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To students of plant anatomy few books have proved to be of greater service than Solereder's *Systematische Anatomie der Dicotyledonen*. It is a book that contains a vast amount of information as to the work that has been accomplished in anatomy thus far, and gives in concise and clear form the most important results in respect to the general characters of the dicotyledonous families, as well as a number of purely generic or even specific peculiarities observed in their internal structure; the classified lists of the enormous literature bearing on this subject are of no less importance. Whether the book be consulted for the sake of ascertaining the distinguishing characters of certain families or genera, or for obtaining a general view of the structure possessed by the dicotyledons, one is always sure to obtain exact information as to the plants that have been treated from this particular point of view. The number of dicotyledons that have thus far been studied is of course very large, and very few of the most interesting families or genera have escaped the attention of investigators. Most of the parasitic, saprophytic, and climbing plants, with their more or less anomalous structure, have already been duly considered and very carefully described.

However, when we remember that most of the literature has been contributed by European botanists, it is readily understood that very
many of the extra-European plants have been studied either from specimens cultivated in botanical gardens or preserved in herbaria. This may be the cause why, for instance, the root-structure has not been studied to the same extent as that of the other organs, for the root system and rhizomes are not satisfactorily represented in herbaria, or may be entirely wanting. Also, only a very few of the more common genera and species of the North American flora have been studied anatomically, because European botanists have not been in a position to study the American plants, and because American botanists have not paid sufficient attention to anatomical botany. American students, therefore, have an important and interesting task before them in undertaking an anatomical investigation of their native plants, the common as well as the rarer ones, in order to assist in the completion of a work so well begun and so very instructive as that of Solereder and his predecessors.

Moreover, the study of plant structures is necessary to the fuller understanding of ecology. The plant societies, so excellently outlined by Warming and Schimper, should not be determined merely by the social occurrence of a number of types that characterize a certain vegetation, but they should be investigated much farther; thus we might be able to distinguish between characters that may be looked upon as those of the family and those that are purely epharmonic. Very frequently, so far as we know, these structural characters do not correspond with what might be expected from the nature of the habitat. Halophytes and xerophytes are often not to be separated by means of their structure alone; for example, many bog plants exhibit peculiarities that are familiar to us as xerophytic, and vice versa. If the structure of all the most significant components of these societies was so well understood that we were able to distinguish between epharmonic characters and those that are generic or specific, we might gain a clearer idea of the real factors that have brought these plants together so as to form societies.

Another and perhaps more important problem is the application of the structures as a means of distinguishing genera and species; in other words, to bring together such points of distinction as may be observed in both the external and internal morphology of plants. For this purpose almost any contribution, large or small, may be of
some service; and the writer is under the impression that a detailed account of a few plants, hitherto left unstudied, may prove more useful than a broad anatomical treatment of a number of genera and species more or less vaguely described or insufficiently compared.

Among the North American plants that have not been studied fully thus far are the Rubiaceae, at least the genera enumerated in the title of this paper. With the object of presenting a contribution to the knowledge of some of these plants, the writer has endeavored to gather as many data as possible from the vegetative organs which may be of some interest to students of plant anatomy. The following species have been studied:

Cephalanthus occidentalis L. (swamps near Brookland, D. C.), Oldenlandia glomerata Michx. (swamp near Brookland, D. C.), Houstonia coerulea L. (open thickets, D. C.), H. purpurea L. (with the preceding), Mitchella repens L. (wooded ravines near Sligo, D. C.), Diodia teres Walt. (open fields, Brookland, D. C.), Galium pilosum Ait. (thickets, Brookland, D. C.), G. triflorum Michx. (woods near Anacostia, and on the Potomac shore, Va.), G. circinaezans Michx. (with the preceding), G. latifolium Michx. (Biltmore, N. C., the specimens kindly furnished by Mr. C. D. Beadle).

Cephalanthus occidentalis (Naucleaeae B. et H.)

The root.—In small shrubs, too young to produce flowers, the primary root persists and is quite large; it is of a brownish color and measures about 1.5 cm in thickness at the base. At a depth of about 9 cm it commences to branch, dividing into a few slender, very long branches. Numerous white lateral roots develop on all sides, which are very hairy and branch freely. A lateral root of first order shows the following structure. Inside the epidermis is an exodermis (fig. 1, ex) of thin-walled, pentagonal cells which covers a stratum of several cell-layers, a tissue representing cork (fig. 1, p). The cortical parenchyma consists of ten strata of thin-walled cells arranged radially and with very wide intercellular spaces, sometimes wide enough to be called lacunae. Neither starch, crystals, nor raphides were observed in the cortex. The innermost layer of the cortex is differentiated as a thin-walled endodermis with the Casparyan spots plainly visible. A thin-walled pericambium surrounds the leptome and hadrome, the primitive structure of which could not be ascertained since secondary tissues had already become developed; the
conjunctive tissue is quite thick-walled, but represents only a minor portion of the central cylinder.

In the capillary lateral roots of second order, in which no increase in thickness has taken place, there is only one tangential division of the phellogen and only three layers of cortex. The root is hexarch, six groups of leptome alternating with six rays of wide vessels, and with a central group of thick-walled conjunctive tissue. The development of a phellogen has thus taken place in these roots before the increase in thickness of the central cylinder has commenced.

The formation of cork inside the exodermis seems to be a point of interest. In roots of dicotyledons the cork usually develops from the pericambium, and DeBarry records only two cases (Clusia and Bignonia capreolata) in which the formation of cork takes place in the peripheral strata of the primary cortex, as described by Van Tieghem. A similar structure, however, has been detected in Artanthe pothijolia, Jasminum humile, and Ruyschia Souroubea by Olivier. Since this peculiarity in regard to the superficial development of cork has been obscured in Bignonia, I examined also the roots of Tecoma radicans and found the same structure; thus Cephalanthus and Tecoma may be added as examples of this very rare structure of roots.

**The stem.**—In the flower-bearing shoots the leaves are generally in whorls of three, and the internodes become obtusely triangular. A smooth but thick cuticle covers the small-celled epidermis, which is moderately thick-walled, and inside of which several (about six) layers of cork are to be observed. Between the phellogen and the cortex proper is a broad continuous zone of collenchyma, which contains much chlorophyll. The cortical parenchyma is here differentiated into two very distinct zones: a peripheral, of about nine layers of large cells with wide, irregular lacunae; and an inner, of about eight compact strata of smaller cells, interrupted here and there by small, isolated strands of typical stereome. Of these two zones the

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2 Vergleichende Anatomie, p. 563. 1877.
peripheral contains chlorophyll, besides calcium-oxalate in the shape of crystalline sand. Inside the cortex is the central cylinder, consisting of a broad zone of leptome, some strata of cambium, and many rows of vessels separated by narrow medullary rays. The central portion of the internode is occupied by a thin-walled but solid pith, in which crystalline sand was noticed.

A somewhat modified structure is to be observed in the shoots of younger specimens, which are yet purely vegetative. In these the leaves are opposite, not whorled in threes as in the floral shoots, and the outline of the internodes is cylindric. The cuticle is wrinkled, and no phellogen is developed; thus the collenchyma borders directly on epidermis. The differentiation of the cortex into two zones is not so distinct, since the parenchyma is more uniformly developed, more compact, and with the cells radially arranged from the periphery to the stele, except where it is interrupted by the stereome, which occurs in very small, scattered groups. There is no endodermis, and the structure of the mestome and pith is identical with that of the floral shoots.

In comparing these internodes of floral and vegetative shoots with the slender peduncle that bears the globose inflorescence, it is interesting to notice that the structure is almost identical, with the exception that the number of strata of the various tissues is smaller, that no cork is developed, and that bicellular pointed hairs abound.

