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I.—*The Nature and Origin of Stipules.*

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The investigation which has resulted in the preparation of this dissertation was undertaken with a view to determine the true nature and phylogenetic origin of those appendages of the bases of the petioles of leaves which are known as stipules and which are present in so large a number of the families of flowering plants.

The data have been collected from every available source; the evidences to be gathered from known geological facts have been taken into consideration, observations have been made upon the morphology and anatomy of the foliar organs in a large number of cases, and the gradual modification of leaf-forms in the annual growth of plants from simple scales to adult leaves has been carefully studied. In addition to the data so gathered, the literature dealing with the subject, relatively scanty though it is, has yielded much valuable material both by the record given of the observations of others and by the suggestion of lines of investigation.

With all this material in hand, I have endeavored to ground the theoretical consideration of the problem upon the broadest foundation possible in the present stage of the progress of science, and from a comparative study of the evidence gathered from all the various sources of information, have drawn the conclusions set forth at the close of my paper.

The results of my investigations are herewith given to the public with the conviction that conclusions arrived at in the manner indicated cannot fail of interest to the reader, nor, in some degree at least, of scientific value.

COLUMBIA UNIVERSITY,
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SYNOPSIS.

A Review of Important Literature Pertaining to Stipules.

Owing to the fact that a large part of the literature pertaining to stipules is inaccessible to the majority of botanical students, scattered as it is, for the most part, in the journals of various scientific bodies, it has seemed desirable to preface the consideration of the results of my research on the question of the Nature and Origin of Stipules with a brief summary, in chronological order, of the publications having reference to the general subject of stipules. I have, however, omitted mention of their consideration in systematic works and the general allusions and definitions as they occur in most general works on the Spermatophyta together with their special consideration in individual species and groups except in the most important cases.

Stipules have not received a very large degree of attention from botanists apart from their morphology as used in classification and the publications to be considered are not very numerous, but it is thought that a review of those following will be profitable and of general interest:

Malpighi, Marcello.—Opera omnia, 22-39. 1686.

This is one of the earliest works in which stipules are treated. A considerable number are figured and described under the name of *foliola caduca.*

Linnæus, Carolus.—Philosophica Botanica, 50. 1751.

A general definition is given of stipules as scales borne at the base of the petiole. Buds are spoken of as formed by stipules, by petioles, or by rudiments of leaves.

Linnæus, Carolus.—Prælectiones in ordines naturales plantarum, 520. 1792. (Cited by Hanstein in Abhandl. Akad. Berlin, 77. 1857.)

In speaking of the whorled leaves of the Stellatæ, Linnæus says that only two of these leaves are true leaves, the remainder are stipules which have grown to the same size as the leaves.

De Candolle, Augustin P.—Theorie de la Botanique, 364. 1819.

The stipule is defined as a foliaceous appendage or accessory leaf situated at the base of certain leaves. The stipel, first so named by De Candolle, is defined as a stipule placed on the common petiole at the base of the leaflets.

De Candolle, Augustin P.—Organographie Végétale, 1 ; 334-341. 1827.

De Candolle's views as here expressed may be outlined as follows: "Stipules do not exist in any monocotyledonous plant,* nor in any dicotyledons in which the petiole has a sheathing base; among dicotyledons with leaves not sheathing, stipules are frequently wanting, especially in plants with opposite leaves. Their existence is intimately connected with the general symmetry of plants, and they occur or are wanting in all the species of a family.

"The only essential character of stipules is their lateral position at the base of the leaves, and it is not impossible that we confound under a common name objects really distinct. Their texture is, in many plants, perfectly foliaceous and in these cases they exhibit so exactly the character of leaves that we can say that they are small accessory leaves.

"In certain verticillate leaves, such as those of *Galium*, it is noticeable that the buds and young branches are not produced in the axils of all the leaves, but only of two among them which are opposite to one another. I presume that these two leaves furnished with buds are the true leaves and that the others should be considered as foliaceous stipules.

"The natural use of stipules seems to be the protection of the leaves during their development, but we must admit that in many cases their smallness or their nature or form make them inappropriate to this use, though we cannot well assign another to them, those which are foliaceous assist in the elaboration of the sap, those which are changed into spines serve for the defense of the plant.

"The tendril in the Cucurbitaceæ is perhaps a modified stipule. The ochrea of Polygonums is a prolongation of the base of the petiole into connate stipules."

In volume 2, pages 213 and 214, De Candolle says in treating of buds, "They have received particular names according as they are formed by different parts of the foliar organs, and according to the degree of their degeneration and adnation.

"1. Buds are called foliar when, the leaves being sessile, the blade itself, reduced to the form of a scale, forms the buds, as in *Daphne mezereum* L.

"2. They are called petiolar when the bases of the petioles dila-

*See also A. Richard. Précis de Bot., 126.

ted into scales form the covering of the young shoot. This occurs in petiolate leaves without stipules, as in the walnut, ash and horse-chestnut.

"3. Buds are stipular when the scales are formed, not by the leaves, but by the stipules which are not united with the petioles. Of these there are two sorts,—those which are formed by a great number of stipules enclosing a young shoot collectively, as in oaks, willows and elms, and those in which the stipules, free or united by their exterior margins, form a peculiar envelope for each leaf, as in *Ficus* and the magnolias.

"4. When the stipules are adherent with the petiole, these two organs united into one form the bud scales, and are named fulcral. This occurs in most of the Rosaceæ, and the scales are frequently three-lobed or three-toothed, indicating the origin of the scale formed by the petiole and the two stipules united together." Plate 21, figure 9, shows the progressive change from scales to foliage-leaves in buds that are fulcral in nature.

Bischoff, G. W.—Lehrbuch der Botanik. 177-183. 1834.

The subject is here more fully outlined than in De Candolle's Organographie. Stipules are defined as peculiar leafy expansions at the base of a free middle leaf. They are recognized as belonging to the leaf on the ground of their frequent connection with the petiole, the receiving of their vascular bundles from those of the leaf and the absence of buds from their axils. Various kinds of stipules are described and the ochrea, the ligule, the stipule in the Naiadaceæ and the ochrea of palms are included with stipular formations.

Lindley, John.—Introduction to Botany, 99. 1832.

The following statement is of interest: "The exact analogy of stipules is not well made out. I am clearly of opinion that, notwithstanding the difference in their appearance, they are really accessory leaves; because they are occasionally transformed into leaves, as in *Rosa bracteata*, because they are often indistinguishable from leaves of which they obviously perform all the functions, as in *Lathyrus*, and because there are cases in which buds develop in their axilla, as in *Salix*, a property peculiar to leaves and their modifications." The character of stipules is denied to the tendril of the Cucurbitaceæ and the tendrils of *Smilax* (p. 96) are regarded as lateral branches of the petiole.

Henry, A.—Recherches sur les bourgeons. Nova Acta Acad. Nat. 18 : 525–540. 1836. (Cited by Clos in Bull. Soc. Bot. Fr. 26 : 193. 1879.)

Henry says that he recognizes in the Betulaceæ and Cupuliferæ that the bud-scales are formed by stipules in an anamorphosed condition, and that in *Platanus* they are formed by the ochrea as he terms the basal foliar appendage in this genus.

Lestiboudois, Them.—Etudes sur l'anatomie et la physiologie des vegetaux. 1840. (Cited by himself in Bull. Soc. Bot. Fr. 4 : 746–747. 1857.)

The author states that he has shown that stipules are parts of the leaf, formed by the bundles or lateral fibers of these organs, whether they arise from bundles not yet having left the stem, from anastomosing arcades which unite the leaves as in the Stellatæ, or from the fibres of the petiole, as in the adnate stipules of Rosaceæ, or whether they are in part supplied by bundles directly from the cauline cylinder, as in *Platanus*.

In relation to the tendril in the Cucurbitaceae, he states that its bundles are derived from those which pertain to the axillary bud; that it is therefore not a stipule, but the first foliar appendage of the axillary branch for its fibro-vascular bundles are not disposed like those of stems, but are analogous with those of petioles.

St. Hilaire, Aug.—Leçons de Botanique. 170, 1840. (Quoted by Colomb in Ann. Sci. Nat. (VII), 6 : 28. 1887.)

It is stated that the tendrils of *Smilax* are to be considered as lateral leaflets of a compound leaf.

Agardh, J. G.—Ueber die Nebenblätter der Pflanzen. (Reviewed by Fries and Wahlberg in Flora, 33 : 758–761. 1850.)

Agardh believes that, although stipules have been considered as degenerate appendages of the leaf or modifications of it, they are not at all a part of the leaf because they are formed before it, and must be considered as independent organs. The outer bud-scales and also the protective coverings of the earliest shoots of a plant are a kind of stipule-formation, leading to the conclusion that in the lower part of a shoot or the outer part of a bud the stipule-formation preponderates, and in the upper or inner parts, the leaf-formation, so that often at the lowest nodes the leaf does not develop and at the upper stipules are absent. In *Tussilago* there are special leafy shoots and the flowering shoots are provided with stipules only.

From these considerations Agardh concludes that there are two kinds of appendicular organs instead of one, namely stipules and leaves.

Astaix.—Essai sur la Théorie des stipules, thése de l'Ecole de pharmacie de Paris. 1-25. 1841. (Cited by Clos in Bull. Soc. Bot. Fr. 1 : 302. 1854.)

The conclusion is reached that the leaf is not a primitive appendage of the stipule and that the stipule is nothing more than an appendage of the leaf.

Regel, E.—Beobachtung über den Ursprung und Zweck der Stipeln. Linnæa, 17: 193–234. 1843.

Regel has studied the development of stipules in seedlings and in the growth of individual leaves. He believes, but does not feel ready to assert, that stipules are present in all Angiosperms in the earliest stages of growth. He therefore includes in stipular formations the ligule, ochrea, sheathing petiole and the supernumerary leaves of the Stellatæ. He concludes from his observations:

1. "That all the leafy organs of phanerogamic plants are divided into two entirely distinct formations, the stipular and leaf-formations.

2. "That the stipular formation arises from the base of the meristem tissue of the leafy axis, covering the summit, but always with a longitudinal cleft or one passing transversely across the apex.

3. "That perfect stipules are formed by the occurrence of two, four or more clefts in the original stipular sheath, giving rise to as many stipular leaflets.

4. "That the stipules receive their vascular bundles directly from the stem, and are usually parallel veined because of their forming originally a completely encircling sheath.

5. "That they serve always for the protection of the growing point and of the true leaves, when these are present, during their development.

6. "In all plants, organs adapted for protection belong not to the leaf-formation but to the stipule-formation.

7. "That stipules are to be regarded as a formation preceding the leaf-formation, since they appear before the leaves.

8. "That they belong primarily to a nodal ring distinct from that producing the leaves and situated either above or below it.

From these relations, as regards the leaf, interior and exterior stipules are distinguished.

9. "Interior stipules protect the formation of the following node and leaves. The leaf at the same node develops somewhat earlier or at about the same time.

10. "Exterior stipules develop before the leaf at the same node and therefore protect their own node with its leaf.

11. "As stipules are limited in the time during which they are functional, they lose their significance as soon as this purpose is fulfilled. They do not produce buds in their axils except in cases where true leaves are not developed."

The following statement (p. 227) should be noted. "In some species of *Thalictrum* the membrane rising above the inner margin of the base of the petiole is the analogue of the ligule."

Kirschleger, F.—Flora, 28 : 615. 1845.

The tendril of Cucurbitaceæ is regarded as a normal stipular formation.

Mercklin, C. E.—Entwicklungsgeschiote der Blattgestalten. 1846. (Translated into the French in Ann. Sci. Nat. (III), 6 : 215–246. 1846.)

