DUPLICATE EVOLUTION OF PECULIAR PERIANTH STRUCTURES IN THE SEDGE FAMILY AND THE COMPOSITES

Studies in Determinate Evolution, VIII[1]

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It is not at all surprising to find similarity of structures and parts in closely related forms. Such similarities are at present usually taken for granted because we know that segregative evolutionary movements, although they establish barriers beyond which no further evolution is possible, do not prevent progressive changes of a parallel nature in the segregated groups. Thus two related groups may evolve series of almost identical characters. In the past, such duplicate developments have often been described as examples of mimicry. But the old teleological hypothesis of mimicry, as developed by the followers of Darwin, is almost entirely a figment of a very vivid imagination and very commonly was based on the most ridiculous propositions and fancies. No one without a very enthusiastic credulity would at present attempt to maintain such fantastic explanations of biological phenomena except those to whom teleological theories are a sort of confession of faith handed down from a former generation of teleologists, who could not conceive of any biological structure except in terms of some special advantage or use which would preserve the individual in an unfortunate and cruel world, where tooth and claw, heat and cold, and the like determined the whole course and direction of evolution.

In the present paper is presented a series of remarkable, parallel developments from two groups of plants which are not only widely separated in relationship but exist in very different environments. The species of the sedge family represented are mostly hydrophytes, some growing as partially submerged aquatics and others in moist or wet habitats, while those of the composite series are nearly all mesophytes, some of them growing in quite dry soils. Both groups are far advanced along evolutionary lines and far removed from any past connecting links. The sedges are monocotyls with closed vascular

[1]Papers from the Department of Botany, The Ohio State University, No. 334.

bundles, parallel-veined leaves, and trimerous, hypogynous flowers, while the composites are dicotyls with open vascular bundles, netted-veined leaves, and pentamerous, epigynous flowers.

The primitive type of flower of the sedges has a dicyclic, trimerous perianth. In the species of Oreobolus the perianth segments are all broad and resemble somewhat the sepals and petals of a Juncus. From this condition there is a gradual modification and reduction until in the extreme forms there is no vestige of a perianth left. In Figure 1 is represented a mature flower of *Fuirena hispida* Ell. The three petals are stalked and have broad blades with forwardly projecting barbs, but the sepals are reduced to bristles with backwardly projecting barbs. In the genus Scirpus, the perianth is reduced so much that all the segments, whether representing sepals or petals, are reduced to bristles. These bristles are attached to the base of the achene when it is shed. In some of the species the bristles have no barbs whatever, as in *Scirpus caespitosus* L. (Fig. 2). The plant is entirely indifferent in this respect. In *Scirpus cyperinus* (L.) Kunth. (Fig. 3), the bristles are also destitute of barbs, but a new factor causes them to be developed as long and flexible hairs, which are responsible for the plants common name "Wool-grass." Many of the higher species of Scirpus have developed barbs on the perianth bristles. In *Scirpus americanus* Pers. the perianth bristles have very prominent, retrorse barbs (Fig. 4). *Scirpus planifolius* Muhl. (Fig. 5) has outwardly projecting barbs on the perianth bristles. Thus of these four species of Scirpus, two are indifferent as to barbs, one has retrorse barbs and can thus hold on to things while the other has forwardly projecting barbs which prevent the bristles from being attached to objects. All three types of perianth bristles, non-barbed, forwardly barbed, and retrorsely barbed, are also found in species of Rhynchospora and Eleocharis, although in the latter genus the bristles are mostly retrorsely barbed. All types exist in the same ecological conditions and it is evident that the different types did not originate through the direct influence of the environment nor through a life and death struggle for existence in the environment. All are successful. Any teleological explanation would be a mere fairy tale.

Turning now to the composites which show similar developments, and which have been used extensively by teleological biologists to prove their case, we find a strikingly parallel series in the genus, Bidens, only in this case the calyx alone is involved, the corolla continuing as a normal structure. *Bidens tereticaulis* D. C. (Fig. 14) has entirely smooth sepal awns corresponding to the bristles of *Scirpus caespitosus* L. It is also entirely indifferent as to whether it is to catch on to anything or not. But *Bidens frondosa* L. (Fig. 13) has prominently retrorsely barbed sepal awns which are able to catch on to the fur of various animals. Thus the seed may be carried far from the paternal acres and perhaps deposited in very sterile or unfavorable soil. Various other species of Bidens have these retrorsely barbed awns or bristles, one of the commonest being *Bidens bipinnata* L., the Spanish-needles. Now in *Bidens bidentoides* (Nutt.) Britt. (Fig. 12) the sepal awns are again outwardly barbed as in *Scirpus planifolius* Muhl.