**The leaf.**—The blade shows a bifacial structure. The cuticle is somewhat irregularly thickened so as to form striations, especially lengthwise (parallel with the midrib). Very characteristic is the small-celled epidermis with the radial walls straight on both faces of the blade; the stomata, which are confined to the lower face, have mostly two subsidiary cells parallel with the stoma (fig. 2), but variations are frequent, there being sometimes two subsidiary cells on one side of the stoma and only one on the other, or the differentiation of the epidermal cells surrounding the stoma may be so slight that no typical subsidiary cells are observable. The stomata are level with epidermis and the air chamber is quite wide and deep. While the upper surface of the blade is glabrous, the lower is hairy with uni- and bicellular hairs, which are long, more or less curved, with the apex acute, thick-walled, and covered by a striately thickened cuticle.
The chlorenchyma is differentiated into a typical and very compact palisade tissue of two strata, and a pneumatic tissue of oblong cells (in transverse section) more or less vertical to the blade and with very wide intercellular spaces. The mechanical tissue occurs only as collenchyma, which follows the veins and which is best developed on the leptome side. A small isolated mass of this tissue is also found in the margins of the leaf-blade. The collenchyma is quite thick-walled and is located directly inside the epidermis, but only as isolated masses above and below the nerves, besides in the margins. A thin-walled, colorless tissue, which evidently represents a water-storage tissue, is amply developed in the midrib and the larger secondaries, where it surrounds the mestome completely. Crystalline sand was observed in some of the cells of this tissue.

The mestome strands are all collateral, but the arrangement of the mestome is somewhat different. The smallest veins show an orbicular outline in transverse sections, and they are surrounded by a very distinct parenchyma sheath; in these the hadrome is located exactly above the leptome. On the other hand, in the midrib or the secondaries the mestome is in the shape of an arch with the ends curved inward, whose concave face looks toward the upper face of the leaf. In this arch the leptome follows the lower face and takes part in the curvature of the end; thus actually the leptome becomes moved from the lower to the upper portion of the mestome bundle. The hadrome is represented by numerous but short rows of vessels arranged above the leptome in the middle of the arch, but beneath it at the ends.

The petiole.—The structure is exactly the same as that of the midrib in the blade. The single, very broad, and arch-shaped mestome strand is located in a mass of colorless parenchyma with crystalline sand, and possesses a support of well-developed collenchyma, while chlorenchyma is completely absent.

The characteristics of Cephalanthus, therefore, are the location of the phellogen inside the exodermis of the root; the absence of stereome in the leaf; the differentiation of the cortex of the stem into two distinct cones interspersed with stereome; and finally the structure of the larger veins in the leaf with the arch-shaped mestome strand.
OLDENLANDIA GLOMERATA (HEDYOTIDEAE B. et H.)

An annual plant and the last of the Rubiaceae to bloom. It inhabitants wet places on borders of swamps, being associated with Hypericum mutilum, Ilysanthes attenuata, Cyperus diandrus, and Fimbristylis autumnalis, but is very rare in the District of Columbia. The short stem is erect from a decumbent base, and all the leaves, which are opposite and short petioled, subtend small cymose inflorescences; the apex of the stem is also terminated by an inflorescence. The basal internodes and the hypocotyl soon become bent towards the ground, and secondary roots develop freely from the full length of the internodes. There are buds in the axils of the cotyledons (one at each) which develop into small floral shoots of one or two internodes, but so late that their flowers are just beginning to open when those of the primary shoot are in fruit. The primary root is short, but has many lateral branches.

The roots.—The main root is hairy and has no exodermis. The cortex consists of three strata of very large, thin-walled cells, and the endodermis is thin-walled, with the Casparyan spots very distinct. The stele showed secondary formations in the leptome and hadrome, so that the primitive organization could not be ascertained. The lateral and secondary roots, on the other hand, do not increase in thickness and remain as diarch. They have long hairs, and show the same structure as the primary, but are much thinner. In the stele there are two strands of leptome, and the center is sometimes occupied by a wide vessel or by a small mass of conjunctive tissue. In these capillary roots the endodermis and pericambium are thin-walled and continuous.

The stem.—The hypocotyl is cylindric in contrast with the internodes above, which are quadrangular, and is perfectly smooth and glabrous. A thin-walled epidermis covers a cortex of three strata of very large cells in which raphides occur. The innermost layer is differentiated as an endodermis, which consists of small, thin-walled cells, surrounding the central cylinder. In this the leptome forms a closed ring around the hadrome, of which the rays are quite long, separated from each other by narrow medullary rays. A thin-walled pith occupies the center of the stele.

The upper internodes are obtusely quadrangular in cross-section,
with two slightly convex and two concave faces; pluricellular but relatively short hairs are to be observed along the angles. The cuticle is quite thick and shows longitudinal striations. The epidermis consists of rather large cells, with the outer wall somewhat thickened; there are several stomata of the same structure as those of the leaf, but the lateral walls of the subsidiary cells are straight, not undulate. Several of the epidermal cells contain large druids.

There is no collenchyma and no stereome, the cortex thus forming an uninterrupted cylinder around the stele. The cortex consists of six layers in the angles, and of four between them; it is a very thin-walled parenchyma of quite large cells with wide intercellular spaces. It contains chlorophyll, raphides, and druids of calcium oxalate. An endodermis of small, thin-walled cells, with the Casparyan spots very distinct, surrounds the stele of collateral mestome strands. In these the leptome forms an almost confluent zone, while narrow rays of parenchyma (one or two rows) separate the short hadromatic rays with only two or three vessels in each row. The greater portion of the central cylinder is occupied by the pith, which is thin-walled but solid, and in which druids are frequent.

Druids were thus observed in the parenchyma tissues as well as in the epidermis, and they are very conspicuous on account of their unusually large size.

The leaf.—The structure is bifacial, with the stomata confined to the lower face, and with the chlorenchyma differentiated into a typical pneumatic and a palisade tissue.

The cuticle is thin and smooth except where it covers the hairs and the midvein of the lower surface of the blade, where it shows a distinct wrinkling longitudinally. Viewed \textit{en face} the lateral cell walls of the epidermis are undulate on both faces, and the stomata have two subsidiary cells, the lateral walls of which are frequently undulate like the others. Hairs are frequent above and below the larger veins; they are pluricellular, with mostly four cells in one row and the apical one pointed; the cell walls are rather thin. Along the margins of the blade the hairs are more frequent, but much shorter, consisting of only one or two cells. Viewed in transverse section, the leaf is perfectly smooth on the upper face, but on the lower—the midrib forms an obtuse keel. The epidermis is thin-
walled on both faces, except below the midrib, where the outer walls become moderately thickened; a difference in regard to the lumen of the cells is very distinct, that of the ventral face being considerably wider than that of the dorsal. The stomata are slightly raised, and the air chamber is wide and deep.

A small water-storage tissue of two strata separates the epidermis from the parenchyma sheath of the median mestome strand on the dorsal face; on the ventral face this tissue is represented only by two or three cells underneath the epidermis and bordering on the parenchyma sheath.

The chlorenchyma, as already stated, is composed of two strata of palisade tissue on the ventral, and of pneumatic tissue on the dorsal. Of these the former is not quite typically developed, since the cells are rather low and broad. The pneumatic tissue is very open, the cells being irregular and branched, with wide intercellular spaces; cells with raphides are frequent in this tissue. There is neither collenchyma nor stereome in the leaves, and the parenchyma sheaths of the collateral mestome strands are thin-walled and the cells large. The midvein has a broad group of leptome and hadrome with narrow vessels, and is partly surrounded by the water-storage tissue.

The stipules.—The stipules in Oldenlandia are extended into two setae, which are terminated by a short, unicellular hair; while the margins bear a few (mostly three) much longer and pluricellular hairs, such as those described above from the stem. At the base of the petiole, but only on the ventral face, glandular hairs were observed. These have a very short stalk and resemble those of Houstonia (fig. 6); they are arranged in two small clusters, one on each side of the axillary bud, but without extending to the stipules.

The characteristics of the genus are the complete absence of collenchyma and stereome from the stem and leaves; the occurrence of very large druids of calcium oxalate in epidermis, cortex, and pith of the stem; also the pluricellular, pointed, and glandular hairs. But neither stem nor leaves indicate in their structure that the plant is a hydrophyte, any more than do the species of Houstonia.

