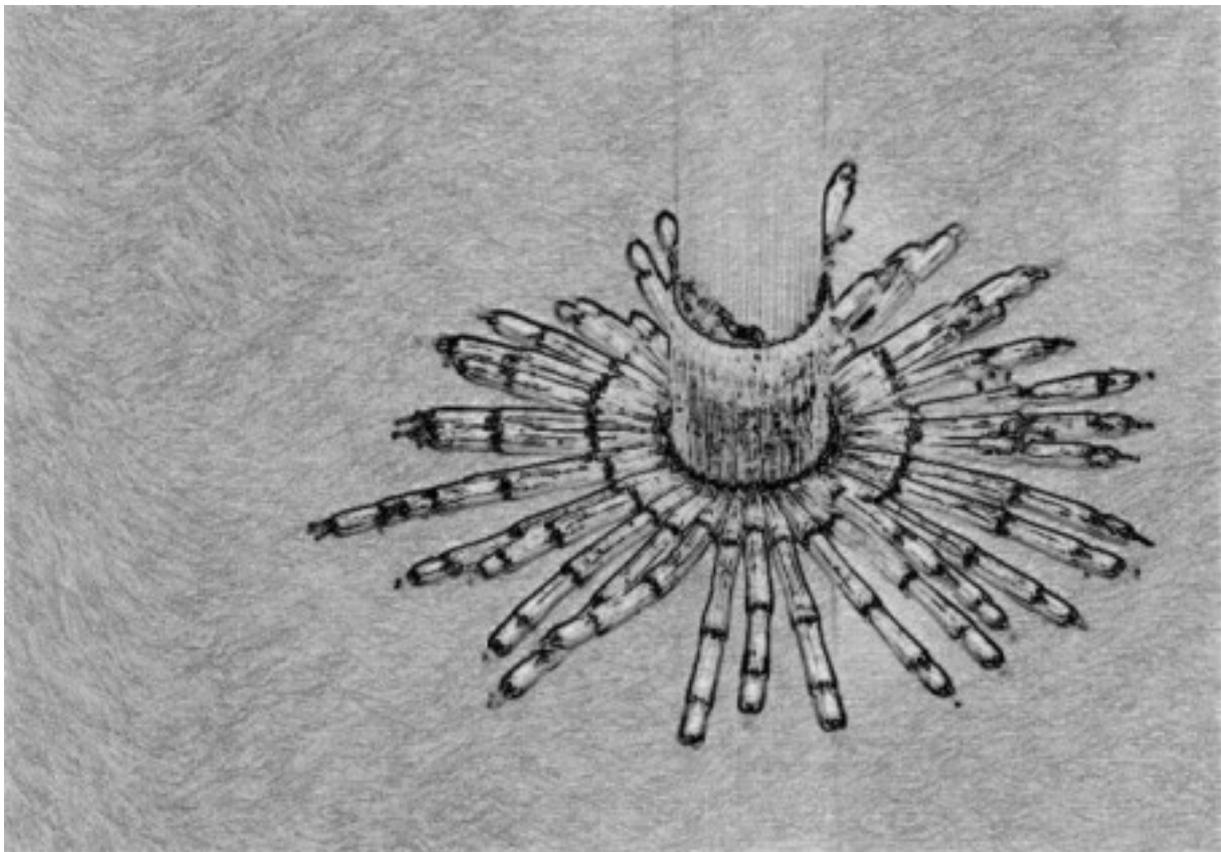


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**Botanical Report**



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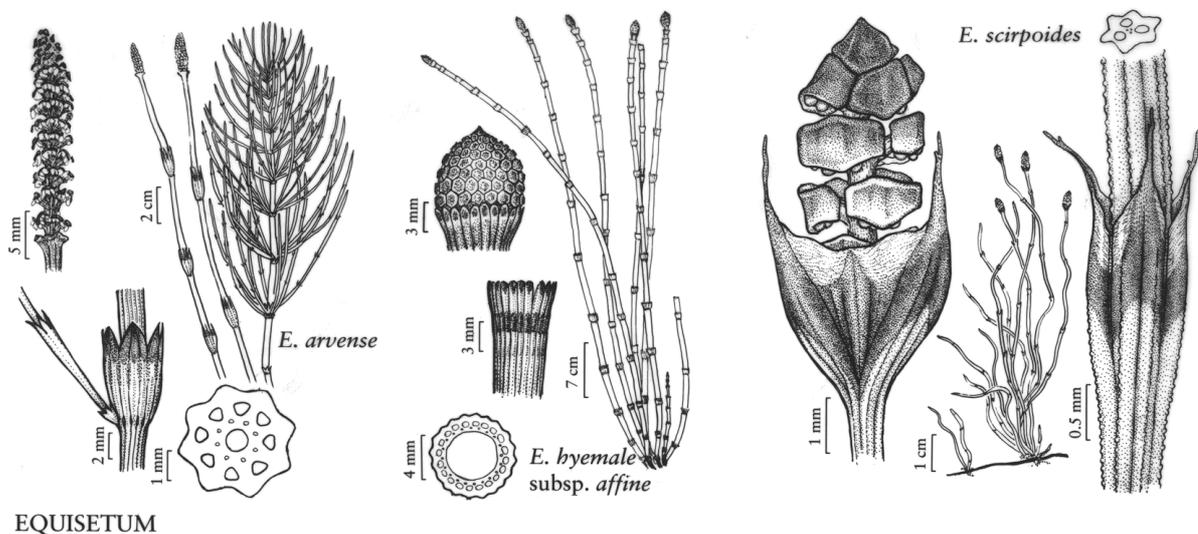
