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Thoughts on high systematics, phylogeny and floral morphogeny, with a note on the origin of the Angiospermae

LÉON CROIZAT

In the space of a few months four different works have appeared which, regardless of their bulk, are of equal importance as regards *high systematics* [1]. In the order of their appearance these works are the following:

1. HUTCHINSON, *The families of flowering plants*, 2 volumes (about 800 pages), 1959.
2. CROIZAT, *Principia botanica*, 2 volumes (about 1820 pages), 1960.
3. MELVILLE, *A new theory of the Angiosperm flower*, an article of about 5 pages, *Nature* **188**: 14. 1960.
4. TAKHTADJIAN (or Takhtadzhyan), *Proiskhozhdenie pokrytosemennykh rasteny* (The origin of angiospermous plants), a booklet in Russian of about 130 pages, 1961.

These works differ radically in their spirit and purpose; HUTCHINSON and TAKHTADJIAN defend essential points in an orthodox doctrine which was that of GOETHE, CANDOLLE, etc., nearly two centuries ago. MELVILLE and myself, on the other hand, move towards the future; although postulating but little new matter, our papers pay far less attention to the past.

Although MELVILLE's contribution is of only five pages in a total exceeding 2780, it is far more important than its bulk seems to imply. Firstly, it is backed by long well documented enquiries. Secondly, it is all the more relevant owing to the fact that, while working and thinking quite independently, MELVILLE and I have reached identical points of view as regards the fundamentals of floral morphogeny and phylogeny. This unanimity in the essentials rather than in theories of very long standing is well worth stressing. It would appear to indicate that the facts, if candidly

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N. d. R. — Les idées et opinions exprimées par l'auteur n'engagent pas la responsabilité de la rédaction.

[1] I would understand as high systematics a science, or doctrine, interested in the philosophical and practical handling of morphogeny, phylogeny and dispersal as one. Obviously on the rebound, this science, or doctrine, vitally influences formal classification.

studied, are of such a nature that they must lead to like conclusions, and that from these conclusions it is thus safe to open new paths to phylogeny and classification.

Authors who publish simultaneously on the same subject cannot be expected to furnish mutual cross references. Such is the case for MELVILLE and myself. TAKHTADJIAN on the other hand, although his work appears at a later date, makes no reference to mine bar a perfunctory mention of my name as technical author of the Austrobaileyaceae.

It is true that I happened to mention my Russian colleague only at the end of my own chores (*Principia botanica* **1b**: 1723.1960), but my readers cannot ignore the difficulties under which I laboured constantly (see, e.g., *Panbiogeography*[2] **1**: xxiv-xv.1958; *Princ.* **1a**: 708; **1b**: 1207, 1215, 1344, 1368, 1376, 1413-1414, 1505-1506, 1723, etc.) to secure literature available to the average botanist for the asking. HUTCHINSON I have of course mentioned at least 20 times in the *Principia.* No one would expect him lavishly to reciprocate, but no informed botanist who runs across HUTCHINSON'S Capusiaceae (Hutch. **1**: 325) will ignore that the interpretation given by the British systematist of this curious plant quite closely parallels the one I offered of my own Celastraceae Siphonodonoideae (in *Lilloa* **13**: 31-43.1947); a reference to this work being required to complete the basic records of so important as group as the Celastraceae. In sum, the titles I have stressed appear to be hardly connected by proper cross-references whilst dovetailing on the contrary most closely whether in the affirmative or in the negative. A review of the entirety of this output is accordingly both necessary and timely.

To agree with the standards accepted today as virtually mandatory, in the pages to follow I should feel bound to refer to extensively and to quote from, numerous

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[2] In order to simplify my references, I will abbreviate the titles currently to be cited as follows:

1. Hutch. = HUTCHINSON, J. The families of flowering plants. 1959 (repr. 1960).
2. *Man.* = CROIZAT, L. *Manual of Phytogeography.* 1952.
3. *Panbiog.* = CROIZAT, L. *Panbiogeography.* 1958.
4. *Princ.* = CROIZAT, L. *Principia botanica* 1960.
5. Melv. = MELVILLE, R. *Nature* **188** (No. 4744): 14-18. 1960.
6. Takht. = TAKHTADJIAN (Takhtadzhyan), A. L. *Proiskhozhdenie pokrytosemennykh rasteny* (in Russian: The origin of angiospermous plants). 1961.

Volume and page-reference will normally follow.

Of TAKHTADJIAN'S *Proiskhozhdenie...* there exists a translation into English made on the first edition in Russian (1954). This translation is titled: Origins of angiospermous plants (transl. Hess Gankin, O.; edit. Stebbins, G. L.) 1959. I owe the copy of *Proiskhozhdenie...* 1961 to Dr. A. L. TAKHTADJIAN'S personal courtesy, and a copy of its translation (1954-1959) to the generosity of Dr. L. CRANWELL of Tucson, Arizona, U.S.A.

Whatever opinion I may express on the *Proiskhozhdenie* (1961), of Dr. A. L. TAKHTADJIAN it is based on first-hand acquaintance with the Russian original. Occasional references to the English translation will be listed as:

6. Takht. 1954-1959.

[3] If nothing be sought beyond what is the current best, and in part at least also absolutely speaking, HUTCHINSON'S *The families of flowering plants* is an extremely useful title. Its iconography stands as first-rate, and the wealth of accurate descriptions it contributes ranks as outstanding. Without HUTCHINSON'S text by my side, I would many a time have experienced grave difficulties from which it rescued me. TAKHTADJIAN'S Proiskhozhdenie is laid out by a clever writer. Both these works are rich in facts and observations in which I fully concur. The matter becomes readily otherwise, and such is far from being the case, when I am forced to judge of these works in reference to what I would understand as basic *Principia botanica.* I evidently think out what I understand as a science of plant-life along lines which are not those followed by HUTCHINSON and TAKHTADJIAN. At this level, we break sharply apart, and it is but fair to the subject and to the readers that the fact be clearly recognized at the start.

authors, even myself, to utter more or less apt personal opinions without much thought of cogent proof, to compile far afield, etc. This I will not do, because I do not believe that time must be spent with side-matters. Practically at my own pleasure, I could prove that I am wholly in agreement with HUTCHINSON and TAKHTADJIAN [3], or that, on the contrary, I do most strenuously object against what they stand for. I could likewise condition my agreement with MELVILLE in certain minor respects, etc. Of course, I feel that nothing of this is being here owed to my readers. What I will try to do in the pages to come is to discuss a number of concrete cases of precise interest to my subjects giving of course proper reference whenever required. In citing and quoting, I do not primarily intend to be controversial, laudatory, censorious, etc., only to present thoughts about which the readers may be privileged to think for themselves at their own good time, and in their own quite personal ways. It is not given to man born of woman genuinely to know anything about which he has not thought out himself. SOCRATES was a great figure because he forced mankind to think what mankind would otherwise but take for granted. That, according to human standards, SOCRATES must be executed as a busybody, a gadfly, etc., is obvious. That, according to divine law SOCRATES did deserve ambrosia rather than hemlock is clear.

First glance at the problems and their nature

HUTCHINSON's classification lays marked stress on orders (groups of families under names in -ales), which it combines into formally unnamed, yet conceptually important " climaxes ". The composition of the first three " climaxes " of this classification, and their inter relationships as understood by HUTCHINSON (Hutch. **1**: 104 ff.), are of vital importance for a great deal of current systematics and phylogeny, and we will accordingly examine them.

Formally, these " climaxes " run as follows:

1. Magnoliales: *Magnoliaceae, Illiciaceae, Winteraceae, Canellaceae, Schisandraceae, Himantandraceae, Lactoridaceae, Trochodendraceae, Cercidiphyllaceae*; Annonales: *Annonaceae, Eupomatiaceae*; Laurales: *Monimiaceae, Austrobaileyaceae, Trimeniaceae, Lauraceae, Gomortegaceae, Hernandiaceae, Myristicaceae*;

2. Dilleniales: *Dilleniaceae, Connaraceae, Crossosomataceae, Brunelliaceae;* Coriariales: *Coriariaceae;* Rosales: *Rosaceae, Dichapetelaceae, Calycanthaceae;* Leguminales: *Caesalpiniaceae, Mimosaceae, Papilionaceae;*

3. Cunoniales: *Pterostemonaceae, Cunoniaceae, Philadelphaceae, Hydrangeaceae, Grossulariaceae, Oliniaceae, Greyiaceae, Escallionaceae, Baueraceae, Cypteroniaceae;* Styracales: *Lissocarpaceae, Styracaceae, Symplocaceae;* Araliales: *Cornaceae, Alangiaceae, Garryaceae, Nyssaceae, Araliaceae, Caprifoliaceae;* Hamamelidales: *Tetracentraceae, Hamamelidaceae, Myrothamnaceae, Platanaceae, Stachyuraceae, Buxaceae, Daphniphyllaceae, Bruniaceae;* Salicales: *Salicaceae;* Leitneriales: *Leitneriaceae;* Myricales: *Myricaceae;* Balanopsidales: *Balanopsidaceae;* Fagales: *Betulaceae, Fagaceae, Corylaceae;* Juglandales: *Rhoipteleaceae, Juglandaceae, Picrodendraceae;* Casuarinales: *Casuarinaceae.*

Three " climaxes " do accordingly contain, in the classification and by the phylogeny of HUTCHINSON, 67 different families, or about 20% of the dicotyledonous families (342 of them) accepted by him. The first " climax " contains 3 orders and 18 families, with an average of 6 families per order; the second 4 orders and 11 families, or about 4 families per order; the third 11 orders and 38 families, or about 3.5 families per order. The low ratio of families per order of the third "climax" is readily made clear in reference to the score of the " amentiferous " forms in its ranks. Salicales, Leitneriales, Myricales, Balanopsidales, Fagales, Juglandales, and Casuarinales yield but 11 families for 7 orders, and of these 7 orders 5 (Salicales, Leitneriales, Myricales, Balanopsidales, Casuarinales), or fully 70% are monotypic. Not so in the balance of the orders and families making up the third " climax ". Here we face 4 orders (Cunoniales, Styracales, Araliales, Hamamelidales) and 27 families, that is, about 7 families per order. In other words: the third Hutchinsonian " climax " is statistically unbalanced. Its " floral ", non-amentiferous orders include each about 7 families, while its amentiferous orders hardly exceed each 1-5 families. This is a fact worth immediate underscoring, as we shall presently see, and also later remember. With an average of but 1-5 family each, the " amentiferous " orders are plainly far more fragmentary than the rest of their presumed, non-amentiferous allies of which each has 7 families. The implication from the figures thus is, that the Amentiferae represent today an old " decadent " aggregate with a long history of extinction that has finally dismembered into oligotypic or monotypic orders, archaic, well differentiated types of vegetation such as oaks, alders, willows, etc. This creates at least a valid presumption that, instead of being " derivatives " and recent in general, the Amentiferae are, on the contrary both " primitive " and ancient in their own right. How this presumption stands up when tested critically against the whole of a large evidence is a question which we will of course not fail to settle.

HUTCHINSON explains the arrangement we have just reviewed with *Notes on affinity (origin and further development)* that can be summarized as follows:

Climax 1. The Magnoliales are an entirely woody group [4] including: *Probably the most ancient types of existing dicotyledons.* Though " more advanced ", the

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[4] The " tree " showing the *Probable phylogeny and relationships of the orders of angiosperms* by Hutchinson (Hutch. **1**: 24) begins lowermost with hypothetical " proangiosperms " leading to Dicotyledones (see for Monocotyledones, *op. cit.* **2**: 517) which forthwith split up into *Lignosae* and *Herbaceae*. I see no reason to discuss here this arrangement, which would doubtless be more convincing:

1. If an exact definition were possible of what is "herbaceum" against what is "lignosum". My guess is that, if we except from reckoning definitely fugacious annuals, this definition is virtually impossible to fix on account, for example, of underground parts, etc., that being themselves, perhaps, quite " lignosa " do yield growth that is " herbaceum ". Then, of course, what is " root " and " rhizome " is not easy to discriminate (*Princ.* **1a**: 1096 ff.).

2. If it were not disturbing, to say the least, to find that the distinction in phylogeny and relationships (nothing less !) foisted upon high systematics by the Hutchinsonian split throws widely apart Araliaceae and Umbelliferae which, as everybody will know, can be closely brought together by, e.g., *Myodocarpus* (*Princ.* **1b**: 1731 fn.). The pollen of this genus also exhibits " cornaceous " characters, accordingly involving within a common phylogeny Cornaceae, Araliaceae, and Umbelliferae.

I see it useless to continue citing a number of other cases which do not favour at all what HUTCHINSON has decided. See next for Schisandraceae, Sargentodoxaceae, etc.

Annonales are close to them. The Laurales mark a step in reduction beginning more or less at the Winteraceae.

Climax 2. The Dilleniales are distantly related to Magnoliales, and might connect them quite as much with Rosales as with Bixales, Theales, and Guttiferales.

Climax 3. The Cunoniales occupy a key-position. They are allied to the early Dilleniales, Rosales, possibly even Celastrales, and stand as the connecting-link between Rosales and the " higher evolved " Hamamelidales. The Styracales may be " derived " from the Cunoniales. The Araliales are probably " derivative " from Rosales via Cunoniales and Cornaceae. The Hamamelidales are closely related to Rosales leading to the Amentiferae, which begin with Salicales. The " ressemblance " of willows and poplars to Flacourtiaceae or Tamaricaceae, says HUTCHINSON, is but superficial.

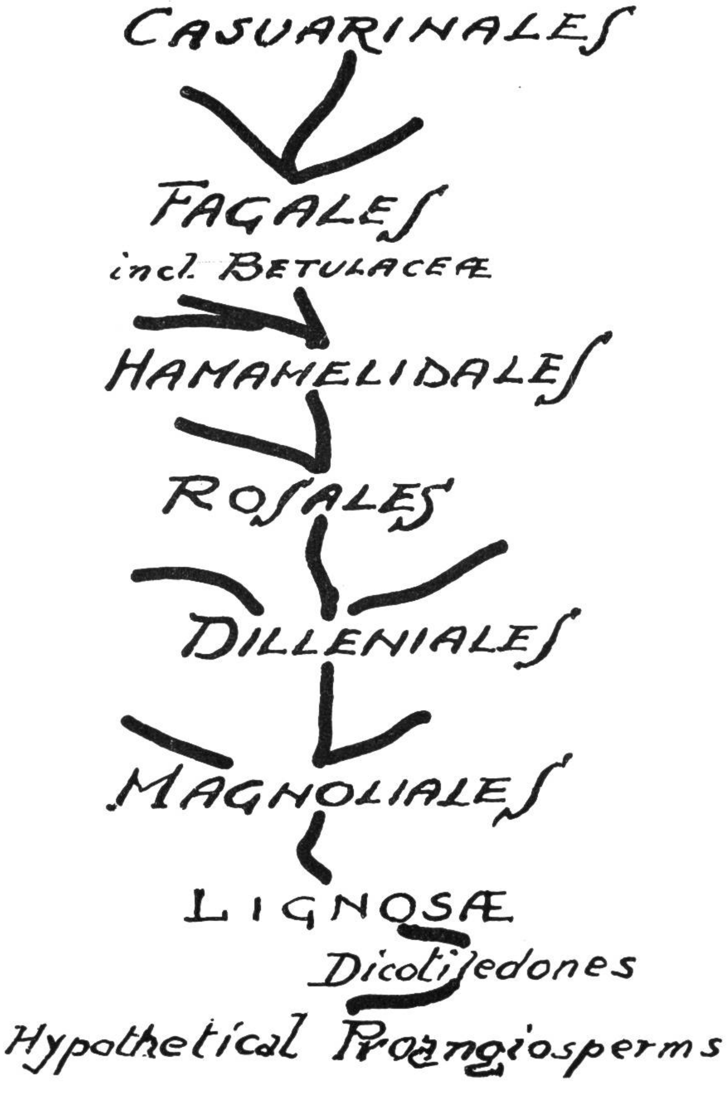

FIG. 1. Hutchinson's " tree " of angiospermous ascent (abridged).

Figured out overall, and construed on the basis of a conventional " tree " (fig. 1), these relationships, naturally, force upon the student the necessity of " deriving " the cone of, e.g., *Alnus* and *Casuarina* from the strobile of *Magnolia* via the flower of *Rosa* and *Hamamelis.* I see for myself, and I might as well state it without delay, a " derivation " of the sort as impossible. Common consensus is of course never tantamount to proof, but there is a sizeable body of opinion including, e.g., ENGLER, WETTSTEIN, and representing a long tradition [5], which inclines to viewing the cone of Betulaceae as possibly more primitive than the flower of the Magnoliaceae, and accordingly to begin classification with the " Amentiferae ". This sizeable body of opinion is not wanting solid reasons in support. I would for example not see as entirely forbidding, at least hypothetically, an attempt made at bringing together the strobile of *Magnolia* and the cone of *Alnus* at a level of evolution not to exceed the " Amentiferae ". Accordingly, and as a strict matter of first impression, I would rather side with ENGLER & PRANTL in beginning classification with Betulaceae than with Hutchinson in standing by Magnoliales.

The core of the matter is however not with the academic issue whether it is better to begin formal classification with Magnoliales or with " Amentiferae " for begun with the one or the other group the question forever remains how efficiently and concretely to bridge the gap between a flower of *Magnolia* and a cone of *Alnus*, and how to assimilate the flower of *Magnolia* to that of *Ficus*. The real issue is in devising methods, principles and concepts fit to serve as constructive tools of synthesis and analysis in the task of understanding plant life whether in reference to a scheme of formal systematics beginning with Magnoliales or to a scheme starting with " Amentiferae ". Beginnings that look very different do lead after all to the very same hurdles, and it is the hurdles that count for much more than the starting point. In brief, let us not worry so much how we should begin, passing first in line this or that group in -ales. Let us rather figure the safest way of ending what we are to begin without ever losing track of commonsense along the road.

In the first place, what is the basic reason why HUTCHINSON chooses to start building his entire system of classification with Magnoliales? This question, we may not doubt, is finally and simply answered taking into account the *general principles* which HUTCHINSON follows. These *general principles* (Hutch.: 20-21) consists of 24 different dicta of which 14 relate to flower and fruit. The first of these *general principles* affirms the following: *Bisexual (hermaphrodite) precede unisexual flowers,*

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[5] The fact is well known to HUTCHINSON. He credits ENDLICHER (Hutch. **1**: 15) with having begun in his *Genera plantarum* (1838-1841) the trend which culminated with the current systematic schemes of ENGLER, WETTSTEIN, etc. Quoth HUTCHINSON: *Instead of commencing with families in which both sepals and petals are present, as in the Jussieu—de Candolle system, he* [Endlicher] *began with a group without petals. Thus commenced the great divergence of the two main systems still in use.* The two main systems are, of course, BENTHAM & HOOKER'S which HUTCHINSON hopes to refurbish; and ENGLER & PRANTL'S which rules in continental Europe, the U.S.A., etc. I should point out that ENDLICHER is antedated by BARTLING, author in 1830 of an outstanding *Ordines naturales plantarum*, in which the statement occurs (*op. cit.*: 97) that: *Salicinis remotis Amentaceae seriem satis naturalem Coniferas inter et Urticinas constituunt.* It is very likely that BARTLING was in his turn preceded by other systematists in beginning natural classification with the conifers among the Angiospermae, i.e., with the Amentiferae. What A. P. de Candolle thought of his own classification we will presently learn. It is alas certain that Hutchinson did not read A. P. de CANDOLLE'S *Théorie Elémentaire de la Botanique* (1813), very carefully, which he refers to (Hutch. **1**: 13-14) as a classic, most important text.

and the dioecious is probably more recent than the monoecious condition. Corollaries of this dictum are other *general principles*, such as, for example: *Petaliferous flowers precede apelatous ones, the latter being the result of reduction; free petals (polypetaly) are more primitive than connate petals (sympetaly);* etc. These *general principles* are by no means unimportant because not only do they mold out the systematic thinking of Hutchinson, but they also furnish the essential standards, for instance, of the phylogeny of Takhtadjian (*Proiskh.*: 9 ff.) which rests on the assumption that the ancestral " flower " of the Angiospermae was bisexual. Of course, this once believed, it follows that the magnolioid strobile must be primitive against the betuloid cone.

Since Hutchinson does implicitly at least acknowledge (Hutch. **1**: 13) the primacy of A. P. de Candolle as the systematist who already in 1813 advanced a classification essentially based on the characters of calyx and corolla, and beginning with a group Thalamiflorae identified by petals free and hypogynous, etc., it can but interest us to consult the *Théorie élémentaire de la Botanique*, 1813, in which that classification was first formulated. What did A. P. de Candolle himself think of it?

I regret that to meet this question I cannot quote here the whole of chapters VII and VIII of the *Théorie élémentaire*, which I strongly advise the readers of these notes to digest in their own time with sustained attention. I will here summarize the substance of these two epochal chapters, as follows:

1. As a prelude to the task of actually writing out a formal scheme of classification, Candolle saw it necessary to understand something at least of what he called (*op. cit.*: 196-197) " le plan de la nature ".

2. Following an excellent discussion of the facts (*op. cit.*: 197-203), Candolle reached the wholly logical conclusion: *Qu'il n'existe pas dans la nature des séries continues; que les êtres se groupent à des distances fort inégales; qu'il est impossible d'exprimer leur véritable rapport dans un erdre linéaire.* However, he continued (*loc. cit.*: § 168): *Cependant, pour la forme habituelle de nos livres et même pour l'enseignement et la disposition des collections, il est nécessaire d'adopter une série, bien entendu que cette série n'est destinée qu'à la commodité, et est vraiment artificielle au moins dans ses détails.* Thus begun, the argument of Candolle next broaches the question (*op. cit.*: 203-205) how " la série " (that is, the sequence of formal presentation) should be started, concluding quite logically on the basis of the data available to him in 1813, as follows (§ 170): *Puis donc qu'il est en soi-même absolument indifférent de commencer la série par une extrémité ou par l'autre, je crois que c'est ici le cas de céder à la commodité de l'étude et de disposer le règne végétal d'après le même principe que le règne animal; c'est-à-dire en commençant par la classe la plus compliquée, celle des Dicotylédones, en finissant par celle qui paraît l'être le moins, celle des Acotylédones.* In order to translate this conclusion into practice, Candolle took the simplest possible way out, thus precisely (*op. cit.*: 205, § 170): *La manière dont j'ai considéré plus haut les degrés de complication des êtres, me donne un moyen fort simple de distribuer les familles dans chaque classe. Je placerai donc au premier rang les Dicotylédones qui ont le plus grand nombre d'organes distincts et séparés les uns des autres et à mesure que je verrai des familles où quelques-uns de ces organes

se soudent ensemble, je le rejetterai dans les rangs inférieurs: ce principe me donne pour série: 1^o les Dicotylédones polypétales hypogynes; 2^o ...... périgynes; 3^o ...... monopétales périgynes; 4^o ...... hypogynes; 5^o ...... apétales ou à périgone simple.

So thoroughly aware was Augustin Pyrame de CANDOLLE that the arrangement resulting could not be natural that he capped his classification, beginning with Ranunculaceae, Dilleniaceae, Chlenaceae, Magnoliaceae, Annonaceae and ending with Euphorbiaceae, Monimiaceae, Urticaceae, "Amentaceae", and conifers, with the following (*op. cit.*: 213): *Esquisse d'une série linéaire et par conséquent artificielle, pour la disposition des familles naturelles du règne végétal.*

Let us summarize:

1. CANDOLLE thoroughly understood that the knowledge available in his times was not sufficient to face the difficult task of arranging the families shown to be natural by JUSSIEU and his followers into a natural system. He pointed out that a lineal series must be adopted which would as such be necessarily artificial.

2. This settled, he chose to begin with the plants best known, i.e., Dicotyledones, arranging them into an admittedly artificial sequence on the basis of artificial characters such as polypetaly, sympetaly, apetaly. In short, maintaining firm natural classification by families in the wake of JUSSIEU, A. P. de CANDOLLE returned to an essentially artificial sequence of the natural families ultimately in the wake of LINNAEUS (CROIZAT, *Bull. Torrey Bot. Club* **72**: 52.1945), and for no better reason than convenience of the pedagogical kind.

It is, then, a clearcut historical fact CANDOLLE definitely understood the dicta that bisexual flowers (Ranunculaceae, etc.) precede unisexual ones (Amentiferae); that petaliferous flowers (Magnoliaceae, etc.) come first before apetalous ones (broadly speaking, Euphorbiaceae, Urticaceae, etc.) that polypetaly (Annonaceae) takes precedence over sympetaly (e.g., Campanulaceae); etc.; as convenient and artificial. This CANDOLLE did in 1813, and the reason is not clear to me why dicta of the kind should be introduced in 1962—that is, at a distance of about 150 years!—as the mainstay of schemes of classification intended to be natural.

It will of course be retorted (the pastures of botany are an *Elysium* of objectors against winds and tides) that, whatever A. P. de CANDOLLE might have thought in 1813, still subsequent findings have let it proven in 1962 that it is true that the bisexual flower is primitive against the unisexual one, etc., etc.

It is easy to test this contention. If well taken, it should be statistically demonstrable on the basis, for example, of HUTCHINSON's first "climax", which includes probably the most ancient types of existing Dicotyledons together with forms directly derived from them. Using HUTCHINSON's own data (Hutch.: 122 ff.), the record stands as follows:

1. Magnoliales: *Magnoliaceae:* bisexual but unisexual in *Kmeria* by " tepaloidy of the stamens "; *Illiciaceae:* bisexual; *Winteraceae:* bisexual to polygamous ; *Canellaceae:* bisexual; *Schisandraceae:* unisexual; *Himantandraceae:* bisexual; *Lactoridaceae:* polygamo-monoecious; *Trochodendraceae:* bisexual or polygamous; *Cercidiphyllaceae:* dioecious.

2. Annonales: *Annonaceae:* mostly bisexual but also unisexual; *Eupomatiaceae:* bisexual.

3. Laurales: *Monimiaceae* (incl. *Amborellaceae*): bisexual, unisexual, polygamous; *Austrobaileyaceae:* bisexual; *Trimeniaceae:* bisexual, unisexual, polygamous, dioecious; *Lauraceae:* bisexual, polygamous, dioecious; *Gomortegaceae:* bisexual; *Hernandiaceae:* bisexual, monoecious, polygamous, *Myristicaceae:* dioecious.

Tabulating:

1. *Magnoliales:* 33% of the families (Illiciaceae, Canellaceae, Himantandraceae) are bisexual, 66% variable in expression.

2. *Annonales:* 50% steadily bisexual.

3. *Laurales:* 28.5% bisexual (Austrobaileyaceae, Gomortegaceae), ca. 70% variable.

It looks as though statistics give cold comfort to the notion that the primitive flower was bisexual, and I see little justification for entering into arguments on the score of what they show. Purely to illustrate: " tepaloidy of the stamens " yielding unisexuality in the magnoliaceous *Kmeria* is in itself clear indication that sexual expression is subjected to hormonal controls no less so than are cleistogamy (*Princ.* **1a** : 525 ff., 566 ff.), and peloria (*Princ.* **1a** : 546 ff.). In Trimeniaceae (*Princ.* **1b** : 1170), the flowers are transitional from unisexual to bisexual, and manifestly strobiliform. The sexual expression of the Amborellaceae is rather less than well defined because the female flower may bear staminodes. If these " staminodes " be functional as stamens, the female flower would then be sexualized into maleness and accordingly become bisexual. We will have ample reason to return to the subject in pages to come, but granting that A. P. de CANDOLLE might be well advised in 1813 in stressing bisexuality against unisexuality, sympetaly vs. polypetaly and apetaly, etc., I doubt whether a serious student will be found today who, well informed of sexual expression and the like, will be inclined to take much stock in " general principles " of the kind favoured by HUTCHINSON, TAKHTADJIAN, etc.

As a check on the returns we have just secured in regard of unisexuality vs, bisexuality, let us verify the score of the Ericales identified by HUTCHINSON (Hutch. 1959. **1** : 111) as: *Clearly one of the most primitive groups of families with sympetalous corollas.* The tally stands as follows:

1. Clethraceae: petals free. — 2. Pyrolaceae: petals free or very shortly united. — 3. Ericaceae: corolla mostly sympetalous. — 4. Epacridaceae: *corolla sympetalous .... lobes imbricate or valvate, rarely the lobes coherent and then the tube opening transversely near the persistent base* [6]. — 5. Diapensiaceae: corolla sympetalous. — 6. Monotropaceae: petals free or united into a lobed corolla. — 7. Lennoaceae: corolla sympetalous. — 8. Vacciniaceae: corolla sympetalous.

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[6] I have never had the opportunity of verifying what HUTCHINSON reports. As it is well known, the " berries " of forms like the " ericaceous " *Pernettya* have usettled morphology. The tube described by HUTCHINSON may give valuable clues to their morphology. It is probably compound of different layers (*Princ.* **1a** : 339, 342 fn. 497, etc.), and it " opens " by circumscission.

It is accordingly clear that the Ericales are sympetalous for only 50% of their families. What would be the result of a genuinely critical enquiry is of course speculative, cases being well known (e.g., *Byblis*, *Saurajia*, *Vinca;* Princ. **1a** : 234) in which slight intercalary growths, etc., may render a definition of sympetaly and dialipetaly virtually impossible. Even at but a glance, I should doubt that HUTCHINSON's Malvales have right to figure among the " dialipetalous " groups. Petals that are described as follows (Hutch. 1959. **1** : 254) : *Free from each other but often adnate at the base of the staminal column* are rather not " dialipetalous ", which their manner of falling very clearly proves.

Concluding overall: I cannot understand why modern systematists should display, and factually stress, as " natural " characters that are definitely " artificial ", and were positively identified as such by the botanist who first introduced them to classification 150 years ago. The question is not with one or the other system whether it is sounder botany to begin with Magnoliales, or with Amentiferae or with Asterales, or the like forever. The question concerns primarily with forming a sequential idea of morphogeny and phylogeny, and next on working out a " lineal series " of families and orders which, as necessarily lineal once in print, must forever be unsatisfactory unless commented upon rationally and completely. In sum, it is not the way we begin but the explanation that we can give why we begin as we do; how the various groups of classification stand connected step by step along the road of evolution through time over space; how and why (to speak pointedly) a flower of *Magnolia* differs from one of *Ficus*, etc.; that must count in the end. After a long time patiently spent in hammering out new methods of enquiry and observation, NEWTON could (300 years ago already) flatly decline to indulge in theoretical thinking, and to mix what he knew to be certain with what would not seem to him to be such. Over 200 years ago, LINNAEUS was thoroughly awake to the fact that natural classification is a lofty philosophy, and he ridiculed the efforts of unimaginative souls who hoped to master it with technical descriptions artificial characters, keys, and the like. Of course, both NEWTON and LINNAEUS understood that it is overwhelmingly difficult to teach to a mass of more or less intelligent students and hearers the sheer stuff of ideas, and how to handle these ideas efficiently at all times. The former wished above all to be left in peace to his work; the latter used but descriptions and keys to instruct the bulk of his students [7]. In the end, however, science and reason affirm their rights, and " unpopular " books, memoirs, etc., must be written that, at first hard to finance and to sell, become eventually the landmarks of the future. No one may be blamed for declining to write stuff of the sort, but

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[7] Most interesting is also the preface written by PERSOON (for his *Synopsis plantarum* **1** : V-XII. 1805). He drew a sharp distinction (*op. cit.* : X) between a method : *Qua plantarum genera serie naturali in diversas disponantur tribus, quas facilius ob eorum multitudinem mente complecti et illorum diversitatem observare possimus*, and an artificial system *(systemate ... mere artificiali)*. Believing the *Genera plantarum* of JUSSIEU to be : *Opus vicissitudines in scientia saepe obvias non facile subiturum*, he observed that several of the " classes " of the artificial system of LINNAEUS could be considered as virtually natural. Accordingly, he proposed for these " classes " both the artificial Linnaean designation and the natural name (e.g., *op. cit.* : **2** : 109, 138 ff. : " *Didynamia Gymnospermia* " = Labiatae; " *Didynamia Angiospermia* " = Verbenaceae, etc.). Augustin Pyrame de CANDOLLE transparently understood in 1813, as we heard, that natural families could only be listed in an artificial sequence based on arbitrary characters. In short, whatever authors of the kind did, they did, knowing what they were doing and why.

everybody should know enough, whatever he may write, not to confuse different needs and ideas as one. Botany is behind the times in higher thinking from three (NEWTON for general method) to one and a half centuries (A. P. de CANDOLLE; for the task of writing out a " natural " system of classification), and its adepts ought to know it.

How to begin, and what to think after beginning

Statistical grounds alone would be sufficient, as we learned, to discredit " general principles " intending the " primitive angiospermous flower " to be bisexual, dialipetalous, etc. It is additionally written in the historical records of botany that, when advancing principles of the sort, A. P. de CANDOLLE knew them to be artificial. Maintaining the natural classification of JUSSIEU for groups of genera (families, in the main), CANDOLLE freely made use of an artificial classification above these groups. Clear to CANDOLLE in 1813, this essential distinction has since been lost, and it is one of the main purposes of these notes not only to restate it, but to draw from this restatement whatever main conclusion is warranted by the present state of factual knowledge. It must be clear on the spot to every botanist that proper phylogeny cannot rest its case on artificial characters mistaken for natural ones. Since this confusion has been, and still is being perpetrated, it follows that, alas, a great deal of high systematics must be rewritten from the ground up.

