

STUDIES IN THE GESNERIACEAE OF THE OLD WORLD XLVIII:

Calcium accumulation and excretion in *Paraboea*

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ABSTRACT. It is shown that in a few species of *Paraboea* calcium salts accumulate in localized patches of cells in the adaxial surface (epidermis or epidermis and hypodermis) of the leaves. This results in necrosis of these cells and the formation of blister-like patches. In another species multi-cellular chalk-glands are described. Other instances of apparently excessive calcium uptake in Asiatic Gesneriaceae are mentioned.

INTRODUCTION

When studying herbarium specimens of *Paraboea* from the limestone cliffs of the Gunung Mulu National Park, Sarawak (Burtt, 1982), it was noticed that in certain species the dried leaves had curious raised blister-like patches on the upper surface. One of us (K. T.) therefore undertook a microscopic investigation. The results are presented here, together with some general notes on special features of some gesneriads that grow on tropical limestone.

As a preliminary, the available species of *Paraboea* (44 out of 65) and the closely allied genus *Trisepalum* (10 out of 14) in the Edinburgh herbarium were surveyed (taking these genera as re-defined in Burtt, 1984). Of all these just four species of *Paraboea* showed the blister-like structures (they can easily be seen under a $\times 10$ hand lens). These four were *P. caerulescens* (Ridley) B. L. Burtt, *P. effusa* B. L. Burtt, *P. meliophylla* B. L. Burtt and *P. verticillata* (Ridley) B. L. Burtt. In addition one species, *P. acutifolia* (Ridley) B. L. Burtt, appeared to have calcium-excreting glands; these too were investigated microscopically. A brief description of normal leaf-structure is given first.

OBSERVATIONAL DATA

a. General structure of lamina of *Paraboea*

Leaves dorsiventral, hypostomatic. Adaxial epidermis 1-layered, very rarely 2-layered in parts (*P. caerulescens*, B. 1822), with a moderately thick cuticle giving a smooth upper surface to the leaf. Trichomes of various types occur on both epidermides: uniseriate, bi- and multi-cellular hairs on tuberculate bases (Figs 1Ab, D), branched hairs (Figs 1Aa, 2A), and stalked glandular hairs (Figs 1Aa, 2A). In most species the indumentum forms a dense white cobwebby mat, often caducous from the upper surface but persistent below. Hypodermis 1-layered, very rarely 2-layered; if so, in the midrib region, sometimes incomplete. Palisade well developed, consisting of a single layer usually occupying half, or more than half, of the leaf depth. Small druses develop in many, but not all, of the palisade cells (Fig. 1Ac); in the spongy mesophyll they are rather less frequent (Fig. 2A). In the midrib region there is collenchyma on the adaxial side; the ground parenchyma is thin-walled often with prismatic crystals. The midrib itself shows, in transverse section, a shallow vascular crescent dissected into separate strands with other associated bundles

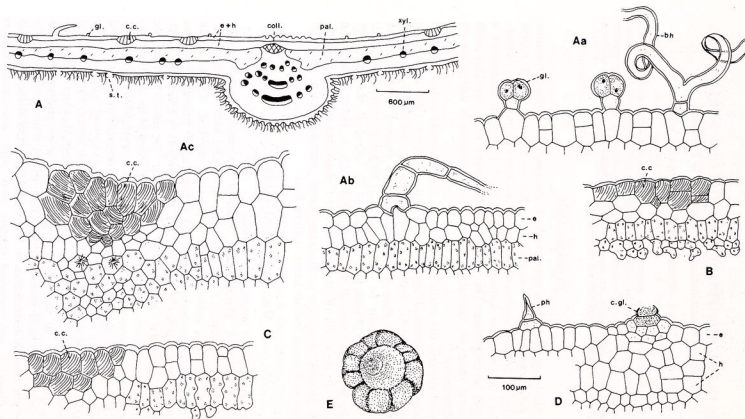


FIG. 1. A–Ac, *Paraboea meiophylla* (B. 2281); B, *P. effusa* (B. 2347); C, *P. effusa* (B. 2309); D & E, *P. acutifolia* (B. 1777). A, leaf midrib T.S.; Aa–D, leaf adaxial sections; E, calcareous gland with radially arranged basal epidermal cells ($\times 115$). All drawn to $100\ \mu\text{m}$ scale shown except A & E. gl. = stalked glandular hair, ph = prickly hair, bh = bifurcate hair, c.c. = calcareous cells, c. gl. = calcareous gland, e + h = epidermis + hypodermis, coll. = collenchyma, pal. = palisade tissue, xyl. = xylem, s.t. = stomatal turret.