It will be seen that in each of these two genera the awns or bristles have evolved all the possibilities in respect to the presence and position of barbs and the species of the several types are often found growing side by side in the same locality and in the same habitat, those of Scirpus in hydrophytic conditions, those of Bidens in ordinary mesophytic fields or waste places. There is neither an advantage nor a disadvantage in having barbs or in not having them, nor does it make any difference to the plant in its survival or in its ability to be distributed whether the barbs project forward or backward. All the multitude of articles and books which have dilated on the advantage to the species of being widely distributed through such means are based on imaginary presumptions. We might just as well presume that any plant was at a disadvantage in possessing special structures which would facilitate removal from its original favorable habitat. There are genera in both the Cyperaceae and in the Helianthaceae which have no special structures whatever for distribution which are among our most widely distributed plants. In Cyperus the perianth is entirely absent and the achene has no appendages whatever. In *Anthemis cotula* L. and *Chrysanthemum leucanthemum* L. the achenes have no pappus bristles nor any other kind of appendage, but just as in the case of various species of Cyperus, they are among the most widely dispersed species in the world. The notion developed in the past and for a time held as a fundamental principle of biology, written into almost every elementary text-book of botany and nature study, that these special structures were evolved through a life and death struggle for existence or as a result of the direct influence of environment is highly irrational and is evidence of an extreme credulity in the scientists of the past generation.

As noted above, *Scirpus cyperinus* (L.) Kunth. has evolved its six perianth segments into long flexible threads. This change of perianth segments to long thread-like structures has been highly evolved in the genus, Eriophorum. The species of Eriophorum form a prominent orthogenetic series in this respect. In *Eriophorum alpinum* L. (Fig. 6) there are only the six original perianth segments in the flower, but these are greatly elongated. In Figure 6 the perianth hairs are represented one-half their comparative length. From this condition the various species represent a series in which the perianth cycle consists of a greater and greater number of pappus hairs until a very extreme condition is reached in *Eriophorum viridicarinatum* (Engelm.) Fern. which has about 70 pappus hairs (Fig. 7).

Passing from these bog plants to the dry land plants of the composites, one is again impressed by the remarkable similarity in the evolutionary development. Among numerous genera that might be taken to represent a condition corresponding to *Eriophorum alpinum* L., *Elephantopus tomentosus* L. shows a close parallel (Fig. 8). There are five sepal bristles, the petals not being affected as they are in Eriophorum. These bristles have flat bases but are very slender toward the top. In *Elephantopus spicatus* Aubl. (Figs. 9a, 9b), a Guatemalan plant, the pappus bristles have a very peculiar character in that each one has a characteristic double fold toward the outer end. This is one of those oddities which one finds when approaching the extreme limits of most of the higher phylogenetic series. That the Guatemalan climate or politics has nothing to do with this remarkable oddity is shown by the fact that *Elephantopus scaber* L., another Guatemalan species, has straight bristles like our own *Elephantopus tomentosus* L. and *Elephantopus carolinianus* Willd.

In some composites there is a double whorl of pappus scales. Thus in *Cymbia occidentalis* (Nutt.) Standley, a dry prairie plant, there are five flat scale-like sepals and five extra bristles at the angles, making an inner series and indicating that multiplication of the pappus units has begun (Fig. 10). This double series of broad scales and slender bristles simulates such forms as *Fuirena hispida* Ell. In both the Helianthaceae and Cichoriaceae there are many series ending in numerous pappus bristles. The ultimate members of each series have no direct relation to each other but were evolved through a series of steps from more simple ancestral types. Figure 11 represents an achene of *Lactuca villosa* Jacq. whose numerous pappus bristles show an extreme evolution from the original and simple five sepals, as those of *Eriophorum viridicarinatum* (Engelm.) Fern. show an extreme development from the original six-parted perianth.

