

A STUDY IN THE CELASTRACEAE

SIPHONODONOIDEAE SUBF. NOV.

POR LEON CROIZAT

RESUMEN

Estudio sobre las Celastráceas : « Siphonodonoideae » subf. nov. — Discute el autor la posición del género *Siphonodon* de las Celastráceas en la botánica sistemática, y llega a la conclusión de que este género es el tipo de una subfamilia nueva para la ciencia, las *Siphonodonoideae*. Habiendo analizado los estudios de varios autores, y en base de la estructura del ovario y de la flor de varias plantas, establece que el género *Siphonodon* difiere de las Celastráceas típicas en razón de que los carpelos fértiles, situados en éstas en el centro de la flor, se ubican por el contrario en *Siphonodon* en la periferia de un tejido central estéril. Incluye en su estudio algunas notas críticas sobre carpelos y la naturaleza del estilo.

This study rests upon observations made years ago, but its publication was delayed because of two main reasons, (a) To make room for the printing of the work of another author (Merrill in *Jour. Arnold Arb.* 21: 108. 1940) who had studied *Siphonodon* in a prior time; (b) To await the publication of the monograph (« Celastraceae » in *Nat. Pflanzenf.* 20: 87. 1942), which I knew Th. Loesener was preparing in Germany when the last World War broke out. It seemed to me unwise to deal with a subject which the authors cited might cover themselves exhaustively, perhaps, publishing simultaneously, or nearly simultaneously at crosspurposes a new subfamily.

As the reader is soon to learn, neither one of these reasons

is of any consequence under date, Notes on the *Celastraceae* in general, and *Siphonodon* in particular, are all the more required, in that botanists not familiar with the evidence might suppose that the position of this genus was finally settled by Merrill and Loesener. This is not the case, because both these authors, true enough, agree that *Siphonodon* is a celastraceous plant, and that Lecomte erred in interpreting as ochnaceous its synonym, the genus *Capusia*, but neither one tells us in detail why Lecomte went wrong, and — which is more important — how it happens that *Siphonodon* is a « Somewhat anomalous genus of the *Celastraceae* ».

GENERAL NOTES ON THE « CELASTRACEAE »

The *Celastraceae* are of very great importance for the botany of the Americas, and the world at large, which a glance at the published record establishes without further. It is also pacific, that their generic and specific limits are hazy as a rule, for accepted authorities themselves are not above reversing their former opinions on the score on the validity of this or that genus or group of species.

It is not my intention to deal with these and similar controversies, because the reader may easily judge of them. I should be concerned here, nevertheless, with a discussion between two well informed botanists. One of them (Perrier de la Bathie in *Not. Syst. Paris.* 10: 173. 1942) insists that the *Celastraceae* have immediate affinities with the *Saxifragaceae* in the kinship of *Brexia*. The other (Loesener in *Notizbl. Bot. Gart. Berlin* 13: 577. 1937; in *op. cit.*) rejects this idea as entirely erroneous.

This controversy is unwelcome, because the *Celastraceae* occupy a capital position in systematic botany, and it is certainly necessary that we understand their affinities throughout, if we ever are to give ourselves a satisfactory account, where they belong in the system, and how they resemble, or differ from, other groups in their consanguinity. The authority of Perrier de la Bathie as regards the flora of Madagascar, and its *Celastraceae*, is in my opinion on a par at least with the

authority of Loesener insofar as the *Celastraceae* in general may be concerned. Disagreement among botanists so well placed and informed may not be dismissed as of no account.

The basic premises of the celastraceous flower are readily expressed by a diagram (Fig. 1), which shows that these pre-

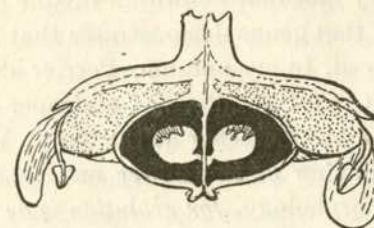


Fig. 1. — Diagram (longitudinal section) of typical celastraceous flower. See text for variations in the position of stamens and « disc ». « Disc » tissue dotted.

mises call for an actinomorphic flower (4- or 5-merous) with a conspicuous « disc » internal as a rule to the stamens. The ovary, which in the early stages of anthesis is pertinently described as semi-inferior — at least within the « disc » — becomes in fruit superior throughout.