The statements of Mercklin are contrary to those of Regel. He says, "In all cases the stipules of the developing leaf appear as portions of the lamina; it is only later, during the development and elongation of the petiole, that they become sufficiently separated to be considered as distinct organs. In all simple leaves the stipules never appear at the same time with the first rudiments of the lamina; they develop only with the inferior parts of the lamina including the petiole."

"From my observations of stipules I conclude that in common with the leaflets they owe their origin to the common petiole and are formed later than the leaflets."

Krause, G.—Einige Bemerke über den Blumenbau der Fumariaceæ und Cruciferæ. B. Cruciferæ. Bot. Zeit. 4 : 137–150. 1846.

Stipules in the Cruciferæ are considered (pp. 142–145) and the homology with stipules of the so-called glands at the base of the leaves is established by a careful series of observations upon their development. The glands of the bracts and floral organs are also included.*

*See also Duchartre, Rev. Bot. 2 : 208. 1845-7 and Norman, Quelques Observ. de Morph. Veg. 1857.

Jussieu, Adrien.—Cours d'Histoire Naturelle: Botanique. 108-111. 1852.

Speaking of the leaf-sheath, Jussieu says that "sometimes the vascular bundles converge little by little, and there is a gradual transition from the sheath to the petiole; sometimes the marginal bundles stop after a course varying in length, or are prolonged in another plane than that of the petiole, and then there is a clear distinction of petiole and sheath. Often, however, the parenchyma does not unite the lateral bundles to the central ones which continue in the petiole, and this is the probable origin of many stipules."

Trécul, A.—Sur la Formation des Feuilles. Ann. Sci. Nat. (III), 20: 288-299. 1853.

The usual classification of stipules is given with the addition of extra-foliar stipules to include those of *Nelumbium.* The author says, "In all adnate stipules that I have seen, they do not envelop the leaf to which they belong, but that which comes next after them, and their own leaf is protected by the stipules of the leaf preceding. Under these circumstances the stipules play the same rôle as the sheath, from which they differ very little. We see thus clearly that there is the closest analogy between the formation of adnate stipules and that of a sheath; the analogy is such that it is impossible to distinguish between them in principle." All the forms of stipules, the ochrea, the tendrils of *Smilax* and the ligule of grasses are classed together.

Among the conclusions those relating to stipules are as follows: In basifugal leaf-formation all the parts are formed from below upward, the stipules first of all. In leaves with basipetal formation, the stipules have their origin earlier than the lower parts of the blade and sometimes even before the upper.

Trécul, A.—Vegetation du Nelumbium codophyllum. Ann. Sci. Nat. (IV), 1: 291-298. 1854.

In the seedling of this plant the leaves are in two ranks on the upper and lower sides of the rhizome and each of them is provided with an axillary stipule. In its later stages the leaves of the lower rank are aborted with the exception of the stipule of every second one and in the upper rank every second leaf is represented by the stipule only. The internodes above the stipules which stand alone remain undeveloped so that three stipules are associated with each leaf, one axillary and two extra-axillary.

One of these last is on the upper side of the rhizome external to the leaf, the other on the lower side.

This paper was presented before the Botanical Society of France, May 24, 1854. M. Ad. Brongniart took part in the discussion which followed. He agreed with Trécul in his conclusions and closed with the statement that "this arrangement recalls that of certain buds in which the scales result from the stipules of leaves of which the petiole and blade are alike aborted." M. F. J. Lestiboudois remarked that "to decide whether stipules are an integral part of the leaf, it is necessary to study them anatomically. In other plants the same fibro-vascular bundles are distributed to the leaf and stipules. Stipules should therefore be regarded as appendages of the leaf."

Clos, D.—Considerations sur la Nature du prétendu Calicule ou involucre des Malvacées. Bull. Soc. Bot. Fr. 1: 289–303. 1854.

The stipular nature of the parts of the involucre or exterior calyx in the Malvaceæ is asserted contrary to the views of Aug. St. Hilaire (Leçons de Bot. 372. 1840) and the term *stipulium* is suggested as applicable to it.

Clos, D.—Du Stipulium chez les Géraniacées, les Légumeneuses et les Rosacées. Bull. Soc. Bot. Fr. 2: 4. 1855.

The term *stipulium* is applied to the exterior calyx of the Malvaceæ and the involucre of the umbel of some Geraniaceæ. In the Cistaceæ the bractlets of the calyx are wanting in exstipulate species.* In many of the Leguminosæ and Rosaceæ the bracts are evidently formed by stipules.

Clos, D.—La Vrille des Cucurbitacées, Organé de Dédoublement de la Feuille. Bull. Soc. Bot. Fr. 3: 545–548. 1856.

The different theories regarding the tendril in the Cucurbitaceæ are briefly stated. They have been considered to be roots; abortive peduncles by Tassi; stipules by De Candolle, Stoks and Aug. St. Hilaire; leaves by Gasparini, Seringe and Braun; degenerate branches by Meneghini; superfluous branches by Link; terminal branches of the axis as in Vitaceæ by Fabre; partly leaf, partly branch by Naudin. Clos concludes that the tendril arises by a division of the leaf, three fibrovascular bundles entering the leaf when there is no tendril and two when the tendril is present and receives the third bundle.

*See also Aug. St. Hilaire. Leçons de Bot. 326 and 371. 1840.

Clos, D.—Les Vrilles des Smilax ni Folioles ni Stipules. Bull. Soc. Bot. Fr. 4: 984-987. 1857.

A summary is given of the literature pertaining to the tendrils of *Smilax*. They are considered as representing two lateral leaflets of a compound leaf by von Mohl (Ueber den Bau und das Winden der Ranken und Schlingpflanzen, 41, 1827), Lindley (Introd. to Botany, Ed. 2, 118, 1835), Link (Elem. Phil. Bot. Ed. 2, 1: 478, 1837), St. Hilaire (Leçons de Bot. 170 and 854, 1840), Le Maout (Atlas de Bot. 23, 1846) and Duchartre (Art. vrille in Dict. Univ. Hist. Nat.).

Mirbel (Élém. de Physiol. et de Bot., 2: 680, 1815), Treviranus (Physiol. der Gewachse. 2: 138, 1838), Seringe (Élém. de Bot. 175, 1841), De Candolle (Theorie Élément. Ed. 3, 321, 1844), Trècul (Ann. Sci. Nat. (III), 20: 295, 1854) and Lestiboudois (Bull. Soc. Bot. Fr. 4: 745, 1857), believe these organs to be stipular tendrils. It is the opinion of Clos that they are neither leaflets nor stipules, but a double lateral prolongation of the cellulo-vascular elements of the petiole.

Rossman, J.—Beiträge zur Kentniss der Phyllomorphose. 1857. (Cited by Clos in Bull. Soc. Bot. Fr. 26: 192. 1879.)

Rossman considers the problem of the nature of stipules, and from a study of bud-scales arrived at his conclusions. He figures the passage from bud-scales to leaves in *Ribes sanguineum* Pursh, *Prunus Padus* L., *Spiræa sorbifolia* L., etc. He notes the presence in the bud-scales of three median veins, separated at the base and joining one another at the apex, where the petiole will originate. The lateral parts of the scale outside of these three nerves he believes to represent the stipules which show themselves at the appearance of the blade in two little points at the apex.

Hanstein, J.—Ueber gürtleformige Gefässstrang-Verbindung in Stengleknoten dicotyler Gewächse. Abhandl. der Akademie der Wissenschaften zu Berlin, 1857 : 77-98. 1858.

The vascular nodal girdle of the Stellatæ is treated of at length. It is shown that from this girdle arise the bundles that supply those leaves of the whorl which are really stipules, and in some cases also the veins of the lateral parts of the true leaves. Similar nodal girdles are shown to exist in other families of plants, notably in *Sambucus*, *Valeriana*, *Verbena*, *Dipsacus*, *Scabiosa*, *Dahlia* and *Silphium*. In *Sambucus Ebulus* L. the girdle sends off vascular branches to true stipules. In the majority of other cases if branches arise they enter the margins of the petioles or the interfoliar portions of connate leaves. In *Platanus* and *Liriodendron* with alternate leaves, each of which receives seven vascular bundles, a similar girdle is shown to pass around the stem posterior to the leaf, and is there joined by another small leaf-trace bundle. From this girdle arise a part of the stipular veins, the others being branches of the sixth and seventh leaf-trace bundles.

Clos, D.—Sépales Stipulaires. Bull. Soc. Bot. Fr. 6: 580-589. 1859.

It is argued from the similarity of the sepals to the divisions of the involucre (stipulium) and also to the stipules of the fully developed foliage leaves which is frequently observed, that they represent stipules. This is held to be true in many Geraniaceæ, Malvaceæ, Begoniaceæ and Cistaceæ. In concluding Clos adds the theoretical consideration that "whether or not stipules are admitted to be organs different from the leaf, analogy seems to demand that in some cases at least they should participate in some degree in floral formation."

Cosson, E.—Note sur la Stipule et la Préfeuille dans le Genre Potamogeton. Bull. Soc. Bot. Fr. 7: 715-720. 1860.

"The stipule in *Potamogeton* is very closely like the first leaf of one of the branches. It is homologous with the ligule of the Gramineæ and Cyperaceæ and is constituted by a single organ, not by two united by their margins."

Eichler, A. W.—Zur Entwicklungsgeschichte des Blattes. 22-31, 1861 (Cited by Martin Franke in Bot. Zeit. 54 : 45. 1896.)

Stipules are said to arise without exception as a product of the leaf base of the primordial leaf. This mode of origin of the stipules is their chief characteristic. Their form, their more or less foliaceous condition and their persistence are secondary.

In individual leaf development in the Stellatæ, the whorl originates in a uniform ring about the growing point. Then arise two opposite prominences in the ring. These develop into the true leaves. After them appear two smaller prominences on each side of the stem between the first. These are the stipules. According to the species they develop separately, forming six-leaved whorls, or grow together giving origin to four-leaved whorls.*

*With this view Göbel agrees (Schenk's Handbuch der Botanik 3 : 230. 1884), except that he does not distinguish the time of appearance of the different parts of the whorl.

Where a larger number of leaves occurs, an additional prominence for each arises between the original stipular prominences.*

Cauvet, D.—Probabilité de la Presence des Stipules dans quelques Monocotyedones. Bull. Soc. Bot. Fr. 12 : 241. 1865.

A number of cases are considered and the conclusion drawn that very probably some Monocotyledones are provided with stipules, but the difference in their form and position has caused them to be considered as another kind of organ.

Meehan, Thomas.—On the Stipules of Magnolia and Liriodendron. Proc. Acad. Nat. Sci. Phila. 114-116. 1870.

Mr. Meehan argues for the origin of the stipules of *Magnolia* as lobes of the lamina similar to the auricles which occur in *M. Fraseri* Walt. by a union of the auricles with the upper surface of the petiole, and a subsequent adnation of their margins and separation from the lamina. He says, " It is scarcely possible to avoid the suspicion that the stipules of *Magnolia* are not formed like the stipules of most plants which are perhaps leaf portions which have never been well developed, but rather are the tolerably well developed side pinnules of a trifoliate or deeply auricled leaf."

Speaking of observations upon the flowers of *M. fuscata* Andr., of East India, the following interesting statement is made : " This observation confirms the views of some botanists as I have learned from Professor Asa Gray, that it is by metamorphosis of the petiolar and stipular parts, rather than by modifications of the leaf-blade, that petals are formed."

Duval-Jouve, J.—Sur quelques tissues de Joucées, etc. Bull. Soc. Bot. Fr. 18 : 231-239. 1871.

The presence of the ligule in the Juncaceæ is treated of. To quote the author, " If in certain species the ligule is so reduced that it appears to be lacking between the separated auricles at the apex of the sheath, in most others these auricles are united by a true ligule, as pronounced as that of grasses, either entire or cleft at the middle."