**Houstonia coerulea** (*Hedyotidæae B. et H.*)

The species is herbaceous, but perennial. The primary root is of short duration and soon becomes replaced by a number of secondary
roots which develop from the nodes (between the two leaves) and from the internodes. A small rosette of green leaves appears at the end of the first season, and this little shoot is the only portion of the seedling that winters over; it is developed from the axil of one of the basal leaves, and consists of a short, but very distinct, internode above ground and is terminated by a rosette of leaves, all opposite and with the internodes hardly perceptible. During the next spring an inflorescence becomes developed terminating the shoot; while at the same time numerous buds become visible in the axils of the leaves of the rosette, each producing a short decumbent stolon of one or two internodes, terminated by a dense rosette of green leaves. The stolons being above ground, all the leaves possess distinct petioles and blades. Secondary roots appear, as described above, at various places; they are very thin, of whitish color, and branch freely. The lateral shoot thus represents two stages of growth: a purely vegetative one during the winter, and a floral one during the next spring; while the primary shoot of the seedling blooms without being preceded by other leaves than those at the base of its own stem, including the cotyledons. Our species thus resembles an annual plant in blooming in the first year; a biennial in producing a rosette of leaves to winter over and to become terminated by an inflorescence in the next year; and finally it remains as a perennial by the continuous development of leafy shoots and inflorescences. The inflorescence is a cyme of the dichasium type, but relatively few-flowered. These introductory remarks are to show that the roots are of short duration, that the stolons are above ground, and that the leaves are either cauline or basal, the latter constituting an over-wintering rosette.

The roots.—As stated above, the secondary roots are very slender; they are very hairy and the epidermis covers directly a cortical parenchyma of three, thin-walled, compact strata. An endodermis with the cell walls moderately thickened surrounds the central cylinder, in which the pericambium is continuous and thin-walled. These roots are diarch, the two rays of the hadrome meeting in the center, alter-

5 A near ally of *H. coerulea* is *H. serpyllifolia* Michx., but in this species the vegetative shoots do not develop as rosettes of leaves, since all the internodes are stretched, with the leaves remote. In *H. rotundifolia* Michx. the habitus is much the same as in *H. serpyllifolia*, but the plant is more robust and the flowers are almost sessile and single in the leaf axils.
nating with two broad strands of leptome, and no increase in thickness takes place. A corresponding structure was observed in the capillary lateral roots, with the exception that the various tissues are much less developed, the cortex consisting of only two layers, the endodermis being thin-walled and the hadrome being reduced to a very few vessels.

The stolons.—The stretched internode is perfectly glabrous, and obtusely quadrangular to almost cylindric. A smooth, quite thick cuticle covers the epidermis, which is thick-walled and contains chlorophyll. There are four layers of compact cortical parenchyma with chlorophyll, and the endodermis is moderately thickened and contains starch. The stele is represented by a confluent zone of leptome and vessels in about five rows, with narrow medullary rays of mostly one row of cells. A thin-walled pith occupies the center and contains starch, but no raphides were observed.

The aerial stem.—The long internodes are glabrous, quadrangular, and four-winged. In these the cuticle is wrinkled, and the outer cell walls of the epidermis are quite thickened. Stomata are frequent; they are level with the epidermis and have a wide air chamber. The cortical parenchyma consists of four strata between the wings, but of eight in them; no mechanical tissue, neither stereome nor collenchyma, was observed. A thin-walled endodermis surrounds the collateral mestome strands and the pith, which is narrow and very thin-walled.

The peduncle.—There is here about the same structure as in the long internodes, but the outline is simply quadrangular. The cortex represents a narrower zone, and the stele consists of several more or less separate mestome strands, but in one circle and collateral as above; the medullary rays are very distinct and the central pith somewhat wider.

The leaves.—The basal leaves, which winter over, have a very distinct petiole and a blade that varies from spatulate to almost ovate. Viewed en face the blade shows a perfectly smooth cuticle, and the lateral cell walls of the epidermis undulate on both faces. Stomata occur only on the lower face (fig. 7), and they have a pair of subsidiary cells parallel with the stoma. Unicellular hairs with the cuticle spirally thickened (fig. 5) are to be observed along the margins, while bicellular hairs with similar spiral striations are distributed over
the upper face of the blade, especially near the apex. Viewed in transverse sections the blade shows a typical bifacial structure. The epidermis is thin-walled on both faces, but the lumen of the cells is considerably wider on the upper than on the lower face; the stomata are level with the epidermis. The chlorenchyma is differentiated into a palisade tissue of two strata and a pneumatic tissue of four layers; the latter tissue is very open and the cells are oblong to almost roundish, with wide intercellular spaces. Neither collenchyma nor stereome was observed; thus the mestome strands are located directly in the chlorenchyma; they are collateral and are surrounded by a green parenchyma sheath. The blade thus exhibits a very weak and simple structure.

The petiole is hairy at the base from pluricellular glandular hairs (fig. 6), but otherwise it is perfectly glabrous. It is triangular in cross-section. The cuticle is somewhat wrinkled, and the epidermis consists of large, thin-walled cells. A compact, chlorophyll-bearing parenchyma surrounds a single central mestome bundle, which is orbicular in transverse section and shows a very distinct, thin-walled endoderm.

The stem leaves are sessile, very narrow, and scabrous along the margins from unicellular, prickle-like, and curved projections of the epidermis. Glandular hairs (fig. 6) are frequent along the margins of the stipules. The epidermis of the upper face shows a very pronounced striation of the cuticle (fig. 4); the lateral cell walls are undulate on both faces, and stomata with one pair of subsidiary cells were observed in equal number on both faces of the blade. While the cuticular striations appear as radiating from the center of the epidermal cells on the upper face, the striae on the lower face are parallel with the longitudinal axis of the leaf. In transverse sections the outer cell wall of the epidermis is moderately thickened and shows the elevated cuticle very distinct on the upper face (fig. 3). Otherwise the structure is identical with that of the basal leaves and shows the absence of mechanical tissues; the chlorenchyma, however, is less developed, there being only one layer of palisades, and the pneumatic tissue is composed of very irregularly shaped cells with wider intercellular spaces and contains raphides.

The characteristics of *H. coerulea*, therefore, are the lack of col-
lenchyma and stereome in the organs examined; the glandular hairs; the striate cuticle; and the presence of stomata on both faces of the cauline leaves.

**Houstonia purpurea**

The rhizome is very short and condensed, being merely represented by short internodes, the basal portion of aerial shoots. Several axillary buds occur on these subterranean stem portions, and some of these develop during the fall into small rosettes of leaves with distinct petioles and green, almost glabrous, elliptical blades. Secondary roots occur in pairs at the nodes, between the leaves, and in addition other roots are formed near the middle of the subterranean internodes.

**The roots.**—The secondary roots are very slender, sparingly branched, and not very hairy. Their structure agrees in all essential points with those of the preceding species, but they differ in showing a slight increase in thickness, due to the development of cambial strata in the stele itself, but without influencing the structure of the peripheral strata from endodermis to epidermis. It appears as if the secondary formations are confined to the leptome and hadrome, and that they are of short duration, the roots persisting only for one or two seasons. The capillary lateral roots are diarch, with two vessels in the center and two broad groups of leptome.

**The aerial stem.**—The basal internodes are quadrangular, with the angles produced into short and very narrow wings. The cuticle is wrinkled longitudinally and quite thick. Unicellular, obtuse, and somewhat bent hairs are frequent; they are thick-walled and show longitudinal (not spiral) striae of the cuticle. Viewed *en face* the cells of the epidermis are rectangular, and the stomata have one pair of subsidiary cells parallel with the stoma. The outer and inner wall of the epidermis is thickened, but not the radial. Inside the epidermis is a cortex with chlorophyll and raphides, but there is no collenchyma, not even in the wings. The strata of the cortex are arranged very regularly in rays toward the center, and the innermost layer is differentiated as a thin-walled endodermis, with the Casparyan spots plainly visible. Directly bordering on the endodermis is an almost continuous band of leptome and hadrome with very narrow medullary rays. The central pith is solid but thin-walled, and con-
tains raphides but no starch. This same structure is to be observed in the upper internodes except that the outline becomes more sharply four-winged as the cortical parenchyma in the wings becomes collenchymatic, and the hairs are more abundant.

The peduncle of the flower, however, is not quadrangular, but cylindrical, and the hairs are reduced to mere papillae, which are exceedingly numerous. There is no stereome and no collenchyma; the cortical parenchyma is thin-walled, very compact, and the endodermis consists of much larger cells than observed in the internodes. The structure of the central cylinder is the same.