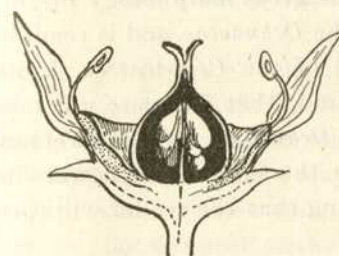


Fig. 2. — Diagram of a saxifrageous flower in the broad affinity of *Brexia*. See text for fuller elucidation.

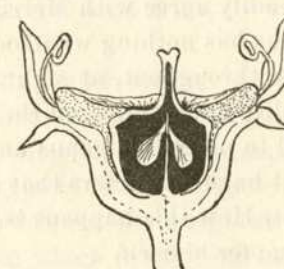


Fig. 3. — Diagram of flower in the affinity of the *Santalales* *Olacales*. See text for elucidation.

By very simple alterations in this basic pattern, it proves possible to secure diagrams which satisfy the requirements of the *Saxifragaceae* near *Brexia* (Fig. 2) or a number of other families (Fig. 3), such as *Santalaceae*, *Olacaceae*, *Loranthaceae*, even *Rhizophoraceae*. Comparatively minor changes in the posi-

tion of the ovary and the «disc» are required to pass from one group to the other, and, indeed, none of these changes demands modifications quite as trenchant as those that separate — as we shall see — *Siphonodon* from conventional *Celastraceae*. Loesener's position in the matter is undoubtedly dogmatic, and, I suppose, the very fact that he proves unable to interpret the floral structure of that genus demonstrates that this dogmatism is not happily placed. In my opinion, Perrier de la Bathie, if not certainly right in all details, has a deeper understanding of the subject than has Loesener at this point. We cannot take a formal and static view of the flower and its significance in phylogeny and morphology, for evolution is by essence the very negation of anything which is fixed, and definitions which — more or less successfully — intend to cover the realities of the moment utterly fail when they come face to face with those of the aeons.

A CONSIDERATION OF «SIPHONODON»

Having seen several specimens of *Siphonodon* in herbarium, I readily agree with Merrill that the gross morphology of this genus has nothing whatsoever of the *Ochnaceae*, and is reminiscent throughout, at sight, of that of the *Celastraceae*. I can readily understand, on the other hand, that Lecomte was misled to place this genus among the *Ochnaceae*, for its flower and fruit have characters that simulate the ochnaceous flower and fruit. How this happens is something that the reader will soon judge for himself.

I am thoroughly unable to understand, finally, why authors who placed *Siphonodon* among the *Celastraceae* failed to give themselves a full account of the reasons of their own disposition. These reasons are for all to grasp at a glance, for they clearly stand out from the discussion, and the drawings in particular, contributed by Hooker *filius* some ninety years ago. I reproduce here some of these drawings (Fig. 4), referring the curious reader for other details to Hooker's own paper (in *Trans. Linn. Soc.* 22: 133. 1857).

Let us notice that in typical *Celastraceae* (e. g., *Celastrus*), the functional carpels are coalescent within a syncarp in the immediate center of the flower. The capsular syncarp so formed, is surrounded by a region of sterilized, but potentially fertile, tissue («disc» or «nectary» of conventional botany). This «disc» may be almost entirely free from the outer walls of the ovary (e. g., *Ptelidium ovatum*, as illustrated by Loesener, *op. cit.* 167, fig. 49) or, on the contrary, coalescent with these walls to a greater or lesser extent (e. g., *Glyptopetalum zeylanicum*, as shown by the same author, *op. cit.* 125, fig. 33). The stamens are inserted immediately into the rim of the «disc» (e. g., *Kokoona zeylanica*, as figured by the same author, *op. cit.*

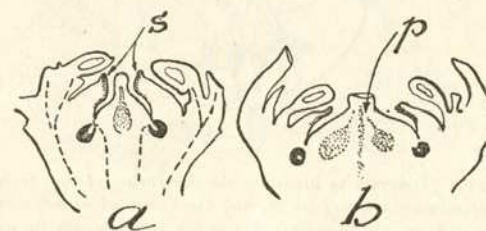


Fig. 4. — Sections through the ovary of *Siphonodon* (adapted from Hooker, as cited in text). Styles in *s*, «disc» in *p*

165, fig. 48), or, which appears to be the most frequent case, outside of it. Next outside the stamens, and alternating with them, are the petals, next again followed in alternation by the sepals.