At present it is probably useless to speculate on the cause of the remarkable parallelism shown in the evolution of the pappus bristles of two groups so distant in relationship and so diverse in habitat as species of Eriophorum and the Cichoriaceae. It is sufficient to note the fact that such developments are very commonly the accompaniments of extreme reductions and attenuations in structures that were originally much more normal organ systems. There are many other extreme groups which show such structures. Very remarkable are the pappus developments in various species of Eriocaulon and Lachnocaulon, which genera are among the most extreme in the Liliales series, having heads of small flowers with involucres simulating closely the heads of many Compositales. In some species the sepals show some transformation into clusters of hairs but the most striking examples are represented by species like *Eriocaulon griseum* Koern. in which, in the carpellate flower, both the sepals and petals have been greatly reduced and transformed into numerous pappus bristles quite similar to those in Eriophorum and Lactuca. The three sepals in this species are, however, still distinct broad structures but with short hairs at the outer tips. In the closely related *Lachnocaulon anceps* (Walt.) Mor. the space representing the petal cycle is also occupied by copious, woolly hairs between the three sepals and the ovulary. In each of these genera a long orthogenetic series of more and more advanced developments in respect to pappus development is also in evidence.

Among the Valerianaceae, *Valeriana pauciflora* Mx. and *Valeriana edulis* Nutt. develop calyx pappus bristles much like some of their distant relatives in the Compositales and the same is true of *Scabiosa arvensis* L. among the Dipsacaceae. In the highest Pandanales, as in species of Typha, the extremely reduced carpellate flowers develop abundant long hairs on the pedicels while their near relatives, the Sparganiaceae, considerably lower in the evolutionary series in nearly every respect, have small perianth segments and no bristles in or below the carpellate flowers. In a general sense the same is true in the higher grasses, where bristles and plumes are very prominent in such highly evolved tribes as the Agrostideae, Paniceae, and Andropogoneae. Among the extreme forms of the Paniceae, like species of Chaetochloa, and related genera, special bristles, some retrorsely barbed and some forwardly barbed and also giving orthogenetic series of greater and greater numbers of cortical bristles around the groups of spikelets, are very prominently developed but are not connected directly with the floral structures and so remain on the dead stalks after the fruits have been shed. In the Andropogoneae, the most extreme tribe of the grass family, bristles and large hairs are often very prominent features of the extremely reduced spikelets, giving rise to the popular names, beard-grass, wool-grass and plume-grass commonly applied to these plants.

All of these developments are to be regarded as the outcome of extreme evolutionary movements which have no relation to a supposed response to environment since they occur in the most diverse environments and circumstances, and in the most diverse morphological systems. Nor, as stated, do they have any relation to utility, for frequently they are so situated that they cannot become a part of the distributional mechanism. Even if they are a permanent part of the fruit and thus accomplish wide distribution through the agency of wind or animals, they are, nevertheless, not at all to be regarded in any special or teleological sense as being produced because of a special utility, since, as shown above, species without any devices whatever for distribution are just as successful and often more so and are able to be just as widely distributed as those which have the special structures as extreme over-adaptations.

These studies again show that even the so-called ecological adaptations may have no relation to special environments, that the most diverse structures occur in the same environment, and that the same structures evolve in very diverse environments. They indicate that evolution is kinetic, orthogenetic, and determinative, and that these remarkable progressions are conditioned by internal causes.