The leaves.—The over-wintering leaves are petiolate; the petiole is triangular in outline and covered by a wrinkled cuticle. The epidermis is moderately thickened on the ventral face, but thin-walled on the dorsal. A thin-walled chlorenchyma with very little chlorophyll and raphides surrounds three veins, the median of which is the largest; it is crescent-shaped and contains a collateral mestome strand surrounded by a thin-walled, colorless parenchyma sheath. The lateral veins are much smaller and round in transverse section. The blades of these basal leaves are sparingly hairy on the upper face from short, unicellular, obtuse hairs with very distinct longitudinal ridges of cuticle; but where the cuticle covers the ordinary cells of the epidermis (not the hairs) on the upper face we meet with a corresponding striation as observed in *H. coerulea* (fig. 9A). The lateral cell walls of the epidermis are undulate on both faces, especially on the lower, and it seems characteristic of this species (when compared with *H. coerulea*) that the lateral walls show local thickenings (fīgs. 9 and 9A). This structure I observed, also, and much farther developed in *Mitchella*, where it will be described more particularly. Stomata occur only on the lower face and show the same structure as those of *H. coerulea*. There is a typical palisade tissue of two layers, and a very open pneumatic tissue with the cells oblong and parallel with the leaf surface. The mestome strands are surrounded by parenchyma sheaths, but have no mechanical support, neither of collenchyma nor of stereome.

The stem leaves are sessile and their structure differs somewhat from that of the basal leaves. For instance, the cuticle does not show the stellate striations, and bicellular hairs (fīg. 8) abound on
the upper face and along the margins, also along the veins on the lower face; moreover the lateral walls of the epidermis are straight, not undulate, on the upper face and do not show local thickenings. Cells with raphides are frequent in the pneumatic tissue, and a collenchymatic tissue occurs on the leptome side of the midrib. All the mestome bundles are collateral, and the median is the largest. Glandular hairs like those described and figured for *H. coerulaea* were observed along the margins of the stipules.

The characteristics of this species are the local thickenings of the lateral cell walls of the epidermis of the leaves, and the presence of collenchyma, which seems to be absent in *H. coerulaea*.

**Mitchella repens** *(Anthospermeae B. et H.)*

In systematic works Mitchella is generally called an herb; “a smooth and trailing small evergreen herb” in the 6th edition of *Gray’s Manual*, or “a small creeping evergreen” in *Gray’s Synoptical Flora*. By Nuttall it was considered as “an herbaceous repent evergreen;” Bentham and Hooker describe it as “herba repens,” with no allusion to the leaves being evergreen; while Linnaea in this same work (*Gen. Plant.*) is characterized as “fruticulus repens, sempervirens.” Finally Schumann (*Natürl. Pflanzenfam.*) describes Mitchella as “kriechende Kräuter” (*M. repens* and *M. undulata*); while in this same work *Linnaea borealis* is called “niederliegende Sträuchlein.” Linnaea and Mitchella are both evergreen and both possess creeping, woody stems. Mitchell, who was the first to describe our plant, called it Chamaedaphne, which shows that he had the correct impression of the plant as being an “undershrub” and not an “herb.” Moreover, a plant cannot at the same time be an herb and an evergreen, and Mitchella is an undershrub in exactly the same sense as is Linnaea.

The stems are creeping, and the roots develop usually near the nodes and often two together, or commonly they develop from one to three at some distance from the nodes, and mostly from the lower face of the internode; the color of the roots is yellowish or light brown. All the internodes are stretched, and the opposite leaves have distinct petioles and green blades, the outline of which may vary from ovate to almost orbicular; no scale-like leaves develop in any place on the
floral or vegetative shoots. Very frequently some very long and purely vegetative shoots are to be observed in mature specimens, and from these develop lateral (axillary) floral shoots, which generally are quite short and bear only a few pairs of leaves, very often only two, though four or five are not uncommon. Whether the vegetative shoots stay as "vegetative," the ramification thus being monopodial, I am not in a position to state. As a matter of fact, it seems very difficult to make out the ramification of Mitchella, even where it occurs in abundance. The difficulty lies in the fact that the younger stages are hard to find and the adult specimens always appear as if they were not entirely complete. Injury to the shoots, for instance, might be the cause of arresting the buds in their farther and normal development.

The shoots of Mitchella, however, appear to be somewhat uniform, since their foliage is identical; and not as in Linnaea, where small, scale-like leaves occur, and the over-wintering buds are of two kinds. The ramification of Linnaea is doubtless much more complicated than that of Mitchella, but nevertheless it would be interesting to know exactly the behavior of the latter, how the shoots develop in young individuals, and especially how soon the stem becomes creeping.6

The roots.—The secondary roots are relatively short, but they ramify freely, and they remain active for several years. They are hairy and possess an exodermis of the same structure as epidermis. The cortical parenchyma is compact and consists of about three strata with the cell walls moderately thickened throughout; the endodermis, on the other hand, is thin-walled and small-celled; cells

6 Professor Wittrock has presented a most excellent sketch of the biology of Linnaea borealis in Botaniska Notiser (1878–79), and calls attention to the fact that the earliest stages are yet unknown. In order to comprehend fully the morphology of Linnaea the following questions must be answered: (1) When does the main stem become decumbent? (2) Is the main stem a direct continuation of the primary axis, or is it developed from an axillary bud? (3) How soon does the ramification begin? (4) When does it commence to bloom? (5) Does the primary root stay unbranched, and how does it remain active? (6) When do the secondary roots develop? These questions may apply to Mitchella also, and I may at the same time quote another paper on Linnaea by Dr. Sernander (Bot. Not. 1891: 225), in which these questions have been discussed and several additional observations recorded. (See also Areschoung Bot. Not. 1879: 1.)
containing raphides occur in the cortex proper. The pericambium is thin-walled and continuous. Secondary formations take place at an early stage of these roots and thus the primary structure is obscured; the leptome occurs as several broad strands outside a much broader zone of hadrome, with many rows of vessels and thick-walled conjunctive tissue.

While studying the roots I noticed the peculiar fact that in some of these the lateral branches did not penetrate the cortex at once, but remained enclosed for some distance, thus traversing the cortical parenchyma although fully developed. The structure of these, however, was normal and they were developed from the pericambium. Such cases were merely exceptional, however, but may nevertheless deserve mention. Similar structures have been recorded for Carpocephalus and Eriocaulon.7

The stem.—An internode from a long, vegetative shoot of the previous year is cylindric, though somewhat flattened on account of its horizontal direction of growth, and it is very smooth. The cuticle is wrinkled, and the epidermis is quite thick-walled; hairs and stomata occur, but they are not frequent. Tannin was observed in the epidermis, also in the peripheral strata of the cortex, which is thin-walled and compact, contains raphides, and occupies the greater portion of the cross-section. A thin-walled endodermis, with the Casparyan spots plainly visible, surrounds the central cylinder. In the outermost stratum of this, thus bordering directly on the endodermis, I noticed about four very thick-walled cells, which resembled stereome but which proved to be secretory cells like those recorded by Solereder as characteristic of Mussaenda, Isertia, Cinchona, and a few other genera; they are quite long and very thick-walled. The stele consists of many leptome strands and broad rows of vessels with narrow (one single row) medullary rays, while the center is occupied by a thick-walled, solid pith.

In shoots of this year’s growth the structure is the same, but cells containing raphides are more abundant, and the stele shows its primary structure more distinctly, with the leptome and hadrome arranged in two large groups on the sides of the flattened internodes.

The erect shoots are strictly cylindric in outline, but show the

same structure as the horizontal; however, they are more hairy and the cortex contains chlorophyll and raphides. In the first year of growth these shoots have no thick-walled secretory cells, and although the leptome constitutes an uninterrupted zone, the hadrome forms only two arches, separated from each other by two very broad rays of parenchyma. The stems of Mitchella increase very little in thickness, but they are woody and persist, as stated above, for several years.