This, then, is what we may call a typical *celastraceous* flower (see fig. 1), and it is obvious that this flower is not a rigid structure, for, not to speak of the ovulation which is very variable, the «disc» itself is not constant as regards its interrelations with ovary and stamens. Moreover, as I have already pointed out, the ovary is neither superior nor inferior in the absolute.

If we now come to *Siphonodon*, we see the center of the flower no longer occupied by a functional syncarp, but by a «disc»-like structure which is prolonged apically into a beaked organ, mistaken by early authors (e. g., Griffith in *Calcutta Jour. Nat. Hist.* 4: 247. 1844) as a true functional style. Hooker's drawings show (see in particular fig. 4 *b*) a most suggestive

deeper shading, indicating a region of special tissue which, in its turn, points to the existence — *within the «disc»* — of an abortive loculation. Outside of the «disc» so formed are functional carpels, fertilized in due course by a ventral commissural stigma and style of thoroughly standard pattern.

This established — be it only in the main — it is not at all difficult to understand why and how *Siphonodon* and the typical *Celastraceae* differ. The structure ancestral to the modern flo-

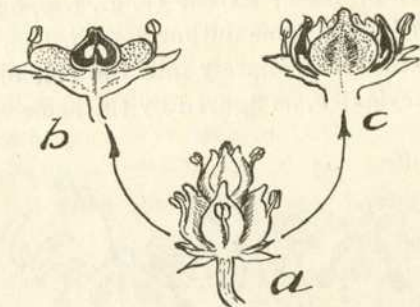


Fig. 5. — Diagram to illustrate the derivation of the typical celastraceous flower (in *b*), and the flower of *Siphonodon* (in *c*) from an ancestral flower (or inflorescence) (in *a*), composed of row of carpels and stamens. «Disc» tissue dotted.

wers was a flower — or inflorescence — consisting of a central axis («rachis») with rows of carpels. It is possible to conceive of variants to this ancestral structure, possibly, for example, consisting of rows of carpels alternating with stamens, or carpels each carrying abaxially a stamen more or less extensively fused with the keels. These variants leave matters very much unchanged as to the main premises.

From this primitive flower — or inflorescence — arose two lines of development, one beyond comparison more successful than the other. In the typical *Celastraceae*, e. g. *Celastrus*, those carpels were maintained in evolution which were apically situated in the ancestral structure, and those carpels (with or without stamens) were suppressed which stood away from the apex, ultimately becoming «disc» tissue. In *Siphonodon*, the exact reverse took place, which a simple diagram (Fig. 5) pertinently shows.

I am aware of the fact that this explanation will by no means satisfy «orthodox» morphologists. Being cognizant of this, and even before to submit further observations, I challenge these morphologists to explain themselves how *Siphonodon* differs from the *Celastraceae* of typical pattern. They have, these morphologists *two facts before them*, one being the flower of *Celastrus*, the other that of *Siphonodon*. These, I repeat, are facts, and since the sum of the characters, gross morphology particularly, indicate that *Celastrus* and *Siphonodon* are closely

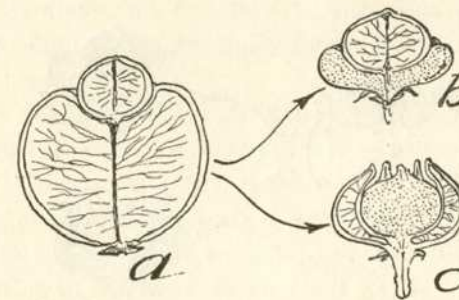


Fig. 6. — The «Navel Orange» (in *a*), and its potential derivatives, with external (in *b*; type *Celastrus*), and internal «disc» (in *c*; type *Siphonodon*). Diagrammatic.

allied, it is for these morphologists to account for the facts with *opinions that meet the facts*, not with definitions beforehand, quotations, citations, flats and the like.