It is commonly admitted (and I also concur) that the primitive inflorescence, or flower that it would be, of the archaic Angiospermae (whatever the archaic Angiospermae themselves could be) was a " strobile ", that is, it was formed by lateral members in indefinite number borne along a central axis. Normally, whenever we think of a strobile we visualize it extended in height, that is formed generally

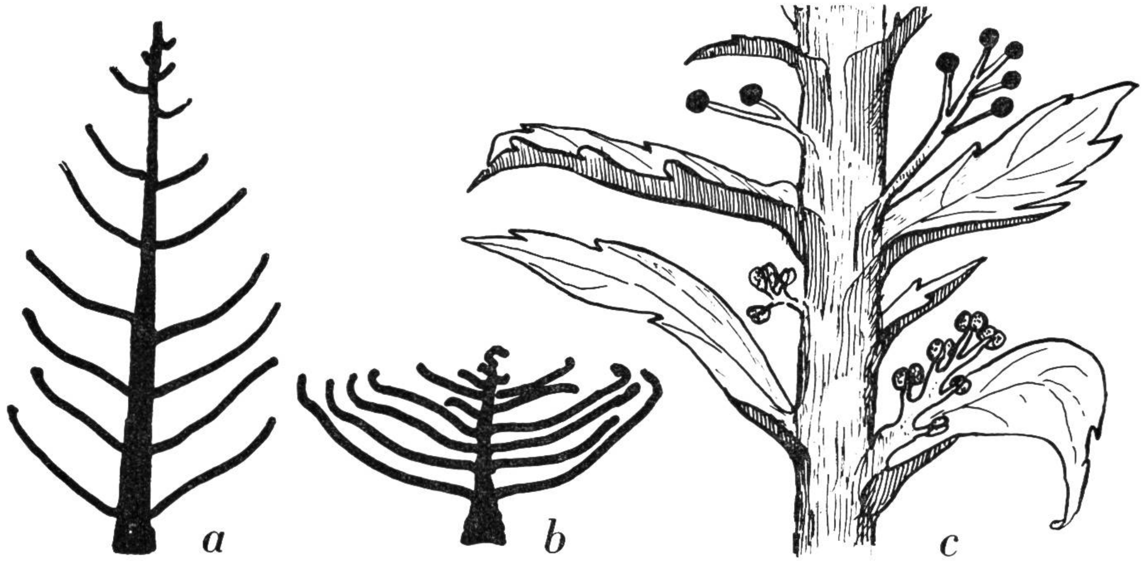

FIG. 2. *a:* " Long " strobile. — *b:* " Short " strobile. — *c:* Component elements of the strobile: macrosporophylls-placentae (tips black); microsporophylls-stamens (tips stippled); subtending (sterile scales or bracts).

to resemble a fir or spruce tree. This is no doubt correct (fig. 2a), but the " long strobile ", as we may call it, admits of a counterpart (fig. 2b) in which (*Princ.* : 354, fig. 42 A, in particular) growth in height is much reduced, and growth in width much increased. This " short strobile " may easily yield, of course, an urceolus, hypanthium, torus, etc., depending upon the degree of its " evagination ". I would like to impress it very strongly upon the attention of my readers, that the " long " and " short strobile " are absolutely not contradictory. They stand in fact but for morphological variants based on the same morphogenetic premises. These premises are of course represented by a structure of lateral members borne upon a central axis of variable length and thickness (fig. 2c), and it is significant that the Monimiaceae sensu lato should easily return examples of both the " long " (Trimeniaceae, Amborellaceae) and the " short " strobile (Monimiaceae sensu stricto), thus implicitly confirming that the two are by far not antithetic and so exclusive. Running here ahead of argument somewhat, but without for this stating anything which is new and challenging (see e.g., *Princ.* : 319, fig. 38), I should point out that the morphogenetic and structural premises displayed by fig. 2 a-c give immediate reason for all manners (fig. 3) of modern angiospermous flowers and inflorescences.

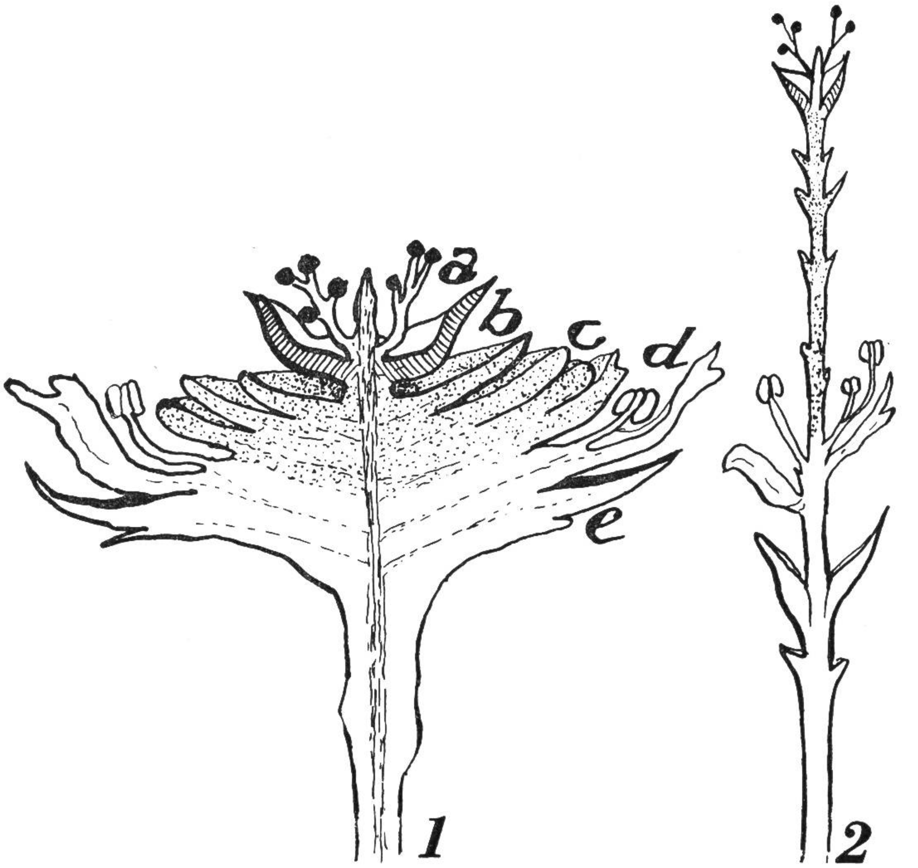

FIG. 3. *1:* Strobile when compressed; constituent elements as follows: *a*, placentae; *b*, scales subtending placentae (= " carpels " auct. p.p.); *c*, scales of unassigned nature generally forming the disc (disc-sector stippled); *d*, stamens, petals, staminodes; *e*, calyculi, sepals, etc.) — *2:* Strobile in " long " condition.

Within premises of this simple kind, even slight differences in degree of compression, locus of immediate sexualization, etc., will return flowers and inflorescences of the most different in appearance and anatomy.

Since everybody is agreed that the " primitive flower " of the Angiospermae was a strobile; since everybody in botany is by now informed that dicta to the effect that this flower must be bisexual, dialipetalous, etc., are compilatory in the worst possible sense, and accordingly misplaced; I ask why the argument should go on for ever whether classification must begin with the strobile of *Magnolia*, or with that of *Betula*. " Strobiles " they both are, and as such either and both are " primitive ". This point is by now so well established that no one should lose time with it any longer. If anything may still be left for settlement, it is the relative degree of " primitiveness " of *Magnolia* vs. *Betula*. This is of course not to be decided by snappy fiats, but by a critical comparison of forms of the kind with both their descendants and their ancestors.

The enquirer who associates a measure of botanical knowledge with an understanding of general methodology, and some familiarity with the byproducts of other sciences, is forthwith impressed by the fact that the average botanist indeed seems to enjoy a privilege of affirming what he likes without feeling for this bound to return sequential proof. To be precise: I may, as a botanist, freely believe that it is possible to " derive " a flower of rose from one *Magnolia* and from a flower of rose and of Witch-hazel eventually to " derive " a flower of birch. I may print this for others of my peers to read and perhaps to believe. So far, so good, but I should feel that, handed that to read, I would like to have some rational explanation of the process of evolution (structural and phylogenetic alike) competent, as it may seem, to turn a flower of *Magnolia* into one of *Betula*. I hold for myself to be impossible to "derive" the one from the other in the light of any "general principle", or like fiat, as now current in botany, and I should genuinely wish that I be concretely and sequentially shown what I apparently do not understand, and have never mastered. My right to learn seems to be perfectly clear but, strange to say, nobody seriously thinks of recognizing it in botany. In this science affirmations exceed explanations (even unsatisfactory ones) by at least ten to one. In the mathemathical and physical disciplines this would be outrightly unthinkable, which implicitly casts botany into a very curious category.

To judge from what the literature has revealed during thirty years to my enquiries, no botanist would like today to be faced by the task of concretely and sequentially explaining how the flower of *Magnolia* managed, as it seems, to some to evolve into that of *Rosa*, *Hamamelis*, *Ficus*, finally, *Betula*. The literature is chockfull of the most detailed accounts concerning the anatomy of these flowers and plants, but above and beyond this reigns an unbroken night of ignorance and neglect. Nobody cares to know, even less to explain.

Out of this night, I have emerged with the conviction absolutely made thanks to my own enquiries that it is impossible outright to " derive " a flower of *Betula* or *Ficus* from one of *Rosa* or *Magnolia* using as connecting-link any of the living Angiospermous families. It cannot be done, and there is no reason why attempts should be made at doing it. If mathematicians have given up long ago as hopeless the task of squaring the circle, botanists ought at long last overdue stop fabulating about " derivations " which they manifestly do not understand, and run against the rudiments of the logics of nature.

If, as I take it by now for certain, the flower of *Magnolia* and that of *Betula* or *Ficus* cannot be constructively compared using the dicta of current botany; if no connecting-link exists for these structures among the living angiospermous groups; this is of course not to prove that these flowers are incomparable throughout and absolutely unrelated by common structural premises. Missing among the angiosperms that we know, the common denominator must exist elsewhere. It may not be extant, which is far from meaning that it is bound to be hypothetical. A skilled mechanic may, by practice and common sense, reconstruct the purpose and plan of a machine of which he is shown but certain pieces. A trained archaeologist can put together a lost world out of sheer scrap. A competent zoologist can use comparative anatomy to quite telling purposes. Well informed, a botanist could not do worse and less: he, too, can sequentially, constructively bring to life again what once was, is no longer, but survives hidden but skin-deep under the appearances of its descendants.

The method of enquiry to follow in botany is of course elementary. Definitely renouncing fabulations woven around *Magnolia*, *Rosa*, *Hamamelis*, *Ficus*, *Betula*, etc., case by case in particular, the competent botanist must abandon the level of angiospermy freely to enter that of pre-angiospermy under the guidance of this time precise morphogenetic and phylogenetic ideas. If we disregard for the moment certain " general principles " of which we have had some unfortunate example before us, we must be sure that HUTCHINSON and TAKHTADJIAN are agreed themselves that the level to be explored is not that of modern angiospermy, but that of pre-angiospermy. Right below the Magnoliales, which rate to him (Hutch.: 19) as the earliest Angiosperms, older even than Ranales and Butomales, HUTCHINSON places certain " Hypothetical Proangiospermae ". TAKHTADJIAN already identifies (*Proiskh.*: 39) as " hemi-angiospermous " *(polupokrytosemennye rasteniya)* the magnolioid *Degeneria*, and certain species of *Drimys*. No clearer hint could be wished for, where to look if one really intends to find. Is it not quite clear that botanists, who map out so tellingly the main outline of the enquiry needed put next seek through the angiosperms what must be looked for among the pre-angiosperms, are bound to be indifferently advised?

This being the case, it is readily seen that the conventional " tree of descent ", that it be a " tree of ascent ", displayed in the literature (see here fig. 1; Hutch. 1: 19, 24; Takhtadjian: 48, fig. 16)[8] is fundamentally ill conceived and as such not fit to convey a proper idea of phylogeny, morphogeny, and basic interrelationships among the living Angiospermae. The correct diagram for the purpose (fig. 4) must embody the following essential concepts:

1. A line, better to say, belt separating pre-angiospermy from angiospermy.
2. An eventual bond, deep into the bosom of pre-angiospermy, making it possible eventually to bring together by structure and affinity, e.g., *Magnolia*

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[8] I view it as significant that no " tree " figures in TAKHTADJIAN's latest version of the *Proiskhozhdenie*. Although still moving within conventional lines, TAKHTADJIAN's thought would not seem in 1961 to be altogether satisfied with them in certain important respects. Of course, my impression that it is so may not be justified. If it is not, I hope that TAKHTADJIAN will duly inform my readers and myself, what we ought to believe.

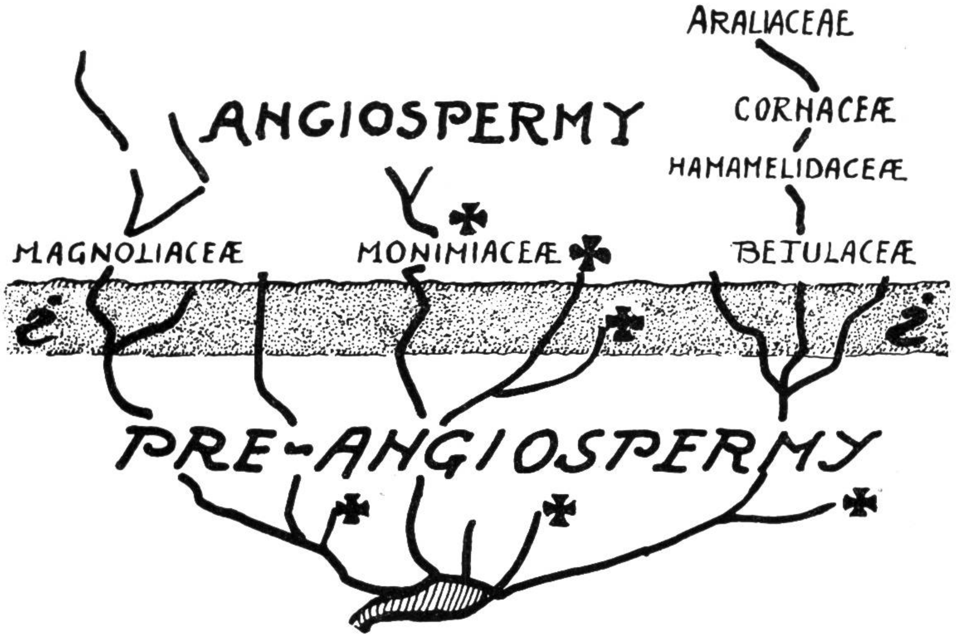

FIG. 4. Modified " tree " of angiospermous ascent: the basic interrelationships among extant and extinct groups and families (latter symbolized by crosses) are forged at the level of pre-angiospermy. Between this level and that of full angiospermy stresses an intermediate horizon (*i*, stippled) out of which immediately emerge a number of key-families. The Betulaceae are indicatively shown connected with the Hamamelidaceae, Cornaceae, and Araliaceae. Observe how this modified " tree " replaces the phylogenetic and morphogenetic bottleneck of fig. 1 with a broad basis of phylogeny, morphogeny, and dispersal without interruption of the angiospermous line of development from its inception to our times. This modified " tree " further makes it possible to account for the phylogenetic and morphogenetic involvements of Magnoliaceae and Betulaceae, etc., against a deep background of evolution through time, space, and form.

and *Alnus*, *Flacourtia* and *Salix*, *Monimia* and *Saxifraga*, etc., etc. In short, the eminently morphogenetic problem how to effect contacts among the flowers, inflorescences, etc., of all these forms (a problem insoluble above the level of angiospermy) is to be uncompromisingly shifted to the level of pre-angiospermy, where a rational solution becomes finally possible.

In proposing these modifications to the conventional " tree " I have very much on my mind a problem of utmost importance for botany at large. I have stated it, as usual, in my own droll way (*Princ.*: 444 ff.), but other students (e.g., HUGHES, *Sci. Progr.* **49**: 84.1961) have felt it quite as clearly. Microfossils are rapidly gaining in importance, and it is virtually certain that botany will have to depend on them for the disposal of numerous problems for which macrofossils may never be obtainable. Naturally, to use microfossils efficiently we must:

1. Have a correct idea of the morphogeny and phylogeny of pollens, in general as well as in particular. I view this as of utmost importance, for so long as we have wrong ideas of pollen morphogeny and phylogeny that long we shall never be in

the conditions of interpreting microfossils correctly. I regret that I cannot hope to work on this problem, for which materials and collaboration are indispensable that I do not have.

2. Form a correct idea of high systematics.

To illustrate: If we finger through the pages of ERDTMAN's *Pollen morphology and plant taxonomy*, 1952, we cannot fail being struck by relationships which we have today no means of rationalizing. For example: no one will wonder that the pollen grains of Gesneriaceae (*op. cit.*: 190) yield similarity in the direction of Bignoniaceae and Scrophulariaceae because these three families do ressemble one another at a glance. Palynology also easily makes sense when it tells us (*op. cit.*: 183) that the pollen grains of Garryaceae and certain Araliaceae have something in common. It is by now accepted that Cornaceae and Garryaceae are allied, and it has already been established (see *Princ.* **1b**: 1731 ff.) that the pollen of *Myodocarpus*, connecting-link between Araliaceae and Umbelliferae, suggests cornaceous characters. Moreover, a direct line running between Cornaceae and Araliaceae (*Princ.* **1a**: 324 ff.) is obvious. If palynology here manifestly hints global, broad relationships it does so in a manner which no longer can catch us by surprise. That the pollen of Empetraceae and Epacridaceae is ericaceous (ERDTMAN; *op. cit.*: 159-160) is common-place, but that the Ericaceae should suggest in their palynology (*op. cit.*: 162) the " saxifragaceous " *Carpodetus* may be baffling. As to Flacourtiaceae (*op. cit.*: 179), it is but normal that their pollen should be reminiscent of Elaeocarpaceae and Euphorbiaceae, but the ressemblance which ERDTMAN claims having detected between the pollen grains of Flacourtiaceae and Salicaceae is a very different matter. It is indeed difficult to visualize *Flacourtia* and *Salix* as consanguineous on the basis of their characters, and HUTCHINSON affirms (Hutch. **1**: 106) that if any ressemblance exists between them it can at the best be superficial. Not so TAKHTADJIAN (*Proiskh.*: 69) who, dissenting from HUTCHINSON for once, insists that the Salicales are " derived " from " Cistales " (including Flacourtiaceae), not at all from " Hamamelidales " as HUTCHINSON implies. Who is to be believed in the end, and may not ERDTMAN be the possible victim of a misunderstood " morphological convergence " between flacourtiaceous and salicaceous pollens? Where is the standard to decide?

All in all, a critically minded student of high systematics will without much difficulty form the opinion (*Princ.* **1a**: 444 ff.) that palynology (or pollen-anatomy as some prefer to call it) is an extraordinarily useful tool of phylogenetic and palaeobotanical enquiry. However (and the case is no other with wood-anatomy) the value of the returns from tools of the kind is far from absolute. What they show only makes the task of eventual synthesis more complex than ever, and furthermore often leads to an all around confusion of methods and ideas when (as the case is with Flacourtiaceae and Salicaceae [9]) palynology returns " pointers " that current botany is not ready to assimilate.

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[9] I have in mss. an enquiry upon the position of the Flacourtiaceae in high systematics. It can easily be shown that both HUTCHINSON and TAKHTADJIAN are in factual agreement when believing that they differ most profoundly on the Salicaceae's " derivation ".

Whatever the case with this or that particular example (and even granting that under the conditions of botanical knowledge now current palynology may at times confuse similarity with consanguinity) the fact that palynology does contribute a very powerful, indeed to an extent unique, tool of analysis of relationships is already undeniable; even when its data do apparent violence to the limits of the extant angiospermous orders and families. Palynology, then, necessarily hits the horizons of pre-angiospermy. If *Salix* and *Flacourtia* yield no indication of direct consanguinity, and cannot be brought together using as intermediate living angiospermous forms (which is surely not the case of, e.g., Gesneriaceae and Bignoniaceae, Garryaceae and Araliaceae) they must come together within the bosom of some very ancient, necessarily pre-angiospermous affinity, unless of course palynology be completely mistaken in what it claims, which I, for one, would not believe without proof. It is meantime obvious that such a " tree " as that shown by fig. 1 is useless for the purpose of exploring the vital pre-angiospermous levels of ascent and descent. It is of course not a question of replacing that " tree " with another that might seem to be more satisfactory on sheer grounds of individual opinion. It is a straight question with thinking out the concepts that will give a " tree " the purposeful, quite general, meaning which its current versions emphatically lack. Obviously, this must be done in a manner which compels reasonable belief much sooner than haphazard opinion.

Strange to say, in a way, the " tree " which I have presented in the *Principia botanica* (**1a** : 424, fig. 49 : 436, fig. 50) to conform with the method and principles just stated is in reality very close to Hutchinson's basic understanding of the interrelationships among the first three " climaxes " of his classification. This understanding (see fig. 1) shoots upward from Magnoliales to Dilleniales, Rosales, Hamamelidales to end with Casuarinales. If instead of being allowed to hit the sky almost vertically, the Hutchinsonian " tree " is broken at the Magnoliales node, and made to lay flat in an horizontal position (fig. 5), this " tree " aligns this time left to right, no

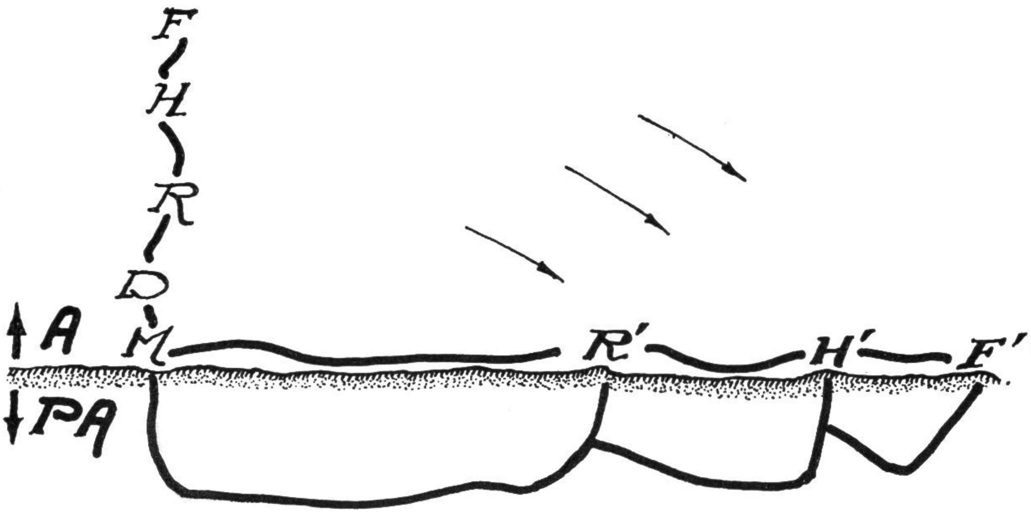

Fig. 5. How to connect the " tree " of fig. 1 with the " tree " of fig. 4 (see the main text).

longer down up, Magnoliales (Dilleniales), Rosales, Hamamelidales, Casuarinales. The horizontal series thus formed is very close to the one I have quite independently found, and exemplified, left to right, with Magnoliaceae, Nymphaeaceae, Monimiaceae, Ulmaceae, Hamamelidaceae, Betulaceae. Together with other authors (*Princ.* **1a**: 1170), I have granted primary significance to the Monimiaceae which the classification of Hutchinson would not seem to highlight. However, that classification does stress the Rosales as a phylogenetic peak, so to speak, between the extremes of Magnoliales and " Amentiferae "; and, rather curiously, it places under Rosales the Calycanthaceae which I would hardly know how to separate from the Monimiaceae sensu lato [10]. In short, the Rosales of Hutchinson do patently involve the Monimiaceae which brings his understanding of interrelationships in line with mine though, of course, in a very different spirit. It must be a matter of gratification that a cytogeneticist like Darlington (*Princ.* **1a**: 630) also agrees with Hutchinson and myself in matters of high essential.

In conclusion: The " tree " which traditionally graces (or disgraces) the pages of standard botanical textbooks is misconceived from its very roots. It narrows the essentially broad, natural basis of angiospermy to a bottle-neck allowing but the emergence of a single group, whether Magnoliales, Betulales, Casuarinales, or the like. This once done, that "tree" is bound to stultify the whole of the interrelationships among groups which cannot be brought together within the limits of living angiospermous forms, eventually postulating the glaring absurdum of " derivations " of *Betula* from *Magnolia* via *Rosa/Hamamelis*, or of *Salix* from *Cistus*. It is very likely that Linnaeus knew better (see Giseke, *Prael. Ord. Nat. Plant.*: 623 ff. 1792) a long time ago. I would of course not encourage the retort that the traditional " tree " has but indicative value. I would not, because:

1. The parameters intended for an indicative graph must be essentially true, not distorted, whatever the purpose immediately sought.

2. It is a very serious matter that the young student be given a false impression at the start of his interest of the nexus between pre-angiospermy and angiospermy.

3. It is, alas, true that the conventional " tree " is not at all meant as indicative. On its branches are, as a matter of fact, hung arguments which make shambles of morphogeny and phylogeny as one.

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[10] Beyond doubt over-comprehensive in the classification of Takhtadjian (*Proisk.* 1954-1959) as a glaring mixture of what is " rosaleous " with what is " saxifragaleous ", the Rosales os Hutchinson (Hutch. **1**: 148) sin, in a way, to the contrary. They consist of but three familiee namely, Rosaceae, Chailletiaceae (Dichapetalaceae), and Calycanthaceae. As to the last, I havt voiced an opinion already. The Chailletiaceae (I use this designation with Hutchinson, withou. being at all sure of its nomenclatural status which I cannot verify; see for Dichapetalaceae, *Princf* **1a**: 425 ff.) are intermediate to Thymelaeaceae (to which they are nearest), Flacourtiaceae, and Celastraceae. The reasonably near kinship between Chailletiaceae and Thymelaeaceae becomes obscure when comparing, e.g. *Dichapetalum thonneri* (Hutch. **1**: 150. fig. 25), and *Daphne mezereum* (*op. cit.*: 216. fig. 85), but can readily be felt when comparing chailletiaceous species of *Stephanopodium*, *Tapura*, *Gonypetalum* (see for informative figures, Engler & Krause, in Engl. & Prantl, *Nat. Pflanzenf.* **19c**: 9 ff., fig. 4-5. 1931) with the genera assigned by Hutchinson to Gonystilaceae and Aquilariaceae under Thymelaeales. In a classification like Hutchinson's, I do not see how the Chailletiaceae can go with Rosaceae when they ought by all means to associate with Aquilariaceae, Gonystilaceae, Penaeaceae, and Thymelaeaceae sensu stricto. I would not be sure that the Geissolomataceae belong here, and I am this time definitely certain that the inclusion of Nyctaginaceae under Thymelaeales invites stringent revision.

Euanthium versus pseudanthium

It is not my intention to discuss in this section of our enquiries what in the literature has passed for *euanthium* or *pseudanthium.* My intention is not to deal with the figments of Man but with the works of Nature and to suggest, if at all possible, how those figments can be replaced by a solid understanding of what evolution did manage to achieve. The finest of theories are vastly below an efficient method of enquiry, and to the latter's establishment concrete, interlocking considerations of straight fact are essential, not learned reviews of a more or less excellent literature.

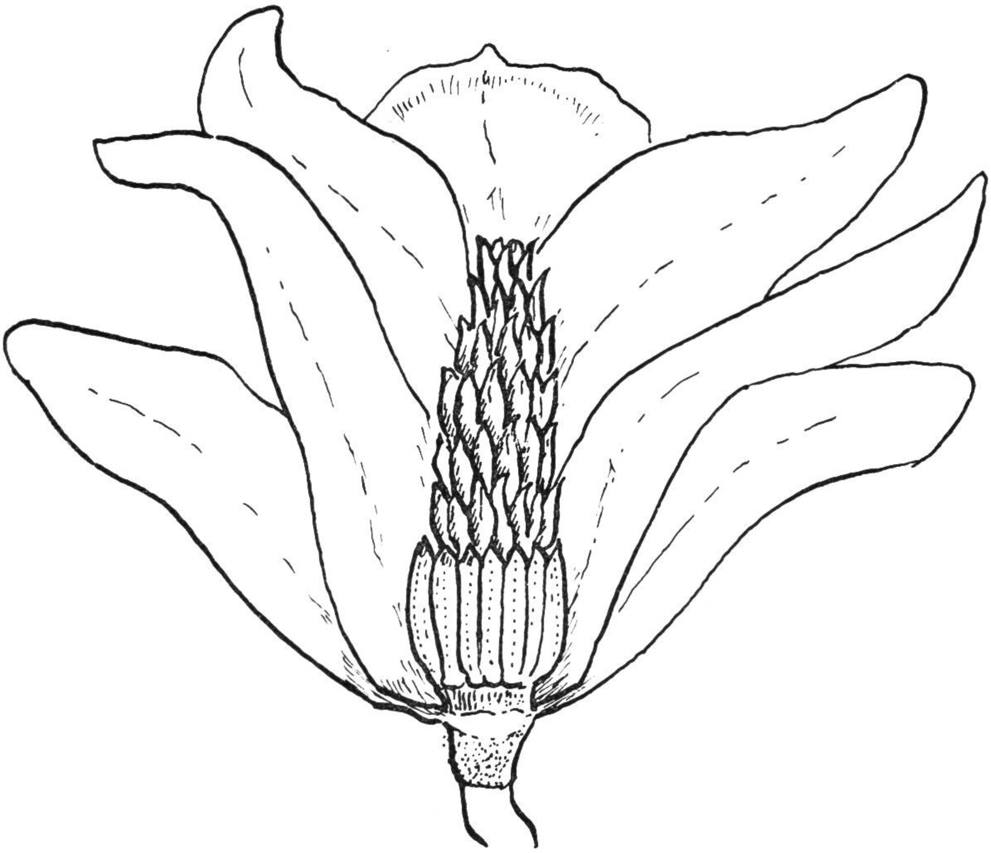

FIG. 6. A flower (strobile) of *Magnolia* (actual).

The flower of *Magnolia* is an euanthium (fig. 6), that is, a true flower, sensu omnium, including myself of course with everybody else in the ranks. So far so good, but may I ask how this classical euanthium can with the least disturbance of its essential anatomy, that is, maintaining it as a strobile, be changed into a pseudanthium? The answer to this question is obviously elementary. All we need do is to distribute the stamens among the carpels in such a way that each carpel is " assisted " dorsally or laterally by one or more stamens (fig. 7). This simple change will turn the euanthium of *Magnolia* into, e.g., the pseudanthium of *Hout-*

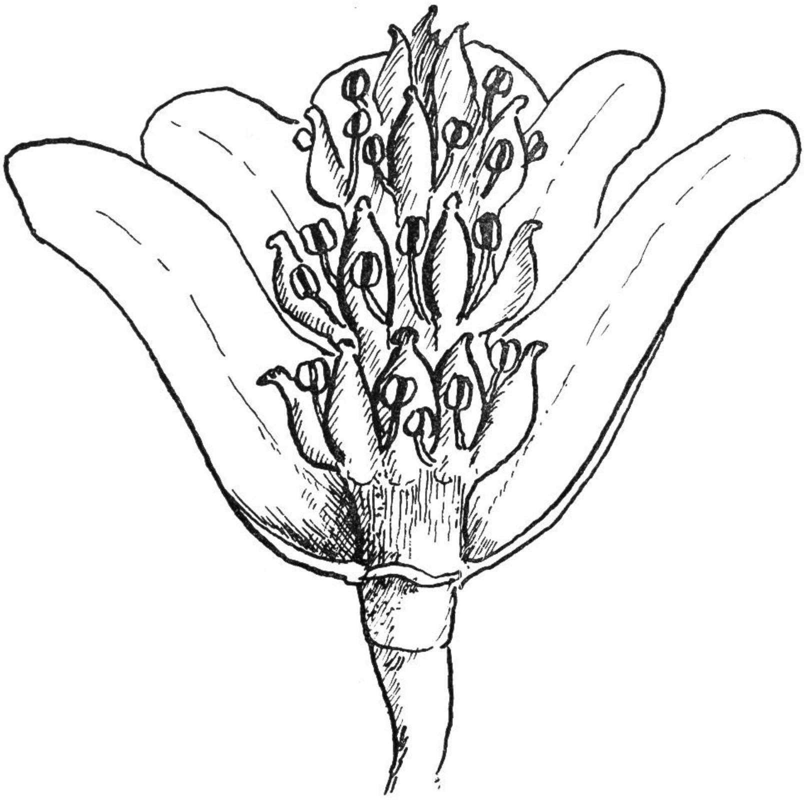

FIG. 7. The same, modified by a different distribution of the stamens, and accordingly turned *ipso facto* into an inflorescence.

tuynia, etc., leaving meantime the strobile to stand as a strobile throughout. Of course, we could change this same euanthium into a pseudanthium by inverting its sexuality, and placing the androecium at the upper end of the strobile. This will readily seem strictly hypothetical to most botanists, but rather not so to a specialist in the taxonomy of the Euphorbiaceae (see, e.g., on *Acalypha*, PAX & HOFFMANN in Engler & Prantl, *Nat. Pflanzenf.* **19c** : 135, fig. 70.1931; CROIZAT, *Princ.* **1a** : 555).

