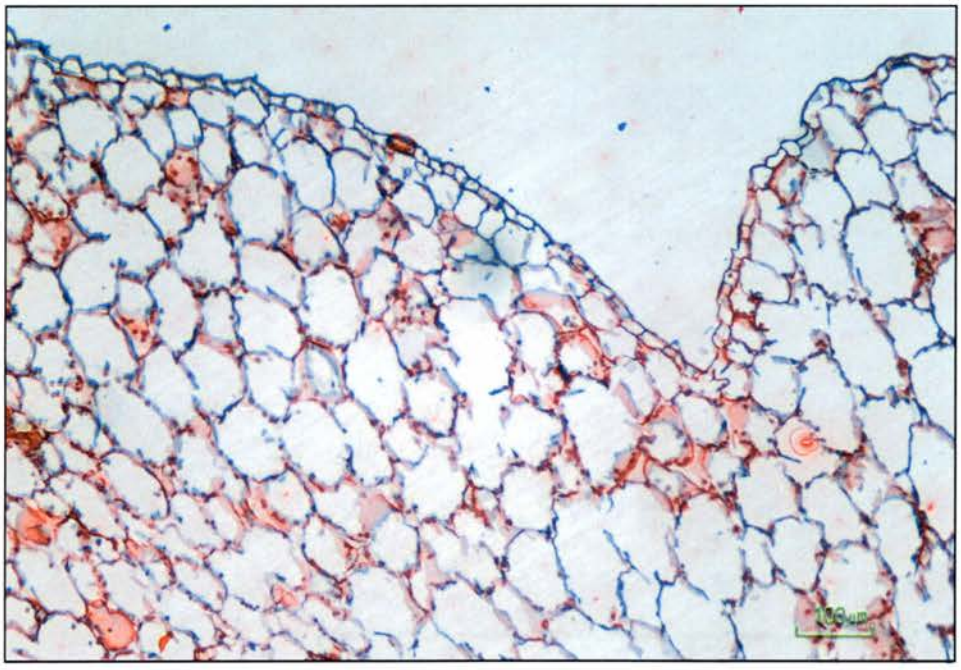

Figure 60. *Stapelianthus decaryi*. Stem cross section showing ridges.

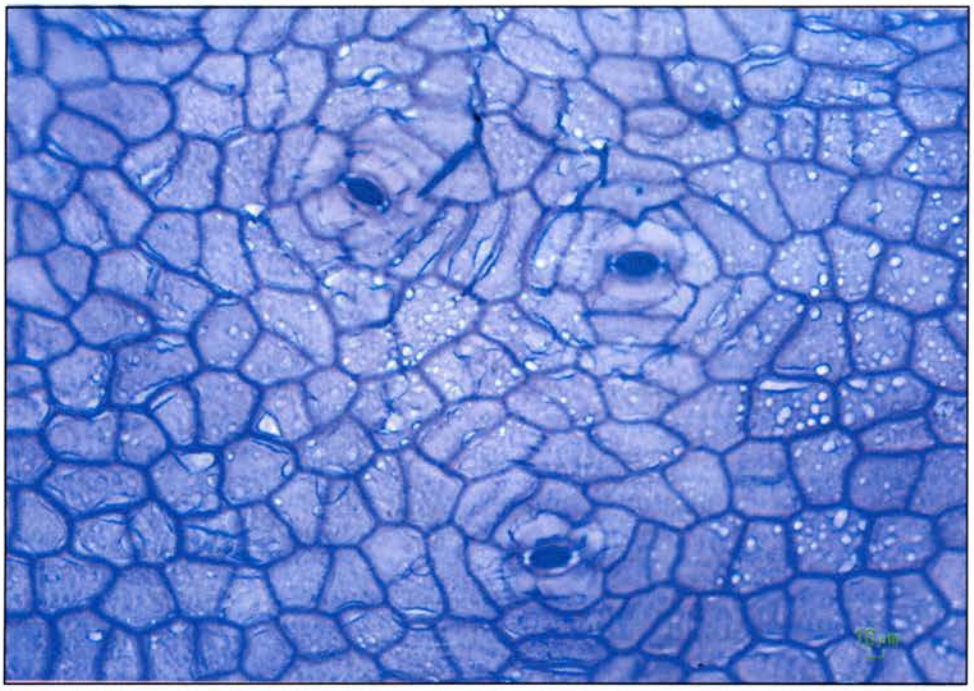

Figure 61. *Staplianthus decaryi.* Stem cuticle showing epidermal cell shape and brachyparacytic stomatal complex.