The leaf-blade.—The cuticle is not very thick, but distinct; it is smooth on the lower face of the blade, except below the midrib, but wrinkled on the upper. The structure of the epidermis is somewhat peculiar. Viewed en face the lateral cell walls are very prominently undulate on both faces (fig. 10); besides that, local thickenings of these cell walls are very conspicuous. A transverse section (fig. II) shows this structure perhaps more clearly, and the thickenings are seen to extend from the outer cell wall to the inner as columns. Whether this structure be common or not, it has not been recorded as characteristic of any of the Rubiaceae in the work of Solereder. It was first described and figured apparently by Mohl in the leaf of Helleborus foelidus, which also is an evergreen. However, it does not seem as if this particular structure is characteristic of plants with persisting leaves, since Lalanne, who examined several genera of various families, does not mention any cases similar to the one described above. But in a paper by Godfrin a somewhat analogous structure is mentioned as occurring in the cotyledons of Aesculus Hippocastanum and Acer platanoides; and Pee-Laby records a similar case from the cotyledons of Mimosa pudica; the thickenings, however, do not extend to the bottom of the cell in these instances, but only to the middle.

The outer cell wall of the epidermis is moderately thickened on

both faces of the blade, and the lumen of the cells is much wider on the upper than on the lower face. The stomata (figs. 12, 13), which are confined to the lower face, are level with the epidermis; they have mostly two subsidiary cells parallel with the stoma and the air chamber is wide, but shallow. No hairs were observed. The chlorenchyma is differentiated into a palisade tissue of two strata and a pneumatic tissue of four layers with broad intercellular spaces (fig. 14). Cells with raphides were observed in the palisade tissue, whose cells diminish in size above the larger veins and become roundish. An almost colorless tissue surrounds the midrib completely and is collenchymatically thickened below this, but otherwise the veins have no mechanical support, since no stereome is developed. The mestome strands are collateral, and the median is very broad, with a large group of leptome and about three rows of vessels; a thin-walled parenchyma sheath surrounds each mestome bundle.

The petiole.—The cuticle is wrinkled and the outer walls of the epidermis moderately thickened. Very thick-walled bicellular hairs occur along the sides of the petiole, while at the base, and especially upon the inner face, numerous glandular hairs (fig. 14, b) were observed. Similar hairs were also found along the upper margins of the minute stipules. The chlorenchyma is quite open and contains only a little chlorophyll, but many raphides. A single, broad mestome bundle occupies the center; it is collateral and surrounded by a colorless, thin-walled sheath. The local thickenings of epidermis observed in the blade do not occur in the petiole.

The characteristics of Mitchella, therefore, are the structure of the epidermis of the leaf-blade; the long and slender glandular hairs; and the secretory, thick-walled cells inside the endodermis of the stem. The peculiarity noticed in some of the roots, where the lateral branches remain enclosed within the cortex for some time, is hardly to be considered as characteristic of the genus, since it was not found to be constant.

**Diodia teres** *(Spermacoceae B. et H.)*

A seedling is shown in fig. 15. The primary root is quite long, sparingly hairy, and the lateral branches short. The hypocotyl is very distinct, erect and hairy, especially above, and the epigeic coty-
ledons are sessile (fig. 16) and hairy near the base on both faces; the stipules are represented by two linear, very small lobes, which bear very long and sharply pointed hairs. The leaves succeeding the cotyledons show the typical shape of the species and the stipules consist of several linear, hairy lobes. In mature specimens, which are annual, the primary root becomes very strong and woody; the main stem is erect, with many horizontal or ascending lateral branches, and the rigid, scabrous leaves are sessile and horizontal.

The roots.—The primary root shows secondary formations at an early stage, so that the primitive organization of the stele becomes obliterated. The epidermis, the cortex, and the endodermis become thrown off, and a cork of about four strata is developed from the pericambium; a large mass of leptome, hadrome, and thick-walled conjunctive tissue occupies the greater portion of the cross-section. In lateral roots of the first order epidermis is partly thrown off and there is no exodermis. The cortical parenchyma consists of four layers of large, thin-walled cells; the endodermis is also thin-walled and shows the Casparyan spots very plainly. Divisions have commenced to take place in the pericambium, and arches of cambium inside the leptome and outside the proto-hadrome have developed. The primitive structure is yet observable, there being five rays of hadrome alternating with five groups of leptome.

The lateral roots of the second order are capillary and show no increase in thickness. The epidermis is hairy and covers directly the cortex of two layers of very large, thin-walled cells. The endodermis is thin-walled, and the pericambium, which is continuous, surrounds two groups of leptome and one diametric row of narrow vessels.

The stem.—Numerous bicellular and rather thin-walled pointed hairs cover the stem from apex to base; the outline of the internodes is obtusely quadrangular, with two concave and two slightly convex faces. The cuticle is very distinctly wrinkled except over the hairs, where it is perfectly smooth. The epidermis is moderately thickened on the outer cell walls, and stomata are quite frequent. A few strata of collenchyma in a continuous zone separate the epidermis from the cortex, which consists of about four layers with narrow intercellular spaces. Chlorophyll was observed in the cortex, though in small
quantity. The innermost layer of the cortical parenchyma is differentiated as an endodermis (fig. 21, end), in which the inner and radial walls are very heavily thickened. The central cylinder contains a closed ring of leptome and about four rows of very narrow scalariform vessels and medullary rays of but one row between each two mestome strands. A thin-walled, solid pith occupies the center of the stem. Cells with raphides are frequent in the stem, but it seems as if they are confined to the cortex.

The leaves.—As mentioned above, the leaves are held in a horizontal position, but nevertheless their structure is almost isolateral, so far as the distribution of stomata and the differentiation of chlorenchyma are concerned. The cuticle is quite thick and smooth on both faces of the blade except the midrib, where it shows prominent longitudinal striations. Viewed en face the epidermis consists of pentagonal or hexagonal cells on the upper face, but of more irregular cells on the lower; the lateral cell walls are straight and not undulate in any part of the leaf. The stomata are most frequent on the dorsal face (fig. 19); the subsidiary cells, normally one pair, sometimes occur one on one side of the stoma and two on the other side, but all parallel with the stoma (fig. 20). Similar irregularities were also noticed in some of the other Rubiaceae examined, as may be seen from my figures. Epidermal projections abound in Diodia; the most common are small warts (figs. 17 and 18) developed merely as protuberances of the outer cell wall; they are very minute, but so numerous that they render the leaves scabrous. Unicellular, rather thin-walled, pointed hairs are also frequent (fig. 19) on both faces of the blade; and along the margins are curved, thick-walled, spine-like projections of exactly the same structure as those well known on the leaves of Gramineae and Cyperaceae (fig. 18).

A cross-section of the leaf shows a large-celled epidermis on both faces, with the outer wall slightly thickened on the upper; the warts appear most numerous on the upper face. The position of the stomata differs on the two surfaces, being raised on the lower and level with the epidermis on the upper. The midvein shows a prominent group of collenchyma and thin-walled water-storage tissue on the leptome side, while no collenchyma was observed above the hadrome. An isolated strand of collenchyma occurs also in the margins of the
leaf, but none accompanies the smaller veins. No stereome is present in the leaf. The chlorenchyma is quite compact throughout and is differentiated into a typical palisade tissue of two strata on the upper face of the blade and around the nerves. Between the nerves on the lower face of the blade the chlorenchyma consists of a pneumatic tissue of more or less oblong cells, with the intercellular spaces quite distinct but not so wide as in the other genera examined; raphides were observed in the pneumatic tissue, but not many among the palisades.

The mestome strands are collateral and surrounded by a very large celled and thin-walled parenchyma sheath, some of whose cells contain tannin; the midrib is the largest and its outline in cross-section is oval, while the others are much thinner and orbicular. The venation of the leaf is difficult to observe without separating the chlorenchyma from the veins, since the cross veins (secondaries) are so exceedingly thin and completely surrounded by chlorenchyma. The cross-veins are so numerous, indeed, that a transverse section of the blade shows their parenchyma sheaths so distinct "longitudinally" that the leaf is almost divided by them into two zones.