# *An Introduction to the Genus Equisetum ( Horsetail ) and the Class Equisetopsida ( Sphenopsida ) as a whole*

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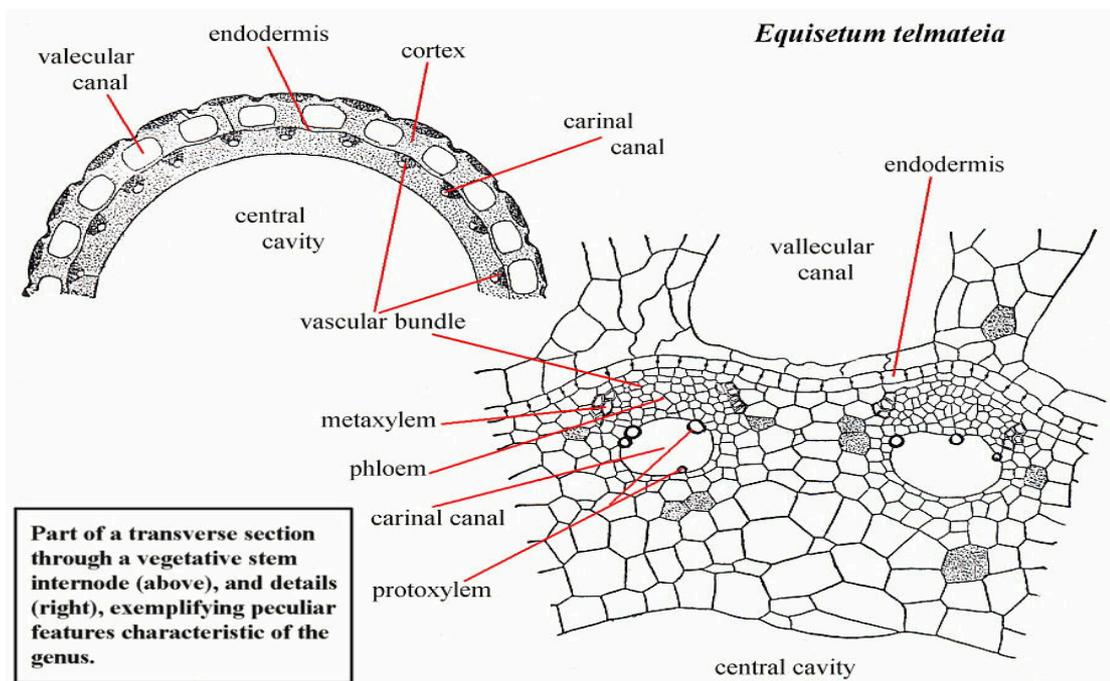
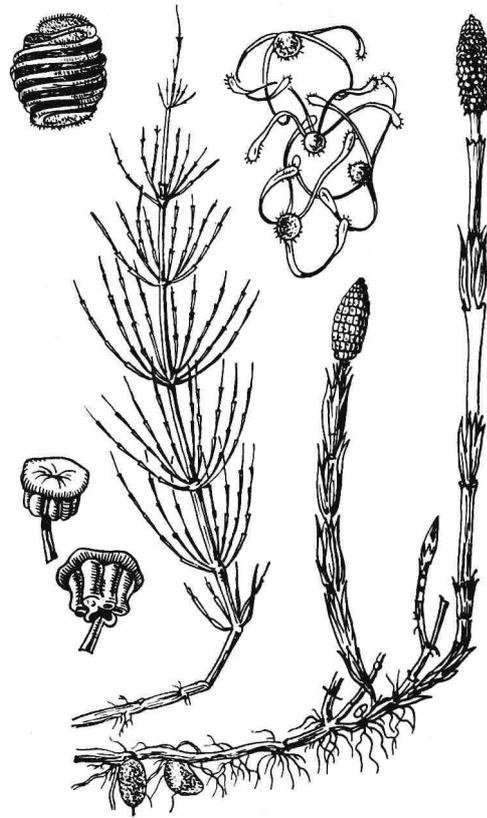
## *Introduction*