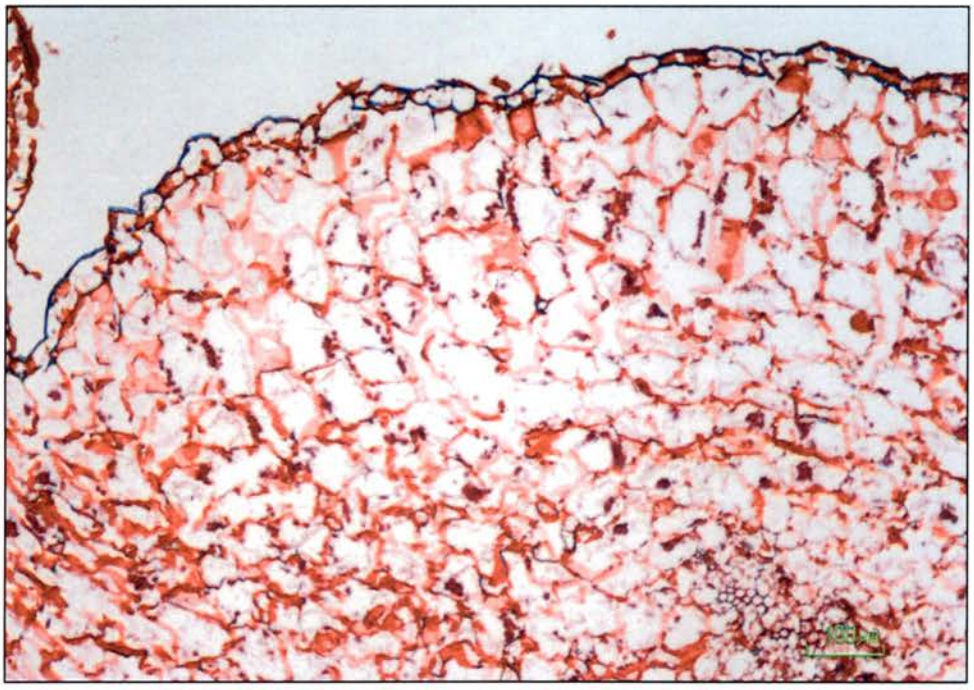

Figure 62. *Tavaresia barklyi.* Stem cross section showing palisade cortex.

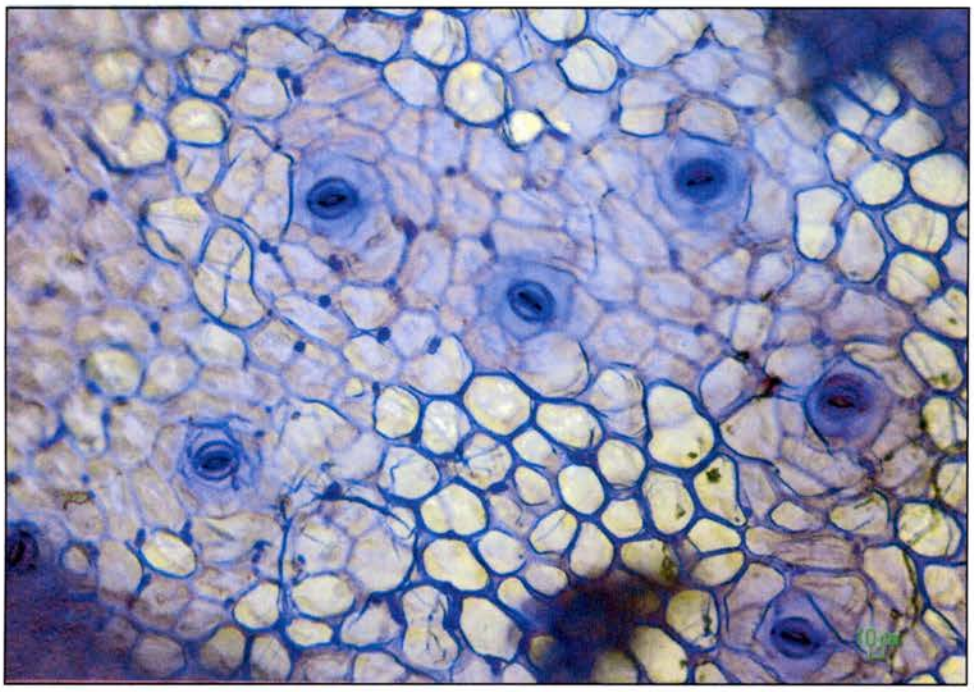

Figure 63. *Tavaresia barklyi*. Stem cuticle showing brachyparacytic stomatal complex.

