IX. *On Bud-protection in Dicotyledons.* *By* Percy Groom, *B.A., Frank Smart Student, Gonville and Caius College, Cambridge.* (*Communicated by* D. H. Scott, *M.A., Ph.D., F.L.S.*)

(Plates LIX. & LX.)

Read 18th February, 1892.

THE welfare, or even the very existence, of a plant is dependent on the preservation of the young growing parts of the shoot. Yet several circumstances conspire to render the life of the bud precarious. A growing bud is more or less exposed in position, and necessarily delicate in structure: hence it is peculiarly liable to physical injury from excess of light, extremes of temperature, and loss of indispensable water. For the same reasons buds are rendered an easier prey to hostile organisms, whilst the nutritious nature of their contents even invites attack. Not only do these young parts of a plant require protection, it is also imperative that the protective mechanism should be of such a sort as to permit of simultaneous or, at any rate, subsequent growth: hence many of the protective measures adopted by mature organs are out of the question.

The most striking illustrations of bud-protection are to be seen when the environment is peculiar. When plants are exposed alternately to a favourable and an unfavourable season, there is frequently a wide difference between the actively growing buds and the "resting buds." The latter are often covered by an envelope of scale-leaves, by persistent petioles, peculiar prophylla, modified stipules (1), &c. Goebel has described the careful manner in which the growing-point and young leaves of succulent plants are buried in the older tissue (13). These cases may be contrasted with those of plants growing under favourable conditions. Submerged plants and many plants growing in a perennially moist and warm region (5) have buds of loosely-packed leaves, so that the growing-point is all but exposed. But the means of bud-protection adopted by a plant depend as much on the character of the plant as on the environment. *Marchantia*, though growing in moist and shady places, possesses an elaborate arrangement of amphigastria curled over the growing-point and a thick coating of mucilage over the young tissue: the reason of this is that *Marchantia* is very sensitive to loss of moisture.

The need for protection on the part of the growing-point and younger leaves explains at once the fact that older leaves cover the younger leaves at the end of the shoot—in fact, that a "bud" is formed in order to permit the younger leaves developing as far as possible under the shelter of the older leaves; they are closely packed and often folded so as to take up the least room possible inside the bud (3). Frequently, too, when the outside leaves of a bud expand, the blades of the younger leaves are not immediately exposed in consequence: the latter may be covered by their own stipules (2), or they may be protected by outgrowths from the base of older leaves (e. g. *Clusia*, *Tabernæmontana*, *Fagræa*) and the outgrowths may take the definite form of stipules.

But the most critical time for the young leaves is when they are first exposed, their epidermal walls being thin and feebly cuticularized, and their chlorophyll dilute and easily decomposed. To avoid excess of light these youngest exposed leaves are frequently directed vertically. Often, too, this arrangement is associated with a diminution of the transpiring surface caused by a folding of the lamina or the close contact of two leaves. In many plants with opposite leaves, the two outermost leaves of a bud are directed vertically with their inner faces in close contact (*e. g.* many *Rubiaceæ*, *Clusia* sp., *Bucklandia populnea*, R. Br., *Veronica imperialis*). In *Durio zibethinus* the pendent arrangement of the conduplicate young leaves gives a characteristic appearance to the tree. In some plants with stalked leaves the change of direction of the lamina leads to the older leaves at the end of a shoot forming an umbrella-like screen over the youngest exposed leaves (e. g. *Gossypium*, *Dombeya Mastersii*, species of *Abutilon*, *Hura crepitans*, *Begonia* sp.). Frequently the young leaves are coated with glistening hairs. That these hairs perform their functions whilst the leaves are young, is proved by the fact that the older leaves may be apparently quite glabrous. One of the functions of these hairs is to protect the young leaves, for they diminish transpiration and radiation and reflect light. The young leaves of many plants are rendered conspicuous by their colour, being generally red, reddish brown, or brown. These colorations are especially common in plants exposed to strong sunlight, *i. e.* alpine plants and tropical plants (e. g. sp. of *Ixora*, *Calophyllum*, *Treculia africana*, Decne., *Garcinia Cambogia* var. *papilla*, *Nephelium Litchi*, *Clusia* sp., *Wormia Burbidgei*). Various experiments make it probable that these colouring-matters protect the young leaves from excess of light (16). At the same time they may be merely the unavoidable results of metabolism, or have some other significance; for we find that the colour is often due to the presence of tannin or tannin-like bodies. Also similar red colouring-matters are found on parts not exposed to light, *e. g.* in villous colleters, &c. (*Cosmibuena*, *Hoffmannia*). These villi are not manufacturing the colouring-matters for the use of the young leaves; for, as far as I could see, the colouring-matters were never transported from the colleters: in addition the leaves of *Cosmibuena* are green when they emerge.

