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A STUDY OF THE GENUS LOPHOPHORA COULTER XI

The Flower (Part VI)

In closing this series of articles I would like to have the reader take a glance at the flower (Fig. 1) here figured. He will notice that this flower differs from the average one of cactus (Fig. 2) in the following, (1) The supposed calyx is not embedded within a sheath formed by the confluent bases of succulent leaves or bracts, but arises from the fusion of several triangular lobes; (2) No petals are present; (4) The ovary is partly but not wholly inferior; (4) The placentation tends to be central, or axile, if the term be preferred, not strictly parietal.

This flower belongs to the genus *Sonneratia,* one of the so-called Mangroves.

Of the four characters I have listed, (a) The first cannot form the base of a serious controversy as between a cactus and *Sonneratia* in regard of the flower. In the Cactaceae we witness to a development of succulence which is obvious and, accordingly, striking. In the Mangroves we have succulence of a more refined and cryptic character, which—as it is understood among plant-students—reveals itself in the internal structure of the leaf, in the presence of peculiar organs, neither root nor stem but quite efficient as storage generally (pneumatophores, so-called), and in the physiological slant of the biotype, so to speak[1]; (b) The absence of petals in *Sonneratia* is not definite. It is well known that flowers with very numerous stamens may, or may not, alter some of these stamens to become petals. Petals, moreover, may occur in *Sonneratia acide* Roxb., which Hutchinson (Fam. Fl. Plts. 1: 146 fig. 74 A, B. 1926) illustrates. In the Cactaceae themselves we observe a gorgeous display of petaloid appendages in many climbing Cereus, *sensu lato,* and a poor to indifferent one in the usual run of *Pilocereus;* (c) The situation of the ovary, whether absolutely inferior, or partly so, is certainly not used by any botanist in his senses to fragment the Campanulaceae, Saxifragaceae and Rosaceae in more or less well meant petty groups. Such a situation is pregnant with meaning along broad struc-

[1] Uphof (in Bot. Rev. 7: 5. 1941) affirms that the succulence of the Mangroves is overrated. Troll (in Ber. Deut. Bot. Gesell. 48: [81]. 1930) avers that though the pneumatophores share in the general respiration, they are primarily intended to hold the physiologically active part of the roots at the best functional level. Chapman (in Jour. Linn. Soc., Bot., 52: 487. 1944) does not contradict Troll, but is inclined to give preeminency to the respiration-factor. For myself, I observe that plants can bring roots, rhizomes, "dippers," "knees," and the like, to any level they choose without inventing pneumatophores, which (Col. Dauphiné in Ann. Sc. Nat., Bot., 9 sér., 3: 319. 1906) has been learned long ago. Plants much sooner mold an old organ to new functions than they do create a new one, which is a *cardinal principle* of evolutionary morphology and physiology. Groom's outline of "Architectural Xerophytism" (in Ann. Bot., 24: 241. 1910), offers a more substantial food for thought than Troll's not always very profound opinions. Among the Cactaceae, certain species of *Pereskia* are not markedly xerophytic. In a sense, xerophytism is just as much a tendency as it is a fact.

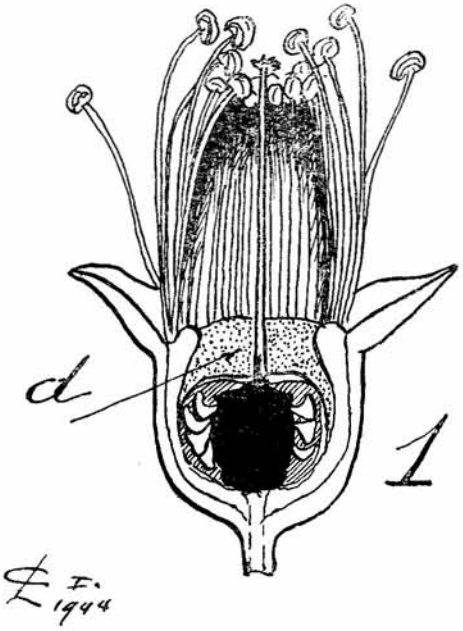

FIG. 1 (Diagrammatic)
Section of flower of *Sonneratia* sp.; disc in *d*.