It should be easy, indeed tempting, to enter into a far more extensive discussion of the matter than I believe to be necessary at present. I will rather deal with examples pertinent to the subject under review before indulging in further observations, brief as these must here be.

We are all thoroughly familiar with a type of orange which is colloquially understood as «Navel Orange». In this orange, we have two fruits (Fig. 6) one atop the other. Should we imagine — by no means a wild dream — that the fruit higher up is suppressed, and turned into inert potentially fertile tissue, we would have before us a structure reminiscent of *Siphonodon* in all essential premises. Should we, contrariwise, imagine that the fruit lower down becomes «disc», we should have in front of

us something very much resembling *Celastrus*. Farther still, a gourd is well known (Hutchins & Sando in *Bull.* 356, *Univ. Minnesota, Agr. Exp. Sta.* 16: fig. 8. 1941) as *Cucurbita Pepo* var. *ovifera* «Ten Commandments», which carries to the periphery of the fruit a number of abortive carpels surrounding central fertile carpels. I have cultivated this gourd for years, and can vouch for the fact that the abortive carpels in question are variable in the extreme.

If we suppose that the sterile carpels of this gourd become functional, and, conversely, the central now functional carpels

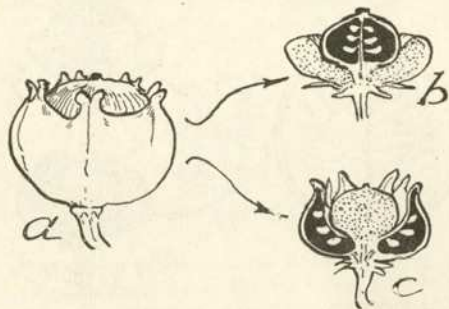


Fig. 7. — The «Ten Commandments» gourd (in a), and its potential derivatives, with external (in b; type *Celastrus*) and internal «disc» (in c; type *Siphonodon*). Diagrammatic.

become «disc» tissue, we again have before us something reminiscent of *Siphonodon*. Reversing the factors, we still see something reminiscent of *Celastrus*, which a diagram (Fig. 7) establishes.

Let us notice that so far reaching is the interplay of sterile and functional carpels, that the peculiar coloration of gourds, green above and yellow below; the appearance in the *Cucurbitaceae* of forms of the so called «Turk's Turban» pattern (in *op. cit.*, 8: Fig. 3. 12), all stem from the same. Hybridization is of course responsible for the vagaries of the cultivated stock, be it in oranges or gourds, for hybridization disturbs the ratio between axes of growth, and releases inhibitions which in pure strains maintain flower and fruit constant. The play of external factors may further concur in these effects.

I feel that *since one and the same explanation* is universally valid to account — with or without a little effort at imagination by the side, imagination being constantly asked for even in mathematics — for happenings in *Celastraceae*, *Rutaceae* and *Cucurbitaceae*, I need not apologize for my belief in sterile carpels. Naturally, if this be necessary to please some of my readers, who believe that sterile carpels are a devilish figment, I will call these sterile carpels «septal glands», thus avoiding the taint of heresy. It suits me, as a matter of fact, to call the sterile carpels «septal glands» (more or less stuffed up, be it clear), for a «disc» is a «gland» in orthodox parlance, and I hold to the belief that potentially fertile tissue left unfertile is «gland» or «disc».

Indeed, I may go further, and finally state that *it is impossible to understand — and even more to teach — botany without accepting from the very start an approach to this science which takes due account of premises such as I have just set forth*. Skeletal anatomy and the like give us facts, but it is only by an higher understanding of the facts as to their prime movers that we may hope to understand and to organize the facts themselves. Only recently (in *Bull. Torrey Cl.* 74: 60. 1947), I had occasion of discussing the findings of supposedly orthodox morphologists as regards *Trochodendron* and *Tetracentron*, showing that gross misinterpretation of vasculature, and a generally sterile handling of the subject, may be charged to authors who have seen all the details of vasculatures well indeed — *as such* — but have failed in their appreciation of generalities, and have proved incompetent to organize the facts in their hands in a constructive manner. The «sterile carpel» is not heresy, *for without it there is no botany*. Only by a constant suppression and alterations in every part of the flower has evolution done its work.