4. DISCUSSION

Examination of transverse sections of 28 species (Table 1) showed that the perennial epidermises were uniseriate with thicker outer periclinal cell walls. In most species the outer epidermal cell wall was also cuticularized. Generally, outer periclinal walls were of three shapes; flat, as in *Huernia leachii* (Figure 33), convex as in *Edithcolea grandis* (Figure 23) or papillate. Species with papillate epidermises included *Duvalia corderoyi*, *D. modesta, Piaranthus barrydalensis* and *Stapelia divaricata* (Figures 9, 11, 43, 52). The average length of epidermal cells ranged from 21 μm in *Huernia hystrix* to 44 μm in *Duvaliandra dioscoridis,* and average widths ranged from 13 μm in *Echidnopsis cereiformis* to 35 μm in *Duvalia corderoyi* (n = 30).

Cuticles showed thirteen species with papillae, for instance, *Caralluma solenophora*, *Duvalia corderoyi* and *Piaranthus comptus* (Figures 8, 10, 45). Conical unicellular trichomes were observed in five species including *Stapelia engleriana,* and *S paniculata* (Figures 54, 56). Striations were present in nine species, for instance *Baynesia lophophora, Caralluma diffusa* and *Huernia hystrix* var. *parvula* (Figures 3, 6, 32). Cell arrangement in all species was random, with a mixture of tetragonal, pentagonal, hexagonal and polygonal cells. But generally pentagonal arrangement (17 species) and hexagonal arrangement (11 species) were more common. The cells in all species had straight end walls and not aligned in rows, except in *Frerea indica* and *Huernia hystrix* var *parvula* (Figures 26, 32) where the cells were in obscure rows.

Also, cuticles showed a variety of stomatal complex types among the species and it was not uncommon to find more than one type of stomatal complex within a species (Table 3). Fifteen of the species mostly had the brachyparacytic complex type. Examples include *Huernia hystrix* var. *parvula* and *Stapelianthus decaryi* (Figures 32, 61). Seven species mostly had the cyclocytic complex type, for example *Frerea indica, Piaranthus comptus, Stapelia divaricata* and *S. engleriana* (Figures 26, 45, 53, and 55). Three species *Echidnopsis lavraniana, Pseudolithos eylensis* and *Stapelia cedrimontana* mostly had the anomocytic complex type (Figures 22 49, 51). The other three species had stomatal arrangements ranging from paracytic to cyclocytic to amphibrachyparacytic. Stomatal index ranged from 0.9 in *Huernia occulta* to 5.4 in *Stapelia paniculata.*

Only three species, *Duvalia corderoyi, D. modesta and Stapelia engleriana,* had a hypodermis. In the remaining species, parenchyma cells underlying the epidermis were similar and only differed in size. Where the hypodermis was present it was made up of only a single layer. Thickening of hypodermal cells walls was similar to that of the epidermal cells (Figures 9, 11, 54). None of the species in this study had an extensive aerenchymatous palisade cortex as do some stem succulents in other studies, for instance *Caralluma burchardii* and *Euphorbia horrida* (Mauseth, 2004). However there were several small intercellular spaces that can enhance gaseous exchange.

Palisade cortex exhibited by tall columnar cells of the cortex, arranged in rows or columns was present in eighteen species (Table 2). Examples include *Echidnopsis cereiformis, Piaranthus barrydalensis* and *Piaranthus comptus* (Figures 16, 41 and 44). The cells of the palisade cortex contained several chloroplasts an indication of photosynthetic ability.

A collapsible cortex or/and pith is an important characteristic for water storage. When water is abundant the cells of the collapsible cortex expand as they absorb and store water. During periods of water scarcity, the cells shrink as water diffuses out especially to the photosynthetic cells. This cycle helps the plants to withstand unfavorable conditions. The cells of the collapsible cortex can shrink without being plasmolyzed (Wiebe and Al-Saadi 1976; Barcikowski and Nobel 1984; Tissue et al. 1991). Where a collapsible cortex is absent the large, thin walled cells of the inner cortex or of the pith provide intercellular exchange of water (Mauseth 2004).