Dutaily, G.—Sur les variations de structure de la ligule des Graminées. Bull. de la Soc. Linnéene, 170. 1878.

*F. Pax (Allgemeine Morph. der Pflanzen, 100. 1890) says, when there are more than six parts to the whorl, the additional parts must have their origin in a division of the blades of the stipules.

It is argued from the presence of a median vein in the ligule of some of the grasses in which this organ is supplied with vascular support that it cannot be formed of two stipules grown together.

Hilburg, C.—Dissertation über den Bau und die Function der Nebenblätter. (Reviewed by F. Hildebrand in Flora, (II), 36 : 161-167. 1878.)

The general neglect of the subject of stipules and the timeliness of this dissertation is referred to by the reviewer.

The functions of stipules as protecting organs are discussed. They are considered under the heads of (1) those protecting the buds in winter, (2) those protecting the growing parts in the spring, (3) those which serve as protection against insects and other animals, (4) those which serve as well the function of assimilation.

The adaptation of most stipules in their form and manner of growth to the special function they are intended to fulfill and the apparent lack of function in others is remarked upon.

Clos, D.—Des Stipules et de leur rôle à l'infloresence et dans la Fleur. Mem. Acad. Sci. Toulouse, (VII), 10: 201-317. 1878.

This paper is the first part of an extended consideration of the subject of stipules. It deals with their occurrence in the families of plants and their importance in classification on account of the great variety of their characteristics.

Clos, D.—De la part des Stipules a l'infloresenoe et dans la Fleur. Comptes Rendus, 87: 305-306. 1878.

The stipular nature of the sepals in *Geranium*, *Helianthemum*, *Begonia*, *Oxalis*, *Alchimilla*, *Viola* and many other genera in different families is maintained.

Dixon, Alex.—On the stipules of *Spergularia marina.* Journal of Botany (Trimen), 7: 316. 1878.

Attention is called to the anomalous connation of the stipules of *Spergularia marina* Griseb. exterior to the petioles of the opposite leaves.

Clos, D.—Des Stipules considérées au point de vue morphologique. Bull. Soc. Bot. Fr. 26: 151-155. 1879.

Under this title a summary of the opinions of botanical authorities as to the true nature of stipules is given and the different theories are briefly discussed.

Various leaves have been considered as stipules, for example the primary leaves of *Asparagus* (Dutrochet), the first leaves of the branches of *Verbena aphylla* Gill & Hook. (Hooker, Bot. Misc. 1: 116. 1830) and of the Piperaceæ (C. DeCandolle, Mém. sur les Piper. 18–19, 1866), and the first two leaves of the axillary buds of many Solanaceæ.

The appendages sometimes accompanying the leaf in some Convolvulaceæ, as *Ipomea stipulacea* Sweet., have been considered as stipules (Jacquin. Pl. Hort. Schoenbr. Descr. et Ic. 2: 39. 1797).

Many have regarded stipules as leaflets, as for example in *Vibernum* (Baillon, Adans. 1: 372. 1860), and the lower leaflets in many plants have been taken for stipules, as in *Cobœa scandens* Cav. (Blume. Rumphia 3: 142. 1837), and *Lotus tetraphyllus* Murr. (Linnæus, Trinius, E. Meyer, Fischer.)

In 1844 Wydler declared that stipules belong to the sheath and cites examples of transition between the two kinds of organs in the Rosaceæ, Polygonaceæ, Leguminosæ, etc. Stipules, in connection with the sheath have been ascribed to *Ranunculus*, *Isopyrum* and *Thalictrum* by Lloyd (Fl. de l'Ouest de Fr. Ed. 2, 1868), to *Caltha* by Wydler, Kützing (Grundz. der phil. Bot. 684, 1851–52) and Hooker. They have been recognized in the scales of the stems of the Aroids.

The so-called "decurrences" of leaves do not differ anatomically from stipules and are to be considered as identical with them, as for example in *Crotalaria*.

The tendril of the Cucurbitaceæ has been regarded as a stipule by Seringe (Mém. Soc. Hist. Nat. Genèv. 3: 1–31. 1825), De Candolle (Organ. Veg. 1: 336. 1827), Kirschleger (Flora, 28: 615. 1845), Stoks (Ann. Nat. Hist. 1846), Payer (Elém. de Bot. 53. 1857–58), Parlatore, etc. Those of *Smilax* have been so considered by Cauvet (Bull. Soc. Bot. Fr. 12: 241. 1865), but are looked on by Clos as "simple prolongations of the fibro-vascular bundles of the petiole without morphological signification."

The spines of the orange are considered as stipules by Du Petit-Thouars (Cours de Phytol. 47. 1820). Clos regards them as branches and those of *Amaranthus spinosus* L. as leaves, though they are considered stipular by Lamarck (Encyc. Meth. 2: 118. 1786). *Ribes* shows stipular spines in some species. The spines of *Xanthium spinosum* L. mentioned by Sachs as occupying the place of stipules, Clos regards as representing pistillate flowers. He looks with disfavor on the doctrine that the glands at the base of the leaves in Resedaceæ, Cruciferæ, *Epilobium*, *Lyth-*

rum and some Euphorbiaceæ and Balsaminaceæ as well as the axillary hairs in some Portulacaceæ are stipules.

Clos, D.—Indépendance, developpement, anomalies des stipules; Bourgeons a écailles stipulaires. Bull. Soc. Bot. Fr. 26: 189-193. 1879.

Stipules have been regarded as appendages of the leaf by Du Petit-Thouars (Cours de Phytol. 46, 1820), Aug. St. Hilaire (Leçons de Bot. 189, 1840), G. St. Pierre and F. J. Lestiboudois.

Clos agrees with Agardh in considering stipules as independent organs, giving as his reason that frequently in the Rosaceæ, Leguminosæ, Malvaceæ, Geraniaceæ, etc., the stipules persist alone, the leaves having completely disappeared, whether in the infloresence or at the base of stems and branches.

Under the head of the development of stipules the conflicting opinions of Mercklin and Trécul as to their time of appearance in relation to that of the leaf-blade is referred to. Agreement with Trécul is indicated and the evidence is not considered sufficient as a basis for the theory of the autonomy of stipules on the ground that they appear before the leaf-blade.

In consideration of stipular bud-scales reference is made to their recognition by Linnæus (Phil. Bot. Ed. 3, 52. 1790), Adanson (Familles des Pl. 246, 1763), De Candolle (Ann. Sci. Nat. (III), 5: 321, 1846)* and Lindley (Veg. Kingdom, 283, 1846).

Göbel, K.—Beiträge zur Morphologie und Physiologie des Blattes. Pt. I. Die Niederblätter. Bot. Zeit. 38: 753, etc.—845. 1880.

This extended treatise deals with bud-scales and the scales of subterranean parts of plants and their homologies with leaves. Speaking of the primordial leaf Göbel says, "it is divided into two parts, a stationary zone which takes no farther part in the leaf-formation and a part out of which the lamina is developed." He calls these parts respectively the leaf-base and upper-leaf and states that the petiole arises after the formation of the blade and is inserted between the two parts.

Bud-scales are regarded as modified foliage-leaves and divided into those formed from the blade (*Syringa*), those formed by the leaf-base (*Æsculus*, *Prunus*), and those consisting of stipules (*Liriodendron*, *Quercus*). In *Prunus*, etc., the formation of the bud-scales by the union of petiole and stipules is denied on the ground that the continuous separate development of the petiole and stipules can be followed.

*See also Org. Veg. 2: 213. 1827.

The scales of rhizomes are divided into those formed by a development of the leaf-base (*Dentaria*, *Chrysosplenium*) and those formed by a modification of the upper-leaf (Labiatæ, Onagraceæ).

Colomb, G.—Note sur l'ochrea des Polygonées. Bull. Soc. Bot. Fr. 33: 506–507, 1886.

"The ochrea of the Polygonums is a complex organ formed of two parts: one opposite the leaf, the leaf-sheath, the other in its axil and detached from the petiole. This is a ligule." "Practically the same conditions prevail in the Gramineæ as in *Polygonum* with the difference that in the former the sheath proper is greatly developed and little prolonged beyond the insertion of the blade, while in the latter, the sheath proper remains short and is much prolonged above the petiole. By union with the ligule it forms an ochrea. So considered the ochrea is not peculiar to the Polygonaceæ. It is found also in *Ficus* and *Magnolia*, establishing the transition between the ochrea and stipules properly so called.

Vuillemin, P.—Apropos d'une recent communication de M. Colomb. Bull. Soc. Bot. Fr. 34: 141–142. 1887.

Commenting on the preceding paper, the author says that the leaf is primitively unifasciculate. The concrescence of a verticil of elementary leaves, such as occurs in the fossil *Asterophyllites*, gave a sheath analogous to that of *Equisetum*; the bundle of one of these elementary leaves becoming predominant and functioning as a midvein gave rise to an aggregate leaf, the first stage of a high differentiation. In this way the origin of the leaf-blade in *Polygonum*, *Platanus*, etc. is explained, while the ochrea, the homologue of the sheath of *Equisetum*, remains as a vestige of the primordial state.

Kronfeld, M.—Ueber die Beziehung der Nebenblätter zu ihrem Hauptblatte. Verhand. der Kais.-Konig. Zool.-Bot. Gesellschaft Wien. 37. Abhandl. 69–79. 1887.

The author has made investigations experimenting upon a large number of plants, by the removal of the lamina of the leaves at the earliest possible stage of development, in order to observe the effect upon the development of the stipules and so determine their physiological relation to the leaf-blade. Only in exceptional cases was the ultimate size of the stipules increased, and those where the stipules were normally foliaceous.

Colomb, G.—Recherches sur les stipules. Ann. Sci. Nat. (VII), 6 : 1-76. 1887.

This paper is the result of an exhaustive anatomical study of stipules and their homologues. The results obtained are of great interest and value. They are admirably summed up at the close of the paper as follows :

"When a leaf is sheathing, the sheath may be prolonged in a ligule situated above the point of insertion of the blade upon the sheath.

"In this organ three regions may be recognized :

"1. The lateral regions into which the marginal bundles of the sheath are merely prolonged. These regions naturally do not exist if all the bundles of the sheath enter into the leaf.

"2. The stipular regions, the bundles of which arise from a doubling of the last bundle of the sheath entering into the leaf.

"3. The axillary region, which unites the two stipular regions, a lamina, usually of parenchyma, but which may receive bundles arising from the internal doubling of those bundles of the sheath which become petiolar.

"The sheath may be reduced even to complete disappearance without a consequent disappearance of the ligule.

"1. If the ligule is complete with its three regions, I give it the name of an axillary ligule.

"2. If the stipular and axillary regions only persist, the sheathing regions having disappeared, we have an axillary stipule.

"3. If finally the axillary region divides into two halves, right and left (which would not be remarkable, considering its purely parenchymatous nature), the stipular regions exist alone at the base of the petiole, and we have then stipules properly so-called.

"Stipules and the ligule are then organs of the same nature, between which it is possible to find all forms of intergradation, the stipule being a portion of the axillary ligule.

"When, finally, the manner of origin of the bundles of the stipule is studied, we arrive at the following definition of the organ: An appendage inserted on the stem, at the base of the leaf, all the bundles of which arise exclusively from the corresponding foliar bundles."

Each of the tendrils of a leaf of *Smilax* is characterized as a demi-ligule, the "stipule" of *Potamogeton* as a ligule identical with that of grasses, the ochrea of *Polygonum* and *Platanus* as axillary stipules, the stipules of *Ficus elastica* Roxb. and *Magnolia grandiflora* L. as axillary ligules.

Ward, L. F.—The Paleontologic History of the Genus Platanus. Proc. U. S. Nat. Mus. 11: 39–42. 1888.