Many buds have a great protective auxiliary in the secretion which covers and fills them. This secretion consists of gummy mucilage or resin, or both together (7 & 17); it is secreted by the general epidermis, by colleters, or by "leaf-teeth." These "blastocolla"-secreting glands are characterized by their early development and their short-lived activity. The colleters, further, occur only on that essentially protective organ, the leaf-base, or on its outgrowths (stipules). After functioning for a short time the colleters, and often the stipules which bear them, dry up or drop off. These facts sufficiently indicate that these external secretory organs are definitely formed for the sake of the bud. It is, unfortunately, impossible to excise these structures early, and thus give confirmatory evidence of their importance to the bud; I did, however, remove the secretory hairs of the youngest exposed leaves of a species of *Ochna*. The hairs occur at the margin of the leaf and only secrete in the bud, and not later in life.

The result of the excision was *nil*. The experiment merely showed that the hairs are not essential to the older leaves. The following points are worthy of note with reference to the secretion :—(i.) the secretion, being adhesive, glues all the young parts together; (ii.) forming a thin coat over the young exposed leaves it diminishes transpiration by reflecting some of the sun's rays; (iii.) mucilage, being hygroscopic, diminishes the loss of water due to transpiration. In addition it might be suggested that mucilage prevents the bud being drained of moisture by excessive transpiration of the older leaves. Wiesner states that in the well-known sympodial shoots of dicotyledonous trees the death of the growing-points is occasioned by the older leaves draining the apex (14). Pfeffer's measurements of the osmotic power of gum arabic give an idea of the energy with which the secretion sucks in water. Attention does not appear to have been called to the fact that the employment of a hygroscopic substance like mucilage (and tannin) is an admirable means of controlling the water-supply of an organ for two reasons: first, the osmotic power of a solution increases with a rise of temperature; secondly, the osmotic power increases with the concentration of the solution. The result is that when a bud is in greatest danger of losing all its water—*i. e.* when the temperature is high and a considerable amount of water has been evaporated from the mucilage—the remaining water is held most firmly or a first supply of water is absorbed most fiercely.

It is probable that this external secretory apparatus is also of use in removing excreta from the young cells. The following reasons may be given in support of this view:—(i.) the precocious development of internal excretory organs suggests the importance of a speedy removal of products which would retard the activity of the young cells; (ii.) many plants which possess colleters &c. also have internal structures which manufacture or store up the same substances, resin and mucilage, e. g. *Rubiaceæ*, *Apocynaceæ*, *Asclepiadeæ*, *Guttiferæ*, *Dilleniaceæ*; (iii.) we are unable to attach any significance to the secretion of mucilage by the leaf-tips of certain submerged water-plants, e. g. *Myriophyllum*, *Ceratophyllum* (8); (iv.) it is suggestive, too, that laticiferous tubes should penetrate the colleters, as I have shown to be the case in the *Apocynaceæ*. This view of the double nature of the service performed by colleters affords a means of conceiving of their primary mode of origin in several distinct unconnected families. Originally, then, the young epidermis of the plants became the recipient of excreta. The plant soon found the advantage of completely ejecting the excreta, so that deeper tissues need not share in their storage or removal: so the excretion oozed through the epidermal walls first over the whole surface of the leaf, and subsequently in localized places. The plant discovered the benefit of the secretion as a protective agent, and thence the external secretory apparatus was elaborated till it reached its present state of perfection. The various stages above mentioned actually occur in different plants. The whole process may be compared to that by which substances which were originally coloured katabolites (tannin, &c.) subsequently became also protective in function.

Many plants possess other glands which may be protective in function—water-stomata. Gardiner (12) and Moll regard these as species of safety-valves to permit the escape of excess of water, and thus prevent rupture of the delicate tissue of the young leaves.

Special Work *.

The following observations refer chiefly to colleters. It may therefore be briefly stated that it is to Hanstein alone that we are indebted for our knowledge of colleters of Dicotyledons. He considers that colleters were always trichomes, whilst he supposed that the mucilage part of their secretion first appeared as a colligenous layer in the cell-wall.

My own observations refer to plants belonging to *Rubiaceæ*, *Apocynaceæ*, *Asclepiadeæ*, *Guttiferæ*, *Dilleniaceæ*.

RUBIACEÆ.

Cosmibuena obtusifolia is a native of tropical S. America. The opposite stalked leaves have between them two large leaf-like stipules which possess no midrib. On closer examination it is seen that the bases of the stipules are continuous with a short outgrowth from the inner face of the leaf-base. So the stipules may be described as sheathing, but the axillary portions of the stipules are very small. This sheath bears a number of villi, which thus form a complete zone round the stem.