Duplicate Evolution
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PLATE I

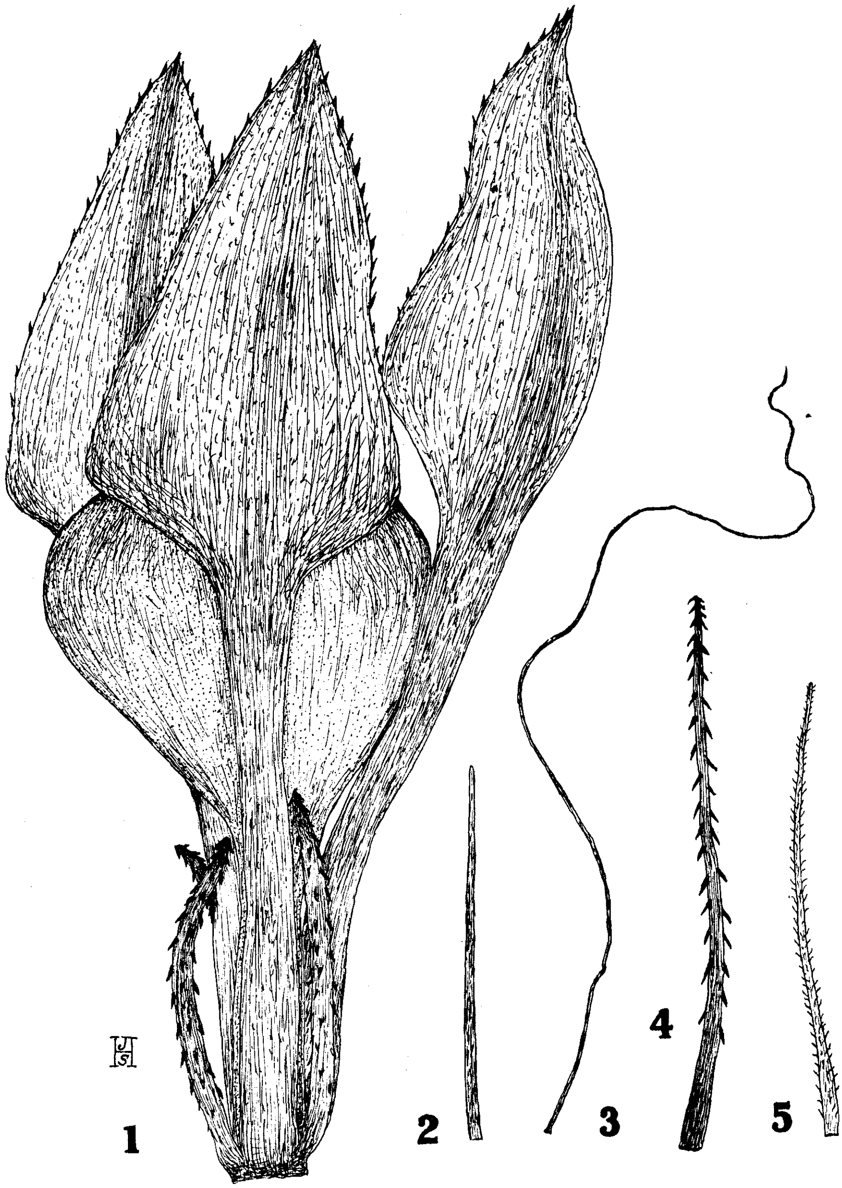
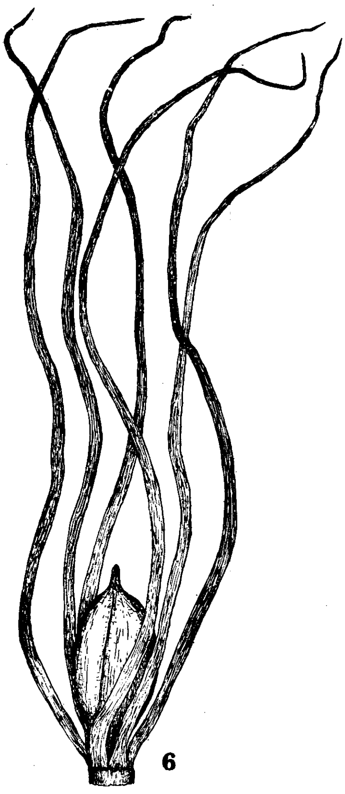


Fig. 1. *Fuirena hispida* Ell. Mature flower with achene and six perianth segments, the sepals reduced and with retrorse barbs.
Fig. 2. Perianth segment of *Scirpus caespitosus* L., without barbs.
Fig. 3. Elongated, flexible perianth segment of *Scirpus cyperinus* (L.) Kunth.
Fig. 4. Retrorsely barbed perianth segment of *Scirpus americanus* Pers.
Fig. 5. Perianth segment of *Scirpus planifolius* Muhl. with outwardly projecting barbs.



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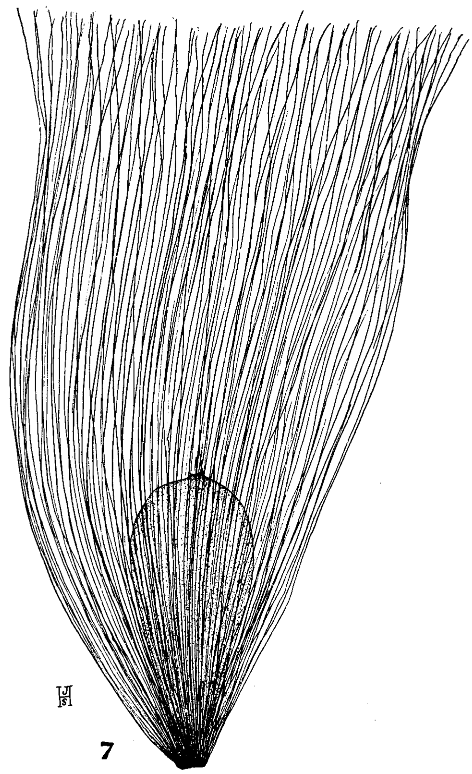

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Fig. 6. Flower of *Eriophorum alpinum* L., with the six elongated perianth segments represented half the comparative length.