Professor Ward says (p. 41) in speaking of the fossil leaves of *Platanus basilobata* Ward, of the Yellowstone valley, that some of those found had "a remarkable expansion at the base of the blade, projecting backward on the leaf-stalk and having two to five lobes or points.

"These expansions are to be interpreted as evidence that the leaves all belong to *Platanus* or to some extinct ancestral type of the genus, since something quite analagous to them is found in our American plane-tree. The ordinary leaves of this tree are, it is true, destitute of basilar expansions, but those on young shoots, and sometimes those on the lower or non-fruit-bearing branches of trees exhibit this peculiarity.

"In place of this backward expansion of the blade many sycamore leaves have an appendage similar in shape at the base of the leaf-stalk, as though the once basilar appendage had been separated from the blade and crowded down the petiole to its point of insertion." This is shown in a short-petioled, wedge-shaped leaf from a young shoot of *Platanus* corresponding to the fossil form of *Platanus appendiculata* Lesq. from the auriferous gravels of California. The indication is that "the constriction seen in the fossil forms between the blade of the leaf and the appendage would seem to represent the beginning of this process of detachment."

Ward, L. F.—Origin of the Plane-Trees. Am. Nat. 24: 797–810. 1890.

The same cases as those in the preceding paper are discussed, the appendages in *Platanus appendiculata* Lesq. being described as stipular, while those of *P. nobilis* Newb. and *P. basilobata* Ward are not so considered.

Lubbock, Sir John.—On Stipules, their Form and Function. Jour. Linn. Soc. Lond. 28: 217–243. 1890.

"The primary function of stipules seems to be to protect the bud. In other species, however, they serve as accessory or deputy leaves. Their protective function is confirmed by the fact of their early fall. Some are more persistent than the leaves and protect the leaves of the following year.

"When-stipules are present [in *Helianthemum*] the petiole is always very narrow, semiterete, and tapered to the base. Where they are absent the leaf is often sessile and, whether or not, its base is always dilated and concave on the inner face, completely enclosing the bud up to a certain stage of its development."

The presence of stipules in the lower imperfect leaves of *Ailanthus glandulosa* Desf. is noticed, though the family of the Simarubiaceæ has been described as exstipulate. In *Ribes sanguineum* Pursh. the bud-scales are described as consisting of the dilated base of the petiole, the lamina being represented by a small black point. "One or two succeeding leaves bear a small lamina sessile on the sheath, which is wholly adnate to the thin dilated base of the petiole and membranous, especially outside of the three vascular bundles. The next one or two have a well-developed lamina, and the sheaths partly separated from the petiole and corresponding to stipules. Farther up the stipular sheaths are shorter and wholly adnate to the petiole."

The form and function of the stipules in a large number of species are described.

Lesquereux, L.—U. S. Geol. Surv., Monog. No. 117: Geology of the Dakota Group. 1892.

Well-developed stipules of a species of *Betulites* from Kansas are described (p. 65) as having been found in their original connection with the leaf, and the discovery of leaves of a *Cratægus* with large undoubted stipules, from the Devonian of Wyoming is mentioned (p. 254). Speaking of a leaf of *Aspidiophyllum* (p. 232). Professor Lesquereux says, "the basilar appendage or pelta is like a primordial form of stipules, as in *Platanus basilobata* Ward of the Laramie group of Wyoming, *P. appendiculata* Lesq. of the auriferous gravels of California and definitively in *P. occidentalis* L. of the living flora."

Henslow, Rev. George.—On a Theoretical Origin of Endogens from Exogens. Jour. Linn. Soc. Lond. 29: 485–528. 1893.

The absence of vascular bundles in certain stipules is noted (p. 494).

Hollick, Arthur.—Wing-like Appendages on the Petioles of *Liriophyllum populoides* Lesq. and *Liriodendron alatum* Newb. Bull. Torr. Bot. Club, 21: 467–471. 1894.

These peculiar wing-like appendages are described and figured. Their similarity to the appendages in fossil species of *Platanus* as described by Professors Lesquereux and Ward is mentioned, and the probability suggested that we have here an explanation of the origin of the stipules of *Liriodendron Tulipifera* L. in the same manner as that indicated for those of *Platanus occidentalis* L. by Professor Ward. The presence of an unwinged portion of the petiole next to the blade in what is evidently the mature form of the leaves of *Liriophyllum*, and its absence in the immature ones is mentioned as tending to confirm the theory.

In commenting on this paper, the *Botanical Gazette* (19: 515, 1894) says, "The phyllopodium is to be regarded as an axis which has a tendency to develop wing-like appendages at any portion, notably, of course, in the epipodium. If stipules are branches of the hypopodium their origin has simply to do with the branching of that part of the phyllopodium, without any reference to the method of winging found in other regions."

Lubbock, Sir John.—On Stipules, their Form and Function. Pt. II. Jour. Linn. Soc. Lond. 30 : 463–532. 1894.

This paper is a continuation of the author's former publication. The presence of stipels in *Sambucus Ebulus* L. is noticed. The membranous protective margins of the sheath in *Thalictrum aquilegifolium* L. and the "membranous stipular processes at each trifurcation of the lamina" are mentioned, the latter "appearing to differ somewhat in their origin from the primary sheath." In treating of *Ranunculus aquatilus* L., the author says, "The terminal bud is enclosed by the stipules of the two uppermost expanded leaves. The developing leaves push their way out at the apex of the stipular sheath. Similarity of conditions have therefore developed in the aquatic Ranunculaceæ, an arrangement very similar to that of the Potamogetons."

The following remarks are of particular interest: "In *Magnolia glauca* L. the winter bud is covered by a pair of connate stipules adnate to a petiole that is less than half their length. Succeeding leaves are perfect, and the stipules are two or three times as long as the petiole, the free portions being connate by both edges, like a candle extinguisher, over the bud, so that the leaf appears to spring from the back. As they are adnate to the petiole, there is some reason to assume that the stipules once formed a sheath pure and simple to the leaf of some ancestral form."

Franke, Martin.—Berträge Zur Morphologie und Entwioklungsgeschichte der Stellaten. Bot. Zeit., 54: 33-60. 1896.

In the part of this paper which treats of the development of the leaf-whorl the author agrees with Eichler that the stipules originate later than the principal leaves. But he says that in the species having four-leaved whorls never more than four prominences arise to develop into the parts of the whorl, and that if the parts number six or more, there is a distinct prominence for each. In the last case the supernumerary stipules first make their appearance in the course of development of the whorl a little later than the first pair of stipules.

Hollick, Arthur.—Appendages to the Petioles of Liriodendra. Bull. Torr. Bot. Club, 23: 249. 1896.

The author, referring to his former paper, describes and figures some abnormal leaves of *Liriodendron* collected from saplings, seedlings and new shoots from old stumps. One in particular of these leaves is of interest on account of its similarity to the fossil leaves of *Liriophyllum populoides* Lesq. both in the form of the lamina and especially in having a short petiole with broadly winged margins which extend from the base of the petiole and connect with the base of the leaf-blade.

The question is put whether in this case we have "stipules adnate to the petiole and leaf-blade, or portions of the leaf-blade which are acting the part of stipular appendages."

Such, in brief, is the import of what has been written on the subject of stipules, so far as I have been able to learn. The results of my own observations are not at variance to any very considerable degree with the opinions of most of the botanists who have studied the subject carefully, as will appear from the following exposition of my investigations and the conclusions at which I have arrived. To these I shall pass at once, deeming unnecessary farther comment on previous writings, except such as the statement of my results may imply.

The Nature and Origin of Stipules.

Though it is not part of the purpose of this paper to discuss the problem of the phylogeny of the plant world, it is nevertheless necessary in order to define our field of inquiry to make a brief statement concerning the probable relationship of the higher forms, namely of those in which foliar organs are developed, including in the widest interpretation the Characeæ, Bryophyta, Pteridophyta and Spermatophyta.

As, in the Characeæ and Bryophyta, the plant body represents the gametophyte stage of development, there can be no homology of the leaves of these plants with those of the Pteridophyta and Spermatophyta in which the plant body is the sporophyte. For this reason the so-called stipules of the Charas, together with the basal lobes or saclike and straplike appendages of the leaves of many Hepaticæ need not be taken into consideration.

Accepting the general theory of evolution in nature, we must admit that the origin of all the higher plants is algal, but just what the relationship of the Pteridophyta to the Spermatophyta may be is still an open question. The same is true in greater or less degree of the affinity of the Monocotyledones, Dicotyledones and Gymnospermæ in the latter group.

This question of relationship is of considerable importance in connection with the problem before us as determining the homology of the foliar appendages in the several groups. The evidence in support of the doctrine of the common origin of all the Angiospermæ is particularly strong and may be considered as conclusive. But the relationship of the Gymnospermæ to the Angiospermæ is more remote, and that of the Pteridophyta still more so-and, though there are many points of resemblance, the similar characters may be cases of parallel development rather than indications of a common origin. It is my present opinion, however, that the Gymnospermæ sprang from some generalized hetero, sporous Pteridophyte,* that the early Angiospermæ were differentiated from related forms, and that therefore, the foliar organs in the three groups may be considered as homologous. But this homology can apply to the leaves of Pteridophytes in a very general way only, namely, to such undifferentiated forms of leaves as the ancestors which gave rise to the early Gymnospermæ and Angiospermæ may be supposed to have had. While, therefore, the foliar organs in the three classes are to be considered homologous in their origin, they cannot be so considered in their differentiation and the evolution of leaf-forms in the Pteridophyta and Gymnospermæ, though analogous in many points to their evolution among the Angiospermæ, should be regarded as independent. We may then consider the "stipule" of the Ophio-

*See Campbell, Mosses and Ferns, *300. 1895.*

glossaceæ, Marrattiaceae and Osmundaceæ and the "ligule" of *Selaginella* and *Isoetes* as special developments and as properly placed in a separate category from the appendages bearing these names among the Angiospermæ. The Gymnospermæ present nothing to represent either stipule or ligule and we have left for our special consideration the ligule, stipule and their homologues as they occur in the various groups of the Angiospermæ only.

Having thus defined our field, we should have, for the consideration of the problem before us, some conception of what sort of plant the earliest Angiosperm was. In the absence of geological evidence this conception must be purely hypothetical and, basing it on a generalization which would admit of the differentiation from it of all the varied forms of the modern group of Angiosperms, we can see that it must have been a plant of very simple organization indeed. For our present purpose we need not concern ourselves with any other organs of this primitive Angiosperm than the leaves which, from the point of view of the proposed generalization, must be conceived of as hardly more than the bare rudiments of leaves, mere sheathing scales at the nodes of the plant, serving slightly, if at all, the function of assimilation which was still subserved, as in its ancestors, by the general surface of the plant, but confined chiefly to that of protection. The primitive leaf was probably parallel-veined or approximately so, giving rise in its earlier differentiation to the parallel-veined leaves of the Monocotyledones. The geological evidence indicates that these appeared before the Dicotyledones* which must have sprung from them later at one or more unknown points, and netted-veined leaves are of a more recent evolution. Consequently the tendency of aquatic Dicotyledones to revert toward monocotyledonous structure is rather a case of atavistic degeneration than an indication of the origin of Monocotyledones from Dicotyledones in ancient times through the effects of aquatic habit.†

Now, as advance in evolution proceeded, the need of greater assimilative capacity arose and, as the foliar organ was the one best

*Professor L. F. Ward. Sketch of Paleobotany. Fifth Ann. Rep. U. S. Geol. Surv. 448, 1885. Professor A. C. Seward, on the contrary, does not believe that we have satisfactory evidence of pre-Cretaceous Monocotyledones. Notes on the Geologic History of Monocotyledones. Annals of Botany, 10: 220. 1896.