Concluding the very concept of flower rests essentially on two factors, that is :

1. A factor of reduction, meaning, a crowding of (sexual) organs and parts within a minimal area.

2. A factor of distribution, meaning, a staggering of the sexes, the androecium being basal or lateral to the gynoecium.

The first one of these factors we will presently analyze. The second, obvious on its face, leads on to a somewhat unexpected consequence (fig. 8). What we call the carpels of the strobiliform euanthium of Magnolia can of course be also understood as flowers " unisexualized " into femaleness on account of the failure of stamens to develop at the base or sides of the ovary. The same is true of the stamens, which may well represent an androecium left without ovary.

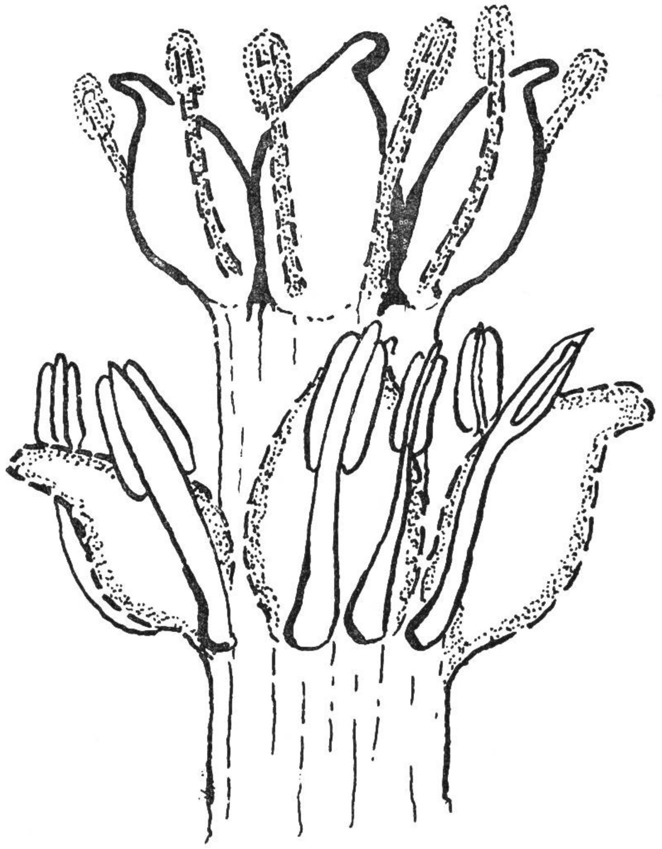

FIG. 8. Diagram to illustrate the fact that, given the sexual expression shown by fig. 7, " bisexual flowers " shorn of their stamens become " carpels-ovaries ", and shorn of their " carpels-ovaries " turn into groups of stamens. Suppressed parts in broken outline and stippled.

Somebody is sure to tell me that I must be downright crotchety outright [11] in imagining something so weird and captious. I do not think so because of a number of good reasons, as follows:

1. The limit-cases which void of their meaning the definitions of botany are very numerous. We will see some striking instances of this in this same article, not to mention, of course examples that I have underscored elsewhere (*Princ.* **1a** : 472 ff., 555, etc.). To meet a limit-case successfully a precise understanding of the minimal and maximal structures in play is advisable, from stamens and carpel to inflorescence overall.

2. Stames will make carpels (*Princ.* **1a** : 534 ff.) under normal or abnormal hormonal controls inducing a change in sexual expression.

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[11] I have been treated as such in good print already, rather politely by LAM (*Vakbl. Biologen* **2** : 31. 1953), quite less than so by POLUNIN (*Intr. Pl. Geogr.* : 21. 1960). Of course, crotchety and objective are relative terms, and I prefer by far being the former alone than the latter, hopefully of course, in the good company of the authors mentioned.

3. Female flowers consisting of absolutely naked ovaries are well known (see e.g. *Eucommia*, HARMS in Engler & Prantl, *Nat. Pflanzenf.* **18a**: 348 ff. 1930; *Daphniphyllum* (female flower wanting minute staminodes), ROSENTHAL in *op. cit.* **19c**: 233 *ff.* 1931). The objection that the ovary of *Eucommia* is 2-carpellate, and that of *Daphniphyllum* virtually such, while the carpel of *Magnolia* is 1-merous is not sequential in the premises. A limit-case of the clearest is at any rate in play. In sum, and here concluding insofar as we have progressed in investigation, I will affirm that the limits between flower and inflorescence, carpel-ovary and naked female flower, stamens and male flowers, are evanescent, certainly not such at any rate to justify theories based on the phylogeny of the unisexual and bisexual flower, of the euanthium of the pseudanthium of the strobile, etc. Everything in flower-making is skin-deep, so to speak. It may become quite well fixed in one or the other group on the basis of tendencies by now firmly in the saddle (e.g., unisexuality in the Euphorbiaceae[12]: " pseudanthia " in Saururaceae and Compositae; etc.) but a ground-level of morphogeny is proved to be extremely shifty. No one will be surprised, of course, who is informed of what cleistogamy and peloria (see *Princ.* **1a** and refer to Indices in detail) can do to " metamorphose " flowers and fruits quite radically under the spur of slight changes in temperature, maturity of tissue (whatever this might imply), illumination, etc. Summing up, I would say that I view as incredible that " General principles " such as we have seen displayed in an earlier part of this article can be thought of as meaningful props of phylogenetic and systematic work. Stuff of the sort is obviously misplaced as currently used.

The factor of distribution of the sexual organs essential to the concept of flower is self-explanatory in the majority of the cases, though it may suggest additional considerations of general nature that, unfortunately, cannot be dealt with here. The question why the androecium is never central to the carpels in a flower begs of course a very simple answer. A flower in which the androecium be central to the carpel becomes ipso facto an inflorescence, which ends the argument. Moreover, as we shall soon learn, the normal process of sexualization into maleness of a female flower consists in turning into stamens certain scales or enations on the ovary wall. This means that the stamens are necessarily located in the tract between the base of the style and the base of the ovary, whether immediately or mediately, that is, across an intervening " disc ". A glance at fig. 3 will orient the reader concerning these elementary observations, and more will be added on the subject in pages to follow.

Concerning now the factor of reduction on which the idea of flower rests, it must be obvious on the spot that reduction, unlike distribution which is normally

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[12] I may not open here a long parenthesis or contribute a string of bulky footnotes in order to discuss the Euphorbiaceae. That they are related to Flacourtiaceae is today pacifically admitted. Weighty issues in flower-making sensu amplissimo center as will presently learn around Scyphostegiaceae/Flacourtiaceae. The Euphorbiaceae directly take part in this basic phase of morphogeny and phylogeny. Genera like *Stachystemon Acalypha* and *Euphorbia* sensu lato contain an epitome in flower- and inflorescence-making (and unmaking) of the most instructive and far-reaching. I hope that it may be possible for me to return on the question in a coming article, or series of articles. Already at the end of my days, I feel, after long years spent in hammering out but a few principles, and the method how to have them work smoothly and efficiently, as if my work tackling particular cases is just beginning. My dearest wish is that what I must leave undone may be achieved eventually by somebody much better than I ever could be.

quite clearcut, is a matter of degree, therefore hardly liable to easy definition. There are indeed cases in which reduction undergoes significant alterations from the stage of anthesis to that of fructification [13] which may create serious doubt as to the " nature " of structure ultimately in play. Of cases of the kind I will discuss here one, drawn from the Schisandraceae, one of the magnolioid families.

The Schisandraceae consist of two genera, *Schisandra* and *Kadsura*. As usual, HUTCHINSON diagnoses them quite satisfactorily for general description (Hutch. **1**: 129 ff.). Broadly speaking, the male flower looks like nothing so much as a piece of the catkin of *Liquidambar* subtended by deciduous tepals. The female is at first a conelet (*op. cit.*: 130, fig. 5 b, d) with a perianth to match the male. Evidently much compressed and reduced when in anthesis, the female flower of *Schisandra* markedly elongates at maturity, finally bearing its carpels discrete upon a thickisch, often vividly coloured rachis. In *Kadsura*, the fruit consists of a more or less globose head beset with carpels. In the allied *Sargentodoxa* the carpels are pedicellate, as I will again mention and, accordingly, definitely reminiscent of annonaceous fructifications [14].

Seeing a mature female flower of *Schisandra*, hardly anyone would call it a flower. It obviously is a raceme, and as such it has been described by REHDER (*Man. Cult. Tr. Shrubs*, ed. 2 : 255.1940), a most methodical taxonomist. Though thoroughly familiar with *Schisandra* at all times of the year, still REHDER let his pen wander using to describe the fructification of *Kadsura* (which is a " head of carpels ") a term like raceme that belongs to an inflorescence by definition.

REHDER, then, grossly erred in a way. But, on second thought, what he identified as a raceme looks so much like one that the question legitimately arises, what is it that *Schisandra* really bears? A flower or an inflorescence? And how may we hope to tell? HUTCHINSON may be cited as authority of the quid being a flower; REHDER does imply something else. OZENDA who had full opportunity of investigating the anatomy of *Schisandra* is manifestly perplexed. He found in the male flower of *S. henryi* (*Publ. Lab. Biol. Ec. Norm. Sup. Paris*, **2**: 80.1949) that: *Les rapports de la pièce périanthaire* [= *sepals, petals, tepals, bracts, etc., auct.*] *avec le cylindre central du réceptacle sont ... absolument comparables à ceux de la feuille avec la tige.* This is all the more unexpected, in a way, in that the male flower of *Schisandra*

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[13] Superficial as usual, botany has hardly ever paid attention to matters of the kind. The tiniest of flowers may yield in time the most massive of fruits (e.g. *Swietenia*), and originally perfectly " angiospermous " flowers may return glaringly " gymnospermous " fruit and seeds (*Celastrus, Habropetalum*). See CROIZAT, *Lilloa* **13**: 40 (in particular). 1947; *Princ.* **1a**: 386, 394 fn.

[14] HUTCHINSON gives " W China " (Hutch. **1**: 408) as the range of *Sargentodoxa*, lone extant genus of Sargentodoxaceae with a single species *S. cuneata*. Considering that West China stands as the heart of one of the most formidable hotbeds of relictual angiospermy of the world (*Cathaysia* of TAKHTADJIAN and Russian authors in general; see also Panbiog. **2a**: 742 fn.), crediting to it also the unique *Sargentodoxa* is a venial slip. However, this relic is actually recorded from Central to East China (Hunan, Hupeh, Kiangsi; see CHUNG, A catalogue of trees and shrubs of China. *Mem. Science Soc. China* **1** (1): 48. 1924; REHDER, *Man. Cult. Trees Shrubs*, ed. 2: 222. 1940). Although West China (Szechuan, Yunnan in the main) is included in the range of the Lardizabalaceae, still most of the records of the family do concentrate, as they do for *Sargentodoxa*, in East to Central China (Kwantung, Chekiang, Kiangsi, Kiangsu, Hupeh, etc.). Biogeographically, Southwestern and Southeastern China are well worth being discriminated. I regret I cannot give more time to the issue here.

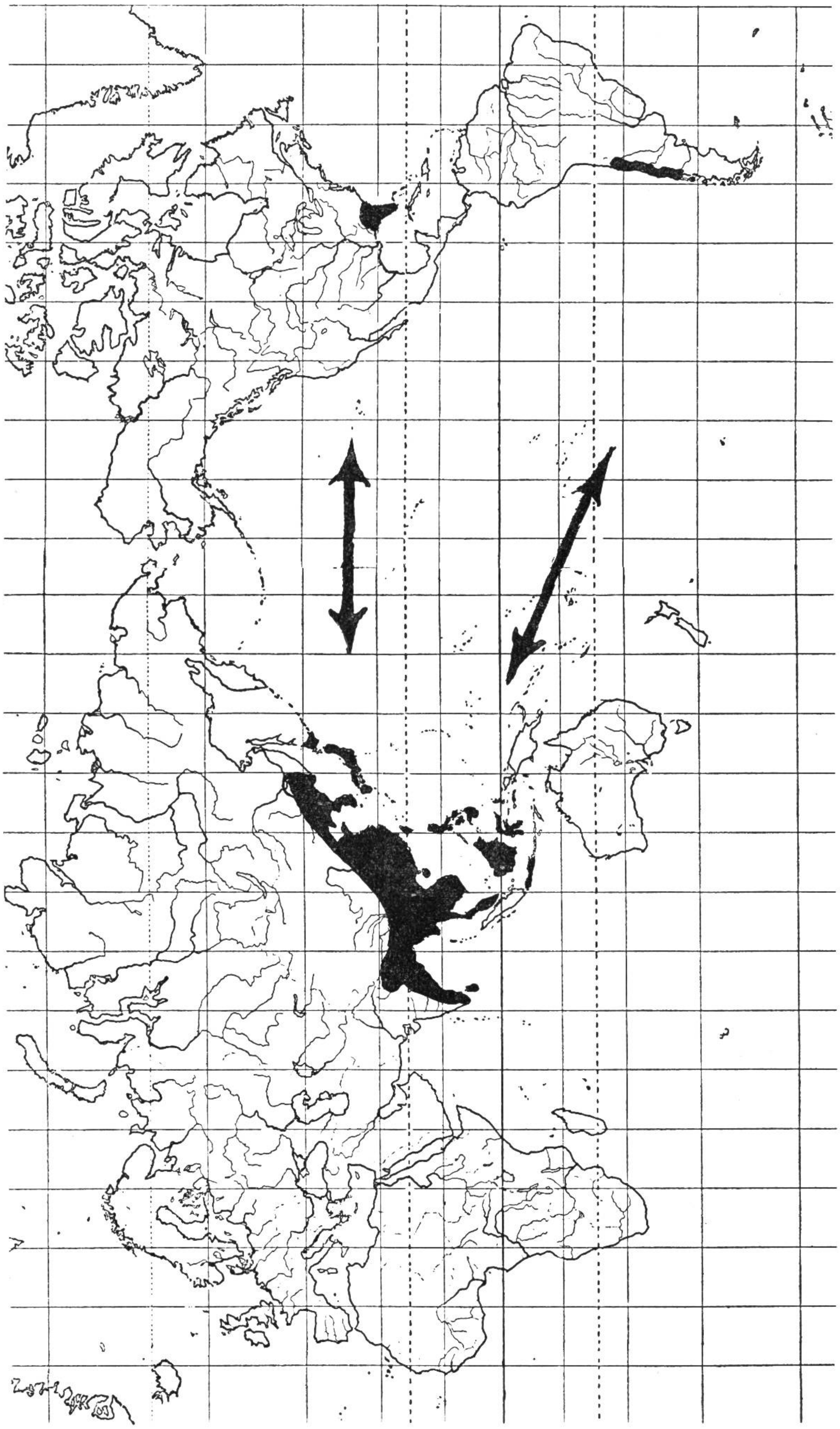

FIG. 9. The transpacific dispersal of Schisandraceae and Lardizabalaceae. The Oriental range partly overlapping. In the New World: Schisandraceae in the Southeastern U.S.A.; Lardizabalaceae in Chile.

is in appearance quite more " flower " than is its female counterpart. Moreover, OZENDA comments on the receptacle of *Schisandra* (*op. cit.*: 83-84) rather cryptically (or, perhaps, quite transparently) as follows: *Le dispositif vasculaire du réceptacle est déjà bien différencié à une époque où celui du carpelle est encore inexistant ou rudimentaire. Ce fait est conforme aux observations faites par Grégoire chez diverses plantes ... Signalons simplement le fait ... sans chercher pour le moment à en tirer une conclusion.* Of course, if a conclusion must be drawn, this conclusion is bound to be that the " flower " of *Schisandra* is an inflorescence. Already upset (*op. cit.*: 153; *Princ.*: 375) by the discovery that the " pistil " of the Magnoliaceae could not be made to square up with the " classical theory of the carpel "; that the foliar trace of *Schisandra* is 1-lacunar while the carpel is 3-lacunar (*op. cit.*: 154), OZENDA would of course see his whole world crumble to pieces were he forced to admit that the " flower " of *Schisandra* is an inflorescence! That far no dutiful student may dare go, whether in A.D. 800 or in A.D. 1962. Starting revolutions, in botany particularly, is not permitted to students, technical assistants, and such lowly personnel. The right to do so is theoretically vested in loftier figures, but since those figures hardly ever will think of using it botany remains there, where it always was, and it still is.

Quite soundly, HUTCHINSON points out (Hutch. **1**: 407) that the Sargentodoxaceae combine in their two sexes the characters of Lardizabalaceae and Schisandraceae, having male flowers similar to the former, female flowers like the latter (especially *Kadsura*; the ripe fruit of *Sargentodoxa* is indeed, rather annonaceous in several respects). In sum, the Schisandraceae do start a unisexual development trending to Sargentodoxaceae and Lardizabalaceae for a quite striking sum total of " transpacific " dispersal (fig. 9) suggesting *Coriaria* (Man.: 72, fig. 23) and *Chrysosplenium* (*Panbiog.* **2b**: 1409 ff. 1427 ff.).

It is dispersal that, whatever the " crossing " in detail (see *op. cit.*: 1526, fig. 271 for an additional reference), falls in with what CAMP has, imaginatively yet quite scientifically, identified (*Ecol. Monogr.* **17**: 175, fig. 26.1947) as the " *Gaultheria* ring " (see also *Man.*: 167, fig. 44a; 146, fig. 36, etc.). The Western Pacific marks indeed the great " gate of angiospermy " for the " magnolioid " quite as much as for the amentiferous alliance. It is understandable that TAKHTADJIAN should have been induced to situate in *Cathaysia* (*Proiskh.*: 93 ff.; *Botanichesky Zhurnal* **42**: 1635.1957) the heart of the dispersal of the Angiospermae. Correct for over half of the tale, this conclusion of course becomes totally wrong if generalized to cover the whole of the tale. Biogeography must be satisfactory for plants and animals on a world-wide basis before proving efficient for only plants or animals on but a provincial scale [15].

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[15] So transparently elementary, yet so basic a scientific requirement is violated today wholesale in a manner difficult indeed to understand. For example: In their present distribution, the Aristolochiaceae could be said to be mainly " bicentric " (Orient and Tropical America with several particular local genera; *Aristolochia* is wide). In a phylogenetic sense their involvements are far-reaching (see, e.g. *Princ.* **1a**: 433 fn. 440, 592 ff. 594 fn. 610 fn.), so particularly with the Cucurbitaceae along the axis: South China-Madagascar. By nothing daunted, certain authors insist on placing the " origin " of Aristolochiaceae in " Cathaysia " on the ground that, e.g. the American genera are less primitive than the Asiatic ones because of more definitely zygomorphic floewrs, etc. One would like to know:

Believing that the original " flower " of the Angiospermae must be bisexual, Hutchinson argues, of course (Hutch. **1**: 130) that the Schisandraceae have apparently been " derived " from the Magnoliaceae. I see this derivation as more hopeful than possible. The truth is that Schisandraceae, Sargentodoxaceae, and Lardizabalaceae do form, teste Hutchinson ipso, a perfectly consistent development from a condition of " flower/inflorescence " to one of " flower " (Schisandraceae to Sargentodoxaceae/Lardizabalaceae), the whole strictly 1-sexual from beginning to end. I see little reason to separate these three families, as done by Hutchinson, the first under No 5 in sequence, the last under Nos 254 and 255, on no better ground than that Schisandraceae are " woody ", Sargentodoxaceae and Lardizabalaceae " herbaceous ". All are climbers, all are closely related within a series morphogenetically and phylogenetically quite consistent, all are congruously distributed, and my feeling is that a classification intending to be even only in part natural cannot have 250 different families stand inbetween *Schisandra* and *Lardizabala*. Hardly credible, yet true : guilty already of a *faux-pas* of this momentuous kind, the Hutchinsonian classification further treats the Berberidaceae sensu strictissimo as " herbaceous " !

Concluding :

1. The " flower " of Schisandraceae stands at the limit between flower and inflorescence. In anthesis it looks like the former; at maturity it yields a raceme *(Schisandra)*; its anatomy and organogeny clearly suggest an inflorescence. In ultimate nature it is exactly comparable to a pseudanthium of, e.g., *Rhodoleia* shorn of stamens [16];

2. Schisandraceae, Sargentodoxaceae, Lardizabalaceae form a perfect series in phylogeny, morphogeny, classification and biogeography;

3. This obviously natural series is unisexual throughout. Unique on a sum total of characters, its secondary growths in fruit are much more reminiscent of Annonaceae than of Magnoliaceae.

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1. How authors of the kind understand the fact that some of the most important centers of angiospermous endemism of the world are located in Eastern South America (*Duida-Roraima* system, Brazilian " serras " the major part at least of the Amazonian " Hylaea ").
2. How do they explain away the bonds effecting contact between these centers and the rest of the world (e.g. for *Croton* along the arc : Antilles-Brazil and Madagascar, with continental Africa hardly affected.
3. How do they figure out what is "primitive" against what is "derivative", and how do they square up what they understand, or assume, as such with rigorous distributional requirements of time through space for plants and animals alike.
4. What do they understand by zygomorphy (see, for example, *Princ.* **1b**: 1817; index where 30 different references proving that what is " zygomorphous " and " actinomorphous ", respectively, is hardly to be separated at all in critical botany).
5. What is their idea of " origins ", " derivations ", " migrations ", etc., etc.

[16] I would not honour with a long discussion the objection (easily anticipatable, of course) that *Rhodoleia* is bisexual, therefore I have no right arbitrarily to imagine it shorn of stamens thus to support some " theory " of my own. I but remark that Harms (in Engl. & Prantl, *Nat. Pflanzenf.* **18a**: 335. fig. 175e. 1930) figures the ovary entirely surrounded by stamens, while I (*Bull. Torrey Bot. Club* **74**: 73. fig. 9. 1947) have found it staminate only on one side. It is very likely that the inspection of a material large enough of this remarkable hamamelidaceous plant will reveal " flowers " that are wholly female, and " heads " of which the component " ovaries-female flowers " are part unisexual, part bisexual. Whatever be the case, nothing fundamental is in question.

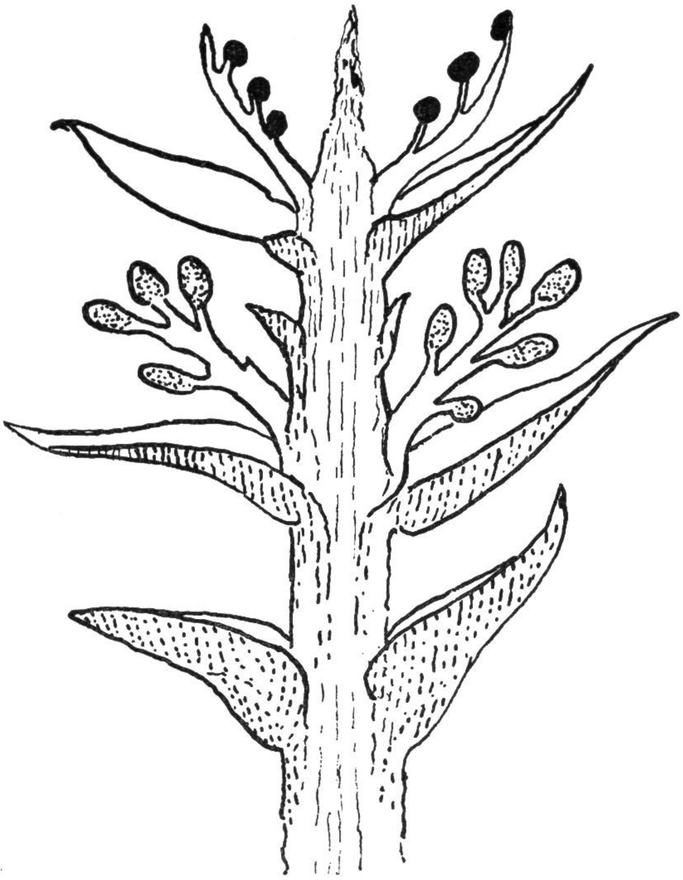

FIG. 10. A " strobile " of the type current in the literature of phylogeny modified in the sense of its having scales subtending sporophylls (see the main text for further details).

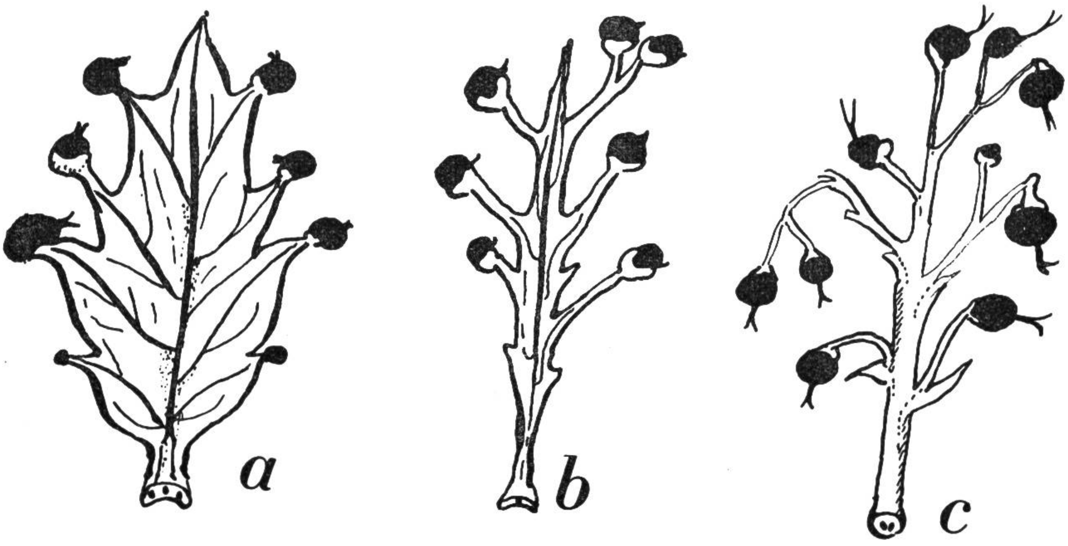

FIG. 11. *a*: Placenta (macrosporophyll) in its "foliar" aspect; *b:* Placenta intermediate between " phyllome " and " telome "; *c:* Placenta in its " rameal " aspect.

The claim that the " primitive flower of the Angiospermae " was bisexual can quite safely be rejected on morphogenetic, phylogenetic, statistical, historical grounds alike. Augustin Pyrame de CANDOLLE was in the right when affirming in 1813 already that the question how to start a lineal series of taxons beginning with families is anything but fundamental. As a matter of obvious fact, whether begun with Magnoliales or with " Amentiferae ", a system of classification intending to be natural runs into the same difficulties if not properly conceived and planned out at the start. The primary question is certainly not whether one or the other group is to stand first in page-sequence, but how all groups can be made to dovetail (insofar as possible today) within a rational scheme of interrelationships true to phylogeny, morphogeny, biogeography, practical needs of classification as one.

On sexualization

The classical theory representing the carpel as a body of foliar nature hardly accounts of course for the actually and potentially extreme complexity of the endocarp, mesocarp, pericarp, and epicarp making up the ovarian wall. Cases are well authenticated (see, e.g., *Princ.* **1a** : 317, 565 ff.) in which the pericarp contains fascicular and interfascicular cambia, the ovary's pedicel intercalary meristems, etc. Overall, the angiospermous carpel is quite as complicated as the scale of a pinaceous cone, or as the valves of the cupules of Fagaceae (*Princ.* **1a** : 286) which, while looking like foliaceous scales, are in reality secondary or tertiary axes of dichasial inflorescences. As a matter of fact (*Princ.* **1a** : 501 fn.), anatomical evidence has also been found that the carpel is a true dichotomous branch-system. No one who has seriously investigated the carpel can fail concluding that it is assuredly not a simple, foliar body, but a vastly reduced and originally complicate quid, which we will identify better presently.

Conventional figurations of the ancestral angiospermous strobile (see, e.g. ZIMMERMANN, *Phylog. der Pfl.* : 327, fig. 230.1930) represent it as formed of lateral fertile and sterile members, the former occupying the upper tiers of the structure. In deference to the classical theory, the female members are construed more or less outspokenly as leaf-like carpels (see, e.g. WETTSTEIN & al. *Trat. Botánica Sistem.* (transl. Font-Quer) : 556, fig. 393.1944) bearing ovules upon their margins.

In agreement with my own findings (*Princ.* **1a** throughout) and those of MELVILLE (in *Nature* **188** : 14.1960), I would slightly modify conventional figurations of that strobile (fig. 10) in the sense of its having each ovule-bearing body subtended by a protective scale, leaving sterile of course, the lowermost scales in the way that Zimmermann, and virtually every other author, show. Insignificant as the change seems to be that I thus propose, it has nevertheless unsuspected importance in several directions. It identifies, for example, two intimately correlated yet conceptually thoroughly distinct organs, that is, an immediately fertile, ovule-bearing body " foliar " or " axial " that it be (fig. 11), which fully deserves to be identified as placenta or (macro) sporophyll. This body is subtended (fig. 12a) by a protective scale with which it may fuse more or less extensively to the eventual extent of a

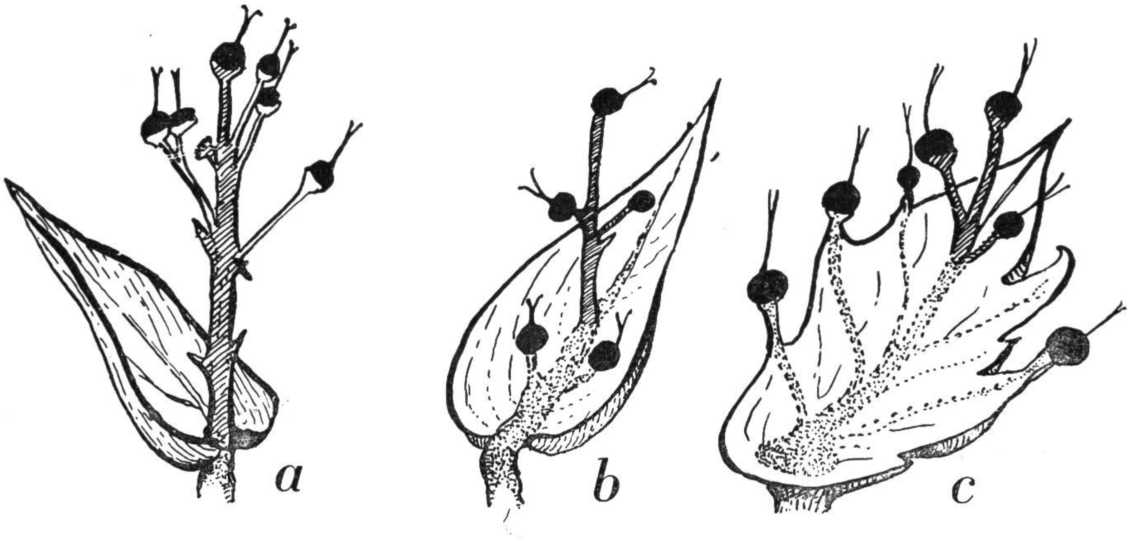

FIG. 12. *a:* Placenta (macrosporophyll) with subtending scale (= " sterile carpel " of HAGERUP, etc. = " gonophyll " of MELVILLE); *b:* Placenta in part " transfused " within the subtending scale; *c:* Placenta fully transfused within the subtending scale and creating the illusion of the " carpel " as a unitary " leaf carrying the ovules upon (or toward) its margins ". A transfused placenta of the kind can hardly be distinguished from the placenta shown in fig. 11*a* (see the main text throughout for further details).

full transfusion (fig. 12b,c). This scale is, in part at least, the " carpel " of most authors, and the " gonophyll " of MELVILLE.

Thus retouched, the " ancestral strobile " (see fig. 2, 3) readily accounts for the complexity of the ovarian walls, for puzzling dehiscences (e.g. *Princ.* **1a**: 496. fig. 57 b, c), for odd discs (*op. cit.*: 339) for phycostemes (*op. cit.*: 341. fig. 41 b, c). All these particular morphologies rest at bottom upon a single morphogeny [17] which has for its basic structural premise a " strobilar " arrangement of scales (see fig. 2 c) actually or potentially sexualizable [18]. These scales are not at all hypothetical because

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[17] Morphogeny stands in my understanding as the sum total of characters and tendencies which collectively belong to different forms. It is by developing their morphogenetic potential in different directions (quite generally in answer to orthogenetic tendencies, that is, to tendencies not primarily, even often not secondarily, bound with " adaptation ", and the like) that the Magnoliales eventually yielded Magnoliaceae, Illiciaceae, Winteraceae, etc.; the Magnoliaceae genera like *Magnolia*, *Talauma*, *Kmeria*, etc. Morphogenetic potential belonging, e.g., to Magnoliaceae is eventually responsible for the different morphologies characteristic of *Magnolia*, *Talauma*, etc. Morphogeny and morphologies accordingly stand in a chain, morphologies going back to morphogeny on a line of ascent; morphogeny answering for morphologies on a line of descent. Whenever a systematist speaks, e.g., of " essential magnoliaceous characters " he evidently refers to morphogeny; when he differentiates, e.g., between *Magnolia salicifolia* and *M. kobus* he stresses morphology. Since morphology and morphogeny do overlap all along the chain, it may seem that discriminating them as I do is unnecessary. I do not think so at all. The concepts are two: Morphogeny essentially stands for a whole of which morphology is but a subordinate part. Systematic thinking is indeed essentially morphogenetic. Rationally understood, phylogeny is but a sequential account of morphogenetic alterations eventually leading to the establishment of related and unrelated groups. If current systematic thinking is still catastrophically behind the times, responsible for it is an abuse of morphology divorced from morphogeny. See: CROIZAT, L., *Space, Time, Form: The Biological Synthesis.* 1962.