The Bud.—The apex of the shoot may be seen to be surmounted by two (rarely three) stipules glued tightly together by the "blastocolla." On separating these two stipules the next two leaves are seen directed vertically upwards, just within, with their inner faces closely adhering (Pl. LIX. fig. 1); these leaves by their growth force the apices of the stipules apart and so emerge. Thus the stipules do not protect the leaves to which they belong; they protect the younger leaves. The stipules subsequently drop off, and the scars are covered with cork. The actual growing-point is at the base of a relatively deep pit, the wall of which is formed by the concentric sheaths belonging to several successive pairs of leaves and stipules. The growing-point is of course covered with secretion.

Development of the Stipules.—In the earliest stage I succeeded in observing that there was an annular outgrowth of tissue common to leaf and stipule: this was thicker where the young leaves had already made themselves visible. The stipule was merely represented by a tiny triangular protuberance.

Structure and Development of the Villi.—Each villus is, roughly, pear-shaped, and consists of a single layer of palisade-like secreting-cells, which cover a mass of thin-walled "conducting parenchyma" cells. Each villus arises as an elevation of a few cells. The young epidermal cells at this spot are, in general, more elongated at right angles to the surface, and possess larger and more deeply-staining nuclei than the adjoining cells (fig. 2). The cells below them are smaller and stain more deeply than the rest of the parenchyma. The epidermis of this slight protuberance divides radially only: these divisions and those of the subjacent cells lead to the formation of a considerable outgrowth. At this stage the young external secreting-cells possess large nuclei and a deeply-staining granular protoplasm. The size of the nuclei and the depth

* Unfortunately, owing to my leaving England, I was unable to complete the work as I should have wished. It was not till too late that I found how easy it was to be deceived by the use of Hanstein's reagent in testing for resin; so that I cannot positively state that resin is present in all the secretions, though gummy mucilage is.

of staining of the protoplasm decrease as the cells approach the non-secretory epidermal cells. The subsequent changes consist in the radial division and elongation of the external (epidermal) cells to form a secretory layer, and the division and elongation of the internal cells to form the conducting parenchyma (fig. 4). As the secretory cells grow older their staining qualities diminish, and the nucleus finally becomes a feebly-staining bubble-like body. Thus it is seen that the villus is an emergence. The villi are red in colour and secrete mucilage and resin.

Coprosma Baueriana (and *C. Baueriana* var. *variegata*) is a native of New Zealand. Its leaves are opposite, stalked; their bases are continuous with small triangular interpetiolar stipules. But the stipules are really sheathing in that they are continued as a small cushion on the inner face of the leaf-base. The villi form a complete zone round the stem, being perched on the top of these peculiar sheathing-stipules. Each triangular stipule possesses about five villi, the median one of which is the largest and is situated at the apex of the triangle (fig. 6).

The growing-point is at the bottom of a small pit formed just as in *Cosmibuena*.

Development of the Stipules.—The development of the leaves and their stipules is so nearly simultaneous that I only succeeded in discovering leaves without well-defined stipules in a few lateral buds. The young lateral bud is flattened in contour; the first leaves arise as distinct swellings in the transverse plane of the bud. Very shortly after the tissue between these two leaves grows up, so that at this stage there is an annular outgrowth with two considerable prominences, which are the two leaves. But the interpetiolar part soon grows more vigorously at its median point, so as to form the large median terminal villus (fig. 6). The other villi arise successively lower down, those lying in an axillary position forming later.

Structure and Development of the Villi.—Each villus is a pear-shaped, shortly-stalked body, possessing the typical palisade-like secreting layer and a central mass of conducting parenchyma-cells. Amongst the latter are many large cells containing raphides. The villus develops like that of *Cosmibuena* (figs. 7 and 8). The modified nuclei of the old cells are especially noticeable.

Hoffmannia macrophylla (syn. *Higginsia macrophylla*) is a native of Guatemala. Between each pair of large opposite leaves lie two small triangular hairy stipules. The whole of the upper (inner) face of each stipule is raised into irregular glandular ridges and lobes. Each glandular elevation consists of a superficial layer of palisade-like secretory cells covering a tissue of somewhat elongated parenchyma-cells (figs. 9 and 10). Many of these parenchyma-cells are enlarged and contain raphides. As in all *Rubiaceæ*, the stipules and young parts generally are rich in tannin, which is especially collected in the epidermis hairs and subepidermis of the stipule. Resin and gummy mucilage form the secretion. The glandular outgrowths and some (all?) of the stipular hairs secrete. In the latter one easily sees pits in the transverse walls of the cells (fig. 11) and protoplasmic intercommunication. The cuticle of these hairs is raised, but outside the unbroken cuticle of many of the hairs one sees the small masses of the secretion, which, however, may possibly have been secreted by other cells.

The growing-point of the stem is surrounded by several concentric sheaths belonging to two or three pairs of leaves and their stipules. The leaves and stipules arise (almost) at the same time, so that I failed to find leaves without stipules. At first there is only a very insignificant sheath common to stipule and leaf, later it increases in size; but when the leaves are mature, one only sees slight indications of the fact that leaves and stipules originally formed a shallow sheath round the stem.

