The fruit of Opuntia

James Arthur Harris

In the Bulletin of the Torrey Botanical Club for May, 1905, Professor Toumey * presents notes on the fruits of some species of *Opuntia*. No reference to the literature appears, and this circumstance, in connection with the conclusions drawn from his observations, seems to justify a brief statement of similar observations which have been made upon *Opuntia* and other genera of the *Cactaceae*, and some remarks upon his conclusion. No attempt at a complete bibliography is contemplated.

The writer first considers the dissemination of *O. fulgida*, and concludes that it is accomplished largely by vegetative means, through the densely spiny and brittle terminal branches; and that the pendulous clusters of spineless, succulent fruit, which remain for many months on the tree and in easy reach of cattle and other large grazing animals to which it is very attractive, are all important factors in vegetal dissemination, and that this acquired function of the fruit is gradually influencing its character and its form. "It is certainly changing from its original seed-bearing condition to one of sterility. * * * Plants of this species are occasionally observed bearing clusters of short, spineless branches which externally closely resemble the clusters of proliferous fruits. These clusters of branches serve the same purpose as the fruits in attracting animals. It is possible that they have developed because of the intimate relation between animal life and vegetal dissemination."

The writer then refers to a number of species, as *O. tetracantha*, *O. leptocaulis* and *O. arbuscula*, in which many short, tumid, lateral branches not much larger than the fruits are produced in abundance during dry and adverse seasons, while under more favorable conditions they are almost entirely replaced by fruit.

Propagation and distribution in a vegetative manner is undoubtedly of great importance in *Opuntia* and has occupied the attention of several writers. Goebel refers to several species.†

* Toumey, J. W. Bull. Torrey Club **32**: 235–239. *pl. 9, 10.* 1905.

† Goebel, K. Pflanzenbiologische Schilderungen **1**: 70–72. 1889.

Mammillaria gracilis produces small, nearly spherical, lateral processes of the size of a hazel-nut, which are readily detached, even by a dash of water, or may easily cling to animals. On *O. gracilis*, according to him, one rarely finds flowers and still more rarely fruits; the plant depending apparently entirely upon the brittle branches, which may even be broken off by the wind, for propagation. He also mentions *O. curassavica*, *O. Biglovii* and *O. aurantiaca* as forms in which the easily detached branches readily take root and reproduce the plant.

More recently Toumey himself has published * upon vegetal distribution in *Opuntia* and finds that of fourteen species of *Cylindropuntia* examined in the field all are more or less adapted for dissemination in this manner. The fruits of the larger number of the species are not sterile, but "as a generalization it may be stated that with this great group of plants the adaptations for vegetal dissemination are inversely as their seed production."

In a general study of vegetative distribution among plants, Terracciano pays particular attention to the *Cactaceae*,† confining his observations especially to *Opuntiae* which he was able to observe under cultivation. He recognizes four types of vegetative reproduction and dissemination in the genus and adduces several illustrations of each.

As to Toumey's conclusions concerning vegetative dissemination, there can be no question of the importance of vegetative propagation in the *Cactaceae*, and we may possibly regard some of the structures described as adaptations which have arisen because of their usefulness to the species. At the present time perhaps the tendency is to place too little rather than too much weight upon the idea of adaptation, but it seems that much more evidence should be assembled before the suggestion, that the pendant groups of fruits or the spineless branches resembling them have developed because of the intimate relation of animal life and vegetal dissemination, can be admitted even into ecological theory.

The conclusions concerning the fruit are as follows:

1. The fruit of *Opuntia* is caulome in structure.
2. Its caulome nature is probably of recent development.

* Toumey, J. W. Bot. Gaz. **20**: 356–361. 1895.

† Terracciano, A. Cont. alla Biol. Veg. **3**: 52–59, 67–68. 1892.

3. It has become caulome by its once superior ovary receding into a vegetative branch, thus making it at present inferior.

4. The branch which now becomes the ovary is usually modified and ripens into the structure which we term the fruit; it may however become but little modified, resembling the ultimate branches and continuing as a vegetative part of the plant.

The first of these conclusions may be freely admitted in so far as any fruit developing from an inferior ovary is to be regarded as caulome. In the *Cactaceae* the similarity of the portion of the fruit derived from the receptacle to the vegetative shoot is greater than in many other forms with an inferior ovary, and the teratological literature affords many illustrations of even more striking resemblance than those furnished by the normal structures. It seems however unnecessary to discuss all the teratological evidence,* since the case is one largely parallel with that of replacement of floral organs by foliage leaves. If one accepts the latter as proof that the elements of the flowers are derived from foliage leaves, he will also regard the fruit of *Opuntia* as derived from the vegetative branch.

The proposition that the fruit of *Opuntia* is caulome in structure is by no means new. It would require an unprofitable amount of labor to try to locate the first suggestion to this effect, but it was certainly more than fifty years ago.

The second statement, that the caulome nature of the fruit is probably of recent development, seems to be open to question. It may be quite true, but no valid evidence is offered in support of it. So far as I am aware the embryological investigations offer no evidence in favor of this point, and our knowledge of the relationships of the *Cactaceae* is too obscure to permit of valid deductions without an examination of all accessory data. It is, however, a quite general opinion that the *Cactaceae* as a group is of recent origin, but the relationships of the groups are very uncertain.

The third assertion, that the fruit has become caulome by its once superior ovary receding into a vegetative branch, thus making it at present inferior, is also much in need of supporting evidence. Here again the evaluation of teratological evidence for special morphological conclusions must largely decide the problem.