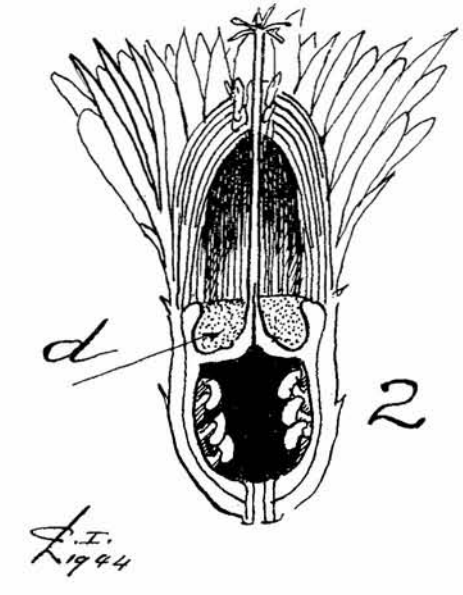

FIG. 2 (Diagrammatic)
Section of flower of Cactaceae, sp.; disc in *d*.

tural lines, but has scarce significance in other respects, hence must be carefully qualified and well understood before being introduced in discussion; (d) The placentation, whether parietal or central, means about as much—indeed, less—as the situation of the ovary. No one has yet come to the fore with a serious proposal to dismember into petty families the Cistaceae and their natural allies, the Dilleniaceae, on the ground that in certain of their genera and species the partitions of the ovary are two millimeters longer or shorter than some fancied average of botanical perfection.

It may be noticed that in *Sonneratia* the seed is more or less curved, a curved seed being supposed to be the key-character of the Centrospermae, to which *Mesembryanthemum* belong. If the shape of the seed be indeed a serious consideration, there is no reason why those who believe that cacti and "mesembs" are allied should not throw together, as one affinity, *Mesembryanthemum,* sundry Chenopodiaceae, *Sonneratia, Cochlospermum* and *Dillenia.* Believers in this classification may readily learn through a casual dissection that the hairy seed of *Opuntia brasiliensis* matches that of *Dillenia indica* and *Cochlospermum vitifolium* quite as well as the seed of *Mesembryanthemum* does that of *Mammillaria.* Would Wettstein have laid emphasis on the seed of the Centrospermae in order to bring under them the Cactaceae, had he read in time Schnarf's (in Oest. Bot. Zeitschr. 80: 45. 1931) review of the seed of *Cochlospermum?* It is an even bet that Wettstein would have stopped, looked and listened.

I have pointed out in a previous article (in DESERT PLANT LIFE 16: 92. 1944) that Hagerup's conclusions do not make of him an authority as regards the Cactaceae and Aizoaceae. I have also revealed that the secondary growths taking place in the ripening ovary of *Mesembryanthemum* are of the same order as those at work within the entrails of the fruit of *Punica.* The pomegranate is very properly associated in classification with *Sonneratia.* Shall we bring together *Mesembryanthemum* and *Sonneratia,* too? In *Sonneratia, Punica* and even *Dillenia* we face a type of flower (the emphasize is on *type*) which, critically seen, is beyond comparison more compatible with that of cactus than with that of *Mesembryanthemum.* Where do we find in cactus the complicated set-up of mediastins which is the rule in *Mesembryanthemum?* Knowing that this genus is certainly and naturally allied with the Amaranthaceae and the Chenopodiaceae shall we be guilty of the crowning folly of visualizing a Sahuaro and a pigweed as member of the same *natural* group, wide as the limits of this group might happen to be?

It often happens that the classification of groups which offer themselves no great difficulty is stultified by the traditional misplacing of some entity, this altering their otherwise clear outline. Such has been the case with the Sonneratiaceae. At one time (Niedenzu in Engl. & Prantl Nat. Pflanzenf. 3(7): 16-21. 1898), they have dealt with as Blattiaceae together with *Crypteronia.* Later on, the Crypteroniaceae have been segregated as a distinct family, but left withal to stand next the Sonneratiaceae. Hutchinson, for instance, maintains (Fam. Fl. Plts. 1: 145. 1926) the Crypteroniaceae between the Lythraceae and the Sonneratiaceae, which sails with the current opinion. Naturally, an affinity so concocted does not lend itself to serious discussion, because it is indeed no affinity at all. Niedenzu's lengthy study of *Crypteronia* (in Engl. Jahrb. 15: 161-179. 1893) boasts of everything sections included, that makes a taxonomic paper perfect, but overlooks, alas,