The first trace of the glandular surface of the stipule is a tongue-like emergence which hangs down from the apex of the stipule on its inner side; this gland, in fact, looks just like the incurved apex of the stipule (Pl. LX. figs. 12 and 13). Gradually the epidermis of the inner face of the stipule assumes the form of a secreting epithelium, the change travelling in a basipetal direction. The modifying epidermis is raised up here and there into lobes and ridges, which at first hang down over the growing-point and younger leaves.

Gardenia florida, Linn., has its leaves in opposite pairs, or, more rarely, in whorls of three. The stipule forms a continuous sheath surrounding the stem, and in the young bud it completely invests the younger leaves till forced open by their growth (Pl. LIX. fig. 14). Numerous villous colleters line the inner face of the leaf- and stipule-base. These colleters secrete the well-known *Gardenia*-resin, which is really a mixture of gummy mucilage and resin: this secretion has a disagreeable odour, and is used in India to protect objects from insects. These colleters also occur on the side of the calyx-base.

Mode of Secretion.—Both the mucilage and the resin arise in the protoplasm of the secreting-cells. Very young secreting-cells are square in outline; they possess a granular protoplasm and a good-sized nucleus. They soon elongate in a direction at right angles to the surface of the colleter. At this stage, sections cut in two per cent. solution of potassic nitrate showed the protoplasm slightly withdrawn from the walls of these cells. Adding iodine solution or potassic bichromate, small bubbles of mucilage (or mucigen) could be seen protruding from the surface of the protoplasm beneath the external and lateral cell-walls (Pl. LX. figs. 16, 17, 18). In the more central parts of the cytoplasm granules or globules of smaller size could be seen. Owing to the small size of the latter, I am unable to state whether they are proteid or mucilaginous in nature; but the appearances naturally suggest that they change into the mucilage drops found towards the outside of the protoplasm. Thus the mucilage arises in the form of droplets in the cytoplasm; the droplets are expelled through the lateral and external cellulose walls, where they fuse to form rod-like or plate-like masses, which in turn unite to form a subcuticular mass. The secretion ultimately invests the cells on all sides, except the inner side, and raises the cuticle to a considerable height (fig. 18). The protruding drops of mucilage within the cell, and the smaller central granules or globules, stain slightly differently from the mucilage which lies under the cuticle, even after the removal of the resin. This suggests that some change ensues as the drops pass through the cellulose wall or after their expulsion from the cell. Thus the mode of origin of the mucilage appears to resemble that described by Gardiner and Ito (15), as occurring in the hairs of the paleæ of *Blechnum* and *Osmunda*. Concerning the origin of the resin, I can only give the bare fact, as Hanstein originally gave it in other types, that resin occurs inside the secretory cells.

Food is conducted to the secretory cells partially in the form of carbohydrates, for transitory starch occurs in the conducting parenchyma of the colleter.

Gardenia laurifolia (?) resembles the preceding, except that the leaves are in whorls of threes, and when young are densely coated with hairs (fig. 14).

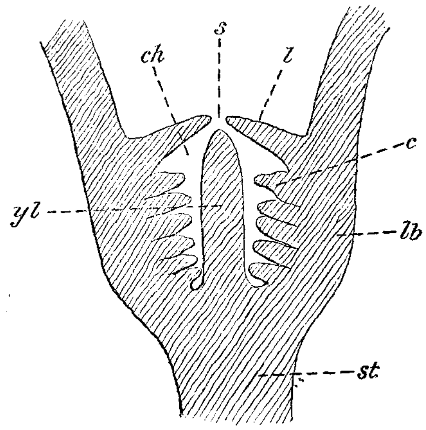
In *Pavetta indica* the long strap-like colleters and the exceedingly elongated, often spirally thickened, woolly hairs form the basis of a complete and striking protective mechanism.

In the evil-smelling *Pæderia fœtida* the colleters are unusually large, and their relatively late development suggests a more lasting function than is usual to colleters.

In *Sarcocephalus* sp. the villi are numerous; the simple hairs are represented by a papillose epidermis on the outer (lower) faces of the young leaves.

APOCYNACEÆ.