†See Rev. George Henslow. Jour. Linn. Soc. Lond. 29: 485-528. 1893.

adapted for specialization in this direction, it was the one upon which the office devolved. Every botanist knows what an endless variety of forms and special adaptations of particular foliar parts have arisen in the course of evolution which was inaugurated when this setting aside of the leaf to bear in future the weight of the assimilative function took place, or rather when this additional function was placed upon it, for the old protective function has always been retained, though it has become less noticeable as the new function has overshadowed the old.

There has been in the line of vegetable descent a progressive development of the foliar organ, and a history of this development, together with that of other organs, if it were obtainable, would give us a complete phylogeny of the flowering plants, and leave no morphological problem unsolved,* but as the geological record is very incomplete, and we have in the lower Cretaceous an already well developed and much differentiated angiospermous flora of the earlier history of which almost nothing is known, we must seek other sources of information in determining the homologies of parts. At this juncture we may safely follow the example of the zoölogists and turn to embryology for the evidence which geology, as yet, refuses to give except in fragments Among animals, as the phylogeny and ontogeny are found to parallel one another, so we may feel confident they will be found to do among plants when the geological record shall be more completely unearthed.

It has become a well established part of the theory of evolution that each individual organism epitomizes more or less fully in its development the historical steps in the evolution of the type to which it belongs.† By the application of this law of re-

* "On this same view of descent with modification most of the facts in morphology become intelligible, whether we look to the same pattern displayed by the different species of the same class in their homologous organs, to whatever purpose applied, or to the serial and lateral homologies in each individual animal and plant." *Charles Darwin*, Origin of Species, 1859. Am. Ed. 6, 2. 264. 1889. See also p. 239, *et seq.*

† This theory, known as Von Baer's law, was promulgated by that scientist in his Ueber Entwicklungsgeschichte der Thiere, 224. 1828-37.

See also F. M. Balfour. Comparative Embryology. Ed. 2, 1: 2. 1885.

Opposed to this law is Adam Sedgewick. On the Law of Development commonly known as Von Baer's Law. Quar. Jour. Mic. Soc. (II), 36: 35. 1894.

capitulation to the development of plants we may arrive at valuable and trustworthy conclusions. The question would at once be asked, where shall the embryology of the flowering plants be studied, and the answer would naturally be, in the development of the seed in the ovary. And here indeed, we trace in outline an epitome of the course of development from the simple unicellular organism, represented by the fertilized egg-cell of the ovule to the highest thalloid form, the "embryo," with its bud (plumule) which is to develop into the full-formed plant perfect in all its parts. For a summary of the further development of the Angiosperms we must look to the growing bud which is the essential reproductive organ of the sporophyte stage and, doubtless, a more primitive one than the seed, for it is common among the more ancient Pteridophytes and these have no seed. The embryo of flowering plants does, however, correspond pretty closely to that advanced stage of development of the egg-cell of some of the higher Pteridophyta now generally spoken of as the embryo and should be regarded as a young plant in a state of arrested development. In this state it remains during a period of rest, in a highly specialized environment in the seed, awaiting favorable conditions for farther growth. Because of the highly specialized environment of the embryo, it has itself become correspondingly specialized and has been variously modified to suit the special conditions of its surroundings. The plumule cannot then be regarded as any longer representing a primitive form of bud and its development is so altered by secondary modifications that the series of phylogenetic changes is disguised and imperfectly represented. A parallel case is found among animals in the development of Echinoderms, in which the changes that have taken place through secondary modification are so great that the relationship of the group cannot be satisfactorily determined by developmental evidence.

It is not then in the seedling that we should expect to find representations of primitive leaf-forms, though later ancestral forms paralleling those of fossil leaves, of which we shall speak, are found in some seedlings, as for example in *Liriodendron.* But it is in the growth of the less specialized buds developing under more primitive conditions that we should expect to find them. Such buds are the ordinary leaf-buds of perennial plants, and especially those occurring on basal and subterranean portions which I conceive to develop under conditions somewhat more primitive than is the case with aërial buds. But in both these the recapitulation of the development of leaf-forms may be traced with a considerable degree of confidence, from the primitive sheathing protective scale to the most highly differentiated and complex of modern leaf-forms.

It is at this point that the fragmentary geological evidence sheds its strongest light on the problem under consideration. In the Cretaceous and Tertiary floras which preceded the modern, the present degree of differentiation had not as yet been attained and but few modern species made their appearance before the close of the Tertiary.* The species, however, which immediately preceded those which now exist were very closely related to them, being their immediate ancestors, and differed from them only in showing a somewhat lower degree of differentiation, and their leaf-forms are accordingly more primitive than those of the existing species which have descended from them.

Now it is a well-established fact that the lower leaves of young branches and shoots, and especially of those which spring from the stumps of felled trees, are frequently unlike the adult forms which occur higher up and bear a close resemblance to the fossil leaves of extinct species, so close indeed, as oftentimes to be indistinguishable from them. This is strong evidence in favor of the doctrine that the lower foliar organs represent not reduced leaves, as botanists have commonly supposed,† but the primitive foliar organs, and that in an ascending series from the lowest scale to the mature adult leaves of the upper part of the stem, giving a more or less perfect summary of the phylogenetic development of the foliar organ from the most primitive type upward to the most highly differentiated.‡ In other words, a single stem may represent the whole phylogeny of the foliar organs of its type. It is true that there are simple leaf-forms which have become so

*Our modern species of *Corylus* are recorded from the Eocene by Professor J. S. Newbury. Later Extinct Floras of North America. Ann. N. Y. Lyc. Nat. Hist. 9:59–60. 1868.

† See DeCandolle. Org. Veg. 2:212. 1827.

‡ "Most modern botanists now regard the varying forms of leaf seen on young shoots and near the base of trees as valuable hints at the probable stages through which the final forms have passed in the history of their development." Professor L. F. Ward. Proc. U. S. Nat. Mus. 11:41. 1888.

by reduction but, as an organ cannot be reduced until it has been developed, these are to be looked for above and not below the perfect leaves, and are found in bracts, involucral scales and the parts of floral envelopes, reduction taking place in inverse order to the course of development, and only the most primitive structure, the simple sheath, persists in the petals of most flowers. Reduced leaves are also common in parasites, and in the flora of desert regions as is well illustrated in some of the Leguminosæ of Australia the leaves of which are little more than spines, or are developed into bladeless phyllodia, while in the seedlings the ancestral pinnate or bipinnate forms occur.*

We thus have shown in each season's growth of a plant, though not clearly in annuals because disguised in the seedling, a more or less complete series of foliar organs which may for illustration be compared with the vertebrate series among animals, the lowest leaf-scales being comparable in degree of development to the simple structures of the fishes and the most highly developed leaves to the complicated ones of mammals. Each leaf in the series is equally perfect for the function it is intended to perform, but the lowest of a lower type of organization, as are the fishes, and representing an earlier stage in the phylogenetic series.

Now in animals we look to the developing egg of the more generalized fishes for the least abbreviated embryological recapitulation of the early development of the vertebrate branch, for in the mammals the early stages are passed through so rapidly and with so many disguises as to be of comparatively small importance in giving the history of the branch, unless viewed in the light of the embryological development of the lower types. So the lower foliar organs of a branch or shoot are embryologically of far greater importance than the upper, for in the beginning of the development of one of the upper leaves we have but the early stages of a highly organized appendage. These early stages are consequently abbreviated and more or less disguised. The formation of the stipules in the growth of the upper leaves is therefore not a salient point in the consideration of our problem though it has had much stress laid upon it, yet it is of interest to note that in general the stipules appear earlier than the leaf-blade, thus giving evidence that they are of more ancient origin. It may be added,

*See Sir John Lubbock. On Seedlings. 1: 474. 1892. See also p. 440 as to the similar case of *Lathyrus Aphaca*.

and it is a matter of common observation, that the petiole is the last portion of the leaf to develop ontogenetically and is therefore to be regarded as the most recent part to be added phylogenetically. This helps to explain the common occurrence of sessile and petiolate leaves even in different species of the same genus, as variation more readily occurs in recent than in ancient structures, while on the contrary it has been a matter of remark among even the earlier botanists that stipules when they occur usually characterize all the species of a family, an additional evidence of the antiquity of their origin.

Let us now take up, in the light of the foregoing conclusions the consideration of the destiny of the primitive foliar organ as it has been modified and developed in the course of evolution. For convenience in making our inquiry, I would divide the primitive leaf into the central-basal, axial, apical and lateral portions. Each of these figures prominently in the evolutionary history of foliar organs, for from the original condition there has been progressive development along several lines of varying degrees of relationship and the morphological result of the development of the several parts has been quite different in the divergent groups, so much so as to render the question of homology a doubtful one to many minds. We shall endeavor to establish its reality.

The lamina of the leaf, as we shall see, has been developed chiefly from the apical portion, usually from scarcely more than a mere point, though it may also include the axial and lateral portions. The true petiole, when present, is developed from the axial portion,* the sheathing petiole from the central basal together with the lateral portions, stipules and structures of the same signification from the lateral portions. It is with the lateral portions, therefore, that we are chiefly concerned.

With reference to the formation of stipules there are three principle types of leaf-development: that in which the several portions of the primitive leaf have developed together into a simple unappendaged blade, that in which a sheathing petiole is formed with or without a ligule or ochrea, and that in which stipules properly so-called are present.

In the first and simplest case the development of all the parts

*See S. H. Vines. Text-book of Botany, 1: 49. 1894.

together gives rise to such leaf-forms as are found in *Vaccinium* and *Sassafras*, the principal portion of the lamina being formed by the development of the apical portion, but including at the base the lateral, central-basal and axial portions which are contracted below into a short petiole.

If we observe the development of the leaf in *Sassafras* the relative growth of the several parts can be readily traced. The first four leaves (fig. 1) are very simple. In the fifth (fig. 2) considerable development has taken place. The apical portion, now forming about half of the organ, is provided with the three typical veins as they appear in the adult leaf, but starting out separately from the very base. The lateral portions have reached their highest development and each is furnished with a pair of veins. In the sixth leaf (fig. 3) there is a very close approach to the adult form. The upper part has expanded and the lower parts have elongated, removing the point of separation of the three principal veins of the leaf to a considerable distance from the stem. At the same time there has been a basal contraction looking toward the formation of the petiole with a considerable degeneration of the lateral portions, one of the veins having disappeared from each of them, while the other has become associated with the midvein. The seventh leaf (fig. 4) represents the unlobed adult form and differs but little from the sixth.

A similar condition is observable in *Ailanthus glandulosa* Desf. (figs. 5–10), but resulting in this case in the final separation of the lateral portions as small gland-bearing fugacious stipules, comparable to those at the base of the leaves of many of the Ranunculaceæ. The comparison of *Sassafras* and *Ailanthus* shows how small a difference in development may determine a leaf as stipulate or exstipulate.

The case of *Syringa vulgaris* L. is like that of *Sassafras*, though more difficult to trace, owing to the larger number of veins in the leaf, but the homologies of parts may be followed more or less distinctly from the second leaf up to the sixth, the first adult leaf (figs. 11–14). The lateral portions are seen to have degenerated almost entirely and, their bundles having disappeared, they remain only in the margin of the petiole.

The Compositæ furnish examples of a similar course of development but often with a closer approach to the true stipular condition, as the lateral portions are supplied with vascular tissue by small branches coming off at the base of the leaf from the main lateral bundles.