[18] I here use the term scale quite generally, referring the reader for a clarification of what I intend to numerous cross-references in the *Principia botanica* (see Index, **1b**: 1791). A scale is neither " telome " nor " phyllome ", but an " emergence " with the potential of " branch "

they can clearly be seen making up the wall of certain ovaries (e.g. *Princ.* **1a** : 320, fig. 39 b). Even less hypothetical are the innumerable interrelationships between placenta and subtending carpel (= MELVILLE's gonophyll), of which a few instances have been shown in fig. 12. Fossil and living forms display interrelationships of the kind (*Princ.* **1a** : 308. fig. 37) as a matter of visual evidence, and literature accepted as standard (e.g. ARBER, *The Gramineae* : 312.1934) records striking, most instructive feats of fusion and transfusion of which, alas, most botanists are all too poorly informed today.

Taking our start from an ancestral strobile (see fig. 2, 10) become by now " flower " (see fig. 3) on account of maximal crowding and adaptation of its component elements, we can reasonably figure two different manners of sexualization of this flower, as follows :

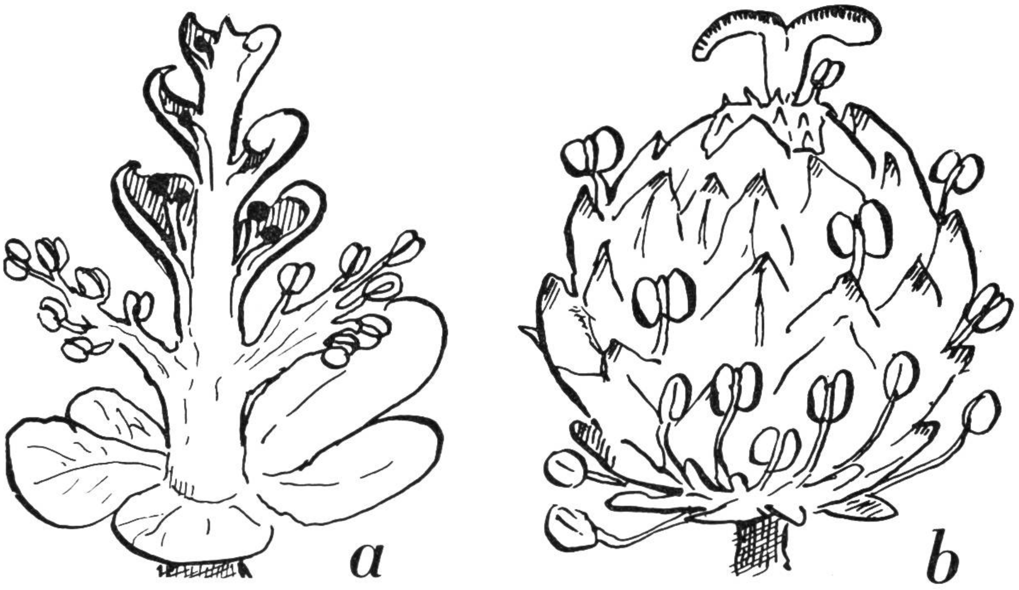

FIG. 13. *a:* Sexualization into maleness of the whole of an ancient strobilar structure (cf. e.g., *Magnolia*, fig. 6) by original destination as stamens of the lower members; *b:* Sexualization into maleness (therefore, bisexuality) of a female flower by additional stamens (see the main text for further details).

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or " leaf ", or of the two variously " fused " and " transfused ". To identify a " sporophyll " as a scale bearing ovules may seem far-fetched, but as everybody knows, placentae (= macrosporophylls in a precise sense) may be " foliar " and " rameal " depending as a rule on the opinion of one or the other author. Accordingly, to assimilate a placenta to an ovule-bearing scale but means, in my judgement, to avoid a useless argument as to whether the placenta is " foliar " or " rameal ", while at the same time referring to a precise interrelationship between ovule or ovules and ovule- or ovules-bearing body. Because of this, fig. 11 represents the placenta as both " foliar " (a) and " rameal " (c) with an intermediate stage (b) between the two extremes. A foliar placenta is of course not at all tantamount to a " classical " (or, Goethian) " carpel ". The subject will be discussed in a page to come in detail. No hair-splitting is involved in these distinctions, which refer to emphatically different concepts of essential organs. By confusing concepts constructive discussion and precise analysis becomes forthwith impossible. See the main text in continuation.

1. The ancestral strobile was bisexual in origin, and the " flower " derived from it (fig. 13 a) endured as such.

2. The " ancestral " strobile was unisexual in origin, and the female " flower " was eventually sexualized into additional maleness (therefore, into full bisexuality, fig. 13 b) by certain of its scales being turned into functional stamens. Simple sketches can make this alternative, and process overall clear.

I have never been privileged to find a precise account how " scales ", whether of the ovary wall or of the disc, can turn into staminodes and stamens. Whether the staminode or stamen represents a new emergence on the ventral (or dorsal) side of a standard scale, or simply a feat of apical sexualization of a standard scale by an adventitious anther (fig. 14), I would just now not know. My feeling is that the former is more likely to prove commonly true (see, e.g. *Princ.* **1a** : 515, fig. 58; 520, fig. 59), but I will gladly accept whatever eventuality proper enquiry may show to be correct.

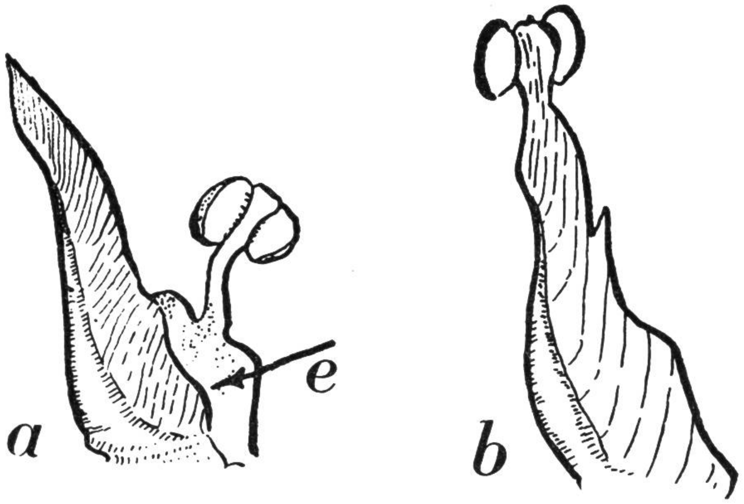

FIG. 14. *a:* Stamen arising on the ventral side of a scale by meristem *e*; *b:* Anther capping a scale (see the main text for further details).

Before proceding with factual evidence bearing ont he stated, I should point out that in the case of " amentiferous " forms with male and female catkins, or like inflorescences, the bisexualization of the female flower renders useless the male catkin. Its function will then be taken over by stamens " grafted " on the ovary-wall or disc of the originally female flower, therefore two tendencies shall develop at the same time, that is:

1. One in the direction of bisexualization.

2. The other in the direction of the eventual full suppression of the male catkin, or similar structure, as by now physiologically useless. This but means overall that

the " Amentiferae " are to be left behind, being replaced by " true flowers " groups. Morphogenetically and phylogenetically, the step is epochal [19].

The line of thinking I have just offered, and the conclusions to which it leads, are supported by an indeed staggering mass of factual evidence of all kinds. I have introduced but part of this evidence to the pages of the *Principia botanica* (see, e.g. *op. cit.*: 258 ff. 287 ff. 300 ff. 317 ff. 324 ff. etc.) following an initial statement of the question (CROIZAT, *Bull. Torrey Bot. Club* **70** : 60.1947) in a current publication. For example: an author who has given considerable attention to sex expression (YAMPOLSKY, *Am. Journ. Bot.* **7** : 95.1920) points out that in the " monoecious " form of *Mercurialis annua* the sex of the plant changes in the course of development from female to male finally ending with bisexual flowers. In the end (as YAMPOLSKY shows): *The line of demarcation between what is male and what is female is wavering and vague*, which no one would think of disputing who has given attention to problems of sex expression, cleistogamy, peloria, etc. In morphogenetic potential both sexes are present as a diffusive tendency to immediate sexualization peculiar to certain sectors of growth, but the flower or inflorescence is finally determined as male, or female, or both by trigger-action of a hormonal nature, liable to release or to inhibit, controled by the apparently slightest provocation of climate, length of night, body-topography, maturity of tissue, etc. [20].

Among the innumerable cases of variable sexualization displayed by *M. annua*, YAMPOLSKY chose to illustrate one (*op. cit.*: 100, tab. 5 (8); here fig. 15) of a female flower bearing a single anther sac without filament budding out of the side of the carpel. This will be put down as a monstrosity by most botanists less than well informed of the subject, but YAMPOLSKY understands it, quite correctly, as but one of many variations (*op. cit.*: 98) that currently take place in this euphorbiaceous weed. Cases of the kind, calling for the bisexualization of an originally female flower by emergent anthers, stamens, staminodes on the walls of the ovary, disc, etc., are legion throughout the " Amentiferae " and their immediate allies, and if the reader turns to the literature he will find both descriptive and graphic evidence of them

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[19] The passage from unisexual catkins to a commonly bisexual flower is but one of the changes in sexual and floral expression displayed by the living Angiospermae. The other, and in no way less important alterations, is the shift from " tubillus " to " style " to be discussed in a page to come. In the last part of this article we will run across still another change, and earliest, which seems indeed to mark the inception of the angiospermous line of ascent. These changes are surely not speculative. If the first and most ancient is still shrouded in uncertainty (as to details) the two following are a matter of sheer visual observation.

[20] If, as is all too often the case, a young botanist is over-schooled in descriptive botany, anatomy (often but amounting to specialized descriptive botany), and the like, he may risk forming of " morphology " a very static concept. I view this forma mentis as highly undesirable. In the first place, even the very dead (in appearance) sheets of an herbarium will show that the basic morphogeny identifying a genus may yield numerous different species quite unlike morphologically. The carnivorous plants are indeed proteiform (see, e.g. *Princ.* **1a** : 134 ff.), and what in certain of their forms (e.g. *Cephalotus*; *op. cit.*: 192 fn.) appears as but a seasonal byproduct is found " fixed " in other genera. Cleistogamy and peloria, wrongly believed to be " curious " or " occasional ", are a constituent part of flower- and fruit-making; etc. To me, morphology is a stream in rapid flow, and if " comparative morphology ", so called, does not yield what it ought to (*Princ.* **1a** : 792 fn.), the reason is that all too few botanists realize how quick and deep run the waters of life.

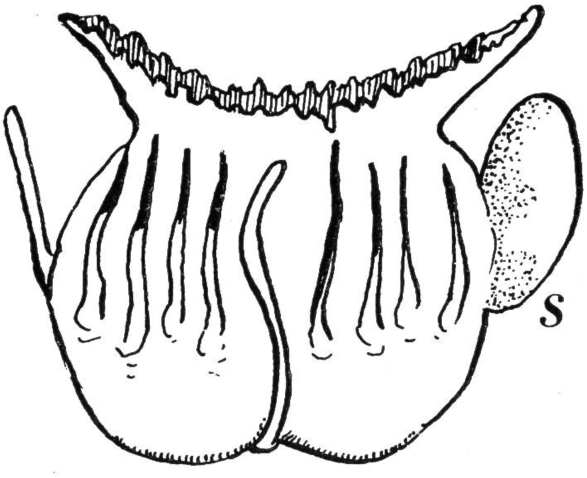

FIG. 15. A female flower of *Mercurialis annua* being sexualized into maleness (consequently also into bisexuality) by an emergent anther *(s)* out of the " ovary wall " (after YAMPOLSKY).

cropping up at all sides [21]. Purely as a passing illustration: the two staminodes incidentally shown by HUTCHINSON in the female flower of *Davidia* (Hutch. **1**: 176. fig. 46 c) [22] bear being compared to those rising at the base of the syle of *Myrica gale* and *Castanopsis chrysophylla* illustrated, again as if wholly incidentally, by SCHNEIDER (*Ill. Handb. Laubholzkunde* **1**: 73. fig. 30 f; 159. fig. 94 d. 1906). HUTCHINSON is himself well aware of the circumstance for, as to the Fagaceae at least (Hutch. **1**: 192), he openly mentions that staminodes may be present in the female flower.

Sporadic and uncertain as it were throughout the "Amentiferae" [23]—although already palpable insofar as the Fagaceae, witness Hutchinson's technical description

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[21] In certain cases, manifestations in Amentiferae of bisexuality and sex reversal (see, e.g. ABBE, *Bot. Gaz.* **99**: 444. 1938) may seem " teratological ", in other cases (see, e.g. *Platycarya; Princ.* **1a**: 272) they are obviously normal, which implicitly proves that frequency, in occurence not an abstract criterium of " aberrancy ", is the determining factor of judgement. Whether seemingly teratological or seemingly normal, these manifestations are perfectly normal in their main premises. " Stamens " will congregate to form " carpels " at ease (*Princ.* **1a**: 534 ff.), which but means that " carpels " may in their turn break down into " stamens " without difficulty. Overall, however, it is the female flower which usually becomes sexualized into maleness (and bisexuality) by additional stamens.

[22] I do not believe that HUTCHINSON is well advised *(loc. cit.)* in reducing Davidiaceae to Nyssaceae. ERDTMAN who does the same (*Poll. Morph. Pl. Taxon.*: 144, 290. 1952) would not seem to be quite sure of the soundness of his disposition, which I challenged (*Princ.* **1a**: 328) as soon as informed of it. Strictly, referring here to technical grounds, it is likely that HUTCHINSON paid no attention to the peculiar " nut " of *Davidia*, a structure which finds its match as stressed by CUATRECASAS (*Contr. U.S. Nat. Mus.* **35** (2): 40. 1961); see for a figure of the " nut " of *Davidia* in germination, MACLEAN & IVIMEY-COOK, *Textb. Theor. Bot.* **1**: 1580. fig. 1440. 1956), in Humiriaceae and *Tectona*. The technical publication of Davidiaceae is to be credited to HUIN-LIN LI (*Lloydia* **17** (3): 330. 1954, December), and I should think that 1954 is its proper date.

[23] It is my definite impression that the sexualization into maleness of " scales " of the female flower eventually to make it bisexual is due to the fact that, when minimally reduced and " adapted " to become a " flower ", the strobile (that was in distal origin essentially vegetative and only locally sexualizable) tended to shed its vegetative, and to increase its sexual potential. As by now a virtually sexual locus, the " flower " would, as some simple sketch will show (fig. 16), easily lend itself to immediate male sexualization virtually all over, with a tendency to acquire

of the female flower of this family, the process of bisexualization I have just outlined reaches a manifest climax in the Hamamelidaceae. In the Liquidambaroideae, a male catkin still lingers together with " heads " of female flowers (see for figures, HARMS in Engler & Prantl, *Nat. Pflanzenf.* **18a**: 340. fig. 178; WETTSTEIN & al.[24]; CROIZAT, *Princ.*: 293, fig. 35 a), but in, e.g., the Hamamelidoideae full bisexualization of the female flower is already achieved, and the male catkin is accordingly eliminated by manifest inhibition in the primordial stage. As if to confirm that the Hamamelidaceae stand indeed at the parting line of a weighty general development in flower-making, the Distylieae (HARMS, *op. cit.*: 331 ff.) still exhibit more or less perfectly unisexual catkins. Pelorization of the male catkin already yields a " flower/inflorescence " in *Distylium* (*Princ.* 296, fig. 36 a), manifestly transforming in the end a whole bisexualized inflorescence into a showy pseudanthium (HARMS, *op. cit.*: 335, fig. 175; CROIZAT in *Bull. Torrey Bot. Club* **74**: 73. fig. 9-10.1947) as the normal flower-making of the Rhodoleioideae. Past the crossroads of the Hamamelidaceae, and of the " rump-families " in their vicinity [25] leading toward the Cornaceae, begins the run of normally bisexual-flowered " conventional " families from Cornaceae to Araliaceae, etc. Overall, the evidence is such as most strongly to imply that the " Amentiferae " are basically relictual in morphogeny and phylogeny, even if morphologically successful, because if their species may be numerous (e.g., *Betula*,

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the two sexes within a minimal area outside the " disc ". An exceedingly fine problem in morphogeny, phylogeny, biochemistery sensu lato (i.e. hormonal controls) opens up right here, which, so far as I know, has not yet been approached, and perhaps, has even never been stated up to the time of this writing. Cleistogamy, peloria, and centrifugal androecia are of course involved in this same problem.

[24] I have in my possession only the Spanish translation of the 4th edition in the German language, 1944, cited once before. In this edition an excellent figure is given of the female " head " of *Liquidambar orientalis* (*op. cit.*: 639. fig. 453/10) pointedly showing the staminodes (omitted by HARMS, as cited in the main text). Since it is likely that the majority of my readers have easier access to WETTSTEIN's work in languages other than Spanish, I omit the indication of page and figure in the main text above.

[25] These families are Davidiaceae (see a previous footnote), Nyssaceae, Garryaceae, and " Torricelliaceae ". They may be construed in either one of two main ways, that is:

1. As "strays", arisen out of the turmoil in flower-making and altered sexuality around the Hamamelidaceae as the " key-group " in the morphogenetic and phylogenetic sense alike.
2. As lone surviving relics of once larger to much larger aggregates including different subfamilies and genera, species, etc. These possibilities are by no means exclusive, for extinction may have contributed to the isolated status of the surviving forms. I should however feel that the former supposition has in its favour the weight of the evidence, general and particular alike. It is challenging, for example, that a " nut " rather closely resembling that of *Davidia* should also turn up in the Humiriaceae, and in *Tectona* (fide CUATRECASAS); this " nut " being manifestly " strobilar " in origin, and morphologically variable in the Humiriaceae for which it stands as a weighty family character. It should not be forgotten that not a few of the families we are accustomed to take for granted do include " strays ", witness the Hamamelidaceae themselves. Rhodoleioideae and Liquidambaroideae are plainly " hamamelidaceous " in a morphogenetic and phylogenetic sense, but by stressing their characters and morphology they might be not unreasonably viewed as types of petty monotypic families. Euphorbiaceae and Flacourtiaceae are notorious aggregates of " rumps " which, if characters and morphology be prevailingly stressed, could easily be broken up into separate families. In short, what keeps a family together is a sum total of considerations that are, in the main, morphogenetic, phylogenetic, and morphological, and a very different formal classification follows if the first two or the last one are stressed.

I may additionally remark here that in Garryaceae (*Princ.* **1a**: 324) both catkins and panicles are represented. *Torricellia* (or *Torricelia* as some would call it) is placed by HUTCHINSON under the Cornaceae (Hutch. **1**: 172), which seems to me a clearly questionable disposition. See for a figure of the flowers of this genus, *Princ.* **1a**: 320. fig. 39c.

Quercus, etc.), still their " type-genera " are not such. The Hamamelidaceae stand at the crossroads, relatively rich in species but poor in genera in, e.g., Africa (*Princ.* **1a** : 289 fn.), running to the opposite in the Orient. Once the Hamamelidaceae are left behind, as stated, then begin the " great families " of " medern " angiospermy. I am at a loss to find reason how and why data of this precise kind can be read to mean that the Amentiferae are derivative.

In accounting for the progress of bisexualization away from the Betulaceae toward the Araliaceae via the Hamamelidaceae as key-group [26], I have of course constantly assumed that the unisexual catkin is primitive against the bisexual flower. This runs of course against Hutchinson's fiat that the " primitive angiospermous flower " is bisexual, and against Takhtadjian's understanding (*Proiskh.*: 37) of this " primitive flower " as virtually equivalent to a coarse " magnolioid " strobile. Moreover, Takhtadjan understands the " Hamamelidales " (*op. cit.*: 65) as the connecting link *(svyazuyushchim svenom)* between the Magnoliales, on the one hand, the Casuarinales, Urticales, Fagales, Juglandales, Myricales, etc., on the other hand. For him, the Hamamelidales have, in general, flowers that are fairly highly specialized, and characterized by a manifest reduction of parts *(yasno vyrazhennoy reduktsiey chastey)*. This, he believes, answers trends in evolution moving away from the bisexual and entomophilous toward the unisexual, apetalous, anemophilous type of flower; from forms with an apocarpous gynoecium toward forms with a syncarpous one.

I have already given several reasons why I cannot believe what Hutchinson and Takhtadjan affirm. The subject is of such a capital significance for high systematics and principia botanica in general, however, that I feel I had better to consider it again this time from a new angle of approach.

Let us, then, lay before us a bisexual flower of " hamamelidoid-cornoid " type (fig. 16) and deprive it of its stamens and petals, making with them a delicate

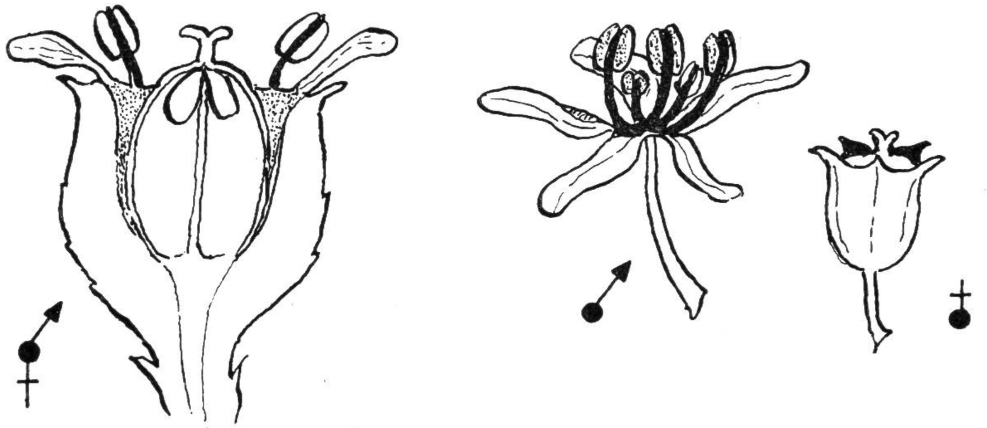

Fig. 16. *Left:* bisexual flower of cornoid-hamamelidoid type; *right:* the same decomposed into its male and female ends (see the main text).

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[26] Trimeniaceae, Daphniphyllaceae and Rhoipteleaceae exhibit interesting cases of bisexualization, the last named particularly in which a male catkin no longer appears. I regret that requirements of space prevent expatiating.

male flower of the kind that is found, for example, in *Garrya* (see, e.g. Hutch. 1959, **1**: 175. fig. 45 b), *Torricellia* (*Princ.* 320, fig. 39 c, right-hand figure), *Quercus*, and the like. This offers of course no difficulty, and could be construed alike from bisexuality to unisexuality, or the other way around.

Matters begin to take another aspect when, moving away from Garryaceae Fagaceae, we hit the corylaceous-myricaceous-betulaceous level. Here we are no longer free to imagine any odd kind of inflorescence to accomodate such male flowers as we may quite easily build up in imagination. Here we face as mandatory inflorescence a catkin or ament. Take it or leave it, the catkin squarely stands across the path of our *Konstruktionen* as an essentially unitary structure in its own right. It may well be true that in the Garryaceae catkin and raceme interchange, the scales of the former looking quite foliaceous as but bracts, etc. However, in the Betulaceae (as Abbe definitely tells us, *Bot. Gaz.* **97**: 64.1935) the floret has the anatomical characteristics of a short shoot, and is undoubtedly of that nature. Likewise, on an anatomical basis the inflorescence is a branch-system which, like the floret, has undergone a long history of concrescence, shortening of internodes, reduction, etc.

It seems to me undeniable that an anatomy of the sort is very ancient, quite as ancient for certain as that of any other angiospermous strobile, cone, flower, etc. I should also feel sure that anyone who has ever paid close attention to the cone of, e.g., *Alnus* and its scales using for the purpose but an ordinary pocket-lens must be sure that (structurally speaking) the whole cannot be far from similar structures in genuine Coniferae. If the scale of the husk of *Fagus* looks by now much more foliaceous and simple than the scale of a cone of *Betula*, still anatomical evidence is there to warn us that so simple a scale also is a branch-system. In the Juglandaceae (*Princ.* **1a**: 268. fig. 33 a, b) the passage is already evident between reduced foliar-lobes and perianth, yet the catkin may be overall a suggestively coarse structure.

Amentaceous or cone-like structures, then witness the additional precedents so clearly established by the Gymnospermae in general, cannot be viewed as recent and easily derivative. Under the circumstance, and having regard to the whole of the evidence, anatomical, morphogenetic, phylogenetic, comparative, etc., as one, I would be able to pass from *Cornus* to *Hamamelis*, from *Hamamelis*, to *Liquidambar*, from *Liquidambar* perhaps even to *Quercus* always imagining bisexual flowers become unisexual and inflorescence to suit, whether racemes, panicles, etc. I would, however, most certainly stop when faced by the catkins and cones of, e.g., Corylaceae, Myricaceae, and above all Betulaceae. Stuff of this hoary, forbidding kind cannot be handled in science with the forceps of " general principles " that piously wish the " primitive angiospermous flower " to be bisexual. Were it ever so that that flower was bisexual, the hurdle remains to be taken of explaining how the flower catkin, or cone, did eventually get together as one. Which one came first? the catkin or the flower it carries? Did the catkin originate without flowers? If so, why did it become reduced, changed, etc., eventually to stand as but a flower-bearing structure?

The *sans-gêne* of systematists, phylogenists, etc., who derive the flower of, e.g., *Alnus* (whatever they may intend as flower in the premises) from that of *Magnolia* via *Rosa* and *Hamamelis* without worrying in the least about the catkin and the cone, and their essential relationships with the flower-floret of the Amentiferae, is indeed surprising. It is of course possible to imagine anything and everything of the "angiospermous flower" launching figments of imagination on the wings of some snappy statement that, yes ... things must have been this or that way in origin, and please ask no more. It is, however, impossible to imagine anything of the catkin and cone contradicting the conclusion that a structure of the kind is (on every count inside and outside science) a primaeval rather more than only primitive structure, scales, rachis, and the whole of it as one.

The argument of course ends right here because, with the catkin on the way, no one in his senses can expect to drive from *Rosa* through *Hamamelis* to *Betula* without cracking up against the stone-wall of ordinary commonsense and immediate visual observation. The path is necessarily running from *Betula* to *Hamamelis*, and to *Aralia*, *Rosa*, for the bridge between *Betula* and *Hamamelis* only works in ascent, not in descent. Augustin Pyrame de CANDOLLE, who like LINNAEUS and Antoine Laurent de JUSSIEU was amply blessed with commonsense, may not have said in 1813 what I am saying here with little merit of my own by now. That he must have felt it is however patent, for had he not, he would not warn that a lineal sequence relegating the "Amentiferae" last is necessarily arbitrary and artificial.

Concluding: The betulaceous cone is at least quite as primitive as the magnoliaceous strobile. At the level of modern angiospermy (see fig. 4) they occupy distinct poles of development, and only find some distal-most structural and phylogenetic

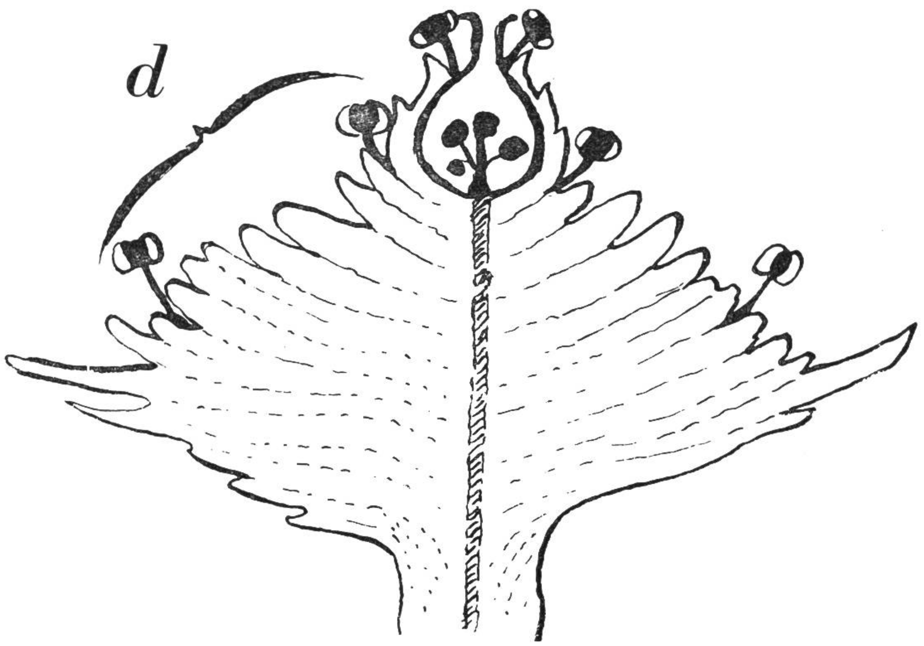

FIG. 17. Archaic reduced strobile ancestral to the angiospermous " flower ". The *loci* of preferential sexualization into maleness indicated by diagrammatic stamens. Sector *d* when left without sexual assignation turns into a " disc " (note that it may contribute also to the building of the "ovary wall"; when developed into maleness as an androecium ripening away from the ovary it yields a " centrifugal flower " (see the main text throughout).

ancestor way down into the bosom of pre-angiospermy. If anything may reasonably be advanced today, this is that the betulaceous cone has, as we will presently see, given the start to a much more extensive line of proximal development than the magnoliaceous strobile. I would be just now inclined to credit to the magnoliaceous strobile (understood in the structural rather than in the consanguineous sense) developments that barely reach beyond Magnoliaceae s.l., Nymphaeaceae s.l., Ranunculaceae s.l., Annonaceae s.l., Schisandraceae, Sargentodoxaceae, Lardizabalaceae, possibly Piperales, perhaps Berberidaceae and Menispermaceae. Of course, I do not believe that CORNER's discovery that the flowers of *Paeonia* and *Dillenia* are " centrifugal " (*Princ.* **1a**: 244, 244 fn.) is irrelevant, as HUTCHINSON does suspect (Hutch. **1**: 400). Far from it, for I rate CORNER's discovery as most important (see fig. 17) in the structural and phylogenetic sense alike. We may not as yet understand the full significance of this discovery, and be accordingly unable today to construe all its byways as they eventually will be with time, patient, candid enquiry, but this is doubtless secondary in my deliberate judgement.

Of course, I would not insist that a scheme of systematic botany which begins with Magnoliales is necessarily objectionable. Whatever we might try to do, we will have to begin a lineal series with some group, whatever it be, and (quite as CANDOLLE firmly asserted in 1813 already) the choice of this group is to be in a way arbitrary. However, I would certainly not approve of a scheme of classification which, arbitrarily beginning with Magnoliaceae or Betulaceae or the like, next hopes to derive one of these families from the other referring for the purpose to forms of modern angiospermy. *It cannot be done, so it must not be tried*[27].

Finally, I should view it as droll outright that, convinced as they seem to be that a strobile is the primitive flower of the Angiospermae, not a few systematists, phylogenists, etc., etc., do not seem to be aware of the fact that a cone of *Alnus* is quite as much of a strobile as the flower of *Magnolia*. Strobile for strobile, both are strobiles. The objection that the strobile of *Magnolia* is bisexual while that of *Alnus* is unisexual breaks down against the fact that the strobile of *Schisandra* is itself unisexual. To assume the strobile of *Magnolia* as necessarily primitive against that of *Schisandra* because the former is bisexual but means to abuse one's privileges as a naturalist, *Schisandra*, *Sargentodoxa*, and *Lardizabala* forming absolute unisexuality! A thoroughly consistent development, as we saw, and to claim that this development must be derived from *Magnolia*, or the like, simply because it is unisexual is most unscientific, as I understand the adjective. Using of the same privilege, I could affirm that, for example, the flower of *Cucurbita* is absolutely primitive for the whole of angiospermy, and build up on this fiat a whole scheme of systematic classification and phylogeny. I would of course find no followers, certainly with ample reason.

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[27] This is not at all a dogmatic statement. It cannot be done, because Magnoliales and Amentiferae have a long past history of diversification begun with ancestors virtually as old as angiospermy itself, and it is through these ancestors and all along this history that these groups have become, in time, through space, by form, what they are today. The past cannot be ignored, because it proves to be in this case the paramount consideration. It must not be tried, first, because commonsense forbids to deal with nature according to man's own whims; second, because what is done against the rules of nature is self-defeating by experience and reason, therefore, plainly unscientific.

If bisexuality is prevalent among the Angiospermae out of a start which, whether with Magnoliales or Amentiferae, is assuredly not primarily bisexual as a statistic fact, it follows that, in tendency, bisexuality is a climax in ascent, not a derivation in descent. I would drop the subject, accordingly, with the renewed statement that botany is still much behind the times in its basic thinking, so much behind the times as a matter of the historical record that LINNAEUS in 1792 had a probably better understanding how to build a " tree " than we have today, and that A.P. de CANDOLLE exactly understood in 1813 what we do not even seem to suspect today.

Were a peculiarly inquisitive reader to ask me what is the reason of this striking lag, I would answer that no student of pedagogy or of the history of the sciences, can be in the dark about so simple a question. Here is the whole of it in a nutshell:

1. As students, we are not trained constantly and sharply to reason about objects which seem to be commonplace. 2. Naturally, as students we learn to take for granted the language of descriptive botany without probing its semantic contents. 3. Faced by a cone of *Alnus* we but see in it an inflorescence, and a few flowers without worrying in the least as to what is really meant by inflorescence and flower, respectively. 4. Rather not well prepared in fundamentals, we forthwith rush to become " specialized ".

