The Leaf Buds of *Archytaea alternifolia*.

BY

R. J. TABOR, B.Sc., F.L.S.

Demonstrator in Botany, Royal College of Science, London.

With Plate LXXIX.

ARCHYTAEA is a small genus of the Ternstroemiaceae comprising only four species, of which two are American and two Malayan. The material under investigation belongs to one of the Malayan species, and was collected in the neighbourhood of Singapore.

A. alternifolia, Szyszyl., is a glabrous evergreen shrub with alternate, oblanceolate, leathery, sessile leaves. The buds are not invested by scale leaves, stipules, or other protective structures. The young leaves are convoluted in the bud, the outer ones unrolling gradually from above downwards; the base of each leaf closely invests the stem for some little distance above its node.

The bud has in consequence the form of a trumpet or a funnel (Pl. LXXIX, Fig. 1), the upper portions of the younger leaves within being freely exposed. All danger of desiccation is, however, apparently obviated by the fact that the buds are borne in an upright position and are filled with a watery fluid.¹

As a consequence the development of the young leaves takes place under water, which must either be collected from the atmosphere in the form of rain or dew, or must be secreted within the bud.

In the well-known case of *Spathodea*, described by Treub (10), the water which fills the unopened calyx of the flower bud is secreted by glands borne on the inner surface of the sepals. Kraus (4) has described flower buds filled with water in *Parmentiera*, and Raciborski (6) has come to the conclusion that very probably a number of genera belonging to the Bignoniaceae and Melastomaceae have a similar protective device. So far as I am aware no leaf buds have been previously described in which the young leaves are protected by immersion in water.

The leaf. The mature leaf is oblanceolate in form, the largest leaf in the material measuring 13 cm. in length and $2\frac{1}{2}$ cm. at its maximum breadth. The surface is glabrous and the margins slightly revolute. A main vein

¹ For this information I am indebted to Prof. Groom, who collected the material.

runs from the base to the apex of the leaf. The secondary veins at some distance from the margin are united by a system of bundles, running parallel to the edge of the leaf. From these bundles short branches run directly towards the margin, to become joined up in their turn by another system of connecting bundles. Finally, short branches from the outer marginal series pass out towards the edge of the leaf and end blindly in the mesophyll. In the lower part of the leaf the margin is quite entire, but in the upper quarter—from the broadest part to the apex—it exhibits a number (40–44) of shallow notches. Towards each notch one or more ultimate branches of the marginal bundles are directed. No water stomata were found in or near the notches. On the other hand, the cells of the mesophyll, among which the vascular bundle ends, are closely compacted and filled with darkly stained contents. The opacity of the cells makes it practically impossible to ascertain the nature of their contents. The presence of tannin in other parts of the leaf favours the suggestion that the contents of these cells included tannin, which has interacted with traces of iron salts, derived from the cans in which the material was preserved. The significance of these notches in the mature leaf will be apparent when the structure of the young leaves is described.

The upper epidermis is devoid of stomata, but these are numerous on the lower side of the leaf. They are of the Rubiaceae type—that is, they show from two to five subsidiary cells arranged parallel to the guard cells (Pl. LXXIX, Fig. 2).

The mesophyll is bifacial, with one, sometimes two, layers of palisade tissue of ordinary type. No sclerotic cells, such as occur in *Thea*, *Camellia*, and other members of the order, are found in the mesophyll of *Archytaea*. The upper epidermis in the young leaf is one-layered, but early divides into two layers, the lower and larger cells forming a conspicuous hypoderm in the mature leaf. The inner walls of the hypoderm cells are strongly gelatinized, the swollen stratified wall encroaching on and occupying the greater part of the lumen of the cell (Pl. LXIX, Fig. 3). Rarely these hypoderm cells undergo a second division. The epidermal cells, on the other hand, invariably become further divided by vertical walls into a group of four to eight cells. The cells of the lower epidermis are not divided, but, with the exception of those connected with the stomata—the guard cells and subsidiary cells—they undergo gelatinization of the inner walls.

Cells with mucilaginous walls also occur scattered throughout the lower part of the mesophyll, and are abundant in the outer cortex of the stem.

The young leaves. The buds examined were composed of four or five leaves. The outermost leaf, which is generally three-quarters grown, has in all essentials the structure of the mature leaf; its basal part is tightly rolled around the inner leaves of the bud. The next younger leaf is clearly visible (Pl. LXXIX, Fig. 1), its apex often extending well above the tubular

base of the outer leaf, and showing very distinctly the teeth with which the margin is beset.

These teeth occupy a position corresponding to the notches on the mature leaf. They are hyaline, conical in form, slope sharply forwards, and have a slight inclination towards the upper surface of the leaf (Pl. LXXIX, Fig. 4). On the next younger leaf—and frequently also on the one following—the teeth are as well developed as on the one described, though, owing to the small size of the leaf, they are more closely set. On the youngest leaf the teeth, though conspicuous, are obviously immature.