The 15 living species of the genus *Equisetum* comprise the plants commonly known as horsetails. The genus name is derived from the Latin *equis*, meaning horse and *seta*, meaning bristle, in reference to the coarse black roots of *Equisetum fluviatile* which resemble a horse's tail ( Hauke, 1993 ). The horsetails range in size from the diminutive *E. scripoides* (stems averaging 12.9 cm tall and 0.5 - 1.0 mm diameter) (Hauke, 1963) to the giant horsetails, *E. giganteum* and *E. myriochaetum*, reaching heights of 8 or more meters (Hauke, 1963) and stem diameters of perhaps 4 cm (see "How large can giant horsetails become"). *Equisetum* species are vascular plants which reproduce sexually by means of spores which are borne on cones. Hence, together with the other spore-bearing vascular plants, the Lycophytes (club mosses), Psilophytes (whisk ferns) and Pterophytes (true ferns), *Equisetum* species are classified as pteridophytes. The genus *Equisetum* is the only remaining representative of the once abundant and diverse subdivision Sphenophytina. However, recent phylogenetic studies suggest that perhaps should be classified within the true ferns ( Pryer et al., 2001 ). Remarkably, *Equisetum* has a history stretching back to the Cretaceous and possibly as far back as the Triassic ( Hauke, 1978 ). As a result, *Equisetum* may perhaps be the oldest living genus of vascular plants ( Hauke, 1963 ).



## *Morphology of Genus Equisetum*

All *Equisetum* species are herbaceous perennials. The plants consist of upright aerial stems which arise from a very extensive underground rhizome system ( Hauke, 1963 ). Morphologically, the genus *Equisetum* is characterized by jointed aerial stems and jointed rhizomes. The stems of horsetails are "anatomically [...] unique among plants" (Niklas, 1997) although they have an external appearance somewhat reminiscent of bamboo. The upright aerial stems exhibit a monopodial branching pattern, having one main axis of growth. This is the pattern which is also found in most gymnosperms and angiosperms ( Scagel, et. al. 1984 ). *Equisetum* species also have small microphyllous leaves that are arranged in true whorls (Rustishauser, 1999) and the leaves of each whorl are fused together to form a cylindrical sheath around each node (Hauke, 1993 ). Some, but not all, species form whorls of lateral branches at the nodes of the aerial stems ( Hauke, 1993 ). Unlike many other vascular plants (such as gymnosperms, angiosperms and some ferns) which produce branches in the axils of leaves, the leaves of *Equisetum* alternate with branches at each node ( Scagel et. al., 1984 ). Like other vascular plants, *Equisetum* produce new branches and leaves from the apical meristem. However, most of the stem lengthening is produced by intercalary meristems above each node and this produces rapid lengthening of the stem ( Stewart and Rothwell, 1993 ). The aerial stems, but not the rhizomes, of some species die back seasonally, whereas other species are evergreen. The rhizomes have the same general morphology as the upright stems, although the rhizomes bear adventitious roots (i.e. roots arising from the stem rather than from other roots) at their joints in addition to leaf sheaths and branches. The plants range in size from the 9 m high tropical species *E. myriochaetum* to the 4-5 cm tall temperate species *E. scirpoides*.