In *Erigeron annuum* (L.) Pers., for example, there are three fibro-vascular bundles in the leaf-trace which pass up through the central portion of the petiole, converging as it narrows. But almost immediately on their departure from the stem each of the lateral bundles gives off a branch in the same manner as when true stipules are present. This branch forks at once and supplies the wings of the petiole. In the cauline leaves (fig. 15) its branches can be distinctly traced into the lower lobes of the leaf. The basal leaves of *Aster undulatus* L. show a condition very closely similar to that found in *Erigeron annuum* (L.) Pers., but in the cauline leaves there is a considerable modification by which the large lobes of the base of the petiole (fig. 16) are formed. The stipular bundle curves outward through the lobe giving off branches which form a net-work supporting its parenchyma. It then passes up through the wing of the petiole and into the basal part of the leaf. In *Solidago juncea* Ait., there are eleven bundles in the leaf-trace and a stipular bundle is given off on each side, supplying the margins of the petiole. *Artemisia vulgaris* L. affords a very interesting variation. The lateral portions of the primitive leaf have branched in a very curious manner (fig. 17), forming several small leaflet-like appendages to the base of the petiole. That they belong to the lateral portions and are stipular in their character is shown by the fact that they are supported by branches of the stipular bundle which is given off a little higher up than in *Erigeron*, passes on through the wings of the petiole after giving off the branches and enters the base of the blade as in other cases. This is the nearest approach to the true stipular condition that I have observed among the Compositæ.

The embryonic development of the foliar organ among the Compositæ is in general too much abbreviated to give much evidence in the consideration of the present question, and it should be so expected from the position which the family holds at the head of the vegetable kingdom.

Petioles of the kind seen in this type of leaf-development are very often short and usually more or less margined or winged by the contracted basal parts of the lateral portions of the primitive leaf. They are evidently genetically different from the petioles of stipulate leaves which are developed by the elongation of the axial portion alone. Sessile leaves also are of this type, hence the absence of stipules, the stipular tissue being incorporated into the basal part of the blade. But even where stipules are present, the lateral basal portions of the leaves are often in the closest anatomical relation with the stipules. This may be seen in *Viola obliqua* Hill (fig. 18) in which, near the bundle which passes into the stipule, a similar one arises, takes its course up the petiole supporting its narrow wing and is distributed to a small part of the basal portion of the lamina. We shall find several cases similar to this when we come to the consideration of the Rosaceæ. There is in this a suggestion of the occasional separation of only a part of the lateral portions to form the stipules and the incorporation of the remainder into the petiole and blade.

The second case is that of the sheathing petiole as it occurs in the Gramineæ, Araceæ and Umbelliferæ. In this case the central-basal portion of the primitive leaf is very largely developed and with it the lateral portions which form the margins of the sheathing petiole. The lamina and true petiole are later developments of the apical and axial tissues. We are strongly supported in this view by the fact that the sheathing petiole is interchangeable with petioles of the ordinary type accompanied by stipules. This occurs in the Umbelliferæ. In *Hydrocotyle* and a few other genera the sheathing petiole is wanting and stipules are present. The closely related *Aralia racemosa* L. also has stipules. Still more striking is the case of *Comarum palustre* L. in which the basal leaves have the sheathing petiole remarkably developed with no indication of stipules (fig. 19), while the upper leaves possess well developed stipules adnate for not more than half their length (fig. 20).

But the identity of the marginal tissue of sheathing petioles is perhaps best shown in the Ranunculaceæ. In the upper basal leaves of *Ranunculus bulbosus* L., the separation of the lateral portions is seen actually to have begun, presenting exactly the appearance of adnate stipules. The development can be clearly traced from below upward. The first leaf has a short sheathing petiole of the ordinary type (fig. 21). This is slowly modified till in the fourteenth leaf (fig. 22) the vascular bundles have drawn closer together, the sheath has grown shorter and the broad lateral portions, hyaline in texture and requiring no special support other than that of the surrounding leaves, are rounded off distinctly at the top at the point of beginning of the true petiole. In the fifteenth leaf (fig. 23) there is a further reduction in size and the tips of the lateral portions are free. Another interesting case among the Ranunculaceæ is that of *Thalictrum polygamum* Muhl. in which the sheathing petiole is of a very generalized type (fig. 24). The lateral portions are chiefly hyaline, though sometimes faintly netted-veined and their margins turn in at the apex and meet in the central dorsal channel of the petiole at its base, forming a ridge between the sheathing and true petioles. This ridge supports a very narrow hyaline membrane which appears to me as the rudiment of a ligule. It would become typical by a little further development of marginal tissue. I believe this to be the origin of the ligule wherever it occurs, though it does not appear so clearly evident in highly specialized groups, nor should we expect such to be the case. There is also present at the first and second forkings of the petiole a transverse hyaline scale very much like a ligule.

It is noteworthy that the ligule always occurs in connection with the sheathing petiole, as in the Gramineæ and Cyperaceæ, or where there is evidence that there has been a sheathing petiole which has disappeared by degeneration, leaving the ligule axillary as in some of the Naiadaceæ which we shall presently consider.

When the ligule has developed sufficiently to require special support, it is supplied by the introduction of vascular bundles. These bundles have their origin most frequently as tangential branches of the main leaf-bundles at their point of passage from the sheathing petiole into the true petiole, or, where the latter is undeveloped as in the grasses, into the blade. This mode of origin of the ligular bundles is seen in some of the tropical grasses and in the ligular portion of the stipule of the Naiadaceæ and the ochrea of the Polygonaceæ. *Richardia* shows an exceptional venation of the ligule.

The best marked examples of the sheathing petiole among the Monocotyledones are found in the Araceæ, the Cyperaceæ and the Gramineæ. If we examine a developing plant of the common hot-house calla (*Richardia Africana* Kunth.), the first leaf (fig. 25) is seen to be a short, broad sheath, the second (fig. 26) has increased to a considerable length and the apical and axial tissues have developed into a minute blade and petiole. The third leaf is of the adult form, but smaller, though all the parts have increased very much in size. This is contrary to what is observed in *Ranunculus* where the sheathing petiole degenerates while the other parts advance. The margins of the sheathing petiole of *Richardia* curve inward at their apices and meet in the middle line of the leaf as in the case of *Thalictrum polygamum* L., but they are much broader and form a distinct ligule which is supported by the incurving and union of the marginal veins of the sheath instead of by tangential branches. In *Arisæma triphyllum* (L.) Torr., the transition is not so well marked, owing to the small number of leaves the first of which is but a sheath as in *Richardia*, while the second bears a mature lamina.

Scirpus polyphyllus Vahl. (fig. 27) will serve well to illustrate the ligule in the Cyperaceæ. It is but little developed as a slight hyaline outgrowth upon the ridge at the union of the sheath and lamina, but the sheath is closed, as is typical in the family, and a little farther development of marginal tissue would produce an ochrea. Typical of the ligule in our common grasses is that of *Phalaris arundinacea* L. (fig. 28). It consists of a considerable outgrowth of hyaline tissue which is continuous laterally with the marginal hyaline tissue of the sheath. This continuity strongly supports the position taken as to the origin of the ligule. The purpose of the ligule is evidently to prevent the flow of water from the upper parts of the leaf down between the sheathing petiole and the stem which together with the axillary bud it invests and protects, and neither the ligule nor the primitive ridge which bears it are found in those cases where the sheathing petiole does not closely invest the stem, at least in the early stages of growth, and its purpose could not be in any considerable measure fulfilled.

The usually axillary position of the "stipule" in the Naiadaceæ has occasioned considerable discussion as to its real relation to the ligule of grasses and to stipules proper. That it is in reality a development of the lateral portions of the primitive leaf, and that it corresponds to the ligule together with the margins of the sheathing petiole of grasses and is rendered more or less nearly axillary by the degeneration of the central-basal portion, becomes clear from the fact that in some species of Naiadaceæ the sheathing petiole retains a considerable degree of what should be regarded as its ancestral development, and a condition approaching that which occurs in grasses is found. *Potamogeton crispus* L. is one of our species which will serve well for an illustration. The first leaves do not develop a blade, but the lateral and central-basal portions are well developed. In the adult leaves there is present a true sheathing petiole (fig. 29). The fibro-vascular bundles of the central-basal portion pass into the blade, giving off tangentially, at the point of transition from sheath to blade, the bundles of the ligular part of the stipule. The bundles of the lateral portions do not in this case curve about to join those entering the blade but are prolonged upward, remaining parallel and supplying the lateral portions of the stipule with supporting tissue directly. In *Althenia filiformis* Petit. (fig. 30), the conditions are more primitive in the larger relative development of the lateral and central-basal portions. In *Ruppia* the ligule is not developed, and the tips of the lateral portions are free as in ordinary adnate stipules.

The condition found in *Potamogeton* is almost exactly repeated in *Polygonella articulata* (L.) Meisn. (fig. 31). The ochrea is cylindrical, surrounding the stem. The central-basal portion is long and narrow, bearing at its apex the terete lamina which is deciduous before flowering. The lateral portions form the principal part of the sheath, are parallel veined with a few anastomosing bundles and are prolonged above the central-basal portion, growing in along the ridge between it and the lamina. This middle portion shows its origin by a deep median sinus and receives its bundles typically as tangential branches from those entering the lamina. We do not have then in *Polygonella* a typical ochrea as it occurs in *Rumex* and *Polygonum*, where, because of the small development of the central-basal portion, the sheathing petiole is very short or almost wholly wanting. The lamina, being of much greater importance than in *Polygonella*, receives all the bundles of the leaf-trace. They are more or less abruptly deflected into the true petiole, generally developed in these genera, according to the degree of degeneration of the central-basal portion. The lateral portions receive their supporting bundles as branches of the lateral ones of the leaf-trace. In *Polygonum sagittatum* L. (fig. 32), the marginal tissues do not extend across the petiole and we have a stipule opposite the leaf. In *Rumex crispus* L. (fig. 33) and *Polygonum Virginianum* L. (fig. 34), the ochrea is complete and the axillary parts receive the typical tangential bundles.

The ochrea of palms is doubtless of the same character, though I have not had opportunity to examine its anatomical structure. In those species which I have examined morphologically, the case is that of the ochrea associated with a remarkable development of the sheathing petiole. There is no true petiole and the ligule may be seen even a little above the base of the blade on the upper surface of the midrib. From this point the lateral portions may be traced down the margins of the sheath, though dried up and very much torn and broken by the more rapid development of the central tissues, till they unite with those parts which in their development have formed the "ochrea." The degeneration of the sheathing petiole with the probable concomitant formation of a true petiole would give the same conditions as in *Polygonum* with its typical ochrea.

The ochreate stipule of *Platanus* differs little morphologically from the typical ochrea, except in the absence of development of the central-basal portion and the possession of a horizontal limb, but there is no fibro-vascular support for the ligular part and this usually splits, leaving apparently a single stipule opposite the leaf.

The case of the tendrils of *Smilax* is one which has occasioned much discussion, but the embryological together with the anatomical characters make it sufficiently clear that in *Smilax* the tendrils are true stipules found in connection with the sheathing petiole. If a young shoot of *Smilax rotundifolia* L. be examined, the first leaf (fig. 35) is seen to be of the typical primitive form. In the second (fig. 36), the apical portion has developed into a blade of considerable size and there is a well-marked sheathing petiole. In the third (fig. 37), the true petiole has begun to develop, the central-basal portion is degenerating and at the same time the lateral portions have begun to separate, forming rudimentary tendrils which in the adult leaves come to considerable length by secondary development in adaptation to their new and unusual function of support. In cross section the bundles of the tendrils are seen to arise as branches of those of the petiole, so that anatomically, as well as embryologically, they answer to true stipules.

Pastinaca sativa L. (fig. 38) furnishes a good example of the sheathing petiole among the Umbelliferæ. The lateral portions are broad and furnished with several vascular bundles parallel with those of the central basal portion. The lateral portions remain of considerable breadth to the top where they are distinctly rounded off, and their bundles, with the exception of two or three of the exterior ones, curve around and unite with those entering the petiole. This free condition of the exterior lateral bundles with the anastomosing network between them shows a considerable degree of approach to the true stipular condition.