These four steps amount in the end to an encouragement not to think about general questions. Since LINNAEUS and Augustin Pyrame de CANDOLLE did on the contrary think long and deeply about questions of the kind, it is in their works that we can find the thoughts and the answers which we no longer find in ours. LINNAEUS and A.P. de CANDOLLE knew little but understood a great deal, we know, perhaps a great deal, but understand by now very little.

How can a flower of Ficus be efficiently compared to one of Magnolia ?

I

Scyphostegia borneensis, type of Scyphostegiaceae, has independently been discussed by HUTCHINSON (Hutch. **1** : 328) and by myself (*Princ.* **1b** : 1344 ff.) virtually at the same time. I think having demonstrated that the by now 70 years old conundrum whether the " receptacle-ovary " of this exceedingly interesting form contains ovaries or ovules involves a limit-case which, easily understood in general, hardly bears being disposed of in some definite manner in particular. Limit-cases of the kind are of course not rare in botany (e.g., the " flower-inflorescence " of *Schisandra*; the " stamen-flower " of the Euphorbieae (*Princ.* **1a** : 472 ff.)), and though childishly simple as such, if approached with proper concepts they prove to be exceedingly troublesome otherwise. The solution of limit-cases of the kind, and the difficulties they entail, is readily furnished by the idea of a nascent structure developing inbetween two conventionally definable extremes. In other words: in the Euphorbieae a stamen, a cluster of stamens, a floret cannot be exactly discriminated having regard to the whole of the intermediates among the three. In *Schisandra* a head of carpels and a raceme are virtually one. In *Scyphostegia* what is ovule or ovary is fundamentally a matter of opinion, and it is altogether conceivable that two flowers of the same plant may yield conflicting evidence for ovule and ovary in turn.

The reader will find in my own work, and in that of HUTCHINSON and other authors abundant material, and references enough to form his own mind on the score of *Scyphostegia.* He will even more remark that there is a radical difference in approach between myself and the majority of authors. They mostly start with a ready-made definition of ovary and ovule as fixed, incompatible organs, and they base their arguments accordingly on technical, mutually exclusive definitions. Since at the level of evolution represented by *Scyphostegia,* it is impossible to provide definitions of the kind that stand under critical enquiry, these authors eventually fall, on a basis of personal opinion, into two camps, for the ovary and against the ovule or the other way around, without either camp ever being successful in proving its point conclusively in the end. My approach is different for, accepting the impossibility of returning a binding definition of ovule and ovary at the *Scyphostegia's* level, I try first of all to understand the problem as a matter of ideas, not at all as a matter of words. To put this otherwise: my peers start with ovule and ovary inscribed on their banners, and next get into a free-for-all at the *Scyphostegia* crossing. I depart from this crossing without binding committments to any preconceived definition of ovule and ovary, exploring all around toward the limits eventually making it possible to identify an ovule or an ovary according to the terms of conventional definitions. In short: botany still is to most of my peers a matter of words. To me it is, I should feel, primarily a matter of ideas. It proved, for example, very easy to prophesy that, endlessly dragged out and by now sunk into futility, the 70 years old conundrum whether the " receptacle/ovary " of *Scyphostegia* bears " ovules " or " ovaries " would continue to smoulder on (*Princ.* **1a**: 1351) for no better reason than that no one seems to have just now ideas tailored out to dispose of it. While I was writing this easy oracle HUTCHINSON went to print to prove it correct. Said he (Hutch. **1**: 328): [SWAMY] considers the large fleshy globose organ [of *Scyphostegia*] to be a 1-locular ovary containing a large number of ovules on a wide basal placenta. An equally feasible view, however, is that it is a very large fleshy disk . . . (not a fig-like receptacle as I suggested previously), enclosing a number of free carpels ". Of course, these views are equally feasible, but the crux of the argument is in giving the ultimate reason why they are both feasible. So long as this reason does not stand clear in print, somebody will periodically come forth to " prove " that, after all, one of these views is rather more feasible than the other. This is what has happened from 1894 to this day, and it may go on for at least 68 years longer. It is only clearcut ideas that can put an end to logomachies.

We have, then, before us a quid, whether receptacle, disc, pome, berry, etc., that it be (fig. 18) which bears on a basal swelling (placenta or torus, etc.), that it may seem certain bodies that are of unsettled nature as between ovules and ovaries (carpels, achenes, etc., etc., that one would like to call them). Instead of losing our time with ready-made definitions, let us objectively consider what follows if this quid contains ovules or ovaries, as follows:

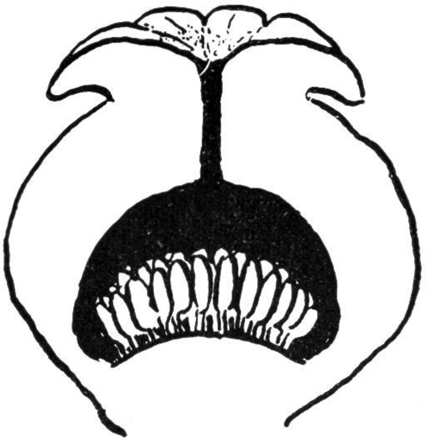

FIG. 18. "Ovary-hypanthium-sycone" of *Scyphostegia* (longitudinal section).

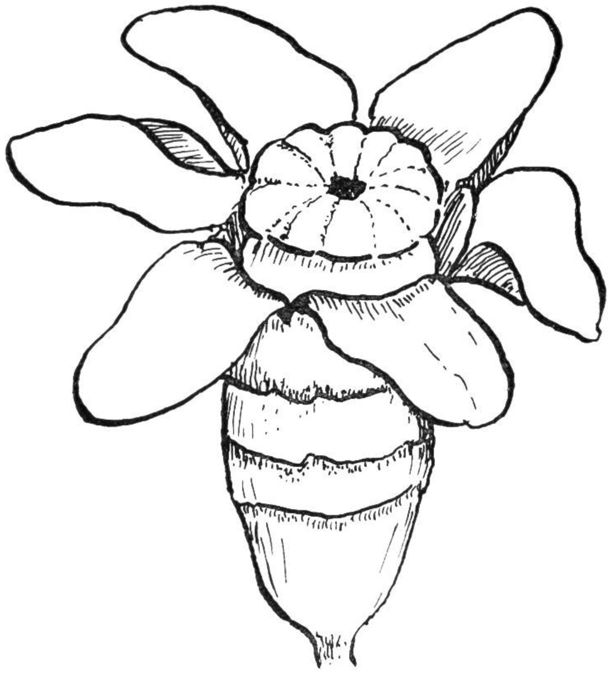

FIG. 19. Female flower of *Scyphostegia.*

1. It contains ovules, the quid is a berry [28], and if the " testa " is hard we face pyrenes. In this case several families are easily suggested as, e.g., Flacourtiaceae, Ericaceae, Empetraceae, Aquifoliaceae, Stachyuraceae depending on placentation. Since in the Ericaceae the ovary may be inferior or superior, I see little risk in adding to this list the Symplocaceae. If the quid were a capsule instead of a berry, we would readily think of Salicaceae and Tamaricaceae. Naturally working around these groups we may reach at will from Flacourtiaceae such families as Euphorbiaceae, Passifloraceae, Tiliaceae, Cochlospermaceae, etc.

2. It contains ovaries, the quid is a receptacle, a hypanthium [29], a sycone or fig-like receptacle [30], a torus. The families it immediately suggests are Monimia-

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[28] It will be clear that all these terms are accurate only to a point. For example (*Princ.* **1**: 500 fn.), authors have argued whether the " berry " of *Vaccinium* may not be a " drupe " instead.

[29] Properly speaking, a hypanthium (see JACKSON, *Gloss. Bot. Terms*: 128. 1900) is an : *Enlargement or development of the torus under the calyx, a syconium.* A sycon, syconium or syconus (*op. cit.*: 262) is: *A multiple hollow fruit, as that of the fig.* A fig is effectively a hypanthium with ovules that are " flowers ", and, if bisexual, with stamens aggregated into " florets ". A beautiful illustration of a bisexual sycone of *Ficus pumila* will be found in WETTSTEIN & al. *Tratado de botánica sistématica* (Spanish, transl. by Font-Quer of 4th ed. in German): 587. fig. 410/6. 1944. I see no reason to exclude here from reckoning the hypanthium merely because it technically opens under a " calyx ".

[30] It is not easy to understand why HUTCHINSON should correct himself, in the text previously quoted, to the effect that the quid of *Scyphostegia* is a " disk " not, as he once had suggested, a " fig-like receptacle ", adding that (Hutch. **1**: 329): *I have come to this more definite conclusion on comparing the female flower* [of Scyphostegia] *with the flowers of Siphonodon (Capusia) related to Hippocrateaceae in the Celastrales, in which the disk completely encloses the carpels and forms*

ceae, Calycanthaceae, and Moraceae. Naturally, from the standpoint of structure, the flowers of these families are not poles apart from the Rosaceae [31].

Overall, then, it is rather not surprising that Flacourtiaceae, Monimiaceae and Moraceae should have been named in turn as the families nearest Scyphostegiaceae. This last is indeed central among the first three, exactly as Dipentodonaceae (see for an excellent illustration Hutch. 1959 **1**: 334. fig. 192) are central among Flacourtiaceae, Hamamelidaceae and Saxifragaceae. The staggering morphogenetic potential of a structure like the scyphostegiaceous quid could indeed be no better highlighted than by the list of the families it interests whether with ovules or with ovaries. In word of the plainest: A quid of the kind is easily basic for the core of angiospermy, and it is by enquiring around it that high systematics may begin to receive a meaning. If I do not believe with HUTCHINSON that the Scyphostegiaceae should go under Celastrales, still I can well understand why he would record them both with Celastrales and Bixales. A family of the kind has long roots in a great many directions.

Before proceding to analyze the relationship between Scyphostegiaceae and Moraceae, thus to compare in the end the " flower " of *Ficus* with that of *Magnolia*, I should stop right here to consider a question of major, quite general importance. As we have just heard, the quid of *Scyphostegia* does immediately suggest a number of families which, were each of them extended to reach the ultimate limits of its affinities, would virtually involve the whole of the living Angiospermae. To illustrate: via Monimiaceae we could reach Lauraceae, Annonaceae, Magnoliaceae quite as much as Calicanthaceae, perhaps even Proteaceae, Rosaceae, Leguminosae. Through Flacourtiaceae we could reach quite as much Caricaceae and Passifloraceae as Tiliaceae, Euphorbiaceae, Cochlospermaceae, Violaceae, Dioncophyllaceae, Drose-

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a false fruit in the manner of a fig (Ficus) ... but a fig, of course, is a modified inflorescence. One may argue almost at will on all these, and like, definitions but I would here conclude as follows:

1. Disc, ovary-wall, calyx are structurally alike (see fig. 3, 17, 27) as ultimate aggregations of " scales " left without immediate sexual destination.
2. As we shall see, the quid of *Scyphostegia* is not at all discriminable as a structure from a fig-like receptacle, indeed from a sycone. It very nearly turns into one if, as Hutchinson wishes, it is made to contain " carpels ".
3. Narrowly speaking, the carpic structures of *Siphonodon*, especially in fruit (see CROIZAT, *Lilloa* **13**: 37-47. fig. 4-6. 1947; Hutch. **1**: 326. fig. 186), yield a hesperidium (an orange-fruit; *Princ.* **1a**: 341 fig. 41c (in particular)). Of course, a hesperidium is an " ovary ", by definition part of a single " flower ", but it would take little indeed (*Princ.* **1a**: 236. fig. 30d, 296. fig. 36a, c) to turn it into an " inflorescence ".

In conclusion, I would say that the various morphologies of disc, receptacle, hesperidium, flower, inflorescence, hypanthium, sycone, etc., are but functions of one and the same ultimate morphogeny (see again, fig. 3, 17, 27 and *Princ.* **1a**: 354. fig. 42). It is easy to discuss all these structures to a purpose if this morphogeny is well understood. In the contrary case, technical terms, as above, readily lose their meaning altogether, and lead eventually to but deplorable arguments. Botany ought to be a science of concepts long before being a science of definition, and on this basis I would refuse to honour with consideration an argument moved only on the strength of definitions preconceived. There is no sense in desultorily debating for decades what, properly stated, can be settled without difficulty on the spot in a few lines of print.

[31] I do not believe that Calycanthaceae are " Rosales ", as HUTCHINSON wishes them to be. They are close enough be genuine affinity to the Monimiaceae to go with the " Laurales " of the Hutchinsonian classification. Doubtless very far from the Rosaceae in perianth, inflorescences, etc., still Moraceae and Rosaceae share a measure of common morphogeny. This does of course not mean that they are even distantly related. See the main text throughout.

raceae. The Moraceae would surely bring in Ulmaceae, Urticaceae, Daphniphyllaceae, etc. Faced of a sudden by this stupendous tangle of families, do we not risk to get hopelessly lost? May we not try to formulate some general rule, or concept, that can direct us to find eventually a way across this overwhelming maze?

I think for my part that two very distinct concepts do face us at this point in enquiry. These concepts are absolutely basic for high systematics and for practical classification as well. Without their steady application I see these two disciplines as hopeless from the start.

Structure is the first of these concepts, affinity the other and considering their importance, singly as well as jointly, I will try to formulate them as clearly as possible bringing here to a head a great deal which is scattered through the pages of the *Principia botanica*, and which the reader will find and verify there in his own time.

Structurally speaking, the quid of *Scyphostegia* stands intermediate between a sycone (a fig) on the one hand, a conventionally syncarpous more or less fleshy ovary on the other hand. The excellent figures by Van Steenis (*Fl. Mal.* ser. 1. **53**: 298. fig. 1. 1957), and by Hutchinson (Hutch. 1959 **1**: 327. fig. 187 a) show that the " perianth-tube " of the female flower (fig. 19) is composed of tiers of bracts (3 to 4) of which only the uppermost is persistent and flaring out into 6 lobes. A longitudinal section that might be taken through this flower (fig. 20) suggests the conclusion that it is made up of a series of bracts or tubular scales which, more or less free and expanded in the lower tiers of the flower, become distally fused to form the fruiting quid. Morphological details remain to be adjusted which no enquirer

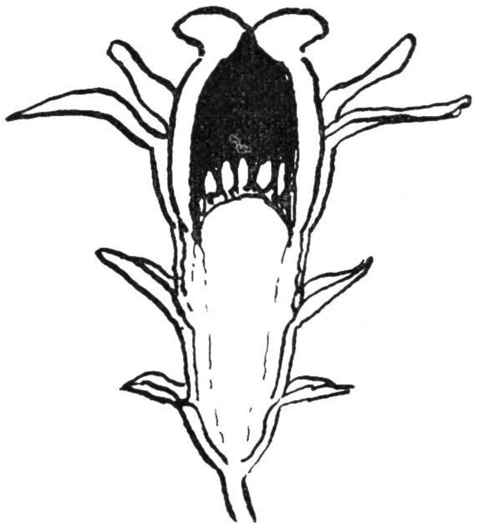

Fig. 20. Longitudinal section through female flower of *Scyphostegia* (the exact level occupied by the placenta in anthesis is conjectural.

Fig. 21. Sycone of *Sparattosyce*: *left*, actual; *right*, in longitudinal section, with constituent " lobes-laciniae " supposedly divaricate.

seems so far to have carefully studied, but there can be no serious doubt about the structural premises or, in other words, the basic morphogeny of this indeed curious flower and "ovary". It is composed of laciniae, lobes, bracts, or what we might call scales, more or less distally free at base, closely fused to form a receptacle apically.

If we now study a sycone of, e.g., the moraceous Sparattosyce[32], we do find (fig. 21) that it, too, is made up of laciniae, lobes, phyllodes, scales that we might call them. The structural premises of this sycone are accordingly the very same as those of the flower of *Scyphostegia.* The difference is that in *Scyphostegia* the lower laciniae (they were in origin pinnate phyllodes, of such a kind as can still be identified in *Sparattosyce* without difficulty) are more or less free, fusing only distally to form the " ovary " (in reality, an apical sycone) while in *Sparattosyce* the sycone is fused cup-like from the base upward.

The common structural denominator of these two "flowers" and "fruits" (fig. 22) is of course a strobile of " phyllodes " which originally bore ovules mainly in their axils. The decomposition of this strobile at its distal end eventually furnished a " pad " for the ovule to sit on (see for homologous structures, *Princ.* **1a**: 296. fig. 36 a; 398. fig. 47/3) with attending elimination of ovules (if there ever were any over) in the axils of the lower phyllodes. There is nothing in this reconstruction that is far-fetched, for everything of it can be traced back to structures but thinly " metamorphosed " either in *Scyphostegia* or *Sparattosyce*, or in both.

It will be seen without difficulty that the strobile in question comes quite close to the still extant cone of, e.g., *Betula* and *Alnus* (fig. 23), in which the archaic disposition of " ovules/ovaries " has been openly retained, each scale subtending as a

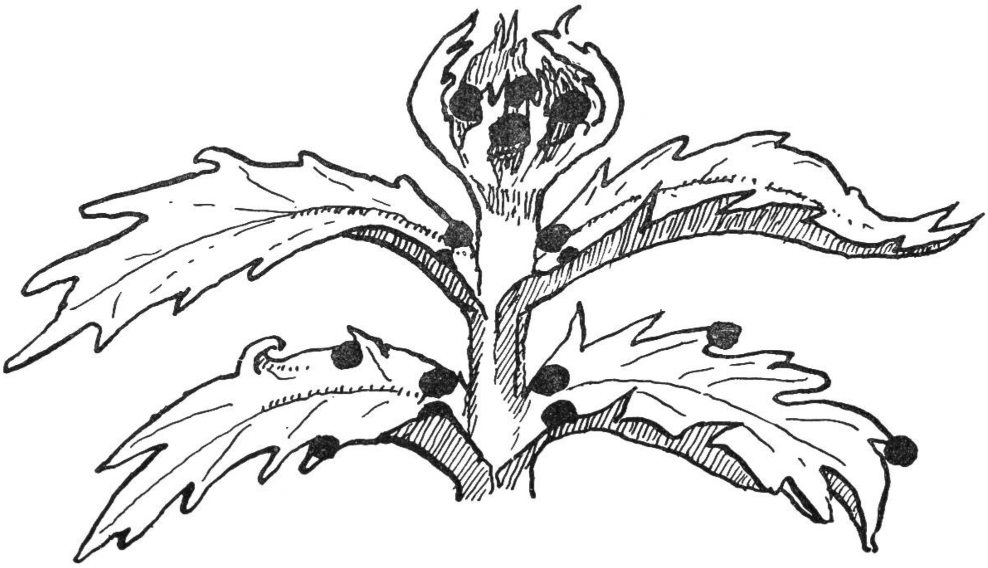

FIG. 22. The archaic strobilar structure common to *Scyphostegia* and *Sparattosyce.*

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[32] Of this striking Neo-Caledonian endemic I have studied only a male sycone of species dioica. It is evidently a primitive fig, New Caledonia being noteworthy (*Princ.* **1b**: 1258) as a center of endemism of *Ficus*.

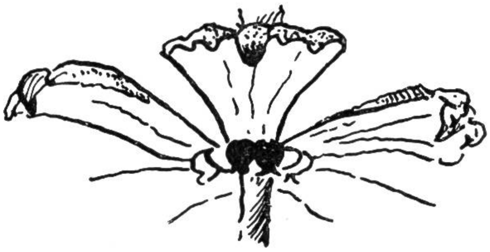

FIG. 23. Tier (partial) of a cone of Betulaceae.

FIG. 24. Lobe (scale, strip, etc.) forming the sycone of *Sparattosyce*, and carrying male " florets " (observe the spicate disposition, and bracteoles).

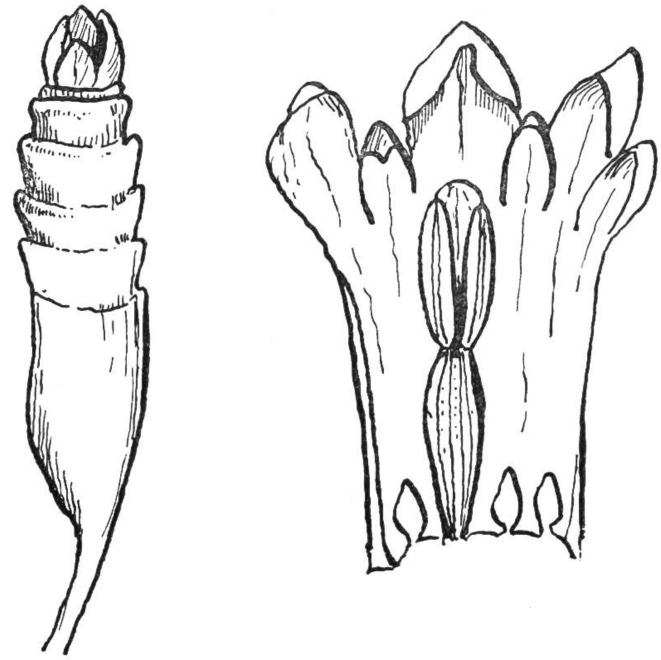

FIG. 25. Female inflorescence (barely unfolding) of *Scyphostegia (left)*; flower of same *(right)*.

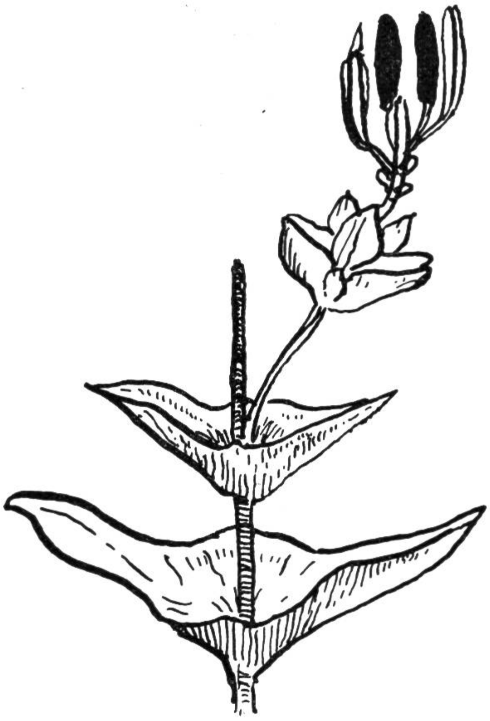

FIG. 26. *Scyphostegia*'s ancestral male strobile and flower.

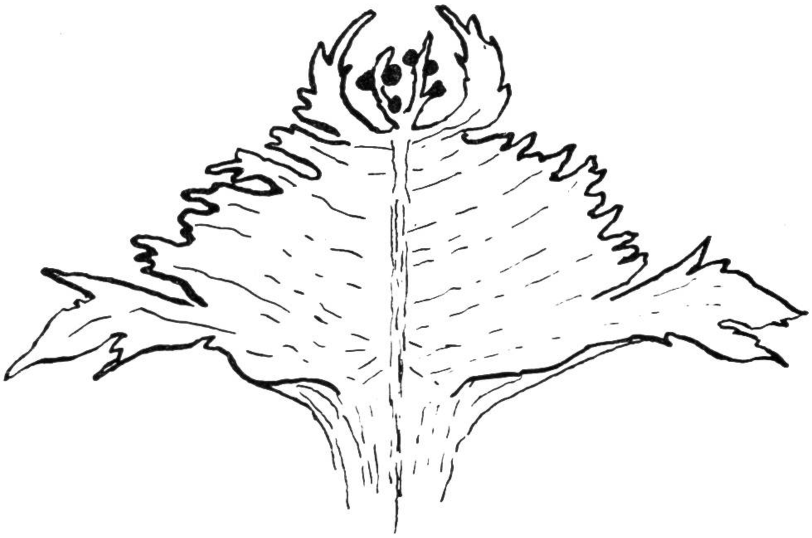

FIG. 27. A compressed archaic strobile as the structure ultimately common to *Scyphostegia*, *Sparattosyce*, *Alnus* (cf. fig. 3, 10, 17 for other groups; and observe that a single type of strobile is virtually common to the whole in distal pre-angiospermous phylogeny and morphogeny).

rule two of them. The scale of this cone is manifestly a compound phyllode or cladode anatomically a branch-system as we heard once before.

Both *Scyphostegia* and *Sparattosyce* are unisexual. In the latter (fig. 24), there is no doubt but that the male florets were borne upon phyllodes, whatever their position basal or apical. In the former, the inflorescence is once more strongly characterized by whorls of tubular bracts (fig. 25) [33], in the axils of which stand flowers. These are surrounded by a perianth of 6 lobes (the outer larger) with basal scales or staminodes. The anthers are aggregated into a column. The basic morphogeny of this structure can be reconstructed (fig. 26) I am sure without unduly straining one's imagination. There is found in it a precise indication that the stamens were borne upon the lower (abaxial) not the upper (adaxial) face of the phyllode, which is an archaic character. A different indication is given out by the male phyllode of *Sparattosyce*, which carries its " stamens-florets " spicately on the upper (abaxial) face of the phyllode as the case might also be with the " florets " in general of *Alnus* and *Betula* (the pendulousness of the ament may be a secondary character broadly speaking; in Salicaceae, the male ament of *Chosenia* is pendulous, that of *Salix* erect) [34].

" Degrading " now the female strobile ancestral to *Scyphostegia*, *Sparattosyce*, *Alnus*, and *Betula* to the utmost, we do get (fig. 27) the essential structural premises of the normal angiospermous flower. The secondary sexualization of certain scales of the ovary-wall or disc can of course make this flower bisexual in the manner so clearly demonstrated by, e.g., the Hamamelidaceae (see fig. 13 b). Bisexualization will eliminate the need of a particular male catkin or strobile.

It will be observed that although bound within an ultimate strobilar morphogeny yielding structural premises common to them all, not only, but to virtually the whole of the Angiospermae, *Scyphostegia*, *Sparattosyce*, *Alnus*, and *Betula* are manifestly consanguineous as to the last two, absolutely not as the first three. Applying here the concept of *structure* we will then say that these four genera yield evidence of a common morphogeny whatever the degree of their individual specialization. This morphogeny they ultimately share in common also with *Magnolia* (see fig. 3, 27),

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[33] I should think that the 1-piece " calyx of the male flower of *Scaphocalyx* (Flacourtiaceae; see for a good figure, Sleumer, *Fl. Mal.* ser. 1, **5** (1): 34. fig. 11. 1954) stands for an originally tubular bract, apically connate and cracking open laterally in anthesis. A " calyx " of the kind reminds me very much of the tubular bracts of *Scyphostegia*. On account of their affinities and relationships with numerous angiospermous families, the Flacourtiaceae look like an epitome of angiospermous " modernity ". However, critically studied, this family turns out to be chokful of ancient structures, of which *Scaphocalyx* exhibits one that gave it its generic name. I hope that I may eventually give to press an article on the Flacourtiaceae in high systematics. They are certainly not far from Scyphostegiaceae.

[34] The problem involved in an exact determination of the primitive symetry of the component parts of the eminently " cladodial " structure represented by the scale of a cone of true Coniferae (and I should think also of Betulaceae, etc.) remains to be critically worked out. Today the ovules of a pine, of a birch, etc., are borne adaxially, but it is a question whether they might not have borne in origin laterally, even abaxially. What looms in the far distance is of course some " pteridospermous " arrangement, which is not yet to mean (structure and consanguinity being different concepts) that the Angiospermae and Coniferae " descend " from Pteridospermae. The Angiospermae are a relatively recent (Carboniferous to Permian) " rejuvenation " of some more ancient stock. One might at least suspect (rather reasonably, I am sure) that Angiospermae arose last into dominance simply because they represent a branch of the tree of vegetable life which proved competent to undergo one more change than their by now extinct relatives. See the last sections of this article.

therefore this morphogeny stands as the ultimate minimum common denominator of the angiospermous sexual parts and organs. This, once agreed on (see also *Princ.* **1a**: 739 ff.), there is no longer difficulty in properly visualizing the distal angiospermous ancestors. Adding to the intelligence that concerns their " flowers ", the positive data furnished by enquiries into their foliage, manner of branching, roots, etc. (see *Princ.* throughout), these ancestors pass from the realm of hazy, bare speculation into the domain of exact research and constructive comparison. Completing the scores with a proper understanding of biogeography (see *Panbiog.*, *Princ.* throughout), evolution in time, through space, by form acquires a new meaning with regards to the positive sciences of morphogeny, phylogeny, and of course higher formal classification.

Using a concept of *consanguinity*, we will on the contrary associate the last two genera, only (i.e., *Alnus* and *Betula*) while sharply setting aside, on the contrary, the first and second.

It should in theory be possible to claim that *Scyphostegia*, *Sparattosyce*, *Alnus* and *Betula* must be consanguineous as all angiospermous. In practice, this claim is far-fetched. These genera have evolved for so long apart as not to exhibit today recognizable bonds of parental affinity. They are scyphostegiaceous, moraceous, and betulaceous long before being angiospermous, so that whenever their angiospermy is stressed in general, their status as well distinct families comes simultaneously to the fore in particular, the latter necessarily qualifying the former quite strongly. Much in the same way, by going back on a direct line of descent to what was the father of all my fathers during the rule of Julius CAESAR I might find that, perhaps, that distalmost sire of mine was but one of, let us say, twelve brothers. If these " uncles " of mine have left descendants I would hardly greet today as my consanguineous " cousins ". In theory they would be; in practice, too much water has run by now under the bridges on the Tiber to make it possible for me to identify those " cousins " otherwise than as " brothers ", this time only within the bosom of *Homo sapiens*.

Concluding, *consanguinity*, although by no means antithetic to *structure*, is a concept of its own, presupposing structural affinity equivalent rather clearly to a bond of proximal joint origin. To illustrate: unlike HUTCHINSON, who places them under Celastrales, I certainly would place the Empetraceae (see also *Princ.* **1a**: 610; Man. 161) either under the Ericales or immediately near them. By a like token, I would not, as HUTCHINSON does, assign the Aquifoliaceae to the Celastrales, but credit them instead to the same order including Flacourtiaceae or to an order nearby. All these plants suggest to me, insofar as I may be able to judge, a direct measure of consanguinity, which the Empetraceae, for instance, do not seem to share at all with Celastraceae. I would of course not hesitate to bring together Monimiaceae and Calycanthaceae because I feel sure that the two groups are genuinely consanguineous. It is seemingly only a bond of structure, on the contrary, that may bring close together Calycanthaceae and Rosaceae. The issue here outlined is of course not new, for questions of " kinship " vs. " parallelism " are ancient battlegrounds of botany. I think that our science will gain in replacing terms of the kind with consanguinity and structure, and in using these concepts with a definite understanding of morphogeny and phylogeny. To illustrate: there is " parallelism " in zygomorphy between *Orchis* and *Viola* but there is certainly no " kinship " between the two. The " parallelism " here in play is of course the result of *Orchis* and *Viola* sharing common morphogenetic premises in flower-making (*Princ.* **1b**: 1698) without there being any consanguinity between the two. Structurally they stand as one; phylogenetically, they are far remote [35].

I do not contribute these thoughts, of course, in the hope of starting a new classification right in the pages of this article [36]. I voice them merely as a preliminary toward the long years of work looming ahead after a lag that has crippled systematic botany virtually for the span of one and a half centuries.

I would not hesitate meantime to affirm that Scyphostegiaceae is one of the cardinal groups of angiospermy. Immediately below the level of evolution to which *Scyphostegia* borneensis belongs (one of the world's most striking and significant monotypes) stretch the ages of pre-angiospermy. At the scyphostegiaceous level, we find associating with *Scyphostegia* different " rump-families " (e.g., Trochodendraceae, Daphniphyllaceae, etc.) not necessarily obscure by morphogeny but surely isolated and, generally, hard to place in immediate phylogeny and affinity. Above the scyphostegiaceous level of evolution (and by nothing more than finally settling the question what is to be " ovule " or " ovary " within the " fruit " of *Scyphostegia*) gushes forth with incredible vigour the bulk by far of modern Angiospermae. These plants flare out in many directions from different particular nodes of which Hamamelidaceae, Saxifragaceae, Flacourtiaceae, Moraceae, Monimiaceae clearly hold each a center. Thus approached and conceived, high systematics stop being the realm of arbitrary " Konstruktionen ", dicta, principles of the tenuous academic kind, etc. They become a joint problem in morphogeny, phylogeny, morphology, biogeography, and what of them is purely philosophic (no doubt, a great deal) is no longer confused into stultification with artificial issues of but formal alignement and treatment [37].

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[35] One of my learned correspondents has recently been pleased to inform me that the Aristolochiaceae must have " originated " in " Cathaysia ", because the large contingent of the family in Brazil (some 130 species of *Aristolochia*, 2 monotypic genera, *Euglypha* and *Holostylis*) are the most " advanced " within the family, with zygomorphic flowers and " specialized " androecium and fruit! I think rather droll this understanding of phylogeny and phytogeography, jointly. Of course, the said learned correspondent " derives " the Aristolochiaceae virtually straight from the " Magnoliales ". How concretely can one discuss the subject with him? I would not know.