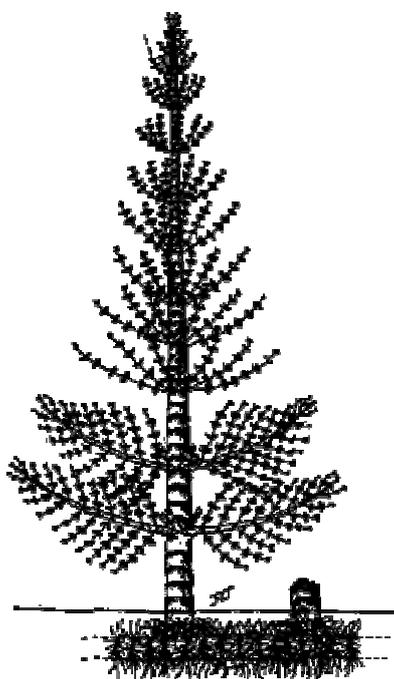


### Fossil history of the Sphenopsids ( Equisetopsids )

**Equisetum** is an ancient genus and comprises the sole surviving representatives of the class *Sphenopsida* (the only class of the subdivision *Sphenophytina*) ( Scagel et al., 1984 ). Sphenopsids first appeared in the fossil record of the late Devonian. The earliest unequivocal sphenopsid that has been discovered is *Pseudobornia ursina*, a monopodial arborescent clonal plant of the upper Devonian which grew up to 20 m tall with stems up to 60 cm thick ( Stewart and Rothwell, 1993 ; Scagel et al., 1984 ). *Pseudobornia* dominated clastic streamside habitats during this time ( Behrensmeier, 1992 ). Later, during the early Carboniferous, a greater diversity of distinctly sphenopsid plants became prominent. These Carboniferous sphenopsids are currently classified into two orders, the *Sphenophyllales* and the *Equisetales* ( Stewart and Rothwell, 1993 ). The *Sphenophyllales*, consisting of a single genus *Sphenophyllum*, were herbaceous plants with whorls of wedge-shaped leaves on a jointed stem. *Sphenophyllum* species increased in abundance until the Upper Carboniferous, but vanished by the end of the Permian. The *Equisetales* include the major families *Archaeocalamitaceae*, *Calamitaceae*, and *Equisetaceae*. The *Archaeocalamitaceae* were arborescent sphenopsids which persisted from the Upper Devonian through the Lower Permian and were similar to the much more numerous *Calamitaceae* ( Stewart and Rothwell, 1993 ). The *Calamitaceae*, which has a single genus, *Calamites* (see also this beautiful reconstruction), encompasses the now extinct arborescent woody sphenopsids, some of which attained heights of up to 30 m and diameters of up to 30 cm ( Scagel et al., 1984 ). Finally, the family *Equisetaceae* consists of the living genus *Equisetum* as well as other extinct herbaceous sphenopsids resembling *Equisetum*. Interestingly, the *Calamitaceae* closely resembled the *Equisetaceae* in having rhizomatous growth, fused leaf sheaths at the nodes, and in many other respects. The chief differences between the two families lie in cone morphology and in the lack of secondary (woody) growth in the *Equisetaceae* in contrast to the presence of secondary growth in the *Calamitaceae* ( Stewart and Rothwell, 1993 ).