The stipules are divided into several bristles, which are terminated by a pointed hair, and a few (mostly three) glandular hairs occur at the base between the bristles; the structure of these glandular hairs is like those of Houstonia (fig. 6), but the stalk is much longer in Diodia. According to Warming, D. radicans Cham. et Schl. possesses dorsiventral leaves with the pneumatic tissue consisting of stellate cells with very wide intercellular spaces; moreover, the stomata, which are said to have no subsidiary cells, are confined to the dorsal face; hence the leaf is strictly dorsiventral.

Diodia teres, therefore, shows the following points of interest: the structure of the epidermis of the leaves; the approximately isolateral blade with stomata on both faces and with the palisade tissue partly extending to the dorsal epidermis; and the scant development of collenchyma and total absence of stereome in the leaves as well as in the internodes.

Galium (Galieae B. et H.)

Wydler\textsuperscript{13} has described the seedling and the structure of the shoots in several species of Galium. His paper contains many points of interest, for instance that the axes of first order in G. cruciata do not become terminated by inflorescences, and that accessory buds are frequent in European species. The seedlings of G. saccharatum and of G. Aparine are figured and described by Lubbock.\textsuperscript{14}

G. pilosum

Seedlings with the first two or three internodes developed may be found in the early part of May. The primary root (fig. 22, r) is quite long and branches freely, and is of a yellowish-brown color. The hypocotyl (fig. 22, h) is very distinct and bears epigeic, petiolate cotyledons with broad blades (fig. 23). While the hypocotyl is cylindrical and glabrous, the succeeding internodes are quadrangular and hairy.

During the first season the hypocotyl becomes bent toward the surface of the ground and secondary roots commence to develop on all sides. The primary root continues to grow in length as well as in thickness. At the end of the first season the primary shoot above the cotyledons dies off, the hypocotyl thus being the only portion of the primary axis above ground that remains and winters over. At this stage, however, two minute buds become visible in the axils of the cotyledons, which in the next spring grow out into leafy shoots. Our species is a perennial herb, whose shoots die down to the ground every fall, while the buds in the axils of the basal leaves winter over, and the same mode of growth is repeated. I have never observed more than one bud in each axil, this species differing in this respect from those studied by Wydler.

In full-grown, fruiting specimens of G. pilosum the primary root persists as a slender, woody taproot of a yellowish-brown color, which changes to a brilliant red when preserved in alcohol. There are many quite strong lateral roots and secondary ones, which develop very freely from the basal internodes of the stem. No real rhizome becomes developed; the persisting stem bases with their buds and

\textsuperscript{13} Kleinere Beiträge zur Kenntniss einheimischer Gewächse. Flora 43:492. 1860.

\textsuperscript{14} Seedlings 2:59. 1892.
the primary root are the only underground organs that winter over, and by which the future development of aerial floral shoots is secured. The term "pseudo-rhizome" seems very applicable to the subterranean stem of this and other species of the genus. It was originally suggested by Hjalmar Nilsson and intended for herbs "in which the basal, subterranean portion does not die off with the aerial, but stays active and produces a floral shoot the succeeding year by means of a lateral bud; and in which this basal portion becomes able to increase in thickness and to nourish the over-wintering bud, and also to develop secondary roots; such a subterranean stem represents a pseudo-rhizome."

The roots.—The primary root persists for several years, and evidently as long as the individual lives. During the first season secondary formations in the stele commence, but the growth is rather slow and causes neither the cortex nor the epidermis to be thrown off. The epidermis thus remains intact, is slightly thickened on the outer cell walls, and is almost glabrous. There is no exodermis, and the cortex represents a compact tissue of about five strata in which cells with raphides are scattered. The endodermis is thin-walled and readily distinguished by the small lumen of the cells when compared with those of the adjoining cortex. The pericambium is also thin-walled and continuous and does not yet (August) show any cell division; but there are additional vessels inside the leptome, so that the primitive structure of the stele is no longer to be observed; the medullary rays are very narrow, consisting only of one row of cells.

The lateral roots of the first order are almost capillary, and the thin-walled epidermis shows many hairs. The cortical parenchyma is very thin-walled and the cells large. A thin-walled endodermis and pericambium surround two groups of leptome and two very narrow vessels in one diametrical plane.

While studying the structure of the primary root of a number of specimens I noticed the same peculiarity as in Mitchella, that the lateral roots stay for some time enclosed within the cortex, which they traverse longitudinally; this peculiarity was noticed in several cases, but not frequently enough to make me believe that it is characteristic of this particular species.

The stem.—The basal internodes are four-winged, and very hairy from long, unicellular hairs with the cuticle minutely granular (fig. 24); otherwise the cuticle is thick and perfectly smooth. A very pronounced thickening with layerings is observable in the outer cell wall of epidermis, the stomata are raised a little above the adjoining epidermis, and the air chamber is deep but narrow. A broad strand of about six layers of very thick-walled collenchyma is located in each of the four wings, just beneath epidermis. Viewed in longitudinal sections the cells of this collenchyma showed the cross walls horizontal to very oblique. The cortex consists of about seven strata inside the wings and of only three between them; it is thin-walled and quite open on account of the very wide intercellular spaces; cells with raphides are frequent in this parenchyma, but no starch was observed. The innermost layer is differentiated as a thin-walled endodermis, directly bordering on a continuous zone of leptome, inside of which is a very broad zone of hadrome with the vessels narrow and thick-walled. The center of the stem is occupied by a thin-walled pith, mostly broken down in the middle. This same structure was observed also in the internodes of the mature stems, but not in the lateral axes that bear the inflorescences. In these the wings are less distinct and the pith is solid. Finally, in the floral peduncle the outline is cylindric and the collenchyma totally absent.

The leaves.—An isolateral structure is characteristic of the cotyledons. The lateral cell walls of the epidermis are undulate on both faces, and stomata occur on the dorsal as well as on the ventral face. The chlorenchyma is represented by a homogeneous tissue throughout, of cells more or less oblong to roundish in transverse section, and no palisades were observed. Several of the epidermal cells contained brown, amorphous clumps of resin, and these secretory cells in the cotyledons did not differ from the other cells of epidermis. The slender petiole has only one broad mestome bundle in the middle and no mechanical tissue.

The small stem leaves and the foliaceous stipules show the following structure. The cuticle is smooth except above the large epidermal cells which contain resin, where it is irregularly thickened so as to form striations (fig. 25). Viewed en face the lateral walls of the
Epidermis are undulate on both faces, and many very large secretory cells occur on the dorsal, besides stomata; the latter have mostly one pair of subsidiary cells parallel with the stoma; unicellular hairs, often with apex hooked, abound on the dorsal face. In transverse sections the epidermis appears to be slightly thickened on both faces, and the lumen of the cells is somewhat wider on the upper than on the lower, excepting the secretory cells, which, as stated above, are very large. The stomata are raised, and in the leaves the air chamber seems constantly to be wide but shallow.

A chlorenchyma is represented by one layer of palisades on the upper face and by three or four strata of very open pneumatic tissue on the lower. Three thick-walled layers of collenchyma are located on the leptome side of the midrib, inside the epidermis; no stereome was observed. A water-storage tissue of thin-walled, colorless cells in about five layers in a very broad group cover the leptome, making the midrib very prominent on the dorsal face. Neither the collenchyma nor the water-storage tissue was observed at the other nerves. Cells containing raphides were only found in the chlorenchyma, between the palisades and the pneumatic tissue. All the nerves are surrounded by parenchyma sheaths of small, rectangular cells with the Casparyan spots very plainly visible, having more the aspect of an endodermis than of the usual parenchyma sheath in leaves. The midrib is the thickest on account of the very broad collateral mestome strand, and because accompanied by collenchyma and water-storage tissue. The lateral veins are very thin, and orbicular in cross-section; they are collateral and the parenchyma sheath is very distinct as in the midvein.

The characteristics of *G. pilosum* are the leaf epidermis with resiniferous cells and their cuticular striations. Secretory cells in epidermis are recorded by Solereder (p. 505) from Rubia, Anthospermum, and Nenax, but not from Galium. They are mentioned however, by Kearney, who found them in the leaves of *G. hispidulum* Michx. The collenchyma is well represented in the stem, but is confined to the midrib in the leaves. The coloring matter observed in the root is well known in other species of Galium, as well as in Rubia.