Tabernæmontana dichotoma.—Treub describes the bud as protected by a coating of a wax-like substance secreted by colleters; but it merits a more close examination. The leaves are decussate, stalked, but connate. Many growing buds present the following appearance:—The shoot ends in two leaves, the fused "bases" of which cover the younger leaves and apex, and only leave a narrow slit between them. This terminal slit (fig. 19) and the parts adjoining are covered by secretion. Forcing these two terminal leaves apart, one sees that not only are the "bases" of the leaves fused, but that there are minute ledge-like outgrowths growing out from the inner faces of the two leaf-"bases." These ledge-like outgrowths, together with the fused leaf-bases, enclose a bell-shaped cavity, in which lie the younger leaves (fig. 22). The only opening to this cavity is the above-mentioned slit which runs in a plane at right angles to the two leaves in question. The walls of the cavity, or chamber, are lined by villous colleters which secrete copiously. From the floor of the chamber rise two more leaves arranged in a plane at right angles to the preceding; they are merely a repetition in miniature of the older pair, except that their interbasal chamber encloses the growing point and tiny leaf-rudiments. When growth takes place the largest enclosed leaves push through the slit, which, it will be noticed, has its plane coinciding with that of the emerging leaves (figs. 20 & 21). The lips of the slit are thus forced asunder, or naturally gape asunder by their own growth, and the young leaves emerge, doubtless, coated with the secretion. Lower down the stem the fused "bases" &c. of the mature leaves form a tight-fitting collar round the stem, and serve to protect the axillary buds.



Diagrammatic longitudinal section through bud of *Tabernæmontana*.—*ch*, chamber; *s*, slit; *l*, ledge (stipule); *c*, colleters; *lb*, base of leaf; *st*, stem; *yl*, younger leaf enclosed in chamber.

Structure of the Villi.—The villi call for no special description; they are perfectly normal in structure, but spherocrystals occur in place of raphides. Delicate vascular bundles run close up to the villi, so that the "nerve-parenchyma" and conducting parenchyma of the colleters are directly continuous. Many laticiferous tubes traverse the leaf-parenchyma and send branches into the colleters (fig. 23).

Judging from the alcohol material at my disposal, the secretion seems to be of a resin-mucilage nature rather than a "wax-like substance." The papillose epidermis on the upper face of the "ledges" aids in the process of secretion.

Alstonia scholarius, R. Br., in its mode of bud-protection reminds one of *Tabernæmontana*. Examining with the naked eye, a circlet of leaves is seen at the apex of the stem. From the base of each leaf a small tooth-like axillary process projects and lies above the younger leaves; this tooth-like process is obviously homologous with the ledge-like process of *Tabernæmontana*, and both may be described as axillary stipules.

Allamanda sp.—The leaves are stalked and exstipulate, and according to the species are arranged in whorls of two, three, or four leaves. On the inner face of the "base" of each leaf of the calyx-lobes is a row of about five villi: these villi cover the bud with a gummy mucilage and resin secretion.

Structure of the Villi.—The villi are normal in structure, but it may be mentioned that laticiferous tubes penetrate them and frequently ascend to the secreting cells even (fig. 24). The secreting-cells resemble some described by Hanstein, so they may be described more in detail. In a mature secreting-cell the general protoplasm is very granular and the nucleus lies in the middle of the cell. Typically a large tannin-globule rests in the inner (basal) part of the cell, or sometimes there are several similar globules. On removing the tannin it is seen that it merely soaked a viscous substance: the latter stains pink with Hanstein's reagent, and is what Hanstein called "amyloid substance" (probably a mucilaginous substance). Outside the cells the secretion first appears in the intercellular spaces between the upper ends of the secreting-cells, rather than outside their outer walls. As the secretion increases in quantity it penetrates deeper between the cells and forms a sort of honeycomb structure. Some of the secretion is visible outside the cuticle before the rupture of the latter; so some of the secretion must pass through the cuticle. It was this sort of appearance which led Hanstein to suppose that two cuticles might be formed. Often in older stages it is visible, so one cannot resist the conclusion that the secretion may dissolve the cuticle.

Landolphia sp.—We might anticipate that the long "feelers" of this climbing plant, with their tiny leaves and elongated internodes, would display a complete arrangement for protecting the young leaves; and the colleters do appear to secrete for a longer period than on plants not possessing those long sunlight-bathed "feelers."

Nerium oleander has colleters and woolly hairs.

ASCLEPIADEÆ.

Asclepias curassavica.—Hanstein figured and described the colleters which occur on the leaf-base. It may be added that villi also occur on the inner face of the calyx-base.

Ceropegia stapeliæformis.—At the base of each small, triangular, succulent leaf is a row of five or six conspicuous yellow colleters (fig. 25). The colleters are more or less pear-shaped; or they may be lobed, as if two colleters were fused. In structure the colleter is a typical villus, but a vascular bundle runs for some distance in the axis of the colleter. Raphides do not occur in the villus. Villi are also present on the calyx.

GUTTIFERÆ.

Clusia rosea has opposite stalked leaves. On the dorsal (upper) face of the leaf-stalk base is a peculiar whitish "cushion" of tissue, which is hollowed out somewhat in the form of a boat. In addition there is a transverse row of colleters situated nearer the point of attachment of the leaf.

