

THE NATURE AND ORIGIN OF STIPULES

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A. A. TYLER

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ORIGIN OF
STIPULES**

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,
NEW YORK, Feb. 8, 1897.

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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*.

Linnaeus, 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.

Linnaeus, 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*, Linnaeus 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 *Polygonum* 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.

ANNALS N. Y. ACAD. SCI., X. April, 1897.—2.

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 *Cupulifereæ* 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.—Études sur l'anatomie et la physiologie des végétaux. 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 *Cucurbitaceæ*, 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*, thèse 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*. *Linnaea*, 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 *Stellatae*. 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.—*Entwicklungsgeschichte 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 Bemerkungen über den Blumenbau der Fumarioideæ und Crucifereæ*. *B. Crucifereæ*. *Bot. Zeit.* 4: 137-150. 1846.

Stipules in the Crucifereæ 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.