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G. *TRIFLORUM*

The seeds of this species germinate very early, and seedlings may be found in wooded ravines in February. The hypocotyl (fig. 28, h) is very long and lies on the ground; the primary root is distinct and amply branched. Very characteristic are the large blades of the cotyledons and the relatively short petioles. Small shoots are already developed in the axils of these, while the primary axis, which is erect, shows long, glabrous internodes. During the first season the plant thus develops three aerial shoots, which however die down to the ground in the fall. The hypocotyl and the primary root do not persist, but the base of the two axillary shoots from the cotyledons remains alive, and the future growth of the individual is secured by small buds in the axils of the basal leaves and some secondary roots that winter over. In mature specimens the root system is thus represented by secondary roots, and the subterranean stem is a pseudo-rhizome like that of the preceding species.

**The roots.—** The secondary roots are very long and relatively thick and strong; they become glabrous very soon. No exodermis is developed, and the cortex, which is very compact, consists of four starch-bearing layers. The endodermis and the continuous pericambium are thin-walled, and the stele shows three leptome strands alternating with three rays of hadrome; while the center is occupied by a thick-walled conjunctive tissue. It appears as if the increase in thickness does not commence until during the winter, when the epidermis and the cortex become thrown off.

The lateral roots are capillary and almost destitute of hairs; there is no exodermis and the structure is identical with that of the mother root, but they do not increase in thickness. I observed no case where these lateral roots remained enclosed within the cortex, as in the former species.

**The stem.—** The internodes are quadrangular and sharply four-winged; unicellular, pointed hairs are common along the wings, rendering them quite scabrous. The thin cuticle shows longitudinal ridges, and the outer cell wall of the epidermis is slightly thickened. Broad groups of thick-walled collenchyma are noticeable in the wings, but otherwise the stem has no mechanical support. The cortex consists of about ten layers in the wings, and of three between them;
it contains chlorophyll and raphides. A thin-walled endodermis surrounds the central cylinder, consisting of a continuous zone of leptome, inside of which the vessels are arranged in short rows with narrow medullary rays bordering on the central, very thin-walled pith.

The leaves.—The structure is almost isolateral in respect to the chlorenchyma. The cuticle is thin and smooth on both faces, and the lateral cell walls of the epidermis show a very pronounced undulation (fig. 26); the outer cell walls are moderately thickened (fig. 27). Unicellular hairs and curved, prickle-like projections are common along the margins and the veins on the lower face, but no resiniferous cells were observed in this species. The stomata are slightly raised and have one pair of subsidiary cells with the lateral walls undulate. No palisade tissue is developed, the chlorenchyma being a homogeneous tissue of roundish cells (fig. 30) with distinct intercellular spaces, especially near the dorsal epidermis, where cells containing raphides are abundant. A small group of collenchyma and a water-storage tissue of a few cells cover the leptome side of the midvein. The mestome bundles show an orbicular cross-section, and are collateral; the parenchyma sheaths show the same structure as observed in the preceding species, with the Casparyan spots very plainly visible.

The structure of *G. triflorum* thus resembles that of *G. pilosum*, but is generally weaker, the epidermis does not show the resinous secretions, and the leaves are almost isolateral.

**G. circaeans**

I have not been able to find the seedlings of this species, and must therefore confine myself to the mature plant. It is very distinct from the two species described above in the relatively long and broad leaves and stipules, also in possessing a true rhizome. The stem bases persist and buds become developed upon them, some of which grow out directly as aerial shoots, while others stay underground, producing stolons with stretched internodes and scale-like leaves. The primary root does not persist, but becomes replaced by numerous secondary roots from the nodes and internodes.

The roots.—The secondary roots are long, slender, and profusely branched; light brown when fresh, but placed in alcohol they attain
rapidly a beautiful crimson color. The epidermis is glabrous and very small-celled; it covers the cortex directly, there being no exodermis. The cortex is thin-walled, but compact; no starch was observed, but globules of resin occur in some of the cells; it consists of about six strata, the innermost of which is differentiated as a small-celled, thin-walled endodermis. Secondary formations have changed the primitive structure of the stele, which shows a confluent zone of leptome and many rows of vessels separated by a few strata of thick-walled conjunctive tissue, which extend to the center.

The lateral roots are also glabrous and have no exodermis. About four layers of cortex with raphides border on a thin-walled endodermis. The pericambium is continuous and surrounds four broad groups of leptome alternating with four short rays of hadrome, with a central group of thick-walled conjunctive tissue. A lateral root of the second order (borne upon the former) is exceedingly thin and slightly hairy. In this the cortex consists only of two layers, the innermost of which is large-celled, with the cells stretched radially and containing raphides. The stele is diarch.

The stem.—The structure of the stolons is rather weak; the epidermis and the primary cortex had been thrown off, and the central cylinder was merely covered by some layers of cork. This cork was evidently developed from endodermis, as in other species of the genus and of Rubia, as stated by Solereder (p. 510). The stele is located directly inside the cork and consists of a confluent zone of leptome separated from the hadrome by strata of cambium. A small pith occupies the center of the internode.

The aerial stem is sharply four-winged, covered by a thin cuticle, which is somewhat wrinkled along the wings, but otherwise smooth. The epidermis is glabrous and the outer cell wall thickened, especially in the wings. Several strata of heavily thickened collenchyma were observed beneath epidermis in the wings (fig. 34, coll). The cortical parenchyma in the wings consists of about seven compact layers with chlorophyll, and of only three between them. The endodermis is thin-walled and surrounds the stele, which shows the same structure as in the preceding species.

The leaves.—The lateral cell walls of the epidermis are prominently undulate on both faces, when viewed en face. Cells with resin are
frequent, but only on the lower face (fig. 31). The cuticle is wrinkled on the upper face, but smooth on the lower, except over the hairs, where it is minutely granular. The epidermis is thin-walled; unicellular, seldom bicellular, hairs cover the lower face, especially the nerves; they are quite thick-walled and the apex is pointed and more or less curved. The stomata, which are confined to the lower face, have two subsidiary cells, one of which is mostly much smaller than the other, but they are both parallel with the stoma. A cross-section of the leaf (fig. 32) shows the lumen of the epidermis to be about the same on both faces; also the structure of the chlorenchyma, which shows a palisade tissue quite well distinguished from the underlying, very open, pneumatic tissue (fig. 33). A small group of collenchyma and water-storage tissue is located underneath the median and the two lateral mestome bundles. The structure of the veins agrees in all respects with that observed in the former species. Besides the secretory cells in the epidermis, there are in the pneumatic tissue many cells containing raphides.

In *G. circaezans* the collenchyma reaches a high development in the stem, but not in the leaf. The epidermal secretory cells show the same structure as those of *G. pilosum*, but the cuticle is uniformly smooth over them, not striate as in *G. pilosum*. The leaf structure is bifacial, even if the palisades are not quite typical.

**G. latifolium**

In habitus this species resembles very much the preceding, but is more robust, taller, with coarse stems and larger leaves. The primary root does not persist, but secondary ones are developed in great numbers; they are yellowish-brown, quite thick, and branch freely. This species has no true rhizome, but a pseudo-rhizome of densely matted basal internodes, that persist for several years. The foliage of these over-wintering stem portions is reduced to small, scale-like leaves of the same length as the internodes. The aerial shoot is stout, with several lateral branches, all of which are terminated by inflorescences.

**The roots.**—The secondary roots are glabrous, and the epidermis is thin-walled. A compact cortex of three strata borders on the endodermis, of which the cell walls are moderately thickened; the peri-
cambium is thin-walled and continuous, with beginning cell division. Secondary formations have already commenced in the stele, where the primitive structure is no longer observable. A thick-walled conjunctive tissue occupies the greater portion of the central cylinder. Some of these secondary roots were quite thick, and were evidently two years old. The cortical parenchyma was thick-walled and consisted of ten compact strata, surrounding a very broad stele, in which the hadromatic rays were considerably longer than in the other roots.

The capillary, lateral roots are also without hairs, and they show the same structure as the mother root, the only differences being that the cortex is smaller and that they do not increase in thickness.

**The stem.**—The internodes above ground show the same structure as *G. circaezans*, but the wings are not so sharp (*fig. 35*); the collenchyma thus represents a broader group. In the basal internodes that winter over, the collenchyma is much reduced (*fig. 36*), while the cortex is frequently more or less thick-walled.