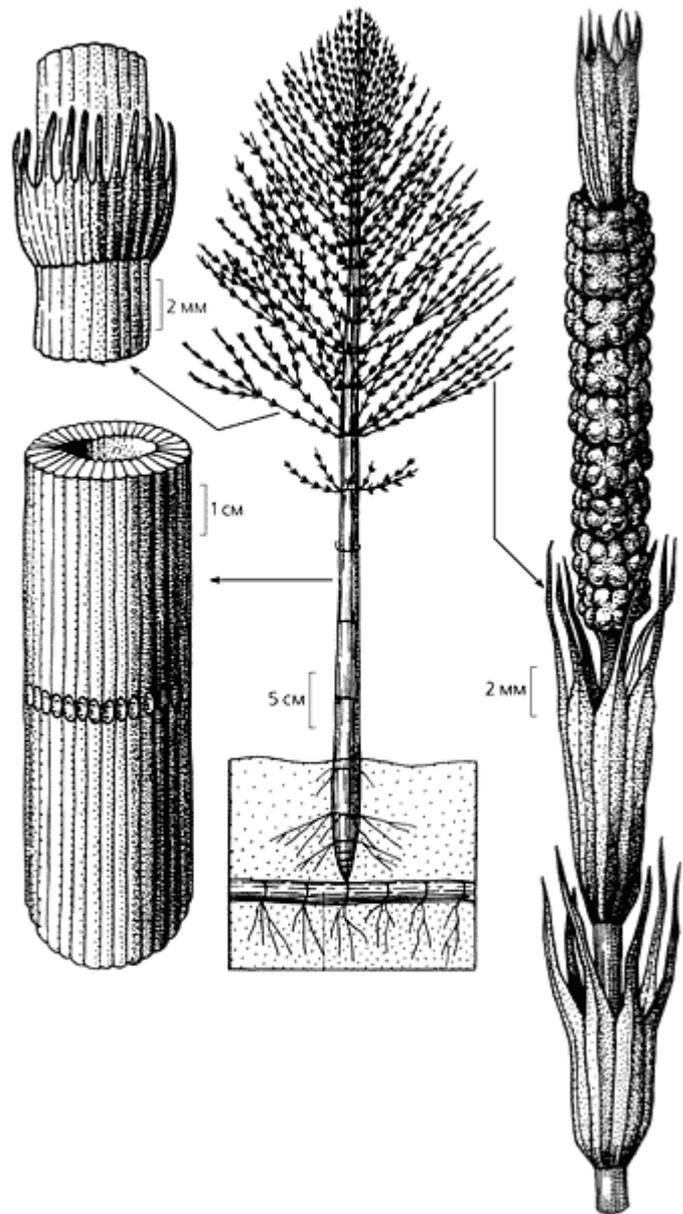
The Carboniferous represented the peak of pteridophyte diversity and abundance ( Rothwell, 1996 ). It was also during this period that about 75% of the world's coal was formed. Hence, there is rich fossil evidence for the ecology and biogeography of this period. The great Carboniferous coal swamps were warm and humid and occupied the wet tropical low-lying areas ( Pearson, 1995 ). These swamps were dominated by giant arborescent Lycopods in genera such as *Lepidodendron* and *Lepidopholios* ( Stewart and Rothwell, 1993 ). Sphenopsids, especially in the genera *Calamites* and *Sphenophyllum* were common members of the flora during the Carboniferous. The Pennsylvanian plant assemblages are probably the best known plant assemblages of the Paleozoic, and possibly the entire pre-Cretaceous. From palynological and coal-ball analysis of Pennsylvanian floras, it is possible to gain insight into the ecology of Carboniferous sphenopsids. *Sphenophyllum* species were ground-cover plants which occurred in nearly all lowland habitats ( Behrensmeier et al., 1992 ). *Calamites* were hydrophytes, like *Equisetum*, and grew on loosely consolidated substrates such as sand bars, lake and stream margins, and other unstable moist substrates ( Tiffney, 1985 ). Therefore, it is probable that *Calamites* were centered outside the comparatively stable coal swamps. *Calamites* were the only Carboniferous lowland arborescent plants that had

the capability for extensive vegetative propagation ( Tiffney, 1985 ). The rhizomatous growth of *Calamites*, like that of modern *Equisetum*, allowed them to form extensive colonies on disturbed wetland areas. However, *Calamites* and *Sphenophyllum* were relatively minor components of the vegetation in terms of overall biomass contribution ( Behrensmeier et al., 1992 ; Tiffney, 1985 ). During the Carboniferous, Laurussia and Gondwanaland collided and thus began the formation of the supercontinent Pangea. In the Late Carboniferous, there was widespread peat formation in the moist

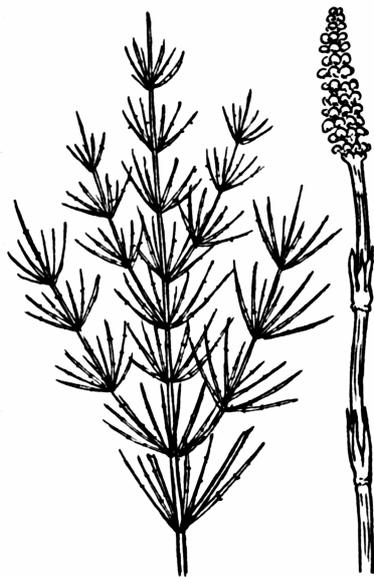


equatorial region coal forests in what is now Europe and central and eastern North America. However, climate changes in the late Pennsylvanian and early Permian began to herald the demise of the great coal swamps. During this time, the equatorial regions of Pangea became drier and rainfall became more seasonal ( Parrish, 1993 ). The climate also became cooler with extensive glaciation in the southern hemisphere. This trend continued through the Triassic when arid to semiarid climates prevailed ( Stewart and Rothwell, 1993 ). This led to a worldwide change from hydric conditions to mesic conditions which are less favorable to sphenopsid growth. In addition, the inability of sphenopsids to grow in the increasingly dry sites probably reduced their ability to compete with the increasingly successful ferns, cycads, and conifers in these drier sites ( Koske et al., 1985 ). These changes probably led to the extinction of *Calamites* during the Lower Permian and the extinction of the *Sphenophyllales* by the end of the Permian. These extinctions left the remaining members of the *Equisetales* as the only representatives of the *Sphenophytina* ( Stewart and Rothwell, 1993 ).