* For much of which the reader will consult Penzig's Pflanzenteratologie.

Those who have had much experience with teratological material, however, will be exceedingly cautious in attaching the significance which Professor Toumey does to the one enlarged pistil containing seeds and which has assumed the color of a fruit. Furthermore it hardly need be pointed out that the derivation of a portion of the inferior ovary from the receptacle of the flower, a structure caulome in nature, removes the necessity of accounting for the structure of the fruit by assuming that the ovary has receded into a vegetative branch.

We may examine a few of the published discussions bearing upon this point.

Ramirez * has published descriptions and excellent colored plates of three malformations in the fruits of *Opuntia*. After a considerable discussion of the morphological nature of the inferior ovary he takes up the three deviations observed.

The first case, as he describes it, is one of fusion, consisting of a cladode, or joint of the shoot, bearing at the tip a mature red fruit which, instead of being articulated with the stem as is ordinarily the case, is continuous with it, the two regions being separated merely by a slight constriction of a whitish instead of green or red color; the whorls of spines and the cushions which they subtend are continuous in the two portions of the structure under consideration.

The second case is one designated as the inclusion of a fruit in a cladode which is somewhat thicker in the middle and on one side, but except for this and the presence of the scar at the apex and the more or less normal ovary inside closely resembles one of the familiar vegetative joints.

The third case is one of "lateral proliferation of the fruit" in which a large number of fully developed fruits are borne upon the side of another.

The interpretation which Ramirez has to suggest for these anomalies has, it seems to me, much to commend it. He considers that the ovaries originate in a normal manner, but that in certain regions they undergo a slight modification and that, due to the hereditary tendency of *Opuntia* to form cladodes, the ovary is more or less completely transformed into structures resembling the

* Ramirez, J. Anales Inst. Méd. Nac. 3: 223–227. *pl.* 5–7. 1897.

joints of the stem. It will be seen that the nomenclature used by Ramirez is not in accord with his explanation, a point of minor importance, however. The second case described by Ramirez, and the one upon which he largely bases his interpretation of the first two cases described, is clearly identical with that illustrated by Toumey (*figs. 11* and *12*) as occurring in *O. Engelmanni* as well as a number of other species.

The fruit of *Opuntia Ficus-indica*, "wholly enclosed in one of the well-known flat branches of this plant," described and figured by Ernst,* is in all probability identical with the forms figured by Ramirez and Toumey. Masters † supposes that this case is analogous to the fruit of *Cereus* described by Zuccarini.

This brings us to the consideration of certain interesting anomalies in *Cereus*. In this genus the flowers are normally lateral but occasionally those which are terminal have been observed, as in *C. azureus*, *C. caerulescens*, *C. serpentinus*, *C. speciosissimus* and *C. splendidus*.

Penzig in his Pflanzenteratologie remarks that when the flowers occupy a terminal position, "sie sind dann meist mehr oder minder tief in die Sprossspitze eingesenkt."

The figures which I have examined represent the flower or the fruit as produced directly from the apex of the main axis. Particularly interesting are the description and figure given by Zuccarini,‡ in which a longitudinal section representing the course of the vascular bundles is shown.

In the large collection of succulents at the Missouri Botanical Garden I have been able to examine several of the cases which have been described in the literature, and Mr. Thompson called my attention to a large specimen of *C. baxaniensis* with several terminal fruits, one of which had other flowers developing from the side. A section of one of these fruits showed it to be sterile. In these cases the meristematic region of the stem probably gave rise immediately to floral organs instead of continuing its growth as a vegetative shoot; this has given rise to the impression that the flower or fruit is sunken in the tip of the axis. This explanation may perhaps also apply in some cases to the fruits of

* Ernst, A. Nature **27**: 77. 1883.

† Masters, M. T. Nature **27**: 126. 1883.

‡ Zuccarini, J. G. Abh. Akad. Wiss. München **4**[1]: 155–161. *pl. 1–2*. 1844.

Opuntia which resemble cladodes, but the other explanation seems the more plausible.

In view of the arguments presented above, the fourth conclusion should be modified to read: "The ovary of *Opuntia* usually ripens into a fruit-like structure, but it may become modified, assuming the features of a vegetative stem, persisting as a vegetative part of the plant and producing flowers or vegetative branches, or becoming detached it may serve as an organ of vegetative reproduction. In many cases the ovules are few or quite abortive, while the portion of the ovary which may be described as caulome in nature persists in the form of a vegetative branch."

In conclusion Professor Toumey remarks:

"The adverse environmental conditions under which *Opuntia* grows is ample reason for this interesting evolution. The ovary which was once superior has gradually become more and more depressed until now it is entirely enclosed in the fleshy branch."

Ganong * suggests the question as to whether there may be a biological reason for the extremely "inferior" nature of the ovary.

It would be highly interesting if such a character as the inferior or superior nature of the ovary could be accounted for as a result of physical environmental conditions, but unfortunately the evidence is entirely inadequate for any such conclusions. Very frequently, as a teratological phenomenon and under physiological conditions for the most part but little understood, a primordium which would normally have developed into a sepal or petal or stamen or carpel, gives rise to any one of the others or to a foliar leaf with the peculiarities of the species. It is not at all remarkable, then, that an inferior ovary should sometimes give rise to leaves or lateral appendages or exhibit other peculiarities of the stem. Of this a larger series of illustrations from various forms might be given. The nature of the vegetative shoot in the *Cactaceae* only makes the condition found in the fruit more striking.

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* Ganong, W. F. Bot. Gaz. **20**: 213. 1895.