Let us now assume — for the sake of pure hypothesis — that I am wholly and completely wrong in visualizing sterile carpels in the central «disc» or «torus» of *Siphonodon*, and that this «disc» or «torus» is in reality a body consisting of the apex a «determined stem», or such other creature dear to the «orthodox» school of morphology. Nothing fundamental of course, will be changed in my interpretation of the difference

between *Siphonodon* and, e. g., *Celastrus*, for the functional carpels will be peripheral in the former, central in the latter, and it is patent that evolution has conspired to produce this pattern in the one and the other genus, respectively. Whether the carpels have been sterilized, or completely suppressed, is a minor issue by comparison with the fundamentals upon which evolution has based its work.

It is curious that it never seems to have occurred to «orthodox» morphologist that the *flower itself is an embryonal structure*, and that in most cases fertilization reaches the flower in its embryonal stage. Out of an ovary barely 2 or 3 millimeters large a fruit develops which in time is a hundred times as big. It is then obvious that the ovary bears to the fruit the very same relation which a rameal primordium bears in the end to a powerful branch issued from its bosom, and that it is futile to study the flower without giving attention to the fruit, not only, but — which is far more important — without visualizing the flower, in many cases if not all, as an embryonal structure. To seek at this stage for evidence of «chorisis» and «fusion», etc., etc., on the strength of ready made definitions based upon vasculature, is quite as sound as looking for evidence in a rameal primordium of all the leaves that are eventually to come upon the twig. That which we face is tissue in bare process of organization, not a finished product, and it is idle to debate generalities, assuming meantime precisely the contrary. Van Tieghem and all his school never seem to have seen that the flower is essentially something *in potential*, and that unimaginative anatomy is about the last of the means in our power to interpret it.

Is, then, the tissue of the «disc» of the *Celastraceae* carpel or stamen or, simply, rachis? My answer is that it is embryonal or, better to say, unassigned tissue, and that its ultimate destination is locked within the prime movers of the plant itself. I may surmise on the score only if I have some information how evolution operates in this plant, not only, but all its allies as well. May we argue, then, that the «disc» is one or the other? Indeed, yes, but this is a minor matter, as I have intimated above.

In conclusion, *Siphonodon* is a celastraceous plant in which evolution has taken a peculiar path insofar as the arrangement of the flower itself is concerned. The difference which set *Siphonodon*, aside from *Celastrus* need not have been reached by a full previous evolution of different floral patterns, later to «reduce» these patterns to a new «adaptation». This difference can easily have been reached by the simpler, and in the end much more probable method, of changing the destination of the tissues in the floral primordium. One cell, or few cells, need have been controlled in one direction in *Siphonodon*, in another direction in *Celastrus* and the typical *Celastraceae* generally. There was, then, nothing in origin which was fully evolved, or fully formed either way, and later manipulated in detail. Orders were issued — as it were — to certain sectors within the primordium, and that was all, for from this followed that entirely different organs were created in time. I will have occasion to expatiate upon this very same point, when dealing in coming writings on the origin of the leaf.

To summarize these conclusions as formal taxonomy demands, I propose, *Siphonodonoideae* subf. nov. — *A Celastraceis typicis primo intuitu discedit floris parte centrali sterili, carpellis circumcirca sitis*. Genus typicum: *Siphonodon* Griff.

I am under the impression that the *Hippocrateaceae*, which are obviously related to the *Celastraceae*, differ from this family in a manner which is basically the same — as to prime movers at least. The very peculiar stamen of the *Hippocrateaceae* strikes me as a «carpel» which has assumed staminal functions, or, possibly, as a sterile carpel carrying in origin abaxially a stamen which has retained its functions throughout, while the ovulation itself has been eliminated in evolution. I refer the reader to notes (see Croizat in *Bull. Torrey Cl.* 74: 69. 1947) on the stamen and carpel of *Platanus*, which may cast light upon the peculiar stamen of the *Hippocrateaceae* and its ultimate origin.