In the third case true stipules are developed. They are formed by a very early separation of the lateral portions from the main body of the primitive leaf, a separation which can be very clearly traced progressively in the embryological history of leaf development. The function of the lateral portions in their primitive connection with the main body of the foliar organ is, in common with the other portions, protective, and while the apical portion, having had placed upon it the special function of assimilation, goes on in its development together with the accessory axial portion in adaptation to this purpose, the lateral portions usually serve their ancient function only, sharing it with the central-basal portion when this has not disappeared by degeneration. The central-basal portion also supports the main body of the leaf, a function from which the lateral portions have been freed by separation.

It is in consequence of this separation that all the main vascular bundles of the leaf-trace in the third type of leaf-development are deflected toward the central one that they may pass up through the petiole into the lamina and give the required support to these important parts. The support of the lateral portions is left to comparatively small lateral branches from the two exterior bundles of the trace, evidently developed expressly for the purpose. This we may conclude, since vascular tissue is the most modern of plant tissues and introduced because of the necessity of support in the evolutionary development of the primitive ground tissues. It would, therefore, follow and not precede the evolution of leaf-forms, being introduced where needed and disappearing again when degeneration or other support of particular parts renders its presence unnecessary. This will appear in some of our examples. In the first and second types of leaf-development the lateral portions may retain in greater or less degree their independent venation.

As the other portions of the primitive leaf have been so wonderfully modified in the course of their development and altered from their original condition, so the freed lateral portions to which we may now apply the term *stipules* have not retained their primitive proportions in adult leaves nor the identity of all their parts. But as the central basal portion has often almost wholly degenerated, the same thing has happened to the basal parts of the lateral portions. The parallel degeneration of the two portions has brought the stipules into closer and closer apparent relation to the stem, so much so as to lead to the enquiry whether they are not accessory leaves and to suggest their origin from the reduction or lack of development of a portion of the leaves as in *Selaginella* and their subsequent association in close relation to the larger ones, but in all my investigation I have not found the slightest evidence in support of this theory. The degeneration of the stipules may continue until they become vestigial or finally disappear altogether. This is evidently the case in those families of plants a few species only of which still possess stipules, as for example the Caprifoliaceæ.

But opposed to the basal degeneration of stipules, there has very commonly been a longitudinal development corresponding to that by which the lamina has been evolved. This has resulted in the adaptation of the stipules to the peculiar requirements of each genus and species. Often in this secondary development they remain membranous, serving the protective function only, and when free are early deciduous. But in numerous cases they have acquired the assimilative function also, developing abundant chlorophyll and sometimes, as in the pea (*Pisum sativium* L.), becoming of equal assimilative importance with the lamina. In *Lathyrus Aphaca* L., they even replace it almost entirely.

Among all these varying forms we should expect to find closer similarities in those plant groups of nearer relationship as we do in floral structures, and conversely these similarities of foliar development should also point to relationship, due allowance being made for parallel development in adaptation to similar environment and for secondary functional modifications which find morphological expression. Also in types more recently evolved and more highly differentiated wide divergence from the typical mode of development may be looked for. The Caprifoliaceæ, before mentioned, are of such a type, with stipules usually wholly aborted;

another is the family of the Rubiaceæ with anomalous stipular development in the group of the Stellatæ. The oaks also, though of lower organization, are an advancing type and still actively undergoing differentiation as evinced by the close relationship and difficulty of determination of the species of any given group. In this genus all but the upper part of the primitive leaf has disappeared by degeneration even in the earliest stages represented in embryonic leaf-development, and the well developed stipules are distinct and separate from the very base of a developing shoot. Not until the fifteenth node, in *Quercus rubra* L. (fig. 39), is there any appearance of lamina. The apical portion of the protophyll must however be regarded as potentially present between the stipules at their base. It begins its development unusually late in the series and exhibits several stages, of which the twentieth leaf (fig. 40) is illustrative, before reaching adult size. The axial portion of the protophyll being aborted, the petiole, here again a short one, is formed by the contraction of the basal part of the lamina itself. The case of *Fagus* is very similar, but the lamina appears as early as the eighth node (fig. 41), indicating a less degree of specialization. In related genera a different course has been followed. The lamina develops still earlier and the stipules of the lowest nodes are united, separating only on the appearance of the first accompanying lamina.

In the family of the Juglandaceæ the genus *Hicoria* furnishes a very interesting example. The lower foliar organs are of the primitive type with an unusual development in size in some species. The transition to the adult leaf-form is commonly rather abrupt, but I have observed, in both *Hicoria alba* (L.) Britton and *H. microcarpa* (Nutt.) Britton, the frequent occurrence of intermediate forms, the lateral portions remaining as typical adnate stipules (fig. 42).

I have not seen the typical representation of embryonic leaf-development better exemplified than in the case of *Baptisia tinctoria* (L.) R. Br. where at a glance one is struck with its clearness. It is also especially full and accurate as occurring in the development of subterreanean buds. The first five leaves are extremely primitive, completely surrounding the node, though only slightly developed on one side. The fifth (fig. 43) shows at its apex a minute apical tooth, the beginning of the lamina which is farther developed in the sixth leaf. In the seventh (fig. 44) the three leaflets are plainly distinguishable, the petiole has begun its development and the separation of the stipules has made considerable advance. The ninth leaf (fig. 45) is well developed, with the large stipules still showing considerable adnation. But in the tenth (fig. 46) they are wholly free and much reduced, and higher up disappear altogether. We could hardly have a more complete series in illustration of the formation of stipules than this, giving as it does all the stages from an extremely primitive leaf-form to that very highly organized condition where the stipules have entirely disappeared. By a comparison of the venation in the seventh and ninth leaves, it will appear that the separate condition of the stipules has been attained in the manner already described, partly by the formation of an apical cleft, partly by the degeneration of the central-basal portion bringing the base of the cleft lower down. Meanwhile there has also been a considerable apical development of the stipule itself. But this increase in size is lost again in the tenth leaf and the reduction continues to final abortion. *Melilotus alba* Lam. presents very similar though somewhat less primitive conditions.

While considering leguminous plants, a few words concerning stipels, which are so characteristic of the family, would be in place. They have been denominated as "the stipules of leaflets," but I am convinced that they have no connection with stipules whatever, but that they represent rudimentary leaflets which have their origin in a tendency to increased compounding. The habit has become so fixed in the Leguminosæ that evidence of its origin is seldom met with. I have however seen, in *Lespedeza capitata* Michx., one of the earliest leaves with the terminal leaflet only developed and the two lateral ones represented by stipels.

I have found more light on the question in other families where the same tendency to increased compounding often occurs. In *Sanguisorba Canadensis* L. (fig. 47) for example, very vigorous plants sometimes show rudimentary leaflets, more developed indeed than typical stipels, but in the same position. Their character as leaflets of secondary rank is evinced by their occasional removal to a little distance from the primary petiole. A more striking case is that of *Sambucus Canadensis* L. In this species the leaves of young shoots springing up where the bushes have been cleared away are frequently partially bicompound and there are all gradations between the ordinary pinnate form and the bipinnate condition (figs. 48–50). In this case it is remarkable that the first appearance of the secondary leaflet is in the shape of a small body with both the form and position of a stipel, with the same small supporting vein and differing only in greater thickness. These facts seem to give evidence sufficiently conclusive that stipels are in reality rudimentary leaflets. That their development is not confined to the Leguminosæ is farther shown by their characteristic occurrence in *Staphylea trifolia* L.

Another frequent foliar variation among the Leguminosæ is the development of the phyllodium, which might be thought to have some connection with stipules, but the presence of both together in some genera disproves the idea.* The stipules in the Leguminosæ often take the form of spines which serve for the general protection of the plant. We have an example in the well known *Robinia Pseudacacia* L. (fig. 51). In some of the tropical Acacias, as for example *A. spadicigera* C. & S. (fig. 52), they take the form of enormous hollow horns which are appropriated as homes by some species of ants.†

Sambucus Canadensis L. presents another remarkable character. The leaves of the vernal shoots from subterranean buds are furnished with stipules of the same form and in the same position as those of *Sambucus Ebulus* L., but smaller. There are four of them at each node, they are ovate or nearly orbicular in form, small, rather fleshy and persist but a short time. Each is supplied with a small vascular bundle, originating as a branch of the nodal girdle which connects the leaf-traces. These facts give evidence of the close relationship of these two species of *Sambucus*, and of the characteristic presence of stipules in the ancestral form. In *Sambucus Ebulus* L., they are still typically developed, but in our species have become so far vestigial as to appear only in connection with the early leaves of shoots from subterranean buds, an additional evidence of the importance of the leaf-forms successively developed from such buds, in their bearing on the evolutionary development of modern adult forms.

If now we turn to the family of the Rosaceæ we shall find many illustrative examples of the same facts as those born out in the case of *Baptisia tinctoria* (L.) R. Br. But it frequently happens that basal degeneration does not take place or is only partial, re-

* Bentham and Mueller. Flora of Australia, 2: 304. 1864.

† Belt. Naturalist in Nicaragua, 218. 1874.

sulting in the adnate stipules characteristic of so many genera and species of the family. *Agrimonia striata* Michx., in the development of its subterranean buds in the spring, presents an excellent series of embryonic leaf-forms. The lower ones are all simple sheathing scales completely surrounding the stem at their insertion. Not until the eleventh leaf (fig. 53), which is three-toothed at the apex, does the differentiation of parts begin. The central tooth is the beginning of the blade with its petiole; the lateral portions with their tips now free are the stipules. To say that they are "adnate" indicates only that they retain their primitive connection with the central-basal portion. In the twelfth leaf (fig. 54), there has been some basal degeneration, as shown by the lower point at which the three main bundles of the leaf converge and the lower position of the zigzag plexus of the stipular veins. The free tips, on the other hand, have increased in size and a small blade supported by a petiole is present in consequence of the development of the central tooth. The fifteenth leaf (fig. 55) shows a stronger development of all the parts, and a branch of the main stipular bundle is seen to pass up the petiole. The adult form is attained in the seventeenth leaf (fig. 56). In it some further basal degeneration has taken place, but the adnation of the stipules is still very prominent.

Prunus Cerasus L. gives a very good morphological series, but the venation is obscure. A view of the several forms can be had by an examination of the tenth, thirteenth, fifteenth, sixteenth and seventeenth leaves (figs. 57–61). They show the transition from the simple primitive scale to the mature condition in which the stipules are rendered entirely free. The series is similar in *Rubus occidentalis* L., *Pyrus Malus* L. and *Pyrus communis* L. In *Rubus villosus* Ait. (figs. 62–66), the basal degeneration is not carried quite so far and the stipules in the adult leaf-forms remain adnate for some distance from the base of the leaf. The tips of the stipules have taken a larger comparative development than in *Agrimonia*. Anatomically, however, *Rubus villosus* Ait. resembles the latter in having a vein which enters the petiole, neighboring to the main stipular bundle much as in *Viola obliqua* Hill (fig. 18). The venation in *Pyrus Malus* L. (fig. 67) is still more like that in *Agrimonia*.