the all essential fact that *Crypteronia* and *Cyrilla* are so close that one wonders whether, after all, they can endure as types of two separate families. If they do, which is as yet not certain, the Crypteroniaceae and the Cyrillaceae stand shoulder to shoulder together with the Corynocarpaceae, and the Pentaphylacaceae, forming a natural affinity that seemingly harks back to the Pittosporaceae. The Sonneratiaceae, and the Cactaceae, lie on their part at the node where several important alliances part company. One genorheitron (to use Lam's excellent concept) moves through certain Rhizophoraceae toward the Belvisiaceae and the Asteranthaceae, which lean in their turn toward the Asclepiadaceae. Another runs in the direction of the Myrtaceae, which have traditionally been accepted as related with *Punica*. The Combretaceae, Lecythidaceae and Lythraceae also arise in this vicinity, with the truly formidable hamamelidoid-saxifragoid phalanx in the background. Naturally, the Thymeleaceae and the Eleagnaceae have no place in this immediate neighborhood. While it may not be denied that the Cactaceae stand apart as a line of evolution having in a certain sense unique characters, the truth will readily be apparent to anybody who studies the floral structures of the families I have just mentioned as related. The Aizoaceae do not touch this alliance even as to genorheitron. They belong to another stream of evolutive potential, and they have consequently nothing whatever to do with the Cactaceae.

It seems to me wholly useless to continue this discussion, because the informed future rather than the opinions current today, whether my own, Wettstein's or Hutchinson's, will have a final saying. Accordingly, I close the matter with the statement that I hold the Cactaceae, Punicaceae and Sonneratiaceae to be naturally allied. The record being taken care of, time will tell. Whether the Cactaceae should be treated under a separate order, Opuntiales, or merged with other broad groups is yet a matter properly left to personal opinion. Names mean at bottom little when the facts are known. Somebody may think one way, somebody else may dissent, and he who emphasizes certain characters is bound to dissent forever in regard of him who emphasizes certain others. Above all, a great deal of systematic botany is to be written before we can use orders with a sound understanding of what they mean. The very concept of order involves two elements, morphological similarities and consanguineity. It is indeed less than easy to decide which one of these elements is to prevail, and to argue the matter without knowing beforehand what is consanguineity both in a narrow and broad sense is sheer talk.

We have recently had the most welcome report (Chaney in Amer. Jour. Bot. 31: 507. 1944) that an unmistakable fossil *Opuntia* has been detected in strata dating from the Early Tertiary. This sets to naught at last all tales about the Cactaceae being a "recent" group, and upholds the belief I have voiced prior to that discovery that this family is an ancient one. Considering that *Rhipsalis* is endemic to Ceylon, South and West Africa, the family to which this genus belongs cannot be a "recent" one. It was easy to see that it must have roots deep in the Cretaceous on distributional grounds alone.

The Cactaceae have evolved in two centers. The first, and most important, ranges along the south and eastern coasts of Brazil, and reaches the West Indies throughout. The second lies in Mexico, and enters our States. The presence of *Melocactus* in the West Indies, Colombia and Peru is significant, and though true *Melocactus* is alien to the United States, forms

like *Echinocastus horizonthalonius* can easily be connected in phylogeny with *Melocactus*. *Mammillaria* is an offshoot of the *Melocactus* and *Echinocactus* group, the parting of which has been marked by the creation of a host of petty genera, *Lophophora, Pelecyphora, Utahia, Strombocactus, Ariocarpus* and the like. In brief, while genera as *Rhipsalis, Cereus, Opuntia, Pereskia* and *Echinocactus* are the root-stuff of the Cactaceae, the rest is pretty much recent, as phylogeny goes, that is, was born from the Eocene on. The dinosaurs wallowing in the shallow lakes of Wyoming and New Mexico saw in their days an abundance of cacti which we could have placed without trouble as to genera, or tribes at least, and these cacti had for their companions species of *Croton* which we would have pronounced without the slightest hesitation to be closely allied by *C. punctatus*. It may be thought on the face of the printed record that many of the systematists of the past had absolutely no conception of the antiquity of the so-called modern plant-world, and even less an understanding of the fact that plants are plastic to an incredible extent. Had we met the ancestors of the cacti where they grew before they became cacti in the modern sense, we would have found them mostly confined to the subxerophytic and xerophytic domains which are still theirs today, preferably at the seashore, sharing company here with their cousins the Mangroves. Let us not forget that the uplifting of the Andes is recent as the geological record goes.

