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GEORGE HARRISON SHULL

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PLATE I.

Sium cicutaefolium Gmel. A jar of seedlings, photographed at the University of Chicago, October 10, 1903, by Dr. W. J. G. Land; spring-growth of an old plant, photographed at Lockport, Ill., May 16, 1903, by W. E. Praeger; and a flowering-stem photographed at South Chicago, September 22, 1903.

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BY GEORGE HARRISON SHULL.

The juvenile forms of leaves have been believed to be so related to the evolutionary history of a plant as to indicate the form of leaf possessed by its ancestors and to furnish satisfactory evidence of the closeness of relationship between allied species. It is impossible, in most cases, to determine the ancestors of any species, and it is likewise impossible, therefore, to demonstrate a close parallel between ontogeny and phylogeny. As there is in both processes the development from some simple condition to one and the same complex condition, namely, the climax type of leaf of the present adult plant, we can scarcely escape the belief that such a parallel does exist in many cases; but how safely or in how minute detail we may reason from ontogeny to phylogeny may well be considered an open question.

The hypothesis of von Baer (1828) has proved a very suggestive one, and, like most suggestive hypotheses, has been given a much wider application than its author would have been willing to sanction. Von Baer did not assume that the adult characters of the ancestors occur as larval or juvenile characters in the descendants, but that the same larval stages occur in both, a given stage appearing earlier in the descendant than in the ancestor. The idea that larval and juvenile characters agree with ancestral *adult* characters was an old conception which was rehabilitated by Louis Agassiz (1848-1849) and became crystallized in the epigram of Haeckel (1866), which is now universally known as the "Law of biogensis"—that "ontogeny repeats phylogeny."*

Great stress was laid upon this hypothesis by Hyatt, Cope, and others who have used it as a most important principle in disentangling difficult phylogenetic problems. More recently Jackson (1899) has called attention to the fact that in organisms having periodically interrupted

*For a history of the development of the idea of repetition see Hyatt, A., "Cycle in the life of the indvidual and in the evolution of its own group." The law of repetition is there called "Agassiz's law of palingenesis." See also Glaser, O. C., "The law of von Baer."

growth, modified characters which he believes to be atavistic occur in definite parts of the organism, particularly in the region where resumption of growth takes place. These local modifications he calls "localized stages" and says that the equivalents of these stages "are to be sought in the adults of ancestral groups." In three recent papers in the American Naturalist, Cushman (1902, 1903, 1904) gives the result of studies similar to those of Jackson, and, besides presenting evidence that at the resumption of growth in perennial herbs in the spring these atavistic modifications occur, lays stress upon senescent stages as showing even more primitive conditions than are to be found in the seedling. It may be said, in passing, that this view of the significance of senescent stages does not fully accord with that of Hyatt (1890, pp. 78, 79; 1897, p. 221), who looked upon senescent stages as indicative of the course any species in question will pursue in the process of degenerative evolution. In Hyatt's view the senescent stages have a prophetic instead of an historic significance, though he recognized, of course, that there are many resemblances between the senescent and the juvenile series.

If the propositions of Hyatt and Cope, of Jackson, and of Cushman are all true, there should be at least three regions in any perennial plant which will agree in presenting ancestral characters—the juvenile leaves following the cotyledons, the earliest formed parts at each renewal of vegetative activity, and the senescent stages approaching and accompanying the inflorescence. In numerous cases there is a general agreement in the forms passed through at these three regions, and no inconsistency arises when they are all looked upon as atavistic, though the mere fact of agreement in the several regions can not be taken as in itself convincing evidence that these characters agree with the adult characters of some ancestral group. On the other hand, certain plants do not show the same modification of leaf-form in the inflorescence that is found in the "nepionic" leaves of the seedling, and it becomes at once evident that no reliance can be placed upon the forms of leaf occurring in any of these regions as having more than the most general significance as indications of ancestral characters.

A plant which most strikingly illustrates this fact is the hemlock water-parsnip (*Sium cicutaefolium* Gmel.), which presents a great range of leaf-form and passes rather rapidly, sometimes suddenly, from one form to another without repetition, so that each of the regions supposed to tell of ancestral conditions tells a different story. This fact is illustrated in a general way by Plate I.

The seedling of *Sium cicutaefolium* is so different from the adult plant that, except when the two are associated together, its identity

would scarcely be suspected. I am not aware that this seedling has ever been described, and the striking variations in the form of the juvenile leaves make description difficult.