The stipules of *Fragaria* and *Rosa* show the highest degree of adnation and little, if any, basal degeneration seems to have taken place, though the lateral leaf bundles curve in toward the median one at but a short distance from the stem. This arrangement of the bundles is probably secondary in these forms for the purpose of giving a firmer support to the leaf by an axial concentration of the vascular tissue in the sheath and a corresponding thickening of the surrounding tissues, a firmer support than could be given by only three bundles if they did not converge till they approached the point of their entering the petiole. The venation of the stipules is also peculiar. In *Fragaria Virginiana* Duchesne (fig. 68), there is a single strong bundle running out into the free tip of the stipule. From this are sent out one or two weak veins above, and below there is a faint vascular network confined mostly to the region of the tip and extending in a long curve toward the outer portion of the base, where it gradually fades out without forming any connection with other vascular tissue below. This condition seems to indicate a former basal connection of these stipular bundles, either with the lateral bundle of the leaf or possibly with those of the stem, forming an additional leaf-trace bundle distributed to the stipules only. The former case is far more likely. A probable explanation of this degeneration of the basal stipular bundles can be found by a consideration of the conditions of the environment. All the leaves being basal, the stipules are clustered together and are supported by one another and by the surrounding soil. They are more or less fleshy, destitute of chlorophyll, and in their moist surroundings loss of water by evaporation is comparatively slight. All these circumstances lessen the necessity of the supply of fresh sap. The rapidly conducting vascular tissue has come into disuse, and its degeneration and disappearance is the natural consequence. The same arrangement in forms with leafy stems is not so readily explainable except by the supposition that the arrangement is ancestral. This seems rather evident in the case of *Agrimonia striata* Michx. (figs. 53–56), where the same condition of the bundles occurs, for the earliest leaves representing the ancestral forms develop under the same conditions as the adult leaves of *Fragaria*. But in *Rosa* it would be by no means clear did we not have such intermediate types as *Agrimonia*. *Rosa humilis* Marsh. (fig. 69) may be taken as typical of the genus. The venation of the tip of the stipules is nearly like that in *Fragaria*, but with a little larger development above the main bundle. The vascular network below is much more extensive and is reënforced by several small branches from the lateral bundle which enters the petiole, below the main stipular branch. This additional supply of vascular tissue is evidently rendered necessary by the exposure of the stipules to the light and air and the development of chlorophyll. It seems to be of secondary introduction.

The nearest approach to the stipular conditions occurring in *Fragaria* and *Rosa* which I have observed among the Leguminosæ is found in the adnate stipules of *Trifolium pratense* L. (fig. 70). There are two sets of stipular bundles. One of these supplies the tip of the stipule and consists of three veins of which the lowest corresponds to the single large bundle of the tip of the stipules of *Fragaria* and *Rosa*. The other has its origin as branches from the lateral bundle of the leaf-trace at the base of the leaf, the usual point of origin of the veins of free stipules. This set of veins is distributed to the lateral and basal parts of the stipules and apparently corresponds to the lower network of the stipules in *Fragaria*. These stipules are mainly protective in function. Their meshes are filled with hyaline tissue, but there is some green parenchyma along the veins.

Two very interesting cases in the family of the Rosaceæ are those of *Cliffortia graminea* L. f. of South Africa (fig. 71) and *Potentilla fruticosa* L. (fig. 72). In the former the leaves very closely simulate those of grasses with the linear lamina sessile upon a sheathing petiole. They differ in having the tips of the lateral portions (stipules) free instead of turning in across the insertion of the lamina to form a ligule. In the latter the conditions are very closely similar to those of the ochrea of *Polygonum*. There is a short sheathing petiole, above the apex of which the tips of the stipules rise. Each of them is supported by a strong vein which has its origin at the base of the true petiole. But instead of being free from one another as in *Rosa*, the stipules are connected back of the petiole by a hyaline ligular tissue. The lateral portions of the sheathing petiole are also united to one another on the opposite side of the stem, at least in young leaves, to a considerable degree. Thus an ochrea is formed, not quite a typical one it is true, yet more nearly so than that of *Polygonum sagittatum* L. (fig. 32).

The fact that such forms as these can occur in the same family of plants along with typical stipules, both adnate and free, goes to show how small is the real difference between the various stipular forms. Not all stipules possess supporting tissues but, just as is the case in the ligule of most grasses, may be without any fibro-vascular bundles whatever. This is the case in *Vitis*, in *Parthenocissus* and *Hydrocotyle*. *Vitis Labrusca* L. (fig. 73) shows a somewhat thickened central streak at the base of the membranous stipule, but in *Hydrocotyle Americana* L. (fig. 74), the thickness is uniform and the stipule very thin. These facts give some authority to the supposition that the pectinate interpetiolar appendages which occur in the Composite *Willoughbya scandens* (L.) Kuntze (fig. 75) are true stipules. They are hyaline in texture, without supporting tissue, and may possibly be merely of epidermal origin. To determine this point requires opportunity to examine their development.

It is of importance to state that the tendril of the Cucurbitaceæ, regarded by many as a stipule, has been determined by anatomical examination to represent the first leaf of the axillary bud.* The spines of *Xanthium spinosum* L., simulating stipules in position, are degenerate pistillate flowers. As proof of this, they often bear a greater or less number of hooked prickles like those of the flowers, and there may be a spine on one side and a flower on the other, showing them to be of the same significance.†

The stipules of *Comptonia peregrina* (L.) Coulter (fig. 76) denied by some to be properly so-called, do not differ anatomically from other stipules notwithstanding their peculiar morphology, and are to be included under the term. One of the chief reasons for their exclusion seems to have been the absence of stipules in *Myrica*. This is doubtless a case parallel with that of *Viburnum*, of which most of the species have lost their stipules by degeneration.

While it is not a generally accepted view, there is no good reason why stipules should not sometimes be distinguishable in floral parts. They are clearly present in the sepals of *Rosa* and *Rhodotypus*, and the smaller intermediate lobes of the calyx of *Potentilla* probably represent pairs of united stipules, one from each neighboring calyx-lobe in the manner of interpetiolar stipules.‡ The teeth of the filament in *Deutzia* are very suggestive of stipules in

* See Lestiboudois, Bull. Soc. Bot. Fr. 4: 746-747. 1857. Cited on p. 6.

† See also Clos. Mem. Acad. Sci. Toulouse, (IV), 6: 66-75. 1875.

‡ See Engler and Prantl. Pflanzen Familien. 3: Abt. 3, 6. 1894.

stamens, and the corona of *Silene* may very probably represent a ligule. The glands of the leaves of Ranunculaceæ which have been homologized with stipules, as already stated, can often be traced up into the flowers and are familiar in connection with the petals of *Ranunculus.*

One of the most interesting families of plants in the development of its stipules is that of the Rubiaceæ, the development being very unusual in the group of the Stellatæ. Though the foliar anomaly in this group was early remarked upon and was anatomically explained as early as 1840,* there are considerations which make its present discussion desirable.

In the greater part of the family the leaves are opposite, or occasionally in whorls of three as in *Cephalanthus occidentalis* L., and are usually stipulate. The stipules are of variable character and often interpetiolar, the adjoining stipules on each side of the stem being connate. In the group of the Stellatæ however, comprising ten or twelve genera, the stipules usually are apparently wanting and the leaves in whorls. There is a tendency toward a verticillate arrangement of the leaves in others of the Rubiaceæ, as shown by the frequent occurrence of whorls of three in usually opposite-leaved species. Now an anatomical examination of the whorled leaves of *Mollugo verticillata* L., *Silene stellata* (L.) Ait. f., *Leptandra Virginica* (L.) Nutt. and *Cephalanthus occidentalis* L. reveals the fact that in other families, as well as in the Rubiaceæ exclusive of the Stellatæ, each leaf of any whorl receives its fibro-vascular bundles directly from the cauline cylinder. But in *Galium* the case is different. Two leaves only of the whorl receive their bundles in the manner stated, and only these two produce buds in their axils. All the others receive their vascular supply from what may be termed a nodal girdle, each half of which is formed by the union of two bundles arising, one from each of the two leaf-traces in the same manner as those supplying stipules of the ordinary form. From this girdle arise the bundles which supply the additional leaves, whether there be only one on each side, as in *Galium circæzans* Michx. and *G. lanceolatum* Torr., two, as in *G. triflorum* Michx. and *G. tinctorium* L., or even three or four, as occurs in *G. Aparine* L. The distribution of the vascular bundles may be seen in a cross section of the node of *Galium tinctorium* L. (fig. 77).

*See page 6.

This anatomical arrangement shows that the so-called additional leaves of the whorls in *Galium* are in reality stipules and that the Stellatæ agree with the rest of the Rubiaceæ in having opposite leaves. The tendency of the family however to produce verticillate leaves has been strongly felt in this group but has taken an unusual course, the increased assimilative area having been evolved through the stipules instead of by an increase in the number of true leaves. The explanation is thus made comparatively simple except in those cases where the number of stipules at a node is more than four.

As a general rule, in plants with stipulate leaves, each leaf is provided with two stipules. But when the leaves are opposite, the two on the same side of the node often coalesce, forming a single interpetiolar stipule, as in the case of *Cephalanthus* (fig. 78). That this coalescence is secondary is shown by the fact that the distal portions only of the veins of the two stipules have united. Now in the Stellatæ also, this must have been the original condition, but the interpetiolar stipules have been greatly developed to serve assimilative purposes, the veins having meanwhile united completely to form a midrib. The increase in size has advanced until in *Galium* the stipules are of the same size and form as the leaves and morphologically indistinguishable from them, except in *G. bifolium* where the stipules are smaller. In this condition they remain in the broader-leaved species, as *G. pilosum* Ait., *G. latifolium* Michx. and *G. lanceolatum* Torr. But in the narrower-leaved species, a still greater foliar expansion being desirable, separation has been re-accomplished, proceeding probably from the tip downward, as is illustrated in *Rubia peregrina* L. with whorls of four. In this species stipules are occasionally found with two midribs (fig. 79), most widely separated at the apex or even coalescing toward the base. In *Galium Aparine* L. and other species in which the number of stipules is abnormal, we may suppose this condition to have arisen from a repetition of the process of division which has produced the six-leaved whorls. This is not improbable, since even in the four-leaved forms the stipules have already entirely lost their original morphological character and have taken on a more generalized nature, making them fit material for development along new lines of evolution. Embryological evidence is not wholly wanting, although the family stands so near the head of the plant series. In

Galium Aparine L., in common with the six-leaved species, the earlier whorls are of four leaves only, representing the ancestral condition. In *Rubia tinctorium* L., the opposite leaves of the subterranean portion of the stem are exstipulate. At the first aërial node there is a whorl of four, interpetiolar stipules being present, and in the higher whorls there are six leaves.* This is a series of long range, though lacking in intermediate steps.

Another case in which there is present a nodal girdle from which the stipular bundles arise is that of *Humulus Lupulus* (fig. 80), but there are three bundles in each leaf-trace. They are placed at about equal distances around the circumference of the stem, and the girdle-bundles proper occupy only about one-third of the periphery on each side. From them a part of the stipular bundles arise, the remainder originating directly from the lateral bundles of the leaf-traces.

It would be to small purpose that examples should be further multiplied. From those already cited we may confidently deduce the following conclusions:

1. The sheathing petiole has its origin independently of the true petiole and is formed by a concomitant development of the lateral and central-basal portions of the primitive leaf.

2. The ligule is a special development of the apical parts of the lateral portions of the primitive leaf along the ridge between the sheathing petiole and the distal parts of the leaf. It may be supplied with veins either by the marginal bundles of the sheath or by tangential branches from those entering the blade. The sheathing petiole may disappear by degeneration, rendering the ligule axillary as in many species of *Potamogeton*.

3. The ochrea is related to the ligule and is generally associated with the sheathing petiole. It consists of the apical tissues developed in those cases where the sheathing petiole completely surrounds the stem or did so in the ancestral condition. The part of the ochrea posterior to the lamina or petiole may be called its ligular portion and is usually supplied by bundles arising tangentially from the main ones.

4. The lateral portions of the primitive leaf, when separated in greater or less degree, constitute stipules in the usual acceptation of the term. They are variously modified by subsequent evolu-

*Sir John Lubbock. Jour. Lin. Soc. Lond. 30:504. 1894.

tionary changes, by increased development, by basal or total degeneration, by secondary adnations and various textural modifications. They receive their vascular bundles typically as branches of the lateral ones of the leaf-trace.

5. The lateral portions of the primitive leaf therefore represent in potential the ligule, the ochrea, the margins of sheathing petioles and stipules, but they are often incorporated with the other portions as the wings of petioles and as lateral basal portions of leaf-blades.