By the Mesozoic, all sphenopsids had the same basic body plan as present day *Equisetum* ( Behrensmeyer et al., 1992 ). The remaining *Equisetales* included the widespread *Schizoneura*, an upright herbaceous genus, with stems up to two meters tall and two cm wide ( Behrensmeyer et al., 1992 ), which first appeared in the Carboniferous and continued into the Jurassic (Stewart and Rothwell, 1993 ). *Schizoneura's* large flat leaves were a distinctive feature of this genus not commonly found in the *Equisetales* ( Scagel et al., 1984 ). Another herbaceous sphenopsid which survived from the Carboniferous to the Lower Cretaceous was the genus *Phyllothea* ( Stewart and Rothwell, 1993 ). Both *Schizoneura* and *Phyllothea* were at first confined to Gondwanaland where they dominated the broad swampy areas, but due to later migration attained almost cosmopolitan distribution ( Hallam, 1973 ). In addition, the genus *Neocalamites*, first appeared in the Upper Permian and survived until the Lower Jurassic. *Neocalamites* resembled small *Calamites* in gross morphology (Stewart and Rothwell, 1993 ) with stems 10 to 30 cm thick and possibly 10 m high ( Behrensmeyer et al., 1992 ). It was widely distributed during the latter Triassic (Seward, 1959 ). *Equisetites*, a genus which first appeared in the Carboniferous, was the other major surviving genus of sphenopsids. *Equisetites* were very similar to present day *Equisetum* and there is some controversy as to whether they may actually have been congeneric with present day *Equisetum*. If *Equisetites* actually were *Equisetum*, then *Equisetum* has existed since the Paleozoic and may indeed

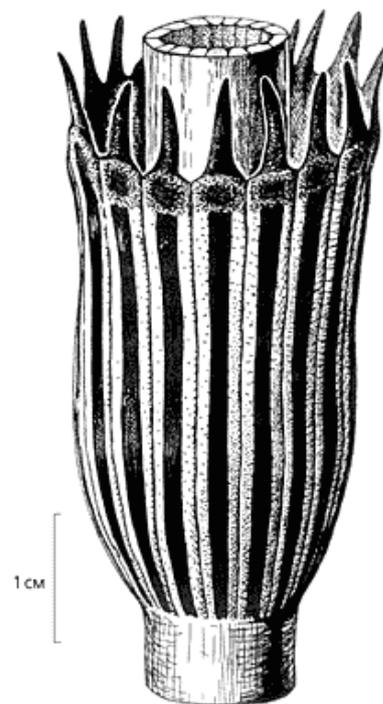
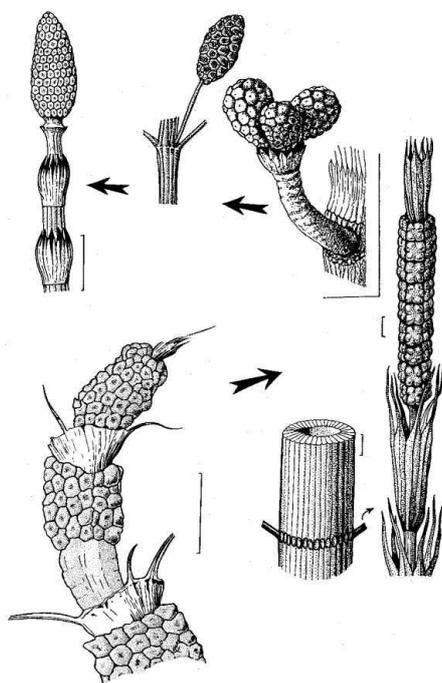


be the oldest extant vascular plant genus ( Hauke, 1963 ). However, some Triassic and Jurassic *Equisetites* were significantly larger than present day *Equisetum*, reaching 8 to 14 cm in diameter