Bud.—Many shoots terminate in two leaves, the cushions of which are closely applied so as to completely enclose the youngest leaves and growing-point (*cp.* figs. 26 & 28). As growth continues the "cushions" gradually separate, and the next pair of leaves emerges through the gaping slit thus formed (fig. 27). The lateral buds are in addition protected by a peculiar "prophylla" (*i. e.* first leaves of the branch), which are small and sessile (fig. 29).

Structure of Colleters.—The colleters are abnormal in structure. The typical palisade-layer of secreting-cells has become split into several layers of cells arranged at right angles to the surface. The conducting parenchyma is present as usual (figs. 30 & 31). In the other colleters the secretion may be seen arising in a lysigenous manner in the secreting layers, and forming irregular star-like masses.

Structure of the Cushion.—The epidermis of the "cushion" is composed of narrow cells with their long axes directed at right angles to the surface. There is a thick cuticle. Between this layer and the ordinary parenchyma of the leaf-stalk lie several layers of elongated, thick-walled, parenchyma-cells. The walls of these cells contain a considerable amount of water and are copiously pitted. Protoplasmic strands pass into the pits and to (through?) the membranes. The cells contain resin, tannin, sphero-crystals, and gummy mucilage. The internal secretory passages pass right in amongst these cells, as if to conduct their products thither.

Loganiaceæ.—I noticed two *Fagræas* in the houses at Kew in which the bud-protection is precisely similar to that in *Clusia* as far as external features go. The young buds, too, seemed to be coated with secretion, so probably colleters are present. Unfortunately I was unable to obtain a bud for examination. (I have in Hong Kong observed colleters in some other *Loganiaceæ.*)

DILLENIACEÆ.

Wormia Burbidgei is a native of Borneo, with alternate leaves. Examining the ends of the shoots at first no buds are visible; but a glance at the youngest leaf visible reveals the fact that the youngest leaves are stowed away in it. What look like the right and left halves of the basal part of the lamina are folded over towards the dorsal (upper) face of the leaf, and are fused to form a cylindrical chamber (fig. 32), which has a narrow slit-like aperture at its top. The chamber is found to contain a younger leaf, whilst the unoccupied space is filled with secretion. This enclosed leaf contains in its sheathing base younger leaves, and finally the growing-point. The young leaf arises in the form of an annular outgrowth surrounding the growing-point. This ring is more developed on the side which produces the lamina. The ring expands later into the "sheath." The oldest enclosed leaf pushes through the slit at the top of the sheath surrounding it, and by its growth ruptures the latter down to its very base. The emerging leaf is coated with secretion and is brown in tint; the brown tint is due largely (solely ?) to the presence of tannin.

The secretion is poured out by the epidermis of the young leaf and by a few capitate hairs. It is worthy of note that there is an internal secretory apparatus producing resin and mucilage. The internal secreting-cells arise very early and are seen in very young leaves and high up the growing-point.

Conclusions concerning Colleters.

1. Villous colleters are frequently emergences; they are emergences in their mode of origin. Frequently, too, their emergence nature is made clear by reason of the fact that laticiferous tubes or vascular bundles penetrate them.
2. They are formed for the sake of the bud, being protective, also probably excretory, in function.
3. *Mode of secretion* in *Gardenia florida*.
   (i.) Secretion commences very early indeed in each cell.
   (ii.) The mucilage (mucigen ?) arises in the form of droplets in the cell-protoplasm.
   (iii.) There are traces of a difference between the secretion inside the cell and that outside the cellulose wall.
   (iv.) Resin occurs inside the secreting-cells.
4. The secretion in part passes through the cuticle in some plants at any rate (*Allamanda*).
5. There never was a trace of the formation of two cuticles in the plants observed.
6. *Contents of the Villi.*—Food is conveyed to the secretory cells in a carbohydrate form, for transitory starch occurs in the conducting parenchyma of the colleter. In addition raphides or sphero-crystals, colouring-matters, and tannin are found in villi.
7. It is significant that laticiferous tubes, containing substances identical with those normally found and even secreted by the villi, pass into the colleters.

I take the opportunity of thanking Mr. Walter Gardiner, F.R.S., for his constant help throughout the progress of the work. Indeed, were it not that he would be rendered responsible for all the statements and views expressed in this paper, his name would be fitly on the titlepage. I desire also to express my thanks to Mr. M. C. Potter for material of *Gardenia laurifolia* and *Tabernæmontana dichotoma* and for a figure of the former.

Literature on Bud-protection.