One fact is evident: the teeth are ephemeral structures which come rapidly to maturity, attain their full development on the second and third leaves, and shrivel and disappear, as soon as the leaf which bears them becomes, in its turn, the outermost envelope of the bud. Their function, whatever it may be, must be performed whilst the leaves are still immersed in their bath of watery fluid. Portions of the leaf—cleared with eau de Javelle—show clearly that each tooth is served by one or two, sometimes three, of the smaller veins (Pl. LXXIX, Fig. 4); these run to within a short distance of the base of the tooth, and there fray out into a number of tracheides. These are, however, continuous with a strand of epithemoid tissue which runs up into the core of the tooth. No water-pores are borne on the teeth, nor are any stomata found in their immediate neighbourhood. If the teeth are concerned with the excretion of water, the latter must find some other exit than a stomatal pore.

The epidermis of the young leaf has a moderately thick outer wall, though this is feebly—if at all—cuticularized. In the second leaf of the bud it has already divided to form the hypoderm, though the upper cells have not undergone the further division by vertical walls. The epidermis which covers the teeth, however, consists of thin-walled cells with rounded contours, not covered by an incipient cuticle, and with numerous definite *intercellular spaces* between them, communicating with the interior of the tooth (Pl. LXXIX, Figs. 5 and 8). The cells forming the core of the tooth are thin walled; those towards the outside are isodiametric, those in the middle are elongated in the direction of the length of the tooth (Pl. LXXIX Fig. 6). The tissue throughout is fairly closely compacted, but narrow intercellular spaces occur at the points where three or more cells meet (Pl. LXXIX, Fig. 7). The central elongated cells of the tooth are continuous with a strand of similar cells, which communicate directly with the terminal tracheides of the vascular bundles. This strand of epithem is not marked off from the mesophyll by a definite sheath of cells.

The leaf teeth of *Archytaea* are in fact hydathodes, though of a somewhat unusual type. The epithem tissue which forms the core, or even the whole tissue of the tooth, has the same relation to the vascular bundle as has been shown to exist in *Tropaeolum*, *Primula*, *Geranium*, and

many Rosaceae, Saxifragaceae, &c., by Haberlandt (2), Reinke (7), von Minden (5), and others.

There is, however, one important point of distinction, and that is that, instead of the water escaping by a well-defined pore between two epidermal cells of special construction, or by a group of such pores, it finds its exit by numerous small intercellular spaces. These are found between all the epidermal cells of the upper two-thirds of the tooth (Pl. LXXIX, Figs. 5 and 8).

At the base of the tooth no intercellular spaces are found between the epidermal cells or the two or three subjacent layers. These cells, moreover, have thicker cell-walls (Pl. LXXIX, Fig. 5), and sometimes show indication of divisions (Pl. LXXIX, Fig. 7).

It is these cells, forming a shallow plinth for the tooth, which later acquire the dark-coloured contents already referred to. They are able to resist the fate which overtakes the thin-walled cells of the tooth, when freely exposed to desiccation by the later growth of the leaf.

Solereder (8, page 133) describes *Camellia* as having leaf teeth which 'figure as secretory organs . . . they contain the termination of a vascular bundle in connexion with an epithemoid tissue, and above the latter a secretory epidermis of palisade-like radially elongated cells'.

This probably refers to an observation of Reinke's (7), who described the structure of the leaf teeth in *Camellia japonica*, and considered the epidermis of the tooth as a glandular tissue, which excreted a mucilaginous secretion through the cuticle.

It was unfortunately impossible to confirm this observation; the only material of *Camellia* available was in a condition too advanced to show functional leaf teeth. In some shoots of *Thea viridis*, kindly supplied by Messrs. Veitch, the young leaves showed prominent teeth with a clear hyaline, viscid apical portion. This terminal portion of the tooth consisted of a central core of cells, covered externally by an epidermis of palisade-like cells; the whole structure strongly resembling the glandular 'villi' figured by Hanstein (3), Groom (1), and others, and obviously corresponding to the teeth described by Reinke (7) in *Camellia*. No excretion of water was observed when a shoot was placed under a pressure of 60 cm. of mercury for four hours, but no definite conclusion can be drawn from this isolated observation.

Similar teeth have been described and figured by Virchow (12) and Tschirch (11) for *Thea sinensis*. In *Thea* and *Camellia* the teeth—even if they should function as hydathodes, which does not seem probable—cannot subserve the same functions as those of *Archytaea*. The buds are small, and the shoot elongates rapidly, so that the young leaves are early separated, and the teeth are apparently functional on leaves which no longer invest the bud.

The liquid which fills the space within the bud of *Archytaea* has been

referred to as water. Unfortunately no information is available as to the nature and reactions of the fluid. In the material, which was preserved in spirit, the space between the young leaves was partly occupied by a soft greyish substance, quite structureless, insoluble in water, alcohol, and ether, staining fairly readily with aniline dyes. There is every probability that this substance is coagulated mucilage, and that the fluid carried by the bud was a weak mucilaginous solution.

