

Main Lines of Evolution in *Equisetum*¹—I

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In general, evolution may manifest itself in two ways in a group of plants. There may be progressive changes which lead up to a higher level and there may also be segregative changes giving rise to characters which are simply different in kind. By the development of segregative characters new groups or branches arise which may go through a series of progressive changes or steps paralleling more or less closely those which are appearing in the original group. In classification, therefore, it becomes important to recognize what is a low type from what is a high type of plant as well as what characters are persistent in the given group and, therefore, of phylogenetic value.

The easiest way to decide on the relative positions of two plants is to look past the characters they may possess to the hereditary properties that produce these characters. For it is often true that an apparently simpler organ or organ complex represents the activity of a much more complex heredity than a more complicated organography which may merely represent repetition. Low types have fewer, more generalized, functional activities and high types have more specialized, complex, functional activities. Besides looking into the characters and the heredity of the plants under consideration themselves, a comparison must also be made with plants admittedly higher in the scale and with those lower.

Applying these principles to the living species of *Equiseta* gives an arrangement nearly opposite to that which has been in vogue for a long time, and shows that

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in the old arrangement still in our manuals the supposed evolutionary series is upside down.

Although undoubted fossil Equiseta occur rather far back in the geological scale, the evidence to be obtained from this source is still too imperfect to be of much assistance in forming a picture of the true nature of the ancestors of the present-day species. But taking the paleobotanical evidence together with what may be seen in the surviving species and related classes, one can set up an imaginary hypothetical ancestry which is probably not very far from the fact. The present genus leads back to a perennial plant with secondary increase in stem thickness and with ordinary sporadic, monopodial branching. Sooner or later the stem was differentiated into aerial shoot and rhizome, the growing bud evolving the property of dimorphic response to gravity, some buds growing up and some staying under ground. At the same time or later, internodes and whorled, reduced leaves came from the more primitive spiral condition without internodes. Also two types of determinate shoots (one determinate in the sporophyll-bearing axis, the other in the aerial, vegetative axis), hollow, aerial stems, leaf sheaths with minute teeth, and whorled branches appeared. The floral development in the living species is of the most primitive type, the cones developing singly at the ends of vegetative branches, never being collected into inflorescences as in some of the higher species of *Lycopodium*. It will be seen, therefore, that *Equisetum* is a primitive type with a highly specialized organography.

The perennial rhizome is fairly uniform in character in all the living species, differing only in such details as thickening of special internodes, and the like. The lowest type of aerial shoot is large, green, and long-lived,

with whorles of branches and is definitely specialized into sterile and fertile systems with the possibility, as in all other horsetails, of occasional intermediate or semi-sterile shoots. The two kinds of shoots are essentially alike except in the presence and absence of cones, which are abundantly produced at the tips and on the branches. The immediate forerunner of the present species probably had rather long, amplified, green sheaths with persistent teeth although these characters are not necessarily retained in the lowest present-day species. The cone axis stops growing very gradually, giving rise to a prominent point at the tip. The stomata are in bands of several straight rows or scattered in the bands. *Equisetum xylochaetum* Mett., *E. pyramidale* Goldm., and *E. giganteum* L. are of this type and are the typical members of the *Equiseta primitiva*. The *Equiseta primitiva* have the sheath teeth more or less tardily deciduous. As stated, the original condition was probably a sheath with persistent teeth. If so, our lowest living horsetails have changed in this respect, although their teeth are much more tardily deciduous than those of *Equisetum praealtum* or *E. hiemale*.

Milde² established five species which if valid properly belong in this group of *Equiseta primitiva*; *E. xylochaetum*, *E. martii* Milde, *E. pyramidale*, *E. giganteum*, and *E. schaffneri* Milde. Baker³ reduced these species to two—*E. giganteum* and *E. xylochaetum*—and also included *E. myriochaetum* as a synonym of *E. giganteum*. The writer has up to the present time not been able to study enough proper material of these forms to come to any definite conclusions in the matter, except that there appear to be at least three good species, as species go in

² Milde, J. Monographia Equisetorum. 1867.

³ Baker, J. G. Handbook of the Fern-Allies. 1887.

Equisetum, namely, *E. xylochaetum*, *E. giganteum*, and *E. myriochaetum*. Whatever the true status of the other three species may be, will not affect our notions of the evolutionary relationships of the higher species, as outlined in this paper, since fortunately all occur in the same general, distributional region—tropical and subtropical America.

One line of evolution passed on from the first group through *E. myriochaetum* Schlecht. and Cham., which has the stomata reduced to single rows, over to *E. ramosissimum* Desf., *E. debile* Roxb., and *E. laevigatum* A. Br., which three latter species are the lowest representatives of the group *Equiseta hiberna*. *E. myriochaetum*, although having single rows of stomata, is large and has abundant whorls of branches, often with cones, and shows a closer affinity to the *Equiseta primitiva*. *E. ramosissimum* is still much branched and sometimes has the stomata in narrow bands but the other two species show a change toward the unbranched aerial shoot and single lines of stomata. Branches, however, may still appear the first season. In *E. praealtum* Raf. and *E. hiemale* L. branching is absent the first season unless the stems are injured and comparatively rare or sporadic afterwards, unless they are injured or have developed cones the first year. Their sheaths are of the extreme cylindrical type, soon becoming discolored and dry. The extreme is reached in the group with *E. variegatum* Schleich. and *E. scirpoides* Mx., which have decided reduction in the thickness and size of the aerial shoots and are developed in dense tufts or clusters. The sheaths are evolved along different lines from those of the *praealtum-hiemale* type, apparently being a direct modification of the primitive, green, amplified condition with persistent teeth. In *E. scirpoides* the extreme re-

duction in size of stem is accompanied by the development of a solid pith which must here be regarded as a secondary condition originating from the hollow type. A similar evolution went on in the branches of the higher horsetails.

From the *ramosissimum-laevigatum* group, the members of which have evergreen stems, amplified green sheaths, and apiculate cones, a small group branches off consisting of two closely related species, *E. kansanum* Schaffn. and *E. funstoni* Eat., the group *Equiseta ambigua*. The aerial shoots have become annual and the cones have lost the terminal points, through a more prompt determination of the growth of the terminal bud of the cone. In these respects they have evolved in the same manner as the two highest groups. In *E. kansanum*, sporadic development of whorls of branches on the main shoot is present but commonly the plant is entirely unbranched, being in its branching habits very much like *E. laevigatum*. In *E. funstoni*, a peculiar branching system has developed in that in typical cases the main, erect, naked shoots are surrounded at the base by a dense rosette of small prostrate branches. The amplified green sheath is also modified, having a strongly incurved limb. *E. funstoni* is plainly the more extreme and represents the culmination in the series, *E. ramosissimum*, *E. laevigatum*, *E. kansanum*, *E. funstoni*.

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(To be continued)



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