[36] In its formal dress, a new classification may look after all very much like any old one. It must be clear that, for instance, the families making up the first three " climaxes " of HUTCHINSON are bound to retain their right of way, whether beginning with Magnoliales (which would not be my first choice), or with Betulaceae (which I should prefer as the start of line driving virtually without interruption as far as Araliaceae-Caprifoliaceae). What would radically change in a new classification are, of course, the methods, the principles, in short, the whole spirit. Were I asked to state meantime what I find in the Hutchinsonian classification that is most immediately objectionable to me, I would say:

1. The setting aside of " Lignosa " from " Herbacea ".
2. The " derivation " of *Betula* from *Magnolia* through *Rosa* and *Hamamelis* doubtless in the name of spurious " General principles " wishing, among other, the " primitive angiospermous flower " to be bisexual.
3. A transparently weak understanding of "Celastrales", "Saxifragales", "Flacourtiales" as cardinal nodes of angiospermy. These three vices are rather serious, of course, in my personal opinion.

[37] One of my deepest regrets is that I had no understanding of the true status of *Scyphostegia* when laying out the main text of the *Principia botanica*. It will interest the reader to compare the tenor of this article with the notes I contributed on high systematics in that book (*Princ.* **1a**:

The problem of delimiting concretely in formal classification an order " Flacourtiales " (or the like; this name may, unfortunately, not be available on technical grounds of nomenclatural priority) is doubtless difficult, and affords a good illustration of what the systematist faces when trying to turn philosophy into formalities. To begin with, the Flacourtiaceae themselves consist of odds and ends (e.g., Paropsieae, Abbatieae, Prockieae, etc.) that tie rather directly toward groups as far apart in a natural system as Passifloraceae and Tiliaceae. Their placentation must perforce be affirmed as " parietal ", because if this be denied the limits between what is " flacourtiaceous " and, e.g., " saxifragaceous " badly blur out. However, in the typical genus *Flacourtia* the placentation may be clearly " axile " (see for a good figure, SLEUMER, *Fl. Mal.* ser. 1,**51** : 74. fig. 31 d,g. 1954); while definitely saxifragaceous forms (e.g. *Ribes*; see Hutch. 1959. **1** : 163. fig. 34 f) have " parietal " placentation. This means, of course, that placentation cannot be appraised correctly unless in function of tendencies and, obviously, of phylogeny, morphogeny, and morphology as one.

There can of course be no question of dismembering the Flacourtiaceae into petty families because too many already are the petty families (see " The Rump "; *Princ.* **1a** : 436. fig. 50) that gravitate in their vicinity. In sum, if it is very easy to understand the Flacourtiaceae, what they are, and what they mean in high systematics, it is on the contrary extremely difficult to dispose of them satisfactorily in a formal scheme of classification. As of today, we neither understand them nor do we classify them formally in a proper manner and it seems to me that doing anything with formal classification that is constructive must be entirely out of the question, until and unless we understand what we face. The " Law of Minimal Ignorance " (*Princ.* **1a** : 868 fn.) does of course apply to systematics.

How can a flower of Ficus be efficiently compared to one of Magnolia ?

II

In the first part of our enquiry, now efficiently to compare a flower of *Ficus* to one of *Magnolia*, we have learned that in the living *Scyphostegia borneensis* is found a hypanthium, or sycone that it be, containing immediately sexual organs which cannot be finally discriminated as either ovules or ovaries. We have enquired

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414 ff.). *Scyphostegia* I could only bring to score in an addendum (*op. cit.* **1b** : 1344 ff.), the title required to write it having, after endless delays, reached my hand with a year of good time lost. Of course, what this article particularly contains is not without its counterpart in the *Principia botanica* (see, e.g. on ovule-ovary, *op. cit.* **1a** : 389. fig. 46c, d, 398. fig. 47a, c; etc.), and my mind had been made up for a long time that " ovary " and " ovule " could no more be finally discriminated than " flower " and " inflorescence ", etc. It must be admitted, nevertheless, that so outstanding and transparent a case as *Scyphostegia* gave me reason to state forcefully and directly at last what I could hardly dare to do before. In short, I had " invented " *Scyphostegia* long before being well informed of it, but it is only after being well informed of it that I could align my argument by now straight and sharp, and speak up and to the point. See also : CROIZAT, L., *Space, Time, Form: The Biological Synthesis.* 1962.

about what follows in the case that these organs are either ovules or ovaries, and thus reached a number of important conclusions in regard of morphogeny, phylogeny and classification.

It remains for us to make a concrete application of what we have been privileged to learn to the task of efficiently comparing a flower of *Ficus* to one of *Magnolia*. Efficiently is heavily stressed. Unsupported opinion cannot interest us any longer, and efficient can only be a comparison which, reasoning the facts of life out step by step, eventually concludes in a spirit of which legal and mathematical logics can approve. Commonsense which is after all the loftiest form of logics cannot have two faces, one for botany, the other for sciences outside it. It must be one throughout.

Around what is the original ovular core of *Scyphostegia* a number of authors have detected " emergences " (see *Princ.* **1a**: 1346) which they have identified as follows:

1. Stapf: A delicate membrane resembling the perianth of a fig flower.
2. Hutchinson: Hyaline sepals, or (Hutch. 1959 **1**: 328) lobules from the receptacle adherent to a short stipe.
3. Baehni: Trichomes.
4. Swamy: Funicular outgrowth.
5. Van Steenis (*Fl. Mal.* ser. 1.**53**: 297.1957): Spongy tissue (around the seeds) of scarious lamellae of placental origin.

It seems clear that these " emergences " escape precise identification in reference to the terms of descriptive botany, and it appears probable that when identifying them, by far not unsuccessfully, as " trichomes " Baehni had in mind the ancipital nascent structures which I have called (*Princ.* **1a**: 974 fn.) trichomoids eventually concluding (*op. cit.* **1b**: 1357) that the " trichomoid concept " finds ready application also to " seed-coats ". This is in agreement with Satina's and Linsbauer's findings (see *Princ.* **1a**: 394) to the effect that the " seed-coats " of, e.g., *Datura* develop from epidermal cells. Satina has significantly added that epidermal cells may readily change their functions at various stages in development.

Whatever might be the case in its descriptive and histogenetic sense, the fact remains that around the nucellus of Scyphostegia (taken as primary point of reference) there come to emersion and to full or partial definition structures which, in the immediate proximity of the nucellus, are conventionally designated as teguments or seed-coats, but pass away from it into " trichomoids " that may be identified as a perianth, hyaline sepals, lobules of receptacular origin, trichomes, funicular outgrowths, scarious lamellae of placental origin, etc. The immediate result of the emersion of these structures is, as we saw, to obliterate the conventional difference between ovule and ovary.

Although without this time immediately referring to the " ovule " of *Scyphostegia*, but in reference instead to the female flower of the genus (*loc. cit.*), Van Steenis introduces a note well worthy of our attention. He says: *Disk glands absent (but possibly disk-like tissue of receptacular origin participating in the ovarial wall).* This indeed shrewd observation does extend the range of action of the " lobules from the receptacle ", which HUTCHINSON restricts to the immediate vicinity of the " short stipe " capped by the " free carpel " of *Scyphostegia.* As a matter of obvious facts, VAN STEENIS thus admits the possibility that receptacular structures (whether " disk " or " lobules ") may directly contribute to the building of the " ovarial wall " itself. I do of course emphatically concur (see, e.g., *Princ.* **1a** : 389. fig. 46c, and relative text; refer also to fig. 16, 27).

Summing up and concluding: STAPF, HUTCHINSON, BAEHNI, SWAMY, VAN STEENIS, myself agree on the essentials of the case, as follows: starting from the nucellus as immediate centre of reference and structure, emergences arise which build teguments (or seed-coats) and ovarian wall alike. Technically identifiable as teguments and ovarian wall in their conventional extreme type of development, these emergences stand beyond the scope of conventional definitions when intermediate to the extremes. That these emergences be definable or not in much detail case by case, they may create a morphological condition which, witness *Scyphostegia,* voids of their scientific value standard characterizations of ovule or ovary. Seemingly exceptional in what it thus reveals, *Scyphostegia* is on the contrary but a match of, e.g., *Euphorbia* (*Princ.* **1a** : 472 ff.), in which " emersions " turn " stamens " into " flowers ". In sum, these plants but illustrate the making of " flowers " or their organs out of rudimentary component parts. In this capacity they are of course not aberrant, but much rather the contrary.

From his courses in basic botany, the young student assimilates a somewhat vague idea that the " teguments " of the ovule and seed are but one or two, with the possible addition of course of certain " arils ", " strophioles " and the like, the whole being fundamentally simple and hardly worth troubling about. In reality, and as always in botany, matters are not quite as simple as that, which at glance at specialized litterature (e.g., SCHNARF, *Vergl. Embryol. Angiosp.* 1931; CORNER, *New Phytol.* **48**: 331.1949; *Phytomorphol.* **1**: 117.1951) will immediately reveal. As a cold fact, our ignorance on the score of " teguments ", " seed-coats ", " arils ", etc., is still rather great at this hour. It is indeed an easy guess that, constructively approached, the matter will prove quite rich in surprises of all kinds.

SCHNARF records the fact (*op. cit.* : 27) that in Myricaceae the nucellus is separated from the lone integument of the ovule by an open space *(Zwischenraum).* In the Juglandaceae, he detected (*op. cit.* : 28) outside the lone integument a pair of " winged emergences " (*flügelartiger Bildung*), which might be construed as an outer integument. The Myristicaceae have (*op. cit.* : 70) two teguments but : *Eigenartig ist der Umstand, dass das Aussenintegument bis zur Chalaza von dem Innenintegument getrennt ist, dass dagegen dieses mit der unteren Hälfte des Nuzellus verwachsen ist.* In the Cactaceae, SCHNARFF reports two integuments, and nothing apparently unusual, but recent litterature (see *Princ.* **1b** : 1699) clearly shows that the ovules of this family may exhibit an " intertegumentary space ", also.

The " Zwischenraum " between nucellus and integument reported by SCHNARFF in Myricaceae is beautifully exhibited in an illustration of the fruit of *Myrica gale* borrowed from an old work of KERSHAW by MCLEAN & IVIMEY-COOK (*Textb. Theor. Bot.* **2** : 1388. fig. 1289), and here reproduced (fig. 28) in essentials.

The original figure is carefully identified as to every part and structure to the exception of one. This part is the one immediately ending with the style, and it

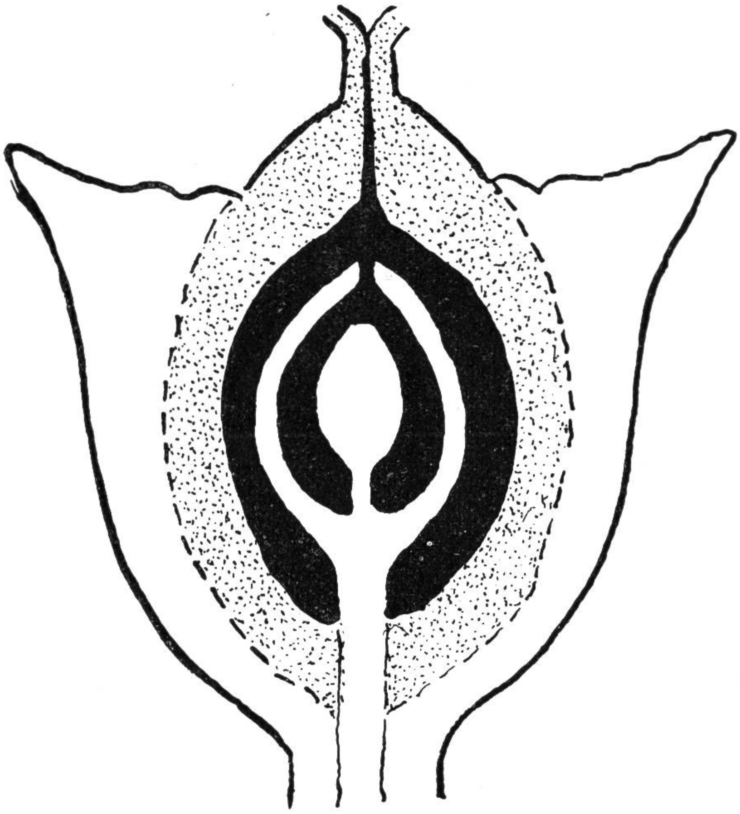

FIG. 28. Longitudinal section through female flower of *Myrica gale* nucellus (white, ovoid with stipe) in center: first tegument; unnamed (or " unmentionable ") layer (stippled); " perianth ".

should accordingly be a conventional " ovary wall " or " carpel " that some would call it. Might it not be instead an " integument "?

The orthodox answer to this question will be, of course, that this cannot be, because a " style " automatically defines a " carpel ". I would for my part not be certain of this at all, because a tubillus fraying atip and extending the inner integument (or seed-coat) occurs (fig. 29), e.g., as a normal feature of the ovule of the urticaceous *Leucosyke* (see CROIZAT, in *Bull. Torrey Bot. Club* **74**: 73. fig. 11; *Princ.* **1a**: 398. fig. 398 c). A wholly homologous structure, if quite reduced, turns up in the annonaceous *Mezzettia* (see *Princ.* **1a**: 389, fig. 46 d), and, this time produced and functional as " style " in *Gnetum*. No tubillus has ever been recorded in the Thymelaeaceae, but that they have one in disguise must be clear (*Princ.* **1a**: 404) because in, e.g., *Passerina filiformis* the inner integument seems to " open up " thus to make contact with the " obturator ". In other plants, e.g., *Tilia* (*op. cit.*: 396 fn.), the inner integument is left behind in growth by the outer. In *Dorstenia* and *Ficus* the inner integument (which should be the " tubillate " one) is so far in a state of regression (SCHNARFF, *op. cit.*: 32) that it blocks the micropyle. The pollen-tube grows at first through the endotrophic tissue of the style then reaches ectotrophically the tissue located around the micropyle finally reaching the tip

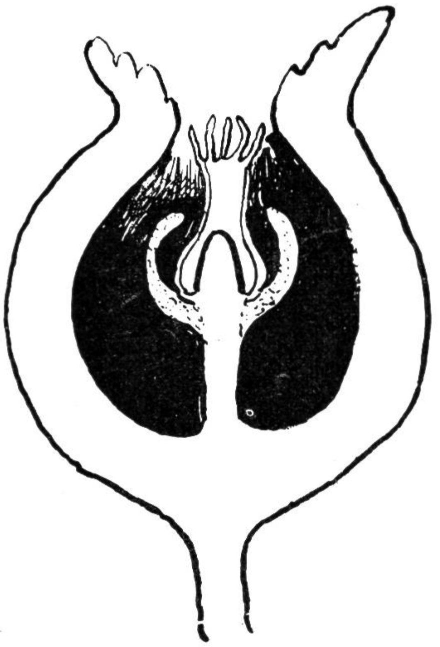

FIG. 29. Moving away from the nucellus: longitudinal section through female flower of *Leucosyke* (the first seed-coat (tegument) is produced into a tubillus fraying atip).

of the embryo-sac. Not so in *Cannabis sativa* and in *Humulus lupulus* (*op. cit.*: 33) in which the pollen-tube may penetrate the inner integument.

I would of course be ready and willing to discuss the issue tubillus vs. style with a botanist intending to deny validity to the evidence I have just brought to record, if I could be sure that this botanist understands what is a style. My suspicion must be, alas, that he may not, for no one is even remotely ready to understand the style who believes in the " classical carpel ", in the " classical ovule ", and, generally speaking, in what general botany takes for granted at this hour without rhyme or reason beyond " general principles ", compilatory dicta, and the like. The style is indeed a very complex structure (*Princ.* **1a** : 398. fig. 47), in the making of which tubillar structures may largely contribute. I hope to return in a separate article on the subject of the " obturator ", for example, which *Passerina* connects with the " inner coat " of the ovule in a challenging manner as we have just heard. I will, meantime, conclude that a tubillus may furnish a quite acceptable substitute for a style, the one passing into the other in a manner that, as usual in botany, forbids to rely on conventional aprioristic definitions.

I have elsewhere compared the " teguments " of the annonaceous *Mezzettia* with those of the ovule of *Gnetum* (*Princ.* **1a** : 396) finding exact agreement between the two. This identity in structure does not mean, of course, that *Mezzettia* is to be " derived " necessarily from *Gnetum* because the path of development of the ovules of these two forms materially differs, and " double fertilization " is an angiospermous peculiarity (see, e.g., HUIN-LIN LI, *Journ. Washington Acad. Sci.* **47**: 33.1957; *Acta Biotheor.* **13**: 185.1960), which stands in the path of hasty " phylogenetic derivations ". Structure and consanguinity are quite different concepts, as we know.

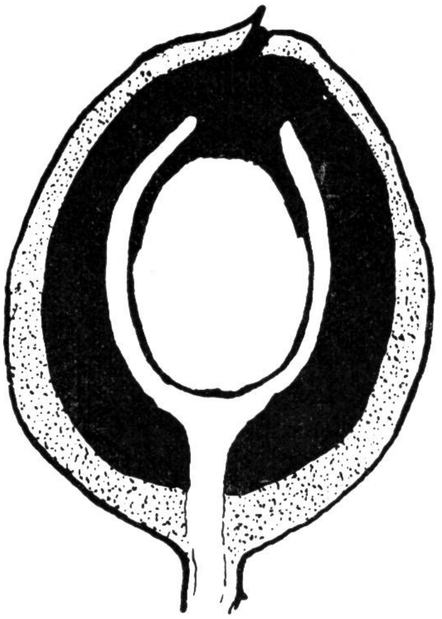

FIG. 30. Ovule of *Lagenostoma*.

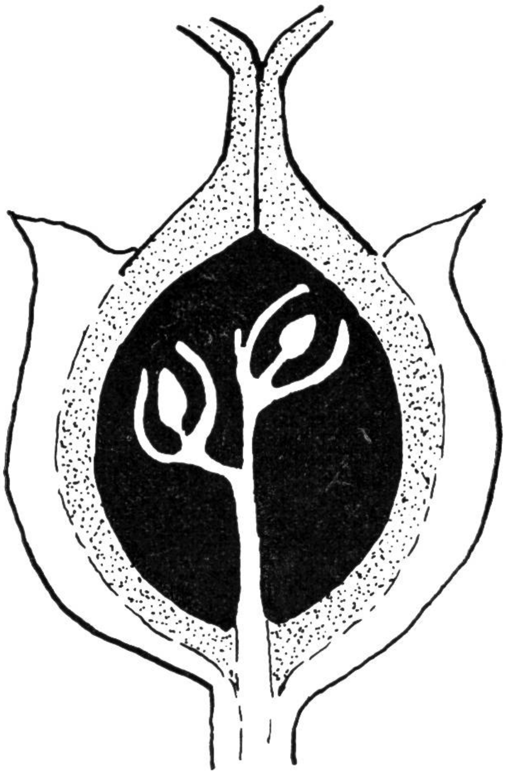

FIG. 31. Female flower to match fig. 28 but with 2 ovules instead of only 1.

By further comparing the " fruit " of *Myrica gale* to the " ovule " of *Lagenostoma* (fig. 30), I would reach the conclusion that that " fruit " and this " ovule " are quite similar though the latter may exhibit no " style " to match the former. I find no reason of course to believe that the unnamed " ovarian wall/seed-coat " of *M. gale* must be a " carpel " by preconceived definition.

In the end, I would conclude as follows:

1. Insofar as I know today, it would seem that a tubillus is usually delivered by the inner integument.

2. There is however evidence (by no means light, if still scanty) that the tubillus which may be delivered by an elongation of the outer integument is what we call today " style " in, e.g., *Ficus* and *Myrica*.

3. Whatever the case, a clearcut transference of function is possible between one and the other integument in the production of elongated structures (tubilli, styles) intended for fertilization [38]. The " micropylar tissue " spoken of by SCHNARFF

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[38] In his account of monstrosa of the ovule (*Veg. Teratol*: 262 ff., 484. 1869) MASTERS insists, of course, on " phylloidy ", and the like, as a key to the academic riddle of the " nature " of the ovule and placenta. He refers to A. BRAUN (*op. cit.*: 270) for the conclusion, surely not misplaced in essentials, that: *The ovule is to be looked on as a bud, the ovular coatings, so often variable in number, representing the scales of the bud, the nucleus corresponding to the end of the axis or growing point.* If this be read to mean that around the nucellus do crowd " total emergences " in indefinite numbers, aggregated within different plays of relationship, some as " ovular coats " (teguments,

in *Ficus carica* demands re-investigation, and I would not be surprised if it were to represent tissue originally intended for a "nucellary beak" or "tubillus" but by now left without destination, therefore used by the pollen-tube as a nutrient, conductive medium.

4. Moraceae and Urticaceae require extensive investigation in regard of the issues just outlined. It is for example impossible to run through the iconography of these families without being struck by of the most challenging "ovular" and "ovarian" arrangements [39].

The objection is certain to be heard that what I have stated may, perhaps, not be altogether crotchety, but that it must be far-fetched cannot be doubted in the end. It is true that *Myrica* is 1-ovulate, but is it not so that, e.g., *Betula* is at least 2-ovulate? Who has ever seen an "ovule-ovary" with 2 ovules? Is it not certain that a 2-ovulate structure is bound to be, necessarily, a "carpel"?

Against this objection I would of course remark, in the first place, that while I have written by now over 2.000 pages to demonstrate that the conventional terms, definitions, etc., etc., of botany hold absolutely no water when critically appraised, those who move an objection of the sort tilt against me using precisely these definitions as their weapon.

The gentlemen are pleased to voice the fiat that a 2-ovulate structure must be a "carpel", and on that they stand. Has *Scyphostegia* taught them nothing at all? Of course, with the precedent thoroughly well established that what A. P. de CANDOLLE clearly affirmed in 1813 is still misunderstood today; that what GOETHE did quite wrongly affirm in 1790 of the "carpel" has become the *Magna Charta* of botany, and still rules today; etc. (this, etc., is charitable); no one may be sanguine. I will at any rate state my case, leaving to the future to take care of what needs be. Personally, I no longer hope for anything from anywhere [40].

One of the oldest quibbles of "classical" botany is whether the orthotropous ovule is truly terminal. There is a huge literature on the score of which, in supine subservience to the "classical carpel" theory, denies this to be possible because the ovule must, by definition as usual, be borne upon a "foliar carpel". As such the ovule cannot be terminal, but must be lateral.

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arils, etc.) others as "carpel wall", it makes of course excellent sense, and it must be regretted that no one ever took up the hint. MASTERS does not mention a monstrosa which seems to be quite rare: VENTURA found ([*Carano*] *Annali Bot.* **18**: 235. 1929) that in *Iris pallida* ovules would grow which had stigmas. Aberrant or not, the circumstance is pregnant with meaning. It is indeed normally the case when what is teratology in one plant is normality in another, to the extreme that, while pursuing the former, MASTERS stumbled heavily, and identified the normal manner of dehiscence of *Cuphea* (*op. cit.*: 210. fig. 113-114) as an aberrant condition identified by MORREN, a "Belgian savant" as *gymnaxony*! See on *Cuphea*, *Princ.* **1a**: 604 ff.

[39] For example: The figures of BAILLON, *The natural history of plants* (transl. Hartog) are, as a rule, very accurate. One of them (*op. cit.* **6**: 161. fig. 127. 1880) shows a longitudinal section of the female flower of the moraceous *Pourouma mollis*. This illustration credits the ovule with, seemingly, two integuments, the outer produced into a distinct tubillar beak. The style is delivered by what would be conventionally called a "carpel", inclosed within an "urceole". I certainly would study the whole of this genus with care.

[40] As usual, I am not alone whether at my best or at my worst. There is found a pathetic appendix at the end of SAUNDER's *Floral morphology* **2**. 1939 (see also *Princ.* **1a**: 507 fn.) in which it is demonstrated in reference to precise facts that glaring errors may persist (or rather, do persist) in botany even for very many years after having been exposed beyond reasonable doubt. It is ghastly or ludicrous in turn, or perhaps even both together at all times.

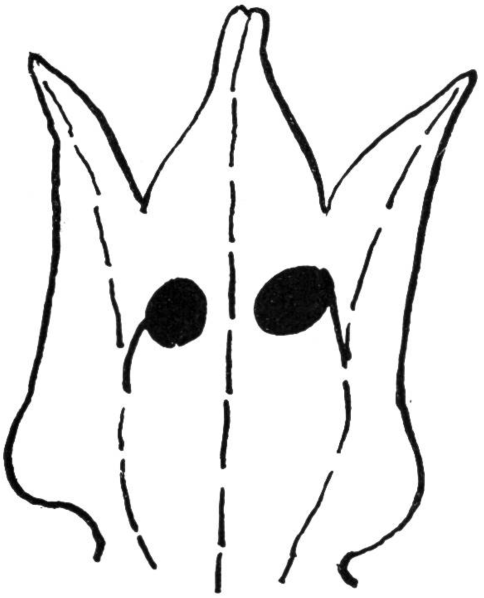

FIG. 32. Carpel of *Magnolia* (ovules in black), after OZENDA.

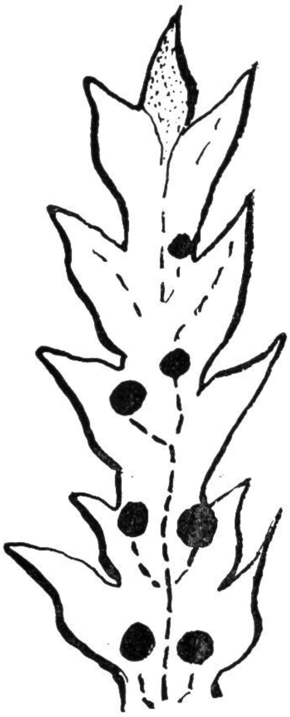

FIG. 33. The same, but supposed free-grown distally.

To me the solution of the conundrum is otherwise. Whether with ovules or other structures (CROIZAT, *Bull. Torrey Bot. Club* **70**: 502. fig. 1-8. 1943), it is virtually impossible to determine the status of a seemingly terminal body. It may be such, but any articulation, or beginning of articulation (which may be reduced to a fleeting cellular primordium, and therefore factually stands beyond the range of anatomy and histology) has it forthwith established that the seemingly terminal body may have usurped its position against (n+1) other bodies that never were allowed to develop. Accordingly, the lone orthotropous ovule may look terminal without being at all such in reality.

Whatever the case, taking as our term of reference the fruit of *Myrica* (see fig. 28), I would see no difficulty at all in supposing that the ovular stalk can elongate and develop into a placentary tract fit to yield other ovules. A simple diagram makes the matter clear (fig. 31), and I should not believe that my peers will find that what I show is fantastic. It is as a matter of fact currently realized in the case when 2 ovules develop instead of 1 in normally 1-ovulate " carpels ", as I have personally verified in, e.g., *Calycanthus*. In short, I would not oppose *Myrica* to *Betula* on the ground that the former is 1-, the latter 2- (or possible more-) ovulate. Nothing alters worth mentioning from the structural and phylogenetic standpoint in one or the other case. *Myrica* and *Betula* are at any rate not poles apart.

We have reached with this the end of the argument, and it remains to show where it can lead us to quite as factually as we have developed it.

A " carpel " of *Magnolia* with its 2 " ovules " (Ozenda, *op. cit.*: 66. fig. 54) looks as shown here (fig. 32), and there is little danger of going wrong if we imagine it extended by distal growth and bearing additional pairs of ovules. Thus produced, this " carpel " is the archetypel " phyllome " which can still be identified in the " sycone " of, e.g., *Sparattosyce* (see fig. 33 and 24), and is plainly represented by the scale of the cone of, e.g., *Alnus* and *Betula* [41].

The ovule of Magnoliaceae has 2 teguments but it bears an additional " false aril " on which much ink has been spilled not always to a trenchant purpose. I would not say that this " false aril " turns the " ovule " of *Magnolia* into an " ovary ", but I would certainly affirm that a " carpel " like Magnoliaceae's does carry two female " flowers ", or " ovaries " that we may like to call them, in *Alnus* and *Betula*. In *Scyphostegia* a sector of the quid making up the " ovary " (that is, the sector of a sycone, after all) bears structures that are as yet intermediate between " ovule " and " ovary ".

What do I conclude? Simply this: The female " flower " of the Betulaceae, the " ovule-ovary " of *Scyphostegia*, the " flower " of *Ficus*, etc., are fully homologous of an " ovule " of the Magnoliaceae, Annonaceae (*Princ.* **1a**: 398. fig. 47A, etc.), etc. One in origin, and all initially bearing " tubilli ". these " ovules ", " ovaries ", " florets ", " flowers ", etc., have in time undergone differential development. In some cases, the tubillus of the inner coat has persisted virtually unchanged (*Leucosyke*; cf. *Gnetum*, *Princ.* **1a**: 389. fig. 46); in other cases it has turned into an " exostome " or " residual tissue " allowing its place to be taken, in a clear play of transference of function (*Princ.* **1b**: 1701 ff. 1816, index: 19 references), by the " tubillus " (= " style " in *Myrica*, *Betula*, *Ficus*, etc.) of the outer coat. Emergences arisen in the *Scyphostegia* manner around the outer coat have added in turn to the " ovule " different kinds of " perianths ", whether arils or more of less genuine " perianths " sensu omnium, making it over into a " floret-flower ". Stopped at this level in certain forms (e.g., Myricaceae, Betulaceae, Moraceae at least in part, Urticaceae and, of course, Scyphostegiaceae, etc.), evolution has in other forms (e.g., Magnoliaceae) taken a very different course, the " carpel " (gonophyll !) here intervening as the chief source of the " stigma " and " style ". Naturally, these different morphogenetic and phylogenetic lines have yielded along the road uncounted morphologies in detail, which have led astray botanists who had of morphogeny and phylogeny a less than clearcut perception, inducing them to overplay the details and to underplay (indeed, to overlook outright) the main substances. The matter seems, to me at least, so clear as to demand nothing beyond direct visual observation.

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[41] The objection that the " carpel " must be " foliaceous " or " foliar " has of course no status. Let us not forget that, on the most orthodox anatomical grounds (see, e.g. *Princ.* **1a**: 376, 501 fn. etc.) the carpel has been identified as a " branch-system ", which the added ocurrence of fascicular and interfascicular cambia in its walls (*op. cit.*: 317) tends to confirm, if it ever were so that at the level of structures like the " carpel " terms like " telome " and " phyllome " have a meaning. Even the androecium has been debated (*op. cit.*: 478, 508) as " branch " and " leaf " in turn. Skeletal anatomy has manifestly definite limitations, now proving, e.g., that the placenta is a " branch " (*op. cit.*: 486 fn.), then again that it does not exist at all, being just some odd end of the " leaf " that must be the " carpel ". If one runs through the literature trying to find out exactly what is the " carpel " (*op. cit.*: 546) time will be lost much rather than well spent.

It will be said that I am crotchety, as usual, in reaching such a fantastic conclusion, but I would not think that I deserve the adjective, flattering in the sense that those who seem crotchety today are generally the ones right tomorrow, and the other way around. In the first place, the " building up " of " florets " out of simple, amorphous aggregates of " stamens " is a matter of visual evidence, too, in the Amentiferae (e.g. *Princ.* **1a** : 308. fig. 37c, d), and Euphorbiaceae (*op. cit.* : 481. fig. 55a, c), quite as the " building " of a " leaf " out of a " branch " is a matter of visual evidence in the insectivorous plants (*op. cit.* : 166. fig. 20, 184. fig. 23d, 188, fig. 24a. c, 199, fig. 25a, and relative texts). It seems to be certain, with precedents of the kind on record all over a vast, deep front of vegetal nature, that they are themselves ill advised indeed (whether or not in the majority today) who have constantly spoken of the " flower " of *Magnolia* as being a " flower " like that of *Alnus* and *Ficus*. How could this be? Suffice it to lay on a table a flower of *Magnolia* and a flower of *Ficus*, and to *think* about the two. How could they ever be the same " flower "? How could the " flower " of *Alnus* be " derived " from that of *Magnolia* via that of *Rosa* and *Hamamelis*? Why not " derive " a man from a carp starting with fish-scales and ending with dandruff?

I will be charitable in not extending the discussion, and in abstaining from citing and quoting further. All I care to affirm is that (most assuredly tomorrow if not today) marked changes will take place in the texts in which botany is taught. The whole of it begs overhauling as by now hopelessly behind the times. As of today, we can isolate a cell, and write on that a volume. However, asked to define the concept of flower we prove completely helpless as if a question of the kind did not belong, really, to botany. If something cannot be made into a slide to go under the microscope, we no longer have eyes for it. Is it bot fantastic, quite genuinely so this time?

The enormity of the difference which separates in evolution *Magnolia* from *Betula* would impress a blind man. In the former, the " flower " is a concept answering a whole strobile (see fig. 6, 7, 10, 27) in the latter but the immediately sexualized parts with their nearest surrounding emergences (see fig. 28-31). The semantic contents of a " flower " of *Magnolia*, and of a " flower " of birch (fig. 31) are accordingly incomparable much as the word is the same in both cases. Since it is the essential purpose of science vesting with precise conceptual and semantic contents the words it uses, in order thus to favour exact comparisons and logical inferences from comparisons, it does not prove hard to weigh out what botany stands for today in the matter of high thinking.

The style which in *Magnolia* is basically delivered from the scale subtending the placentae is on the contrary of tubillar origin in *Ficus* and *Betula*. The " carpel " (i.e., the scale subtending and surrounding the placentae; MELVILLE's gonophyll) is much reduced and altered in *Magnolia*, still expanded in *Betula* [42].