I must stand the temptation of discussing at this point the disc which is so conspicuous a part of the flower of the Cactaceae and their allies the Punicaceae and the Mangroves generally. The subject does not bear being reviewed briefly. Goethe who did botany no service by dealing with morphology as a poet, while not all morphologists are poets, is not very far from the truth there, where he states (Versuch 34. 1790) that Dame Nature built nectaries in order to ease her path in passing from the stamen to the ovary. To put all this poetry another way: The flower is essentially a sporogenous axis and a strobile. Sex expression within this axis, and in this original strobile, is ruled by forces which in our lack of better knowledge we might call hormones. At certain points in the flower the male and the female hormones come into contact in such a manner that neither prevails, and the sporogenous tissue is there barren. This is by no means to be construed to imply that this barren tissue, disc or nectary that it may be called, is physiologically unimportant. Were it such, it would not persist with the tremendous tenacity which it displays both in phylogeny and ontogeny. It has proved most unfortunate that sterilized sporogenous tissue is seldom the bearer of a revealing vasculation; so much has afforded many workers a very commodious excuse for ignoring it altogether, this further tending to create among botanists in general the impression that disc and nectary are, mayhaps, benign tumors or pimples on the fair face of Flora which good manners forbid gentlemen even to mention. Some have gone so far as to read in discs and nectaries hidden phylogenetic messages, which has deservedly earned them scanty return in consideration of the fact that there is hardly a flower, regardless of its affinity, which is without nectaries.

In sum, a disc or nectary is an essential part of the flower, whether it may be regarded as an abortive stamen or an abortive carpel. As such, it has definite taxonomic and systematic meaning, but, let it be added, just as much of it as common sense warrants, case by case. To ignore the disc when dealing with *Lophophora* is fully as mistaken as to neglect it when treating

forms in the Rosaceae or Cucurbitaceae. Since it belongs to the record that we still know almost nothing of the cactoid flower, both as it stands, and as it has come into being; since we have been mislead for long years as to the true affinities of the Cactaceae, let us all accept in humility the verdict that those who know very little in the present are fated to learn in the future, and that we might as well begin to learn from nature, not from the book. There are more things in the world than our philosophy is wont to dream of, and a cactus is still very much of a dream as many textbooks read today.

NOTE: Since it has been admitted in print (Huss in Beih. Bot. Centralbl. 20(1): 86. 1906), I might as well state here that it is often difficult to understand what an embryologist tries to say when speaking, alas, a language wholly of his own. For this reason, I have made no mention in the previous pages of embryological work on the Aizoaceae and the Cactaceae. It might be called to my attention, on the other hand, that Mauritzon (in Bot. Not. 1934: 129. 1934) has definitely "proved" on embryological grounds that the Cactaceae and the Aizoaceae are related. I would like to point out, merely by glance through the literature, that lipped micropyles built by the inner integument of the ovule, supposedly a common character of Mesembryanthemum and Cactus, occur also in the Marcgraviaceae (Gilg & Werdermann in Engl. Nat. Pflanzenf., ed. 2, 21: 100. 1925); in the Fouquieraceae (Mauritzon in Svensk. Bot. Tidskr. 30: 93. 1936); in the Tamaricaceae (Mauritzon in op. cit. 84); in the Violaceae (Mauritzon in op. cit. 98 ex fig. C, D). This list, I am sure, could be extended by anybody who takes time to fill it. The very characteristic sagittate synergids of *Rhipsalis* (Mauritzon in Bot. Not. 1934: 125 Fig. 5 F. 1934) reappear in *Bixa* (Mauritzon in Svensk. Bot. Tidskr. 30: 81 Fig. 1 S), where Mauritzon emphasizes their presence (in op. cit. 82). The nucellar epidermis in this very same genus is seemingly thick from the start, and grows thicker in age, which again Mauritzon notices (in op. cit. 81). A nucellar cap is present in the Violaceae (Mauritzon in Svensk. Bot. Tidskr. 30: 97. 1934), as it is in the Cactaceae.

I have not the slightest doubt that the literature could be made to yield data beyond the ones I bring here, *currente calamo,* to cast suspicion upon the arguments of embryologists who occasionally rush to conclusion. This is not to say that embryology has no greater nobility than any other form of investigation, and is precisely liable to the same limitations that afflict mankind at work everywhere. Mauritzon has contributed excellent work, a very great deal of which is of essential value to systematic botany. His bringing near together the Crassulaceae and the Podostemonaceae, for instance, (in Bot. Notis. 1932: 172-180. 1932) may seem less than inviting only to those who are not familiar with the strange ties that bind these families. Mauritzon's opinions are as a rule most interesting, and liable of deeper applications than at first it may seem. It is patent that we do not need less embryology, *but more of it,* worked out, if possible, on a broader base of comparison than it has heretofore been the case. We need quite as much some interpretation of the *organs* within the ovule, and of their functions and limits.

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