1. FEIST.—"Ueber die Schutzeinrichtungen der Laubknospen dicotyler Laubbäume." Nova Acta Acad. Cæs. Leop.-Car. Bd. li. p. 303 (1887). This paper gives the previous literature.
2. HILBURG.—F. Hildebrand, 'C. Hilburg's Dissertation über den Bau und die Funktion der Nebenblättern.' (Abstract in 'Flora,' 1878, p. 161.)
3. GREW.—'Anatomy of Plants.' Folio, London, 1682.
4. KERNER VON MARILAUN.—'Pflanzenleben.' Bd. i. (1888.)
5. TREUB.—"Iets over knopbedekkung in de Tropen." Handelingen van het eerste Nederl. Natuur- en Genees-kundig Congres, gehouden te Amsterdam, 1887. (Abstract in 'Botanisches Centralblatt,' 1888, Bd. xxxv. p. 328.)
6. REINKE.—"Beiträge zur Anatomie der an den Laubblättern, besonders an den Zähnen derselben, vorkommenden Secretionsorgane." Pringsheim's Jahrbuch, Bd. x. pp. 117–178 (1876).
7. HANSTEIN.—"Ueber die Organe der Harz- und Schleim-Absonderung in den Laubknospen." Bot. Zeit. 1868, pp. 697, 721, 745, 769.
8. BORODIN & VOCHTING.—Quoted in Reinke's paper (l. c.).
9. MIKOSCH.—"Beiträge zur Anatomie und Morphologie der Knospendecken dicotyler Holzgewächse." Sitzungsber. der kais. Akad. der Wiss. zu Wien, Bd. lxxiv. Abth. 1, Nov. Heft (1877).
10. CADURA.—'Physiologische Anat. der Knospendecken dicot. Laubbäume.' (Breslau, 1886.)
11. SORAUER.—'Pflanzenkrankheiten.' Bd. i. pp. 357–362 (1886).
12. GARDINER.—"On the Physiological Significance of Water-glands and Nectaries." Proceed. Camb. Philos. Soc. vol. v. pp. 35–50 (1883).
13. GOEBEL.—'Pflanzenbiologische Schilderungen.' Bd. i. Marburg, 1889.
14. WIESNER.—'Biologie der Pflanzen.' Bd. iii. Wien, 1889.
15. GARDINER & ITO.—"On the Structure of the Mucilage-secreting Cells of *Blechnum occidentale* (L.) and *Osmunda regalis* (L.)." Annals of Botany, 1887.
16. HABERLANDT.—'Physiol. Pflanzen Anatomie,' pp. 75 & 76. (1884.)
17. GOEBELER.—"Die Schutzvorrichtungen am Stammscheitel der Farne." 'Flora,' 1886.

DESCRIPTION OF THE PLATES.

PLATE LIX.

l, l' = leaf; s, s', s'' = stipules; v = villus; se = secretion; c = cuticle.

Fig. 1. View of the bud of *Cosmibuena obtusifolia,* with one stipule removed, to show the enclosed pair of leaves and the secretion rendered opaque by alcohol. g = colleters.

Figs. 2, 4. Development of villus of ditto. (Instead of fig. 3, which was lost in transmission, see youngest colleter in fig. 7.)

Fig. 5. Bud of *Coprosma Baueriana.*

Fig. 6. Longitudinal section of bud of ditto, taken on one side of the growing-point. Shows especially the terminal villus of s and s', s'' developed earlier than the lateral villi. $y.v.$ = young villi.

Fig. 7. Longitudinal section of young villi and growing-point of a lateral bud of ditto. a = apex of shoot.

Fig. 8. Old secretory cells of villus of *Coprosma Baueriana*, var. *variegata*, showing the modified nuclei.
Fig. 9. Transverse section of a stipule of *Hoffmannia macrophylla*.
Fig. 10. Surface section of ditto.
Fig. 11. Two terminal cells of a hair of stipule of ditto.
Fig. 14. Bud of *Gardenia laurifolia* (?).

Plate LX.