At any rate ample means exist for the secretion of the mucilage, in the shape of numerous colleters, which are found in the axils of the leaves, borne on the leaf bases (Pl. LXXIX, Figs. 9 and 10). These glands are club-shaped multicellular bodies, borne on narrow stalks, and consisting for the most part of small isodiametric cells with thick walls and abundant contents. There is no indication of columnar epidermal cells such as were described by Hanstein (3) in *Coffea* and *Viola*, and by Groom (1) in *Coprosma*, *Hoffmannia*, and *Gardenia*.

In the club-shaped part of the glands large irregular cavities occur close to the surface, which are occupied by a deeply staining contracted mass—possibly mucilage (Pl. LXXIX, Fig. 11). In some instances these cavities may be individual cells of large size, but in most cases they seem to have arisen by the fusion of a number of cells, possibly by the mucilaginous degeneration of their walls. The glands are always closely surrounded by the greyish coagulated substance above described, and it seems highly probable that they are largely concerned with its production.

The facts described above all point to the conclusion that the various structures are admirably adapted to serve for the protection of the young leaves from drought and excessive insolation. The structure of the teeth and their relation to the vascular system indicate very clearly their probable function as hydathodes, and water is certainly present in the living buds. The general construction of the bud and its upright position enable the water to be readily retained. The narrow spaces between the leaves and the mucilage secreted by the colleters obviate the danger of desiccation to which the young leaves and axillary buds would be exposed, if the bud became emptied of water, or for any reason the hydathodes failed to maintain a supply. The thick cuticle and numerous mucilaginous cells protect the leaves from excessive loss of water, after their emergence from their watery bath.

It is obvious that these conclusions can only be fully sustained by actual demonstration with living material, which is unfortunately not available to me.

SUMMARY.

I. The leaf buds of *Archytaea alternifolia*, Szyszyl., have a trumpet-shaped structure, are upright and filled with water.

II. The young leaves possess a number of marginal teeth which are probably hydathodes.

III. The hydathodes are connected with vascular bundles by epithemoid tissue, and provision is made for the escape of water by intercellular spaces between the epidermal cells of the teeth.

IV. Colleters are borne in the axils of the leaves on the leaf bases. They are probably concerned in the secretion of mucilage.

V. A mucilaginous hypoderm is present towards the upper side of the leaf, and mucilaginous cells in the mesophyll and in the epidermis of the lower side.

In conclusion I desire to record my appreciation of Prof. Groom's kindness in handing me the material for investigation, and to express to him, and to Prof. Farmer, my thanks for much helpful advice and criticism.

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EXPLANATION OF PLATE LXXIX.

Illustrating Mr. Tabor's paper on *Archytaea alternifolia*.

Fig. 1. Entire leaf bud; leaf teeth are seen on the second leaf at *t*. Nat. size.

Fig. 2. Lower epidermis in surface view. Stomata with 3-5 subsidiary cells. *g* = guard cells, *s* = subsidiary cells. $\times 200$.

Fig. 3. Transverse section of mature leaf. *m.h.* = mucilaginous hypoderm cells with swollen stratified walls, *m.e.* = mucilaginous epidermal cells, *m.m.* = mucilage cell, *g* = guard cell, *s* = subsidiary cell. $\times 175$.

Fig. 4. Portion of young leaf showing three teeth and related vascular strands. Cleared with eau de Javelle. $\times 28$.

Fig. 5. One tooth from the same preparation as that from which the preceding figure was drawn. *i.* = intercellular space, *p* = thick-walled cells forming a plinth for the tooth. $\times 240$.

Fig. 6. Horizontal section of margin of leaf, with tooth in nearly median section. The terminal tracheides of two vascular bundles are seen associated with narrow elongated cells of epithem tissue. *t* = tracheide, *ep.* = epithem, *i* = intercellular space. $\times 265$.

Fig. 7. Similar section in which the tooth was cut almost transversely near its base. In this and in the preceding section the tracheides and surrounding cells were torn by the razor. *p* = thick-walled cells at base of tooth, other lettering as in Fig. 6. $\times 300$.

Fig. 8. Tangential section of the epidermis of a tooth with intercellular spaces. *e* = epidermal cell, *i* = intercellular space. $\times 600$.

Fig. 9. Transverse section of bud immediately above the insertion of the outermost leaf. *st* = stem, *l.t.* = leaf traces, *l.b.* = leaf base, *b* = axillary bud, *c* = colleters. $\times 10$.

Fig. 10. Longitudinal section of base of bud showing portions of five leaves. *t* = row of immature teeth on fourth leaf, other lettering as in Fig. 9. $\times 10$.

Fig. 11. Transverse section of colleter. (Cell contents omitted in most cells.) *m.c.* = mucilage cavity. $\times 265$.

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