Fig. 7. Achene of *Eriophorum viridicarinatum* (Engelm.) Fern., showing the original six perianth segments replaced by about 70 slender bristles, which are represented one-half their comparative length.

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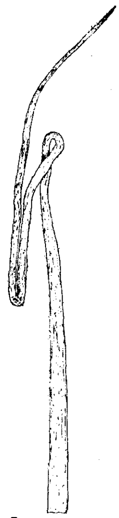

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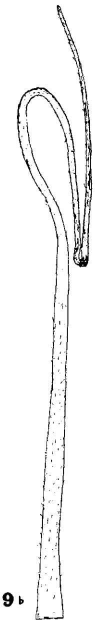

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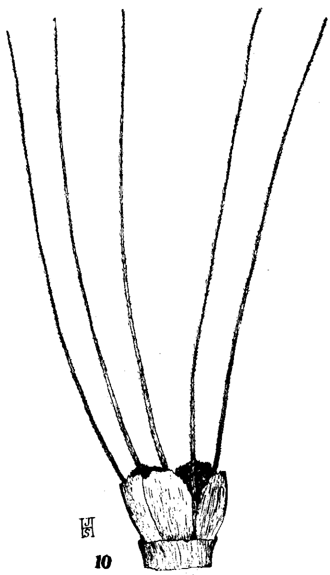

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Fig. 8. Pappus of *Elephantopus tomentosus* L., showing the five elongated calyx segments.

Figs. 9a, 9b. Pappus segments of *Elephantopus spicatus* Aubl., showing a peculiar double fold toward the outer end.

Fig. 10. Double pappus of *Cymbia occidentalis* (Nutt.) Standley, showing five short flat scales and five long bristles.

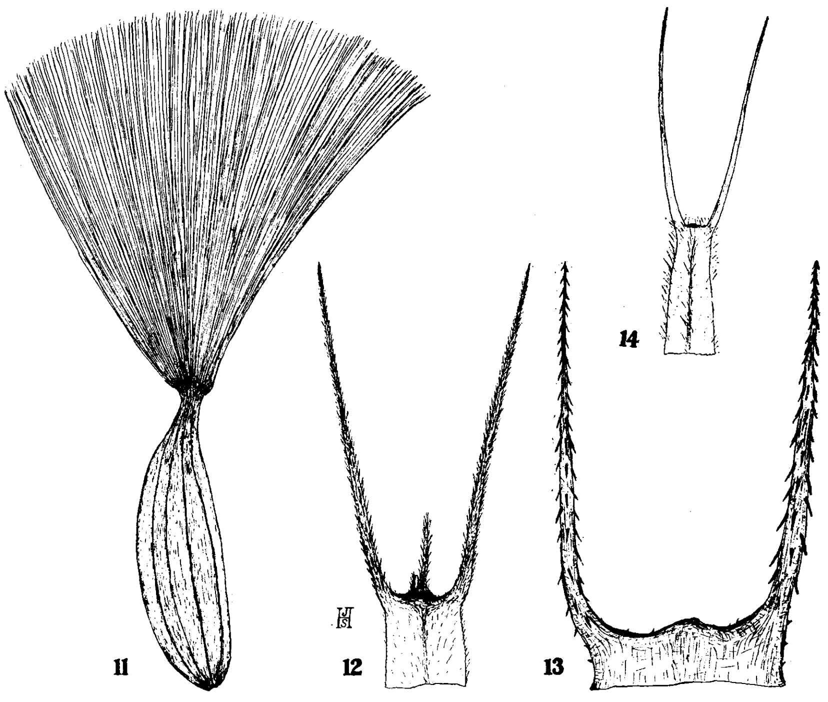

Fig. 11. Achene of *Lactuca villosa* Jacq., showing the very numerous pappus bristles.

Fig. 12. Outwardly barbed pappus awns of *Bidens bidentoides* (Nutt.) Britt.

Fig. 13. Retrorsely barbed pappus awns of *Bidens frondosa* L.

Fig. 14. Awns without barbs of *Bidens tereticaulis* DC.