In the present study, ten species had collapsible cortex in some cases shown by undulate cell walls. Examples include *Caralluma solenophora, Echidnopsis cereiformis* and *Huernia recondita* (Figures 7, 17, 37). Five species with *Piaranthus barrydalensis* and *Stapelia pillansii* (Figures 42, 58), as examples, had a collapsible pith. *Huernia recondita* and *Piaranthus germinatus* had both pith and cortex as collapsible. A parenchymatous pith and cortex was observed in all species. With the exception of *Pseudolithos eylensis* with 0.3, the cortex to pith ratio ranged from 0.4 to 1.7 indicating that in these plants the cortex contributes a larger storage volume than the pith just as in many stem succulents (Mauseth 2004).

Many species lacked cortical bundles probably because most stapeliads do not attain large sizes; therefore an extensive transport system is not necessary (Mauseth 2004). Even then, it was surprising that cortical bundles were observed in the genus *Echidnopsis* (Figures 18, 20). It could also be that *Echidnopsis* is more evolved than the rest of studied genera. According to Mauseth, (2004) in the more evolved stem succulents the epidermis and photosynthetic tissues are located further from the main vascular

bundles. Therefore, presence of cortical bundles enhances efficiency in transportation of water and the products of photosynthesis to the distal parts of the plant. Absence of cortical bundles can be a limitation in the extent to which succulence evolves.

Medullary bundles were seen only in *Caralluma diffusa* and *Duvaliandra dioscoridis* and these comprised mostly of phloem (Figures 5, 15). Laticifers were observed in all species. An example is given in *Echidnopsis lavraniana* (Figure 21).

Compared to some succulents, such as members of the Euphorbiaceae and Cactaceae, stapeliads usually do not grow as large, but the three groups are similar in some of their growth forms (Bruyns 2005). In the present study, stem anatomical features characteristic of stem succulents, especially the Cactaceae that has been studied extensively, (Boke 1964, 1968; Calvente et al. 2008; Gibson 1973; Gibson and Horak 1978; Gibson and Nobel 1986; Loza-Cornejo and Terrazas 2003; Mauseth and Plemons-Rodriguez 1995, 1997, 1998; Mauseth et al. 1995; Terrazas and Arias 2003; Terrazas and Mauseth 2002), were also seen in stapeliads. These include a perennial stem with stomata and a cuticularized outer epidermal cell wall, presence of palisade cortex with numerous chloroplasts, an evidence of photosynthetic ability, collapsible cortex, an adaptation to dry habitats, a high cortex:pith ratio and presence of medullary bundles and cortical bundles. However, a relatively small fraction of carrion flower species have been considered. Studies on stem anatomy of more species are needed for a better understanding of this group of plants.

LITERATURE CITED

Barad, G. S. (1990). Pollination of stapeliads. *Cact. Succ. J. (U.S.)* 62: 130-140.

Barcikowski, W. and Nobel P. S. (1984). Water relations of cacti during desiccation: distribution of water in tissues. *Bot. Gaz.* 145: 110-115.

Boke, N. H. (1964). The cactus gynoecium: a new interpretation. *Amer. J. Bot.* 51: 598-610.

_____. (1968). Structure and development of the flower and fruit of *Pereskia diazromeroana*. *Amer. J. Bot.* 55: 1254-1260.

Brown, N. E. (1907-1909). Asclepiadeae. In Thistleton-Dyer, W. T. (ed). *Fl. Trop. Afr.* 4: 231-503. Lovell Reeve & Co., London.

Bruyns, P. V. (1988). A revision of the genus *Echidnopsis.* Hook f. (Asclepiadaceae). *Bradleya* 6: 1-48.

_____ . (1993). A revision of *Hoodia* and *Lavrania* (Asclepiadaceae –Stapeliae). *Bot. Jahrb. Syst.* 115: 145-270.

_____ . (2000). Phylogeny and Biogeography of the Stapeliads: 1. Phylogeny. *Pl. Syst. Evol.* 221: 227-244.

_____. (2000). *Baynesia*, a new genus of stapeliad from the northwestern-most corner of Namibia. (Apocynaceae). *Novon* 10: 354-358.

_____. (2001). New combinations in the genus *Orbea. Aloe* 37: 72-76.

_____. (2005). *Stapeliads of Southern Africa and Madagascar.* Vol. 1. Umdaus, Hatfield, South Africa.

_____ and Linder, H. P. (1991). A revision of Microloma R. Br. (Asclepiadaceae – Asclepiadaceae). *Bot. Jahrb. Syst.* 112: 453-527.

Calvente, A. M et al. (2008). Stem anatomy of *Rhipsalis* (Cactaceae) and its relevance for taxonomy. *Pl. Syst. Evol.* 276: 1-7.

Gibson, A. C. (1973). Comparative anatomy of secondary xylem in Cactoideae (Cactaceae). *Biotropica* 5: 29-65.