This review may be closed with few additional notes. The *Stackhousiaceae* are best allied with the *Celastraceae* wholly or in part. Certain of the genera of *Stackhousiaceae* (see *Stackhousia*; Mattfeld in *Nat. Pflanzenf.* 20^b: 245, fig. 77-0. 1942) have ova-

ries superior upon a short gynophore and a more or less definitely glandular «disc». In other genera of the same family (see *Macgregoria*; in *op. cit.* 245, fig. 77 E) the style itself is «Mit Drüsenpolstern verbunden», the ovary being *inferior* to this glandular «disc» (see fig. 8). These structure demand careful morphological study to ascertain whether the style of *Macgregoria* does indeed belong to the functional inferior carpels, or is a mere projection of the «disc», both being possible alternatives. It seems necessary to point out that all too many authors who have busied themselves with the origin of the style, believing the style to be the essential ingredient of angiospermy

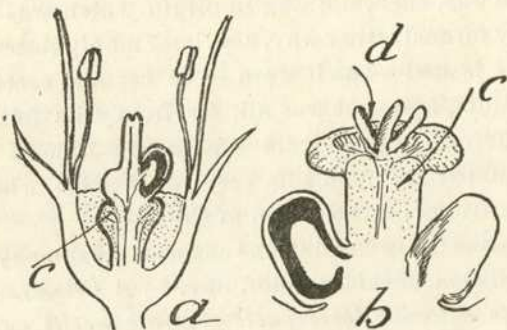


Fig. 8. — Flower of *Stackhousia* (in *a*: «disc» tissue in *c*), and *Macgregoria* (in *b*: «disc» tissue in *c*, styles in *d*). Adapted from Mattfeld, as cited in text.

(see for a meaty bibliography, Frenguelli in *Bol. Soc. Argent. Bot.* 1: 169. 1946) never reached in the first place a correct idea of what the style itself is, or may be. For instance: it is well established that the style of the *Geraniaceae* having a rostrate fruit (see Guillaumin in *Ann. Sc. Nat. Bot.*, 9 ser., 19: 33 1914) is not in the infolded lips of the carpels. The pollengrains eventually reach the ovules through and across the «Bouchon parenchymateux qui obture en haut le canal axial» that is to say, they use for their purposes the decomposed tissue of the axis connecting in origin the carpels, though the original germination of the pollen is effected upon the papillae of the stigmas themselves. In the *Corynocarpaceae*, and *Corynocarpus laevigata* in particular (see Piggot in *Trans. Proceed. New Zeal. Inst.* 58: 69. 1927), «Although a very obvious groove is left

along the style *by the infolding of the sterile carpels* (Italics mine), pollengrains do not grow down the groove. They always penetrate the tissue of the style». Nothing more than these two quotations establish the fact that the style does not necessarily reside in the folded lips of the fertile «leaf-carpel» but interests other organs as well. It is accordingly possible that in *Macgregoria* the styles may belong to the «disc» rather than to the functional carpels themselves, and I should not be surprised if it were eventually established that also in *Siphonodon* some of the pollengrains germinate and, perhaps, reach the ovules taking advantage of the beaked projection of the «disc». All these facts, and possibilities, are in full agreement with our knowledge that the pollengrains come into contact with the ovules by chalazogamous methods in great many families, and that these grains germinate and thrive for a long time upon the ovuliferous scale of such conifers as *Araucaria*. In conclusion: «orthodox» morphology and its conventional «style» are wide of reality, and discussions of angiospermy which rely upon such morphology as this contribute nothing to constructive botany.

It is understandable that Lecomte could be induced to view *Siphonodon* as a member of the *Ochnaceae* by a hasty survey of its ovary and fruit, for in the *Ochnaceae* the fertile carpels are set around a central core. This is also the position taken by the fertile carpels of *Siphonodon*, and for this reason there is a superficial resemblance between this celastraceous genus and that family. Less understandable is that Lecomte should not have been struck by the fact that *Siphonodon* (Lecomte's *Capusia*) has precious little indeed of the gross morphology of the *Ochnaceae*.

In treating *Siphonodon* as a member of the *Celastraceae*, I take a conservative view of family-limits. It is evident that from the standpoint of pure morphology this genus might be erected into a separate family, which I am not prepared to grant at present. It is clear that before a further disposition can be attempted, and *Siphonodon* regarded as the type of a monotypic family, we need know a great deal more of its pollen- and wood-anatomy, to say the least.

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