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[42] BAILLON, as it is well known (see, e.g. *Bull. Soc. Linn. Paris* **124** : 986. 1892), understood as ovule only the nucellus of Coniferae, identifying its " teguments " as ovary. Bitterly fought against by VAN TIEGHEM, the supreme pontiff of unimaginative botany, BAILLON's ideas never found their mark in spite of their being quite often most deserving of attention even when incorrect in detail. It is understandable, in a way, that BAILLON would refer to VAN TIEGHEM as " l'Imposteur ", adding (*op. cit.* : 987) of his notions concerning the coniferous " ovule " : *C'est là une profonde erreur, comme celle qu'il commet sans cesse, en devinant les choses au lieu de les observer.*

Quite noteworthy is the following: whether the female flower is circumnucellar [43] in its origin or rather strobilar, the fact is that it can in both cases be sexualized into maleness (therefore into bisexuality) by emergent stamens of ultimately " receptacular " origin. So far as I know, this form of sexualization does not seem to occur in *Casuarina*, but it has been recorded in *Betula* (Abbe, *Bot. Gaz.* **99**: 444-445. 1938) and, as we heard, in *Myrica.* This but confirms, of course that " seed-coats " and " ovarian wall " are fundamentally the same stuff.

The ancestor common to *Magnolia* and *Betula* can of course be sought only deep into the bosom of pre-angiospermy. I should be inclined, as a matter at least of strong personal preference, to view the cone of the latter as even more " primitive " than the strobile of the former. Anyway, among the angiosperms now living both the strobile of *Magnolia* and the cone of *Betula* do represent extremes, and it will certainly take a considerable amount of candid work to settle the issue how far and how deep structures of this basic kind reach into the bosom of less " extreme " angiospermy. Without for this running ahead of what future is to reveal I should think that the sycone of, e.g., *Sparattosyce* may be viewed as structurally intermediate between a cone of, e.g. *Betula* and a " sycone " of *Scyphostegia.* Once with *Scyphostegia,* we next immediately stand with *Flacourtia* in the thickest of conventional angiospermy which I take to be significant as a general indication.

Van Tieghem, I am sure, observed a great deal, described without end what he had observed, but understood virtually nothing at all of what he both observed and described. Baillon would, on the contrary, construe at times with astounding insight what he had barely seen. It is tragic that botany has held for a century by now Van Tieghem in much higher esteem than Baillon.

Auguste de Saint-Hilaire, a rather brainy student of plant-life, understood the scale of a cone of Coniferae (*Leçons de Botanique*: 287. 1841) as " feuilles carpellaires " outright. In this he was perfectly correct, and I surely would not know how to discriminate, structure from structure, a lacinia of the sycone of *Sparattosyce*, a " carpel " of *Magnolia*, and a cone-scale of *Pinus* or *Alnus.* Structurally, to insist, the whole is virtually identical. The pompous ineptitude of much botanical thinking is nowhere better displayed than in the " criticism " (*Princ.* **1b**: 1693) moved by some high priests of " morphology " against authors who, like Baker & Smith, stressed the resemblance that exists between a cone of *Callitris* and an angiospermous flower. Structurally and morphogenetically that cone and this flower can hardly be separated, and a candid recognition of the fact does of course not entail a belief in the " derivation " of *Magnolia* from *Pinus.* Structure and consanguinity are perfectly distinct concepts, forever to repeat.

[43] I regret being forced to propose a neologism. Circumnucellar is to me the flower (e.g. *Betula*, *Alnus*, *Ficus*) which is formed by receptacular or toral emergences immediately arising around the nucellus. Strobilar is conversely the flower (e.g., *Magnolia*, *Thea*, *Myrtus*) which is the end-result of the decomposition and adaptation of a whole primaeval inflorescence-flower. It will be observed that the limits between the circumnucellar flower and the naked ovary are virtually evanescent. As a matter of fact, we indifferently designate the female end of the cyathium of the Euphorbieae as " female flower " or " ovary ", though tending to prefer the former term in deference to the theory that the cyathium is an " inflorescence ", which it is only in part (*Princ.* **1a**: 472 ff.) as an obvious limit-case in flower-making. I should emphasize the following: The important side of botany is not that we use one or the other term, but that we clearly and fully understand what every term we use does mean and can mean. Accordingly, I advance adjectives like circumnucellar and strobilar in reference to the flower not thus to furnish two brand-new " toys ". With these adjectives, I do intend to invite attention to basically different concepts of flower. Just to illustrate: in pre-Linnaean, and in Linnaean times (see, e.g. Persoon, *Syn. Plant.* **2**: 109, 138. 1807) the Labiatae went under " *Didynamia Gymnospermia* ", and the Verbenaceae, Myoporaceae, Selaginaceae (type-genus: *Selago*), Scrophulariaceae, Pedaliaceae, Bignoniaceae, etc., under " *Didynamia Angiospermia* ". This classification is, if properly understood, not quite as wild and antiquated as it may seem. It shrewdly raises the question what is the morphogenetic and phylogenetic status of the " nuculae " of the Labiatae. Do the Labiatae have true " carpels " (in the sense of gonophyll, of course)? How do they compare structurally with Boraginaceae?

The strobile of *Magnolia*, as I have stated elsewhere already, seems to have but limited currency. At any rate, families like Monimiaceae and Annonaceae may prove to connect that strobile with the sycone of the Moraceae, at least in point of structure. This would be satisfactory, for it may then furnish a single common denominator of structure (not at all of consanguinity, of course) in general for nearly all the Angiospermae, but it will impose upon the objective enquirer the task of determining the scope of the typically magnoliaceous strobile. To this task CORNER's report that the flower of *Paeonia* is centrifugal may vitally contribute, in spite of HUTCHINSON's (Hutch. **1**: 400) animadversions to the contrary.

What is the carpel?

The reader may not have been aware of it on the spot, but the conclusion we have reached that a "flower" of *Ficus*, *Betula*, etc., and an "ovule-ovary" of *Scyphostegia* are tantamount to but an "ovule" of *Magnolia* is bound to alter in every fundamental respect the notion currently accepted today of "carpel". What this notion is the reader doubtless knows. In its crudest versions, the "carpel" is construed as a leaf folded ventrally and carrying ovules upon its margins. In hopefully refined incarnations, the "carpel" is presented as follows (ESAU, *Plant Anatomy*. 1953):

1. *The basic unit of the gynoecium is the carpel which is commonly* [sic] *regarded as a megasporophyll* (*op. cit.*: 530).

2. *The carpel of an apocarpous gynoecium is a leaf-like folded structure ... The folded carpel is commonly* [sic] *described as having infolded or involuted margins ... these margins are pictured* [sic] *as bearing the placentae that give rise to the ovules. The carpel of the woody Ranales shows, however* [sic], *that in the primitive form the carpel is a conduplicately ... folded structure* [44].

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[44] These quotations are transparent, and what the author of the original text herself believes is a question which the reader may answer. I feel a positive need of bringing these statements to record because an incredible amount of quibbling has been, and still is, current concerning the "nature of the carpel", so much of it in fact that a candidly conducted argument on the subject is today virtually out of the question. The stuff I have quoted belongs of course to a standard textbook for the teaching of botanical anatomy in "developed" countries. What is current in "underdeveloped" ones is readily learned from the following, for example (LASSER, *Botánica general*: 107. 1956): *Un corte al través del ovario de una flor de caraota nos permite ver que el carpelo no es sino una hoya cuyas mitades están soldadas por sus bordes cerrando una cavidad. El nervio mediano de la hoja corresponde a la sutura dorsal del carpelo; la linea de union de los bordes, a la sutura ventral. ... El ápice de la hoja ... es el estigma* (A section taken across the ovary of a flower of *Phaseolus* will make it possible for us to see that the carpel is nothing else but a leaf whose halves are soldered by their margins around a central cavity. The mid-rib of the leaf corresponds to the dorsal suture; the commissure between the margins to the ventral suture of the carpel ... The tip of the leaf is the style.) A text of the kind being virtually official in, e.g., Venezuela for the teaching of botany in the higher brackets, it follows that the rudiments of a science of plantlife have no longer place in the classroom and the hall mandatorily imbued with Lasserian "Konstruktionen". It is patent that the nexus between what Essau cryptically states, and LASSER of course more or less happily understands, is one of direct filiation. The state of affairs thus ruling would not be worthy of mention if its consequences were not catastrophic. See the main text in continuation.

The " classical carpel " does of course grossly confuse, as one and the same, two perfectly distinct concepts, that is:

1. A body immediately bearing ovules (= placenta, sporophyll, sporoclade)[45].

2. A " bifacial " body subtending and often enclosing the ovule-bearing organ (= carpel *p.p. sensu fere omnium*, MELVILLE's gonophyll). This doing, that " carpel " destroys at the root the idea of an interplay between a " leaf-like " sterile subtending body, and a placenta which might, in certain cases at least, e.g. Euphorbiaceae; *Princ.* **1a** : 486 fn.) be not improperly construed as " rameal " and accordingly voids floral morphogeny and phylogeny of its scientific edge[46]. A botanist informed of the facts of plant-life can of course not wonder why I have spent a large pagination (*Princ.* **1a**, throughout) in order finally to expose how pernicious with regard to a science of plant-life can be the "classical" (or, "Goethian") carpel. So long as botany entertains it, that long botany shall not progress.

It will seem to most of my readers that the conclusion I have just ventured categorically to affirm is dogmatic beyond reason, and that the difference cannot be capital between a carpel conceived of as a " foliar " body carrying ovules upon its margins or ventral face, and a carpel (see fig. 12) understood as made up of a subtending essentially sterile scale (gonophyll) and of a subtended placenta (sporophyll or sporoclade). Is it not so, at any rate, that the placenta can be so thoroughly " transfused " into the gonophyll as to establish what is to all intents a single body?

Against this apparently logical objection a physicist would of course oppose the consideration, that a seemingly unitary emulsion postulates to be properly understood a prior knowledge of its components as essentially distinct. Failing this knowledge, the entire subject of emulsion ceases to have a meaning in science. A chemist would of course approve what the physicist would thus say. Any science dealing with compound bodies must have clearcut concepts of composition, and of separate elements that eventually get together. Nothing is more simple than

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[45] Sporophyll (=ovule-bearing leaf) and sporoclade (=ovule-bearing branch) are perfectly equivalent terms. At the level of placenta it is certainly impossible to discriminate " leaf " from " branch ". In, e.g. Urticaceae and Moraceae (Conocephalus, etc.) the whole of the inflorescence may not seldom suggest quite as much a " phyllome " as a " telome ". See on the subject of " phyllome " vs " telome ", *Principia botanica* throughout.

[46] Melville has stressed the point (*Nature* **188** : 18. 1960) when stating : *Many facts that formerly appeared to be anomalous in the context of the* [" *classical* "] *carpel theory now fall naturally into place. For the first time it is possible to indicate a link between the reproductive structures of Gnetum and those of the Angiosperms and to point out similarities between those of Glossopteris and the androecium of certain Angiosperms.* This summary does not give, I am sure, the full measure of the change for the better that follows throughout botany when the " carpel " begins to be approached as it must be. It is the whole of the problems of flower-making in regard of morphogeny, phylogeny, structure, high and formal systematics, etc., which receive thus a new meaning. The interplay between gonophyll and placenta is, as MELVILLE has intimated, the very same that has place between an " epiphyllous " flower and the subtending leaf. This interplay is a hypocladial relationship (*Princ.* **1a** : 1028 ff., 1032 fn.), and its manifestations cover a vast field of morphogeny and morphology which is today quite indifferently understood. See for epiphyllous flowers : HUTCHINSON **1** : 362. fig. 216 *(Dobinea)*; ENGLER, in Engler & Prantl, *Nat. Pflanzenf.* **18a** : 224. fig. 131a *(Phyllonoma)*, 1931; ARBER, The Gramineae : 313. fig. 162 *(Hordeum)*. 1934. Varying degrees of hypocladialism between spadix and spathe are indicatively shown, *Princ.* **1a** : 987. fig. 125a; and between pedicel and subtending leaf or bract, *op. cit.* **1a** : 1026. fig. 132c. Hypocladialism inducing " infundibula " of different kinds is shown, *op. cit.* **1a** : 1047. fig. 134. The subject is indeed endless, and in every respect fascinating.

water to the man in the street, but chemistry could not really begin in its strides before having reached the understanding that water is indeed anything but simple, and in fact, represents a compound of hydrogen and oxygen in certain fixed relations. What is thus true of physics, chemistry, etc., is manifestly quite as true of plant-life which represents beyond question infinite morphological combinations and aggregations of but a few, simple structures. Its follows that, without a precise understanding of these combinations and parts, botany must remain in a pre-scientific state of knowledge. The reader of this article may, perhaps, have had reason to suspect that this affirmation is not lacking in solid grounds for support. We only know as much as we can think, and no thought is worthwhile that fails to compare exactly, and to reason sharply, following critical comparison.

How really destructive of sound phylogenetic thinking is the " classical carpel " can easily be shown in reference to certain statements which Takhtajian has incorporated in the last version of the origin of the Angiospermae from his pen. In bringing them before the reader, it is not my intention to take personal issue with a generally well informed botanist. My intention strictly is to use what documents in his work, alas, a state of mind and knowledge widely prevalent at this hour, and to show what are its results.

TAKHTADJIAN observes (*Proiskh.* : 11) that the megasporophylls of Bennettitales were reduced rod-like bodies generally capped by a single ovule. Among these rod-like megasporophylls *(mezhdu takim palochkovidnymi megasporofillami)* stood, alternating with them, sterile rod-like bodies (interseminal scales; *mezhsemennye cheshui*) possibly representing " metamorphosed " ovule-less sporophylls. Coming together with their enlarged apical ends, these scales formed a kind of armour around the ovules *(eti bezplodnye sterzhenki, smykayas svoimi verkhnimi rasshirennymi chastyami, obrazuyut rod pantsirya vokrug semezachatkov)*. For TAKHTADJIAN, an arrangement of the kind proves that the protection of the ovules *(zashchita semezachatkov)* took place in Bennettitales in a manner entirely different *(sovershenno inym putyom)* than in the Angiospermae. It is for him absolutely evident *(sovershenno ochevydno)* that the reduced sporophylls [47] of the Bennettitales and, as he adds, of their living descendants, *Ephedra*, *Welwitschia*, and *Gnetum*, never could give rize *(dat nachalo)* to the carpels of the Angiospermae *(plodolistikam)* [48] *pokrytosemennykh)*.

The discussion by TAKHTADJIAN which I have just quoted and commented upon immediately bears upon the morphogeny and phylogeny of Bennettitales, Ephedraceae, Welwitschiaceae, and Gnetaceae on the one hand, Angiospermae on the other hand. The argument is manifestly spun on the basis of (mega-)sporophylls and

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[47] Since we are here discussing only sporophylls carrying ovules, I will not constantly harp on megasporophylls. In translating accordingly as sporophyll what TAKHTADJIAN calls megasporofil in the Russian original I am not doing violence to his text.

[48] *Plodolistik* (from *plod* (fruit) and *list* (leaf)) is the standard Russian term for carpel in the current sense of the term in descriptive botany. My translation stands accordingly beyond argument, and will easily be verified by comparing, e.g., Takht. 1954-1959: 34 fig. 8, caption (Stages of the evolution of the angiospermous carpels (megasporophylls ", as translated by Olga HESS GANKIN) with the very same figure and caption in Takht. 1961 : 39. fig. 5 : *Stadii evolyutsii plodolistikov (megasporofillov) pokrytosemennykh.* It is thus certain that TAKHTADJIAN understands as synonymous carpel and (mega) sporophyll. This means that his carpel is the " classic " (Goethian) one, that is, a leaf-like body carrying ovules near to, or upon, its margins, which is to be confirmed in a text to be quoted in the next footnote.

carpels, the conclusion being reached that the structural premises of Bennettitales are incompatible with those of Angiospermae because in the two groups the " protection of ovules " is assured in an entirely different way. Moreover, the carpels of the Angiospermae never could have been "derived" from the (mega)-sporophylls of the Bennettitales and their alleged living descendants *Ephedra*, *Welwitschia*, and *Gnetum*. As carpel TAKHTADJIAN does of course understand a " foliar " body carrying ovules upon its margins [49].

To test what TAKHTADJIAN argues out and finally concludes is very easy, two sketches of the simplest bringing the matter to a head on the spot. The first of these sketches (fig. 34), shows, in the Bennettitales, sporophylls true to TAKHTADJIAN's own characterization, surrounded " protectively " as if by an armour of " inter-

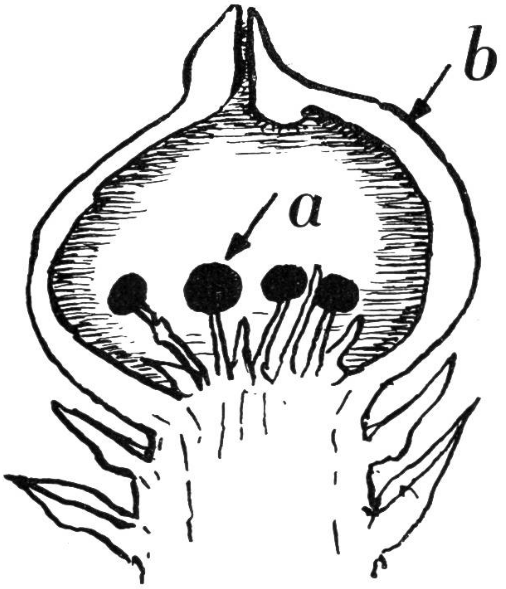

FIG. 34. TAKHTADJIAN's understanding of the interrelationship between " megasporophylls" *(a)* and protective scales *(b)* in the Bennettitales.

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[49] This is definitely established by the additional following (*Proiskh.*: 39): *The carpels (megasporophylls) of the early Angiosperms still were of a primitive, only half-closed type, as we still see them today in* Degeneria *and some species of* Drimys. *These plants were accordingly only "half-angiosperms". These primitive carpels had as yet a wholly foliar character suggestive of folded leaves ... Already approximate but as yet not connate, the margins of the carpels heralded a coming stigmatic surface. In primitive carpels the ovules were boerne on the margins of the abaxial (internal) face).*

I should warn the reader that this translation has not met the entire approval of Dr. TAKHTADJIAN (in litt. Febr. 2nd. 1962) who warned me that: *Zanimali bokovye chasti* means, in his sense at least, a " lateral-laminal-lateral-placentation ". I have no reason to dispute of the matter with an author whose language is Russian. Rokovoy means: lateral, side-long, and bokovushki are margins, which explain why I translated *The ovules were borne on the margins of the abaxial (internal) face*, while I should have said according to Dr. TAKHTADJIAN: *The ovules stand in lateral-laminal-lateral-placentation.* I leave my translation as it stands, in the understanding that the reader is not to find a great deal of difference in the argument, following such rectification as Dr. TAKHTADJIAN requires. His " carpel ", with one or the other placentation, is surely the old " classical " war-horse that clogs beyond repair the cogs and gears of botany as a science. See the main text throughout.

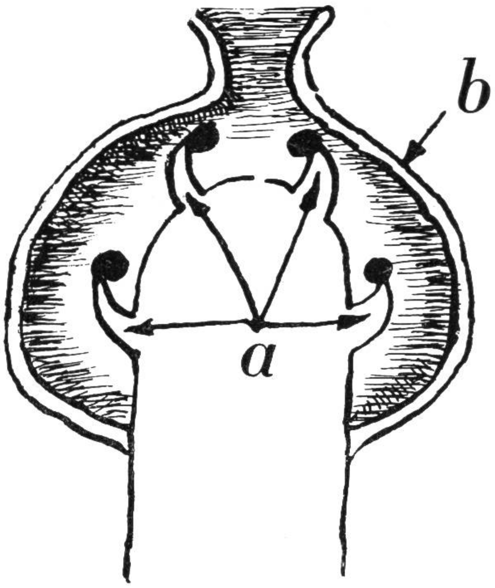

FIG. 35. HAGERUP's understanding of the interrelationships between placentae *(a)* and subtending, sterile " carpels " *(b)*. Homologous coats are stippled in fig. 28-31 : delivered by the innermost coat is a "tubillus" (fig. 29), by the coat exterior to it a "style" (fig. 28, 31.) Absolute structural homology in the set-up carrying and "protecting" ovules rules between Bennettitales (fig. 34) and Angiospermae (fig. 35), regardless of morphological details.

seminal scales " coming together at their enlarged distal ends. The second sketch (fig. 35) is taken from one of the works of HAGERUP (in *Kgl. Dansk. Videnskab Selskab. Biol. Meddel.* **15** (2): 35. fig. 93-95. 1939) displaying the basic morphology of the gynoecium of the Solanaceae, Gesneriaceae, and Orobanchaceae.

It is a matter of immediate visual/evidence that the " protection of the ovules" conform in the two, Bennettitales or Angiospermae, that they be, to identical structural premises. The " interseminal scales " of TAKHTADJIAN are the " carpels " of HAGERUP (which carpels, quite correctly, HAGERUP understands as sterile " protective " bodies around the placentae). TAKHTADJIAN's " megasporophylls " are of course HAGERUP's " placentae ", not " carpels ".

Concluding: TAKHTADJIAN cannot see what is evident for the simple reasons that he confuses as one " carpel " (as by HAGERUP, gonophyll by MELVILLE) and placenta. He takes the " classical carpel " for granted, and his understanding of morphogeny and phylogeny suffers accordingly. In his turn, HAGERUP is lured by a structural homology between the carpic structures of Gnetales and Coniferae, on the one hand, Angiospermae on the other hand, to assume a probable " derivation " of the latter from the former. Structurally speaking this " derivation " is possible, but in point of consanguinity manifested by identical or similar ovulation, fertilization, etc., this " derivation " becomes improbable. In these respects, Gnetales, Coniferae, Angiospermae, etc., substantially differ on different evolutive lines of their own.

Accordingly, it seems quite clear that by confusing gonophyll and placentae as a single " classical " (or, " Goethian ") carpel precise analysis of morphogenetic and phylogenetic points of basic evidence becomes impossible. Likewise, by confusing what is structural with what is consanguineous matters of morphogeny and phylogeny are forthwith thrown out of gear. TAKHTADJIAN and HAGERUP would argue their case to the end of time without ever reaching an understanding, and without making it possible for their readers to grasp the core of the argument, either.

I have shown elsewhere how, by preconceived devotion to the " classical carpel ", it becomes impossible (*Princ.* **1a** : 384 ff. 387, fig. 45b, c, d) to interpret correctly fossils of utmost relevancy. To my mind, the single greatest difficulty on the path of advance of palaeobotany, wood-anatomy, pollen-anatomy, embryology, phylogeny, etc., is precisely to be found in the circumstance that we do not well understand the basic morphogeny of the living plants. Ballasted by false notions to this extent, we find the past even more obscure than the present. The remedy? To assimilate principia botanica as a mandatory part of the elementary curriculum of botany.

The origin of the Angiospermae

In a text quoted elsewhere (see last footnote), TAKHTADJIAN identifies as " hemi-angiosperms " the " magnolioid " *Degeneria* and, in part, *Drimys* on the ground that their " carpels " fail to coalesce completely and accordingly to establish a perfectly well made style. I have pointed out in my turn (*Princ.* **1a** : 271 fn. 376 fn.) that the case is not different with other, this time apparently less hoary, angiospermous plants. The evidence is indeed such as to suggest that searching enquiries may greatly increase the list of the " hemi-angiosperms " among the conventional angiosperms, so particularly if investigated in anthesis [50].

As a matter of fact, and on the basis of observations reported in the previous pages, I would not know how to construe the scale of the betulaceous cone otherwise than as a " carpel " which has remained distended without in the least taking part in the formation of the " style ". This organ is evidently of tubillar origin in Betulaceae.

It seems to me certain (so doubtless also with the blessing of TAKHTADJIAN) that the early Angiospermae were technically hardly angiospermous at all. Their placentae and ovules were carried very nearly in the open, and I would see no difficulty (at least in the sense of structure) in construing a fructification of, e.g., *Umkomasia* (*Princ.* **1a** : 381. fig. 44d, 387. fig. 45b, 398. fig. 47a) as being directly pre-angiospermous. It is of course lamentable that petrifacts cannot, and probably never will, acquaint us with the fine points of the process of ovulation and, even more, fertilization so that we may never be certain that, e.g., the Corystospermaceae are actually

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[50] A perfunctory acquaintance with the literature of morphology is sufficient to reveal that a hiant ovary is much racher the rule than the exception in initial organogeny. Sweeping differential growths intervene later to modify the original lay-out in the sense of conventional " angiospermy ". Of these differential growths MARTEL gave a good example ([*Morot*] *Journ. Bot.* **19** : 85. 1905) showing that in Umbelliferae the pistil, for example, is formed by basipetalous growth only after fertilization. I would say that the Angiospermae rather easily prove to be " hemi-angiospermous " in early anthesis, and " gymnospermous " at maturity. These trends do not strike me as insignificant at all.

proto-angiosperms by their embryogeny. It must be on the other hand certain that the step is relatively short between a group of the kind and the living Angiosperms. All that is required structurally to pass from the one to the other is that the " fructification " be eventually enclosed within a more or less perfectly " angiospermous " ovary.

Of course, the tendency toward reducing within a minimal area sexual parts and organs essential to the establishment of the angiospermous flower is by no means a prerogative of the Angiospermae. " Neoteny ", at least of sorts (CROIZAT, *Lilloa* **13**: 40. 1947; TAKHTADJIAN, *Proisk.* 17 ff.), stands displayed quite as much in their ranks as in those of true Conifers. As a highly adapted brachyblast, the scale of a pinaceous cone is beyond question " neotenous ". It is only extreme reduction and " adaptation " that could turn a cone of, e.g., *Pinus lambertiana* or *P. coulteri* into a " berry " of *Juniperus*. In the Cupressaceae (HUIN-LIN LI, *Journ. Arnold Arb.* **34** : 17. 1953), the cones of *Tetraclinis* and *Diselma* are manifestly " reduced " and " juvenile " by comparison to those of *Fokienia*, *Cupressus*, and *Chamaecyparis*, finally *Juniperus*.

The tendency responsible for these evolutionary current is evidently widespread throughout plant-life, and amounts to little more than to specialization of certain axes for reproductive functions. I have given of this orthogenetic tendency a [51] diagrammatic figure (*Panbiog.* **1** : 166. fig. 21) which makes the point clear. A tendency of the kind must at its distal end allow the fertilization of the ovule within a structure representing a " bud " as yet to unfold, that is, an " ovary ". That this is the case with the great majority of the Angiospermae seems clear, for, even in the Betulaceae and the like, the cone is ready for fertilization in an early stage of development.

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[51] Orthogenesis (or orthogeny) is the subject of endless debates in the literature of evolutionism, cytogenetic, etc. It could alone furnish the subject to a book. I understand it briefly this way: when, for example, the ancestors of Flacourtiaceae, Euphorbiaceae, Passifloraceae, Tiliaceae, Thymelaeaceae, Dipentodononaceae, Saxifragaceae, etc., etc., came to the parting of their ways eventually to establish the modern families by these names, the Euphorbiaceae inherited certain characters of placentation and sexuality, a particularity, which made them what the Euphorbiaceae still are today. By a like token, the Passifloraceae inherited a different placentation and sex-expression, etc. In short: out of the sum total of characters, actual and potential, of an ancestral group common to them all in origin, the Euphorbiaceae took some, the Passifloraceae some others, etc.

Throughout an immensely long history (around 175 million years, at least) the Euphorbiaceae have become " adapted " into an infinity of different forms, some aquatic in the manner of *Lemna* (e.g., *Phyllanthus fluitans)*, others become fitted for dry deserts, and become ball-like (e.g. *E. obesa*). They have yielded humble annuals (e.g. *Chamaesyce*) or enormous trees of the " cloud forest " (e.g. *Alchornea*) in the tropics. Their placentation has undergone certain modification (e.g. *Cleistanthus* vs. *Ricinus*), but (by far and large) what some 175 million years ago was euphorbiaceous is still euphorbiaceous today by the permanence of essential characters of no " adaptive value " proof against " struggle for life ", and the like. The preservation of this core of character and tendencies is the byproduct of orthogenetic morphogeny having yielded untold particular morphologies in development, some with an evident basis in the environment, others not so, while at the same time remaining unvariable around an initial core of interrelationships between gonophyll and placenta, between the different hormonal balances required to maintain basic unisexuality, etc. In the end, adaptation only operates against a background of orthogeny. *Euphorbia peplus* and *E. obesa* are " adaptational ", very different forms, but their common denominator (*Euphorbia* as a genus, Euphorbiaceae as a family) is something against which neither " Mediterranean " nor " South African " climate, etc, etc., had any power. As a concept, orthogenesis is very simple but it appears that, distracted by " darwinism " and its byproducts, not many are the naturalists who understand the matter as simply and as concretely as I do. See CROIZAT, L., *Space, Time, Form: The Biological Synthesis*. 1962.

It is quite possible that even this cone would have turned into an " ovary " if certain tubillar arrangements had not interfered.

Overall, then, " neoteny " is rampant throughout plant-life yet it has managed to reach in the Angiospermae a peak which it has not attained in other groups. What may be the reason of this peak ?

I would not give a direct answer to this question, but I can suggest some evidence that probably bears heavily on the answer eventually to be returned. For example: I view as overwhelming the evidence establishing it, that the typical angiospermous leaf is a compound of " bracts " and formerly fertile axes (*Princ.* **1a**: 178 fn. et passim), the " traps " and " pitchers " of the leaf of the carnivorous plants marking probably a last, rather obvious, remnants of axes of the kind [52]. In *Casuarina*, TREUB detected (*Ann. Jard. Bot. Buitenzorg* **10**: 180. 1891) certain " macrospores stériles " with " tails " that reach even beyond the chalazal region and favour the course of the pollen-tube. There is a moment in the growth of this genus when, after the formation of an original cavity in the ovary, the ovary is again filled solid by some sort of " packing tissue ". Nothing of this bears being pinned down to anything definite, for the literature, quite rich in certain directions, is hopelessly vague in others, those particularly for which ideas are not available to see (no one ever sees what he is not ready to understand when he sees it); but I have never been able to escape the suspicion that at some time during their history the Angiospermae were quite different from what they are today not only in leaf, stem-anatomy, etc., but also in reproductive matters. Their " foliage ", " roots ", " inflorescences ", etc., manifestly are today what they once were not. I should think that to this overwhelming change was due also the inception of " double fertilization " accompanied by a stepping up of the " neotenous " tendencies eventually responsible for the " flower " [53].

Remote as might have been this change in its inception, I still think that a very solid chronology can be established by interlocking distributional and geological data to determine the " age " of the " modern " Angiospermae. Before doing this,

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[52] A fascinating problem, evolving biochemistry, morphogeny, and phylogeny, is exposed here. It has been repeatedly claimed in the literature that " insectivory " (or " carnivory ", that we might call it) is required to provide nitrogen for eventual seed-making. The traps, ascidia, etc., of the " insectivores " stand accordingly bound with sexual functions to this day, though by now indirectly if still essentially. A biology of active digestion is inherent part of the development of most ovules, and of the angiospermous one particularly. It may not be strange that this biology interplays in the " insectivores " between the extant sexual organs and what formerly were sexual parts but are now traps, ascidia, etc. The nexus between the two seems to me to be so obvious as to prove inescapable once thought about. My feeling is that " insectivory " in one or the other of its forms is widespread in plant-life much beyond what is commonly believed at this hour. See on *Roridula*, a form which is morphologically " carnivorous ", biologically no longer so, *Man.*: 469; *Princ.* **1a**: 218.

[53] Quite interesting is the circumstance that, as independently stressed by BUCHHOLZ (*Science* **102**: 135. 1945), and by MARTENS (*La Cellule* **54**: 103. 1951), the seed of a pine and a majority of Coniferae is fully grown and has attained its ultimate size at the time of fertilization. Not so the seed of the Angiospermae, in which manifestations of immediate sexual nature acquire virtually complete dominance over lingering vegetative developments. " Syncopation " and " recapitulation " reach in the angiosperms a pitch which seems unmatched elsewhere. As usual, the literature is rather unsatisfactory in respect of the matters here mentioned. It is lamentable that the time of a promising student is often being wasted or subjects of academic theses of the dullest and most unconstructive type, whillst an immense amount of creative, obviously challenging enquiry finds very few takers today.

however, I would answer the question whether these plants are " monophyletic " or " polyphyletic ". This question has worried many phylogenists, some, like TAKHTADJIAN, affirming that they are " monophyletic ", others (e.g., METCALFE; see *Princ.* **1a** : 351) refusing to stand commited to an answer but viewing the problem, and its direct implications, as one of the great riddles of evolution.

My own answer is as follows:

1. No one who lays on a table a plant of *Lemna*, a flowering shoot of *Magnolia* and *Alnus*, respectively, etc., can hope to argue that stuff of the kind is monophyletic. It cannot be such because it palpably represents divergent, remote lines of differential evolution.

2. No one who considers that this stuff is bound by a basically common morphogeny and physiology in reproductive organs can call it polyphyletic. It is not polyphyletic, either, in regard of the tendency responsible for the ultimate establishment of the " flower " and of technical " angiospermy " of the ovary.

In short, as Angiospermae, these plants are monophyletic. As Lemnaceae, Magnoliaceae, Betulaceae they are polyphyletic. The reader may have his choice, for I think that the conundrum is far more academic than scientific. The truth is that the majority of those authors who have paid any attention to these and similar questions manifestly understand " monophyletism " and " polyphyletism " as would theorists whom I cannot follow.