_____. (1998). Photosynthetic organs of desert plants. *BioScience* 48: 911-920.

Gibson, A. C. and Horak, K. E. (1978). Systematic anatomy and phylogeny of Mexican columnar cacti. *Ann. Missouri Bot. Gard.* 65: 999-1057.

Gibson, A. C. and Nobel, P. S. (1986). *The cactus primer.* Harvard University Press Cambridge.

Grime, J. P. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Amer. Naturalist* 111: 1169-1194.

Laundrum, J. V. (2002). Four succulent families and 40 years of evolution and adaptation to xeric environments: What can stem and leaf anatomical characters tell us about their phylogeny? *Taxon* 51: 463-473.

Loza-Cornejo, S. and Terraza, T. (2003). Epidermal and hypodermal characteristics in Northern Cactoideae (Cactaceae). *J. Pl.Res.* 116: 27-35.

Mauseth, J. D. (1995). Collapsible water storage cells in cacti. *Bull. Torrey Bot. Club* 122: 145-151

Mauseth, J. D. (1999). Anatomical adaptations to xeric conditions in *Maihuenia* (Cactaceae), a relictual, leaf-bearing cactus. *J. Pl. Res.* 112: 307-315.

_____. (2004). The structure of photosynthetic succulent stems in plants other than cacti. *Int. J. Pl. Sci.* 165: 1-9.

_____. (2004). Cacti and other succulents: stem anatomy of "other succulents" has little in common with that of cacti. *Bradleya* 22: 131-140.

_____. (2005). Anatomical features, other than wood, in subfamily Opuntioideae (Cactaceae) *Haseltonia* 11: 113-125.

Mauseth, J. D. and Plemons-Rodriguez. B. J. (1997). Presence of paratracheal water storage tissue does not alter vessel characters in cactus wood. *Amer. J. Bot.* 84: 815-822.

Meve, U. (1987). The genus *Piaranthus* R. Br. (Asclepiadaceae). *Bradleya* 12: 57-102.

_____ and Albers, F. (1990). The species concept in *Duvalia* (Asclepiadaceae). – A preliminary revision of the genus. *Proceedings of the 12th plenary meeting AETFAT. Mitt. Inst. Allg. Bot. Hamburg* 23: 595-604.

_____ and Liede, S. (2002). A molecular phylogeny and generic rearrangement of the stapelioid Ceropegieae (Apocynaceae – Asclepiadaceae) *Pl. Syst. Evol.* 234:171-209.

Mulej, I. and Strilic, M. (2002). Stapeliads, morphology and pollination. *Welwitschia* 5: 1-4.

Terrazas, T. and Arias. S. (2003). Comparative stem anatomy in the subfamily Cactoideae. *Bot. Rev.* 68: 444-473.

Terrazas, T. and Mauseth, J. D. (2002). *Shoot anatomy and morphology*. In: Nobel, P. S. (ed) Cacti: biology and uses. University of California Press. Berkeley, pp 23-40.

Troll, W. (1935-1937). *Vergleichende Morphologie der hoheren Pflanzen* 1 (1). Gebruder Borntraeger, Berlin.

Von Willert, D. J., Eller, B. M., Werger, M. J., Brinckmann E. B., and Ihlenfeldt H. (1992). *Life strategies of succulents in deserts; with special reference to the Namib desert.* Cambridge University Press, New York.

Werger, M. J. A. (1983). Plant form and plant function- an introductory historical outline. *J. Southwest China Teachers Uni.* (Beibei, Sichuan), 4: 141-165.

Wertel, H. P. (1976). Vergleichend-morphologische und entwicklungsgeschichtliche Untersuchungenüber Bau und Stellung der Infloreszenzen bei einigen Stapelieen Gattungen (Fam:Asclepiadaceae). *Trop. Subtrop. Pflanzenwelt* 17: 1-70.

White, A. C., and Sloane, B. L. (1937). *The Stapelieae*, ed. 2. Abbey San Encino Press. Pasadena, California.

Wiebe, H. H and Al-Saadi, H. A. (1976). Matric bound water of water tissue from succulents. *Physiol. Pl.* 36:47-51.

Wyk, B. E. & Gericke, N. (2000). *People's plants. A guide to useful plants of southern Africa. Briza Publications, Pretoria.*

Wynberg, R. (2004). Rhetoric, realism and benefit sharing. Use of traditional knowledge of Hoodia species in the development of an appetite suppressant. *J. World Intell Prcp.* 7: 851-876.

VITA

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