**The leaves.**—There is only one point in regard to the internal leaf-structure in which this species differs from *G. circaezans*, namely the resiniferous cells in the epidermis. These are much more numerous and often occur several together, and viewed *en face* they show branches very often, so as to acquire a very irregular outline, instead of being merely oblong. Over these cells the cuticle is prominently striate, as observed in *G. pilosum*. The only characteristic feature by which this species may be distinguished from the others, therefore, depends upon the abundance and much larger lumen of the secretory cells in the leaves.

**Summary**

According to Vesque, the characteristics of the Rubiaceae are the simple hairs; the absence of glandular hairs; the stomata accompanied by at least one pair of subsidiary cells parallel with the stoma; the crystals simple, druids, raphides, or as crystalline sand; the absence of laticiferous ducts. The peculiar glandular hairs which I found in Mitchella and Houstonia are not glandular hairs in the


18 In accordance with Warming the stomata of *Dodia radicans* Cham. et Schl., from the sandy shore of St. Thomas, have no subsidiary cells. Halofyt-Studier, p. 187.
same sense as this term is generally used. Solereder (p. 504), who
records them from the stipules of Isertia for instance, calls them
Drüsenzotten, but I am at present unable to suggest any better English
name than "glandular hairs." The other characters enumerated by
Vesque are readily recognized in the plants described above.

The epharmonic variations are also discussed by Vesque (p. 202),
but these are not exactly comparable with those observed in our
plants, since the genera treated by Vesque are so very different.
However, the same degree of variation takes place in several instances,
and we might consider these epharmonic characters as suggested
by Vesque. Among the epharmonic variations observed in the
Rubiaceae described above, the following may be enumerated:

The roots.—The superficial development of cork inside the exo-
dermis in Cephalanthus; the lack of exodermis in Houstonia, Diodia,
Oldenlandia, and Galium; the thick-walled cortical parenchyma in
Mitchella and and G. latijolum.

The stem.—The presence of stereome in Cephalanthus; the
development of collenchyma as a continuous zone in the same genus
and in Diodia; the isolated collenchyma strands in the angles of the
stem in Houstonia purpurea and Galium; the lack of collenchyma
in Oldenlandia, H. coerulea, and Mitchella.

The leaves.—The bifacial structure in Cephalanthus, Oldenlandia,
Houstonia, Mitchella, Galium circrizans, G. latijolum, and G. pilosum;
the isolateral structure in Diodia and G. trijlorum; the distribution of
the stomata on both faces of the (cauline) leaf-blade in H. coerulea
and Diodia; the presence of epidermal resin cells in G. pilosum, G.
circrizans, and G. latijolum; the local thickenings of the lateral cell
walls of the epidermis in Mitchella and H. purpurea; the straight
rather than undulate lateral cell walls of the epidermis in Cephalan-
thus, H. purpurea (the cauline on the upper face), and Diodia; the
cuticular striae radiating from the center of the epidermal cell in H.
coerulea and H. purpurea; the cuticular spiral striations over the
hairs in H. coerulea; the wrinkled cuticle above the resin cells in G.
pilosum and G. latijolum; the granular cuticle over the hairs in G.
pilosum, G. circrizans, and G. latijolum; the glandular hairs in Olden-
landia, Houstonia, and Mitchella; the palisade tissue extending to the
dorsal epidermis in Diodia; the non-development of typical palisades
in *G. triflorum*; the lack of collenchyma in *H. coerulea* and in the over-wintering leaves of *H. purpurea*; the presence of a water-storage tissue, amply represented in Cephalanthus, and only on the leptome side of the midrib and larger veins in Galium and Diodia; the endodermis-like parenchyma sheath in Galium.

Some of these characters may not be constant. For instance, the relative development of the palisade tissue may be different, and it would be interesting to know the leaf-structure of *Galium triflorum* from northern Europe, and of the Japanese *Mitchella*.

The family characters, as outlined by Vesque and Solereder, may be augmented, but hardly changed. The family is well represented in North America, and an extended study of the southern and western species would no doubt give many interesting results.

Brookland, D. C.

**EXPLANATION OF PLATES VII–IX**

**PLATE VII**

*Cephalanthus occidentalis*

Fig. 1. Transverse section of root, showing development of cork; *ep*, epidermis; *ex*, exodermis; *p*, phellogen; *c*, outermost stratum of cortex. X320.

Fig. 2. Epidermis of lower face of leaf with stomata. X240.

*Houstonia coerulea*

Fig. 3. Cross-section of stem leaf, showing a cell of epidermis with its cuticle from the upper face. X240.

Fig. 4. Epidermis from upper face of stem leaf with cuticular striations and stomata. X240.

Fig. 5. Hair from leaf margin with spiral striations of cuticle. X240.

Fig. 6. Glandular hair from stipule. X240.

Fig. 7. Epidermis with stomata from lower face of basal leaf. X320.

*Houstonia purpurea*

Fig. 8. Hair from upper face of stem leaf. X240.

Fig. 9. Epidermis with stomata from lower face of basal leaf. X240.

Fig. 9A. Epidermis of upper face of basal leaf, showing cuticular striations and thickenings of the lateral cell walls. X320.

*Mitchella repens*

Fig. 10. Cells of epidermis from upper face of leaf, viewed en face. X560.

Fig. 11. Cross-section of leaf, showing epidermis (*ep*) and part of palisade tissue (*p*). X560.

Fig. 12. Epidermis of lower face of leaf, showing the stomata. X320.

Fig. 13. Epidermis of lower face of leaf. X320.
Fig. 14. Pneumatic tissue of leaf, viewed *en face*. \( \times 240 \).

Fig. 14B. Glandular hair from base of petiole. \( \times 240 \).

**PLATE VIII**

*Diodia teres*

Fig. 15. A seedling; cot, cotyledons; h, hypocotyl; r, primary root. \( \times 2 \).

Fig. 16. A cotyledon with stipule.

Fig. 17. Transverse section of leaf, showing epidermis of upper face with protuberances of outer cell wall. \( \times 240 \).

Fig. 18. Epidermis of leaf margin. \( \times 240 \).

Fig. 19. Epidermis of lower face of leaf. \( \times 240 \).

Fig. 20. Epidermis of upper face of leaf, showing stomata. \( \times 240 \).

Fig. 21. Cross-section of stem internode, showing endodermis (*end*) and cortex (*c*). \( \times 240 \).

*Galium pilosum*

Fig. 22. A seedling; index letters as in fig. 15. \( \times 2 \).

Fig. 23. A cotyledon.

Fig. 24. Hair from stem. \( \times 240 \).

Fig. 25. Epidermis of lower face of leaf, showing stomata and a secretory cell with cuticular striations. \( \times 240 \).

*G. triflorum*

Fig. 26. Epidermis of lower face of leaf, showing stomata and undulate lateral cell walls. \( \times 320 \).

Fig. 27. Transverse section of leaf, showing epidermis and a stoma from lower face of blade. \( \times 320 \).

**PLATE IX**

Fig. 28. A seedling: index letters as in fig. 15. \( \times 2 \).

Fig. 29. Hair from midrib. \( \times 240 \).

Fig. 30. Transverse section of ventral portion of leaf; ep, epidermis; m, mesophyll without palisade. \( \times 320 \).

*G. circaezans*

Fig. 31. Epidermis from lower face of leaf, showing a secretory cell with no cuticular striae. \( \times 240 \).

Fig. 32. Cross-section of leaf; ep, epidermis; p, palisade tissue. \( \times 320 \).

Fig. 33. Pneumatic tissue viewed *en face*. \( \times 320 \).

Fig. 34. Cross-section of internode, showing one wing; ep, epidermis; coll, collenchyma; c, cortex. \( \times 320 \).

*G. latifolium*

Fig. 35. Cross-section of basal (but aerial) internode, showing one of the angles; index letters as above. \( \times 320 \).

Fig. 36. Cross-section of subterranean internode of an over-wintering shoot; index letters as above. \( \times 320 \).
HOL. Mon RUBIACEAE
HOLM on RUBIACEAE