Dating the Angiospermae on the strength of fast interlocking geological and biogeographical data is easy indeed.

It is a matter of common knowledge that the flora of southern South Africa, with stress on the so called Cape Region (GOOD, *Geogr. Flow. Pl.* ed. 2 : 125. 1953): *Has one of the most remarkable, and perhaps the richest, of all the world's floras.* Of the 1.500 genera which turn up within its limits no less than 30% are endemic. The high speciation of certain of these genera (e.g., *Erica*, *Stapelia* s.l., *Mesembryanthemum* s.l., *Euphorbia* s.l., etc.) is characterized by narrow endemisms of a kind which, *Stapelia* for instance (GOOD, *Feat. Evol. Flow. Pl.*: 258. 1956), strikingly exemplifies. Over 40% of the South African forms are species recorded from a single locality, and are presumably known only from it. Several have been found but once, others have remained unknown following the original collection well over a century ago.

Distribution of this same type is well known also on the mountains of Madagascar (PERRIER de la BATHIE, *Mém. Acad. Malgache* **3**: 58. 1927). On the high grounds of Mt. Tsaratana, for instance, authentic species of *Gravesia*, *Medinilla*, *Begonia*, *Impatiens*, Orchidaceae: *Semblent même n'avoir qu'une aire excessivement réduite, n'exister que dans un seul peuplement et n'être représentées que par un petit nombre d'individus. Le fait n'est pas douteux pour les Gravesia, dont chaque station possède, presque en propre, une espèce spéciale.* PERRIER does not believe that species of the kind are the byproduct of casual mutations and seed-tansportation. For him: *L'histoire de chacun de ces peuplements est en somme celle même de la station où il croît ... Ces espèces ne datent pas de hier et pourraient tout aussi bien, si l'on ne considérait que la longueur du temps qu'il a fallu à l'érosion et à l'évolution pour* *constituer ces formes, être considérées comme des relictes.* This summary by an unusually shrewd naturalist with ample personal information perfectly agrees with whatever I have been able to learn during long years devoted to enquiries into dispersal the world over. In a word, life and rocks did evolve together, whether by uplift or by erosion. Geography and topography did change, and so did old form-making die out and a new one come to the fore. Of course, species that score into the hundreds presuppose less of extinction than of form-making, that is, a very old generic age and an even longer time of relatively quiet occupation. If *Erica* still numbers at this hour over 500 species divided into some 40 different sections within a comparatively narrow coastal range of The Cape, it must be so that *Erica* was in the range which we today know as The Cape from ages when angiospermy was young. *Erica* indeed does belong to The Cape quite as fully and as solidly as do its ancient mountains and strands.

How old is the angiospermous Cape flora? Can we know? My answer, to repeat, is, quite definitely, yes.

Southern South Africa numbers close to 200 different species of more or less succulent *Euphorbia* (White, Dyer & Sloane, *The Succulent Euphorbieae (South Africa)*, 2 vol. 1941) of which no less than 150 are typically Southern South African. No botanist at all informed of *Euphorbia* who sees, e.g., forms like *E. caput-medusae*, *E. clava*, *E. squarrosa* can fail locating them on the spot as originating from a definite corner of the map of the Dark Continent. By the same token, Madagascar has about 50 different species (Ursch & Léandri, *Mém. Inst. Scient. Madagascar*, ser. B. **5**: 110. 1954) of *Euphorbia* closely related to *E. milii* (= *E. splendens*) and *E. lophogona*, which are absolutely and fully Malagasy at a glance. These 50 species form a solid compact block east of the Mozambique Channel just as the 150 species in Southern South Africa form a solid, compact block west of said Channel.

So clearcut and so characteristic a pattern of dispersal begs of course the question: How old is the Mozambique Channel? Wild as may be the notions about " casual transportation ", " chance distribution ", " stratospheric conveyance of seeds " current in a great deal of " phytogeographic " work, it is yet probable that no " phytogeographer " will be pleased to imagine that species of *Euphorbia* could fly across the Mozambique Channel like snow-flakes whipped thick and fast by an antarctic blizzard. Two hundred typically local species, about 150 in Southern South Africa, some 50 in Madagascar, do presuppose:

1. Long form-making in situ.

2. Prior establishment in the two regions of ancestors sufficiently distinct, actually or potentially, to insure in time a ripe form-making of morphologically quite different sub-genera and species.

Failing either one of these conditions, *Euphorbia* could not be in Southern South Africa and Madagascar what *Euphorbia* is there today; and but nonsense follows if interlocking, cogent conditions of the kind are credited to " casual agencies " (see, e.g., *Panbiog.* **1a**: 207. fig. 23) supposedly active across Mozambique Channel. Hypothetical " means of dissemination " that might account for one or a few species across the sea no longer have a meaning in regard of massive blocks of species, both of which (be it carefully remarked) are integral part of worlds of vegetations themselves extremely endemic in character. If in Southern South Africa, genera are endemic to the rate of 30% (a very high total by all means), in Madagascar species are such (PERRIER de la BATHIE, *op. cit.*: 59 fn.) to an extent close to 90%.

More challengingly and significantly still: the gross morphology of the species forming the Malagasy and Southern South African block of *Euphorbia*, respectively, is virtually exclusive if direct comparison is sought between the two blocks. It can be connected (CROIZAT, mss.) by intermediates, however, via another genus, *Monadenium* of some 50 species again. *Monadenium* is not only very variable in its morphology and rooted in some of the oldest biogeographic and evolutive cores of Eastern Africa (in Tanganyka, for instance: heights of Usambara and Uluguru), but also geographically vicariant of the euphorbieous blocks facing one the other across Mozambique Channel. *Monadenium* extends from about the Northern Transvaal (broadly speaking, the Drakensberg Mts., marking the approximate divide between the Eastern and the true Southern South African floras) to Somaliland, reaching westward (BALLY, *The genus Monadenium*: 106-107, maps. 1961) to Angola, the Belgian Congo and Ubanghi-Chari. The dispersal and form-making of *Euphorbia* in The Cape and Madagascar, and of *Monadenium* in East Africa, with main massings at three classical nodes of world's biogeography (The Cape, Tanganyika, Madagascar) can in no way be accounted for unless by taking it as a fact that the dispersal of the plants in question (fig. 36) antedates modern geography by far, including in it, of course, the Mozambique Channel.

FIG. 36. The main massing of *Euphorbia* s.l. typical of The Cape within dotted range *1*; of Madagascar within continuous range *2*; of *Monadenium* within broken range *3*. *Euphorbia* in ranges *1* and *2* find intermediates in range *3*. See the main text.

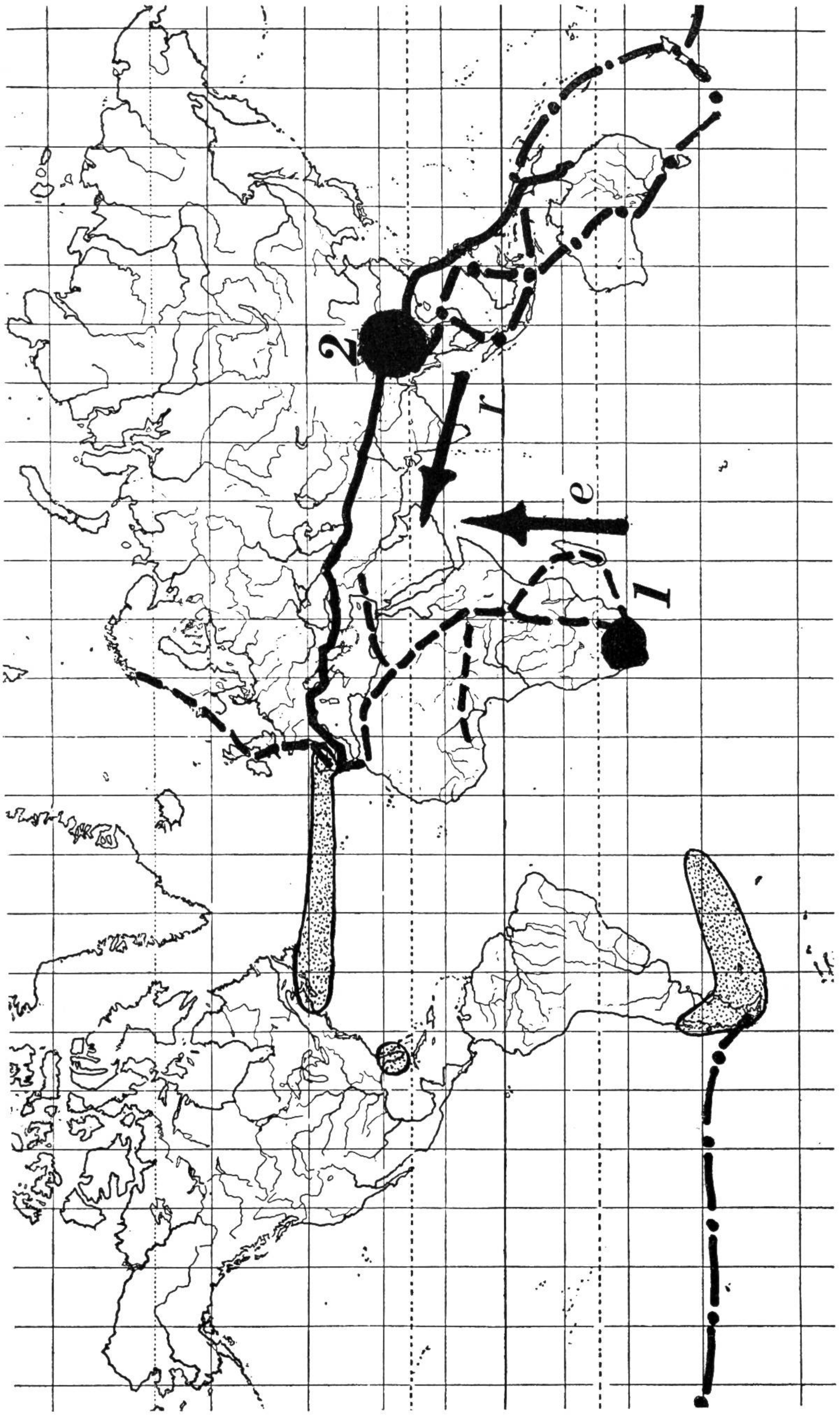

FIG. 37. The dispersal of the Ericaceae-Ericoideae (broken lines; main trends with the longitudes as per arrow (*e*), and Rhododendroideae (continuous line; main trends with the latitudes as per arrow (*r*); centers of main massing (hundreds of species, etc.) for Ericoideae in Southern South Africa (1), for Rhododendroideae in the Orient (" Cathaysia " of Russian authors) (2). Dispersal of Empetraceae stippled within thin lines (the panboreal massing not shown); dispersal of the Epacridaceae in broken-dotted lines. This map is not intended to render the details of the geographic distribution, only to emphasize the main trends of dispersal (see also *Princ.* **1b**: 1820).

It is by now well established (FURON, *Géol. Afrique*: 54, 66, 68. 1950) that the coast of East Africa began to take shape during the Permian (some 200 millions of years ago), and that by Mid-Jurassic (Bajocian-Bathonian; some 150 millions of years ago) only precarious connections stood between Madagascar and Continental Africa. The conclusion obviously follows that the early sires of *Monadenium* and of *Euphorbia* by now in East and Southern South Africa, and in Madagascar had reached the stations where their descendants still mass today at no later time than some 150 millions of years ago.

I will be told that this conclusion is crotchety, but I should once again not think so. As an important constituent part of the highly endemic floras of the Cape and Madagascar, the Euphorbieae cannot be much younger than those floras. An easy check can additionally be had referring, for example, to the Ericaceae, Ericoideae and Rhododendroideae (*Man.*: 161 ff.), two groups of the same family which run dispersal (fig. 37), that, standard in its own right (e.g., that of the Rhododendroideae is very much like that of *Quercus*), is nevertheless quite different. Were climate, casual transportation, and the like genuine factors of the dispersal of *Erica*, this genus would be in the Himalayas where it does not occur at all, and *Rhododendron* could be found in the mountains of East Africa to which it is entirely alien.

Hundreds of species of *Rhododendron* mass in, and immediately around South China. Hundreds of species of *Erica* together with about a dozen of genera in *Erica*'s immediate alliance fill Southern South Africa with stress on The Cape. Two families closely allied with the Ericaceae, Empetraceae and Epacridaceae (see fig. 37) interlockingly vicariate for the Ericoideae in the west, for the Rhododendroideae in the south. Other ericoid aggregates, Andromedoideae, Gaultherioideae, Vaccinioideae, Arbutoideae virtually fill the map of the world. Characteristically (*Man.*: 169): *Vaccinium* has in Africa a scanty contingent which connects East Africa and Madagascar as does *Philippia*, a genus of Ericoideae that if further represented in The Cape. The southermost station of *Vaccinium* in Africa highlights the Drakensbergs' approaches like *Monadenium*. It may hardly be reasonable to imagine that, thus distributed, the Ericaceae (a family correctly identified by Hutchinson as among the most primitive of the " sympetalous " alliance: HUTCH. **1**: 111) can be any younger that the angiospermous floras which they concur to enrich at times with a staggering speciation, as do *Erica* and *Rhododendron* in The Cape, and in and around South China. Even under an elementary approach to phytogeography, the dispersal of the Ericaceae requires the separate recognition of different centers of massing and " tracks ", which are quite distinct in the case of Ericoideae and Rhododendroideae. The whole cease to have a meaning in respect of the three basic factors of evolution, time, space, and form, if imagination is let loose to postulate " migrations " of the sheer hypothetical kind from, e.g., China to The Cape, Norway to New Zealand, Chile to Madagascar, etc., etc. The whole by contrast receives a meaning if the conclusion is accepted as necessary that, for example, genera like *Erica* and *Rhododendron* but stand for the ultimate segregation of definitely generic groups in certain quarters of the map, which were occupied in a prior time by ancestral generalized ericoid forms later in evolution to be individualized as " modern " genera[54]. Obviously, *Erica* and *Rhododendron* are coaeval, quite as the Ericaceae as a whole are coaeval of the Empetraceae and Epacridaceae. This of course means that the entirety of it goes back to angiospermous ancestors distally at least as old as angiospermy itself, and from time of the earliest in possession of the main ranges later bequeathed to their " modern " descendants, whether in The Cape or in South China[55].

Summing up: Some 150 millions of years ago, prototypic euphorbieoid and ericoid forms already held the five continents for, if they could be found by then at The Cape, in Somaliland, South China and Australia they could not fail also being found elsewhere. Naturally, these prototypes were not the modern species, and they only corresponded to the modern genera sensu amplissimo[56]. However, they were on the whole rather well advanced, because typically Malagasy *Euphorbia* could not have had the same proximal sires as *Euphorbia* typically of The Cape. In short, in Mid-Jurassic not only dispersal but basic differentiation was in full swing among Angiospermae the world over.

As recorded by HUGHES (*Sc. Progr.* **49**: 84. 1961), the current theories of angiospermous evolution stand as follows:

1. Angiosperms developed first in Late Palaeozoic (Carboniferous to Permian; some 280 to 200 millions years) in upland areas.

2. They continued in the uplands of a broad equatorial belt, and only invaded the equatorial lowlands in the early Cretaceous (Neocomian or Middle Lower Cretaceous; some 120 millions years ago).

3. They spread in the lowlands progressively poleward in Aptian-Albian times (Mid-Cretaceous; some 100 millions years ago). As positive facts, HUGHES mentions the occurence in few areas of *hints of angiosperm remains, usually requiring confirmation*, of Barremian age (Upper Lower Cretaceous; some 110 millions years), and the possible presence of a flora (Val de Lobos) exhibiting about 10% of Angio-

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[54] This manner of form-making is definitely proved to be standard ! by the *Panbiogeography* and the *Principia botanica*, both for plants and animals the world over. It stands by now above argument, and it has been of necessity adhered to by zoologists and botanists of different schools at different times.

[55] TAKHTADJIAN believes (*Proiskh.*: 93 ff.) that " Cathaysia " is the first center of distribution on the Angiospermae. That "Cathaysia" is important I agree (see, e.g. *Panbiog*, **11a**: 742 fn.), but TAKHTADJIAN has manifestly overlooked a great deal that looms large outside " Cathaysia ". For example (*Proiskh.*: 102 fn.): when indicating that *Saruma* seems to be the connecting link between Aristolochiaceae and Magnoliales (nothing less). TAKHTADJIAN has forgotten to consider the striking similarities between *Saruma* and two archaic cucurbitaceous genera of Madagascar (*Princ.* **1a**: 440 fn. 593, 610 fn.), *Xerosycios* and *Zygosycios*. His suggestions that the Aristolochiaceae may have originated in " Cathaysia " receive scanty support from the records (HOEHNE, *Fl. Brasil.* **15** (2). 1941) of the Aristolochiaceae of Brazil. The tale is evidently much vaster and much deeper by time, space, forms that TAKHTADJIAN has ever thought possible.

[56] Deane understood the matter quite well, and that long ago (*Proc. Linn. Soc. New South Wales* **25**: 475 (in particular). 1900), when he stated that we have no right in assuming that the ancestor of an oak had in every respect the character of the modern genus *Quercus*. It might indeed have been the ancestor of quite a few other genera, and so have had the characters of each one of its living descendants in combination. It is strange that statements of this fundamental, sterling contents hardly ever reach bibliographies.

spermae in the Lower Necomian (Middle Lower Cretaceous; some 120 million years ago)[57].

My own estimate is that the dispersal of prototypic Angiospermae already within close range of modern subfamilies and tribes was necessarily world-wide some 150 million years ago. This figure is assuredly not in conflict with the appearance of fossils and microfossils of widely distributed Angiospermae of modern type some 30 to 50 million years later. Of course, our ignorance of living plants is still so great that our ability to identify correctly scanty fossil remains must be questioned. An improved understanding of the morphogeny and phylogeny of pollen, of high systematics, etc., will better our scores in palaeobotany by far.

The very last thing I believe is the widely held theory (shared by TAKHTADJIAN (*Proiskh.*: 14 ff.) that wishes the Angiospermae to have originated as small populations in the highlands. There is one, and only one, type of distribution that could account for the comparatively rapid angiospermous upsurge. This is the " weedy one "; and I would not hesitate in affirming that the original angiosperms were " weeds " of the shore and its immediate hinterland.

The reason for my conclusion will be obvious to any serious student of the records of dispersal. In the first place, the history of some of the major centers of angiospermous endemism of the world (rather, of the great majority of them) is one of marine and lacustrine conditions eventually yielding through geological time to solid land and highlands. Whether we look (see *Panbiog.* overall) at the Aralo-Caspian, at the Lerma District of Mexico, at the Amazonian Hylaea, at Nigeria/Gaboon, at Southern South Africa, at Australia, at Malaysia and Western Polynesia, etc., the history is the same. Still today, the flora of the strand is remarkably uniform over large sectors of the earth, yet never haphazardly, for even this flora may exhibit (*Panbiog.* **1**: 749) striking endemisms of a local nature together with diffusive " trash ". The connections which, e.g., *Suaeda* documents between the Aralo-Caspian and the rest of the world (*Man.* fig. 73, 74) are striking both in

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[57] To this record must be added the very recent publication by CHANDLER & Axelrod (*Amer. Journ. Sci.* **259**: 441. 1961) of *Onoana californica*, an angiospermous fruit of well established Hauterivian age (first half of the Lower Cretaceous; about 120 million years ago) found in Northern California. The fact that a similar, slightly older fruit (Valinginian) was reported not so long ago (CHANDLER, *Ann. Mag. Nat. Hist. London*, ser. 13. **1**: 354. 1958) from Southern France is most interesting from a biogeographic standpoint. Accordingly, it can not be disputed that between 140 and 120 million years ago authentic Angiosperms had reached both California and Northern France, which dovetails with what dispersal and geology concurrently affirm (see main text in continuation). Concerning the " icacinaceous funicle " mentioned by CHANDLER & AXELROD (*op. cit.*: 446) see *Princ.* **1a**: 306 fn. The statement is rather curious (CHANDLER & AXELROD, *loc. cit.*): *In the case of an endocarp of such antiquity as the present one, the question naturally arises as to whether it shows relationships to the woody ranalian alliance. There appear to be no grounds for regarding the fossil as ranalian but rather as representing a plant that had evolved well beyond that level.* In Hauterivian times, the " Ranalian alliance " (see CROIZAT, *Bull. Torrey Bot. Club* **74**: 60. 1947; *Princ.* **1a**: 356 ff.) had parted from the " Amentiferae " quite a few million years before, and the level of evolution represented by *Scyphostegia-Flacourtia* was by then surely no longer very young. Whatever it be, icacinaceous or not, *Onoana* is a good reminder that angiospermy was definitely "modern" at the end of the Jurassic, and by then of world-wide distribution. The fact that angiospermous fruits were already in California and France at the beginning of the Cretaceous is of average significance both in the sense of morphogeny and biogeography. See the main text in continuation.

sweep and in character, quite as striking indeed as those which *Datura* establishes (*Princ.* **1b**: 1377 ff.) between Mexico (Lerma district) and, e.g., Central Australia. The dispersal of *Gossypium* and its allies (*Panbiog.* **2a** : 148 ff.) is manifestly " weedy ", though nothing could be more precise and satisfactory biogeographically than the dispersal of the species and subspecies of *Gossypium* of economic value. Most numerous are the plant-groups in ranks above the genus which it proves easy to associate with the mangrove, the immediate hinterland of the shore, inland waters and swamps, that is to say, with the conventional haunts of widely distributed forms inside and outside the tropics. Classic is the case of plants of essentially " weedy " dispersal (*Princ.* **1b**: 1380) turning up now as fullfledged weeds, then as endemics of comparatively narrow or narrow range. *Gyrocarpus americanus* widespread at, or near, the marine shore in Tropical America, Asia, and Polynesia is found localized in pockets protected against brush-fires (AUBRÉVILLE, *Contr. Paléohist. Forêts Afr. Trop.* : 49. 1949) on the laterites of the interior of the Sudan. It is virtually impossible to believe that the families forming the " tropophilous " forest of West and Central Africa (*op. cit.* : 13 ff.) were derived from ancestors of highland origin, for the whole of this forest, consisting by order of importance of Leguminosae, Rubiaceae, Moraceae, Combretaceae, Euphorbiaceae, Anacardiaceae, Capparidaceae, Sapotaceae, Tiliaceae, Annonaceae, Burseraceae, Verbenaceae, Rosaceae, points for its origins straight toward the shore and its hinterland. If, for example, *Tilia* may suggest ancestors " in the mountains ", the tale is quite other with *Grewia* and, even more, with *Triumfetta* (*Man.* : 419), and the Brownlowioideae (*op. cit.* : 117 ff.)[58]. The massive development of *Mesembryanthemum* in Southern South Africa is an epitome of psammophilous and halophytic evolution running throughout long geological and biological eras, and it is surely not surprising that, given its background, this tale should involve Australia and Chile with at least a few species of *Carpobrotus*, a minor segregate of *Mesembryanthemum*. A thick volume could be written chockful of facts to prove that theorists intending the Angiospermae to have originated as " mountain populations " have never sufficiently mastered the records of biogeography. Right under our own eyes, and with man replacing in destructiveness the worst of geological cataclisms, the fact stands clearly affirmed that the world belongs to the weeds forever. Beginning as " weedy " and as " marginal ", a flora and a fauna grows, conquers, then turns by degrees " static " and " climatic ", eventually to fall, an easy prey to topographic and geographic change altering the balance of life against climaxes in favour of ever renewed " weeds ". The tale of the aeons, constantly replacing the dinosaur with the mammal, the cycadeophyte with the angiosperm, etc., could never have been such as it was and it were the contrary even remotely possible.

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[58] Time need not be spent to convince a naturalist informed of proper biogeography (= panbiogeography !) that the ancestors of the Malvaceae, Bombacaceae, Tiliaceae originally lived as " trash " on the shore. It is no more surprising to find today the malvaceous (and epiphyllous) genus *Nototriche* (HILL, *Trans. Linn. Soc. Bot. (London)* **7**: 201. 1909) ranging up to 5700 m alt. in the Andes, than it is to find in the high punas of, e.g. Bolivia a bird, Thinocorus, which also thrives on the tropical coast of Southwestern Ecuador, I regret that I cannot discuss the subject further here.

I regret not being in the condition of extending this analysis here, but I am sure that, once informed[59], the reader will bring to a close what I can here but hint. The very last thing thinkable, I am certain, is that the angiosperms originated in highlands. They did originate as " weeds " of the shore and its immediate hinterland, at first by comparatively few types. Their rapid, wide original dispersion was due primarily to their being forms characteristic of far-flung environments of which the shore and its hinterland are the most typical. Originally fit to stand extremes of moisture and drought, fogginess and fierce insolation, seasonal climates of all kinds, biting winds and storms, the ancestral angiosperms took fast possession of every inch opened to their inroads by altering topography and geography in the wake of geological change. The intimate, certain bond between geology and biogeography so amply documented throughout the *Panbiogeography* and the *Principia Botanica* could have no other origin but this. Naturally, in the measure that they spread and gained ground (motion in space through time favours change: *Princ.* **1a**: 631) the angiosperms yielded new form-making of local " adaptation " while older forms of plantlife bound to ancient climaxes were wiped out, characteristically leaving behind survivors which today still belong to such widespread habitats as the " hylaea ", shore and mangrove (e.g., *Cycas*, *Gnetum*) or the desert (*Ephedra*, *Welwitschia*). Characteristically, too, among the angiosperms this time: Tending to be alpine in Madagascar and Africa, Philippina has nevertheless a species which can stand the shore conditions of the island of Mafia (*Man.*: 408), Mangroves turned into " alpines " are well known *(loc. cit.)*. *Utricularia* may enter the tropical mangrove which easily explains why it occurs on certain petty islands (*op. cit.*: 397 fn.) off Indochina; etc., etc.

Concluding, I would outline the history of the Angiospermae as follows:

1. During the " Permo-Carboniferous " glaciations, a group of plants underwent a notable change in its process of ovulation and fertilization. This led to the elimination of its former " sex-bearing " axes which were changed into leaves of a new type, and it generally altered the whole of the morphogenetic and physiological balance of this group, inducing a strong trend toward " neoteny " in the sexual organs which eventually replaced archaic strobiles with potential flowers. I would not expatiate beyond that already stated because the subject is not yet ripe. I am on the other hand certain that by applying the analytical principles and methods introduced in the Principia Botanica and in this article, much can be done to " reconstruct " efficiently the distal pre-angiospermous sires.

2. The pre-angiosperms underwent comparatively rapid and surely extensive distribution as weeds of the strand and its hinterland beginning with the Permian

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[59] For example: In a study, which has remained a classic, on the biogeography of the New Zealand Region (*Journ. Linn. Soc. Bot. (London)* **47**: 114 (in particular). 1925), OLIVER observed that: *The wider ranging the group the higher the percentage of fresh water plants.* According to his estimates, the flora of New Zealand contains 10% of forms of this kind. They again form 25% of the species common to New Zealand and Australia, and 35% of the cosmopolitan species in New Zealand. Be it noticed: New Zealand is today insular and these are fresh water plants. Of course, some will say that the ducks " did it ", but look at the biogeography of the world on a comparative basis, plants and animals as one, before taking anything for granted. Scan, please, the *Panbiogeography* overall.

(some 220 million years ago). It is unlikely that, if ever found, petrifacts of this early age would be correctly interpreted at this hour [60].

3. Some 70 million years later (that is, in the Middle Jurassic), the angiosperms were already within range of modern subfamilies and tribes, and world-wide. The forms living at the time need however not have borne " closed ovaries ", and closely resemble their living descendant. For example: the forerunners of *Euphorbia milii* (= *E. splendens*) may have had a very different type of spinesce than those borne by their living descendants. It is a cardinal error to assume that Jurassic ancestors would look like the modern forms. It is largely sufficient that these ancestors had morphogenetic powers qualifying them eventually to yield the modern forms.

4. Some 30 millions years later, the presence of " modern " Angiosperms began to be felt in the fossil record to increase subsequently into full dominance.

I admit not seeing the history of angiospermous origin as mysterious at all. If approached " panbiogeographically ", that is, with tools of analysis steeped at the same time in correct principles of dispersal, morphogeny, phylogeny, this origin is indeed transparent. Naturally, if the student does not know the records of dispersal of plants and animals; if he has scanty perception of the fact that the flora of highlands is much sooner " climactic " than " weedy "; if he does not grasp the essential mechanism of distribution of plants and animals through time in space; if he has no idea of morphogeny; if he " reasons out " high systematics in reference to fiat discredited these 150 years past, assuming that the primitive flower of the angiosperms was bisexual; if he takes for granted that the " flower " of *Magnolia* and that of *Betula* are conceptually the same flower; if he believes that the " carpel " is a leaf-like body folded ventrally and carrying ovules upon its margins; in short, if he is certain of knowing a great deal while he actually knows much less; the student of botany whether specialized in his later years as a systematist, paleobotanist, cytogeneticist, phylogenist, etc., etc., may not expect to round up scores that (otherwise than technically) are satisfactory. Of all merchandises, thought is the hardest to buy, for thought belongs to every man to be forged out in individual strife and pain. Of course, I am probably only crotchety. How glad I am that everybody else is wise. Let us carry on as we have done so far, boys and girls!

As a parting warning: Those who may think that what I stand for is revolutionary, highly controversial, fantastic, etc., are certainly less than well informed of the history of botanical thought. Ninety years ago, LEMONNIER, one of VAN TIEGHEM'S pupils, clearly voicing the ideas of his master, wrote (see *Princ.* **1a**: 502 fn.): *Peut-être en viendra-t-on un jour à étudier la structure de la fleur, du fruit et de la graine par la description pure et simple des différents tissus qui composent ces organes, de*

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[60] I can but insist that, in view of the increasing importance of microfossils, botany does badly need a constructive understanding of the morphogeny and phylogeny of pollen. This constructive understanding can certainly not be established on the dicta and fiats now current. The whole of botanical thinking needs to be overhauled. I have done my part with the *Manual of phytogeography*, the *Panbiogeography*, and the *Principia botanica*, and *Space, Time, Form: The Biological Synthesis*, not to mention such articles as this, but man is a puny thing, and what remains to be done following the rough trail I have blazed, is positively huge. I hope that these lines are eventually read by some ambitious, energetic young soul.

leurs rapports d'insertion et de forme en abandonnant complètement les idées de Goethe. This day is now, about a century overdue. It is obvious, for example, that no one needs to undertake mighty labours in skeletal anatomy, histology, etc., etc., to learn that a " style " which extends the " coat " nearest the nucellus is a " tubillus ", while the " style " which lies one " coat " off toward the outside is a " style ", of course not of *Magnolia*, but of *Betula*, *Alnus*, *Myrica*, *Ficus*, etc., type. Amazing, even sinister, is the petrification befallen thought which, in botany, can fabulate about everything, citing literature by the stack, yet fail to grasp so simple and so profoundly meaningful a fact.

The conclusions

The main conclusions from this article stand as follows:

1. The conventional dicta used today as props of systematic thinking are false. It is for example not at all true that the primitive angiospermous flower was bisexual, that dialipetaly must precede sympetaly, etc.

2. Discrimination is hardly possible between inflorescence and flower, ovary and ovule, etc. The terms of descriptive botany cannot be used to interpret plant-life in its evolution and phylogeny without a sharp appreciation of their semantic contents and limitations.

3. Sexualization of a formerly female flower into bisexuality by nascent stamens on the " ovary wall " is one of the epochal steps in angiospermous flower-making. The Hamamelidaceae are crucial for this process, theoretically as well as factually.

4. Conventional " trees " of descent misrepresent the facts of life. Angiospermy was preceded by pre-angiospermy. The " modern " angiosperms emerged virtually simultaneously along a broad front between Magnoliaceae and Betulaceae, with Monimiaceae in the center.

5. Structure and consanguinity are essentially different concepts. Plants morphogenetically quite close may not be consanguineous at all.

6. A correct understanding of the status and position in the system of Scyphostegiaceae and Flacourtiaceae is crucial for the whole of high systematics. It is only above the scyphostegiaceous level of evolution that the Angiospermae emerge climatically. The carpic structures of the Scyphostegiaceae are basic for angiospermy of the modern type.

7. Adherence to the " classical " (or, " Goethian ") carpel makes it impossible to understand angiospermous morphogeny and phylogeny.

8. There are two essentially distinct types of flower. One is conveniently represented by *Magnolia* (" strobilar flower ", the other by *Betula* (" circumnucellar flower "). In the latter, the style is of tubillar origin.

9. The history of the origins of the Angiospermae is not mysterious. These plants distally began during the " Permo-Carboniferous " glacial ages. By mid-Jurassic, they were already world-wide, and not far remote from modern subfamilies/genera (at least in the morphogenetic sense).

10. The angiosperms did most certainly not originate as montane populations. They were, on the contrary from the very beginning of the " weedy " type, and mostly distributed near the shore and its immediate hinterland.

11. The closing of the ovary to effect technical " angiospermy " is a comparatively late development in the wake of a prior orthogenetic tendency toward ultimate reduction of sexual axes and organs. This tendency achieves its climax in the angiospermous line of evolution.

12. The Angiospermae are " monophyletic " as such, and by general tendency. They are on the contrary " polyphyletic " family by family.

13. Botanical thinking demands full overhauling.

14. These conclusions should be compared with those reached in the recently issued: *Space, Time, Form: the Biological Synthesis.* 1962, under my signature. See, in particular, chapter 5: 347 ff.