The cotyledons are quite similar to those of many other of the Umbelliferae, being narrowly oblong or elliptic oblong, rather acutely rounded at the apex, and tapering gradually into a petiole at the base. The petiole and blade together are 1.5 to 2 cm. long and the blade is 2.5 to 4 mm. wide.

The early "nepionic" leaves are extremely variable, but it is rare that they do not consist of a single blade constructed on a somewhat palmate plan. The blade is usually of rounded form and quite variously notched, cut, or lobed. In order to facilitate a systematic investigation of the variation in these leaves they were divided into several more or less artificial groups. The first nepionic leaf in more than 120 unselected individuals* presented forms which were placed in six of these categories, as follows:

(*a*) About 10.5 per cent were divided palmately into five nearly equal lobes, one or two of which were sometimes slightly notched.

(*b*) Twenty per cent were 3-lobed, with the middle lobe 2-notched and the lateral lobes each bifid.

(*c*) The leaves in the third group were likewise 3-lobed, but the lobes were quite variously notched. Over 28 per cent of the seedlings had the first leaf of this description.

It will be noted that the form of leaf described under (*b*) is simply a special case of (*c*), and was separated from it because this was the only form of trilobed leaf which could be so definitely characterized, and because this simple definite type of trilobation is almost wholly limited to the first nepionic leaf.

(*d*) Over 15 per cent showed the tendency to trilobation by a single cleft on one side, unmatched by a cleft on the opposite side. These will be spoken of as "half 3-lobed leaves." They pass gradually into a form having one lateral leaflet, and these two conditions were kept together in a single category.

(*e*) Nearly 25 per cent had a generally rounded, ovate or cordate form, merely dentate, or irregularly cleft in a manner which did not suggest trilobation.

*The seedlings were taken up on two small clumps of earth from their native habitat near Robey, south of Chicago, Illinois. The individual seedlings were carefully separated and all were transplanted about 3 cm. apart in a regular pattern in glass dishes. The point of departure for each dish was marked and a number assigned to each seedling, so that drawings made from time to time could be labeled in a manner to allow the progress of each individual to be followed.

(*f*) Less than 2 per cent had one pair of lateral leaflets, and may perhaps be looked upon as an extreme form of the 3-lobed condition of category (*c*), but (*c*) is essentially palmate, while (*f*) is essentially pinnate.

A glance at Plate II will show, better than description, the variability of the first nepionic leaf, and it will also show how truly gratuitous is the division into the categories just described. The leaves were chosen at random from the material at hand, but when more leaves were chosen than could find place in the plate the less dubious forms were discarded in order to show the real difficulties of such a classification and to give a clue to the personal equation of the writer in distinguishing the several categories. The letters A, B, C, etc., illustrate the categories described above under (*a*), (*b*), (*c*), etc.

The first two classes, (*a*) and (*b*), are characteristic of the first nepionic leaf. With the exception of these two forms, all the categories described above are represented in each succeeding leaf up to the sixth, and perhaps occasionally in the seventh, and in these later leaves the various types are much more definitely distinguishable, so that there is rarely any question as to where any leaf should be classed. With rare exceptions every leaf after the sixth is pinnate and shows a marked contrast to the great variability of the first leaf, so that in the eighth leaf a very large majority have three pairs of lateral leaflets which closely resemble the typical stem-leaves of the species, except in texture and in the more ovate form of the terminal leaflet.

In the second nepionic leaf (Plate III, 2) trilobation was found in only a little over 15 per cent of the seedlings, or about one-third as frequently as in the first nepionic leaf, but the half 3-lobed form had increased from 15 per cent to 18 per cent, the unlobed or irregularly lobed form had increased from 25 per cent to over 61 per cent, and the form with one pair of lateral leaflets from 1.6 per cent to about 5 per cent. Just as the 3-lobed form was the modal condition of the first nepionic leaf, the unlobed form was the modal condition of the second.

The third nepionic leaf (Plate III, 3) showed a partial return to the 3-lobed condition, and nearly 24 per cent of the specimens were so characterized. The half 3-lobed form occurred in over 22 per cent, the unlobed or irregularly lobed form in 39 per cent, and the number having a pair of lateral leaflets had increased from 5 per cent in the second leaf to over 15 per cent in the third. Here, although there was an increase in each of three categories at the expense of the unlobed form, the latter was still the modal form of leaf.

The fourth leaf (Plate III, 4) was 3-lobed in 24 per cent, half 3-lobed in 15 per cent, unlobed or irregular in nearly 23 per cent, and pinnate