

**THE NATURE AND
ORIGIN OF STIPULES.
VOLUME X**

Published @ 2017 Trieste Publishing Pty Ltd

ISBN 9780649317141

The Nature and Origin of Stipules. Volume X by A. A. Tyler

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A. A. TYLER

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ANSC/REVISED BY
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A. B., LAFAYETTE COLLEGE, 1892; A. M. 1895.

Presented to the Faculty of Pure Science of Columbia University in Partial
Requirement for the Degree of Doctor of Philosophy.

NEW YORK:

1897.

[Reprinted from the ANNALS OF THE NEW YORK ACADEMY OF SCIENCES, Vol. X.]

ANNALS
OF THE
NEW YORK ACADEMY OF SCIENCES,
VOLUME X.

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

BY A. A. TYLER, A.M.

Read Feb. 8, 1897.

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.

ANNALS N. Y. ACAD. SCI., X, April, 1897.—1.

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.—Praelectiones 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 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.

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 *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.

Lestibondois, Them.—Etudes 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.