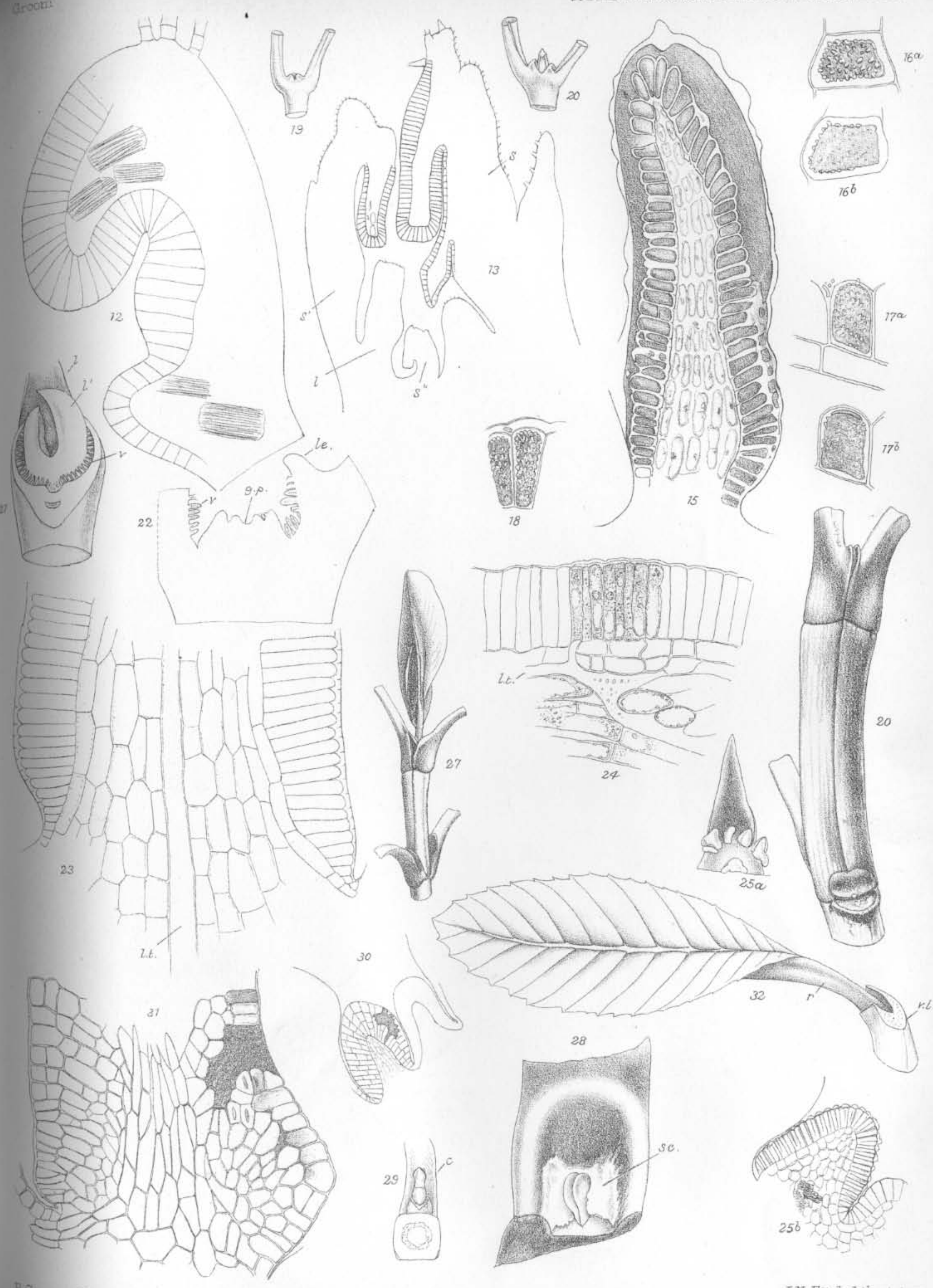
Fig. 12. Longitudinal section of a young stipule of *Hoffmannia macrophylla*.
Fig. 13. Longitudinal section of a bud with older stipules of ditto.
Fig. 15. Mature colleter of *Gardenia florida*.
Fig. 16. Young secreting-cell of colleter of ditto. *a* is focussed to show the minute protuberances of mucilage studding the surface of the protoplasm ; *b* is focussed into the centre of the cell.
Figs. 17 & 18. Slightly older secreting-cells of ditto.
Fig. 19. Terminal bud of *Tabernæmontana dichotoma*.
Fig. 20. Ditto, but showing young leaves emerging.
Fig. 21. The same bud as preceding, but rotated through an angle of 90°, and with one of the covering leaves removed.
Fig. 22. Longitudinal section through apex of ditto. *le*=" ledge" ; *g.p.*=growing-point.
Fig. 23. Longitudinal section through the base of a colleter of ditto, showing a laticiferous tube (*l.t.*).
Fig. 24. Longitudinal section through a portion of a colleter of *Allamanda* sp., showing a laticiferous tube ascending to the secreting-cells.
Fig. 25 *a*. Leaf of *Ceropegia stapeliæformis*.
Fig. 25 *b*. Section of colleter of ditto.
Fig. 26. Bud of *Clusia grandiflora* (?).
Fig. 27. Young shoot of ditto.
Fig. 28. Base of leaf-stalk of *Clusia rosea*, looked at from the side on which the opposing leaf has been removed; shows the enclosed terminal bud enveloped in the secretion, which has been rendered opaque by alcohol.
Fig. 29. Young lateral bud in the axil of a leaf of ditto.
Figs. 30 & 31. Longitudinal sections of colleters of ditto.
Fig. 32. Bud of *Wormia Burbidgei* : *r*=region within which the younger parts are concealed ; *v.l.*= sheath of older leaf.

TRANS. LINN. SOC. SER. 2. BOT. VOL. III. PL. 59.

P. Groom del.

J.N. Fitch lith et imp.

BUD-PROTECTION IN DICOTYLEDONS.



P. Groom del.

BUD-PROTECTION IN DICOTYLEDONS.

J.N. Fitch lith et imp.