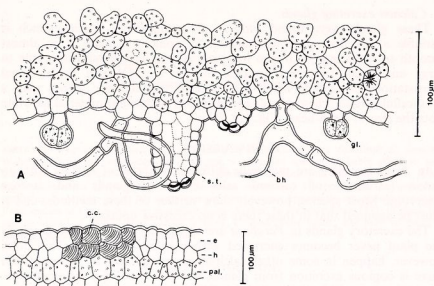


FIG. 2. *Paraboea effusa*: A, leaf abaxial section (B. 8338); B, leaf adaxial section (Anderson S. 30906). Each with individual scale.

above it and at the ends of the crescent (Fig. 1A). The vascular bundles of midrib and lateral veins are not accompanied by sclerenchyma which is also absent from other parts of the leaf. Stomata are restricted to the abaxial surface, raised on 'turrets' (Fig. 2A), and have a ring of three subsidiary cells that are much smaller than those of the surrounding epidermis. Most leaves examined had certain fungi invading the mesophyll and forming sclerotia.

b. Leaf-blisters

The blister-like patches occur on the adaxial leaf-surface and are easily seen (Figs 1A, Ac, B, C, 2B); the leaf-apex and margins usually show them most conspicuously. In herbarium specimens they appear to be raised, but this is due to shrinkage of the surrounding epidermis and hypodermis; when the leaf has been soaked up for sectioning they are, if anything, slightly sunken. In transverse section they resemble air-bubbles trapped in the adaxial epidermis, or epidermis and hypodermis, being greyish and glistening hyaline, looking as if they were gelatinous. They effervesce vigorously when dilute HCl is added. It appears that they are moderately thick-walled cells that accumulate calcium salts and in time undergo necrosis. Although they originate in the epidermis as isolated and discontinuous patches, in time they occur in the hypodermis (Fig. 1Ac), though never in the palisade. The calcium salt is present as a single amorphous, but somewhat laminated, mass in each cell. The patches eventually fuse and the leaf-surface appears 'blistered'. The presence of these blisters may provide a useful diagnostic character that can be used in sorting material as they are only found in *P. caerulescens* and *P. verticillata* on the Malay Peninsula, and in *P. effusa* and *P. meiophylla* in Sarawak.

c. *Calcium-excreting glands*

These glands were found only in *P. acutifolia*, a species which is variable as to the upper leaf-surface. In some specimens it is almost smooth to the touch, in others it is very harsh. This harshness is due to large and small trichomes (prickle hairs; Fig. 1D) and to hardened incrustations of calcium carbonate excreted by sessile glands with a multicellular base. These glands are visible in herbarium material as white dots the size of a pin-head, Fig. 1D, E.

DISCUSSION

In *Paraboea* there are two quite different methods of dealing with an excess (assumed) of calcium salts—excretory glands and storage reservoirs. Most species, however, show neither of these methods, and it must be assumed that in these there is no excessive uptake.

The excretory glands in *Paraboea* are apparently of little importance, as the plant never becomes encrusted with calcium carbonate. This does, however, happen in some other calciphilous gesneriads. In *Monophyllaea* there is copious excretion from glands, but these are of a different type: they have been critically studied by C. Puff (1975) and are described as bicellular trichomhydathodes. Calcareous incrustations are also found in several species of *Cyrtandra* (e.g. *C. farinosa* C. B. Cl., *C. incrustata* B. L. Burtt), but it does not occur in all the species growing on limestone (not, for example, in *C. calciphila* B. L. Burtt, which may be found growing alongside *C. incrustata*). It is noteworthy that, on these plants that are heavily incrusted, the non-glandular hairs (found particularly on the leaf margin in *C. incrustata*) are not incrusted. In a few other species of the family (for example the doubtfully placed *Streptocarpus clarkeana* (Hemsley) Hilliard & Burtt) there is no general incrustation but the hairs themselves have a calcareous coating.

The accumulation of calcium salts in *Paraboea* and the consequential death of patches of cells, is reminiscent of the situation reported in *Monophyllaea fissilis* B. L. Burtt (Burtt 1978, p. 18 & fig. 7); here a zone of necrosis sets in along the underside of the broad midrib and this may proceed so far that the midrib splits down the mid-line and the plant grows, and flowers, with the single cotyledonary leaf split into two.

There is obviously considerable scope for study of the reaction of these gesneriads to the tropical limestone habitat. At present we can only note the morphological situation.

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