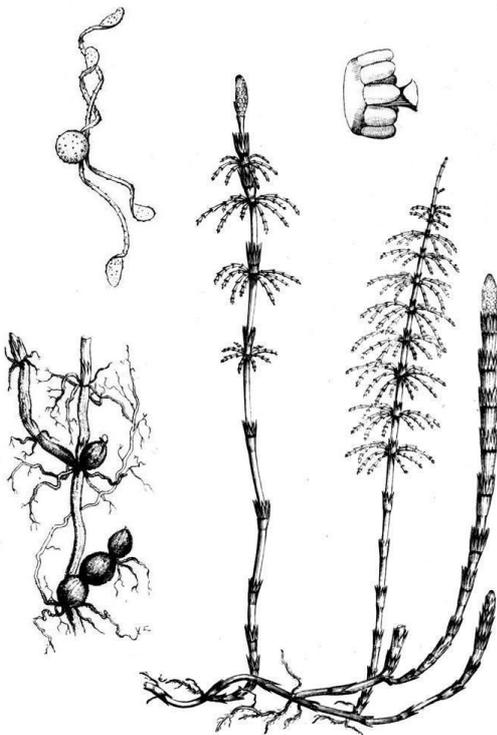
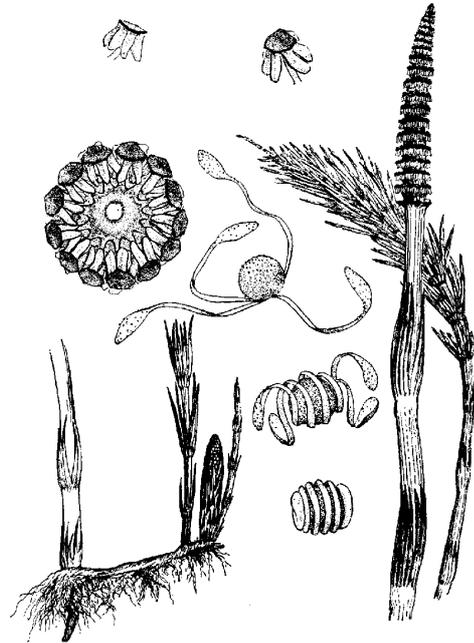
(Stewart and Rothwell,1993) . Perhaps the largest *Equisetites* species, *E. arenaceus* , lived during the Upper Triassic period ( Kelber and van Konijnenburg-van Cittert, 1998 ). This remarkable species had stems that averaged 25 cm in diameter and about 2.5-3.5 m in height ( Klaus-Peter Kelber, 2000, personal communication ). Stewart and Rothwell ( 1993 ) hypothesized that large *Equisetites* may have had secondary growth due to their size, but mention that there is no direct evidence for this. Seward ( 1898 ) mentioned interesting indirect evidence that *E. arenaceus* had secondary growth. Some bamboos have stems approaching the diameter of *E. arenaceus* , yet lack secondary growth ( Judziewicz et al., 1999 ). Bamboo stems are supported by extensive lignification ( Judziewicz et al., 1999 ) and it seems possible that the large *Equisetites* likewise had lignified support tissues. Although Spatz et al.( 1998 ) did not find lignification in the supporting tissues of the *E. giganteum* stems they examined, Speck et al. ( 1998 ) found slight lignification in supporting tissues of *E. hyemale* . The distribution and anatomy of Mesozoic

sphenopsids was consistent with primary colonization of open or disturbed moist habitats. The sphenopsids as a whole became less diverse and increasingly limited to herbaceous forms during the Triassic ( Behrensmeyer et al., 1992 ). This trend was probably due to increasingly arid conditions during the Triassic. However, the surviving order *Equisetales* was widely distributed and diverse during the Mesozoic. During the Jurassic, the large *Equisetites* were present in nearly all parts of the world. From the Jurassic, however, *Equisetales* become smaller and less numerous ( Schaffner, 1930 ). By the beginning of the Cenozoic, relatively small species of *Equisetum* are all that appear ( Stewart and Rothwell, 1992 ). This decrease in size and abundance during the Cretaceous was probably also related to the rapid rise of angiosperms to dominance and the resulting general decline in the prominence of pteridophytes and conifers ( Schaffner, 1930 ). However, despite this decline, during the Quaternary, *Equisetum* species were found to be widely distributed in the temperate zone ( Seward, 1959 ).



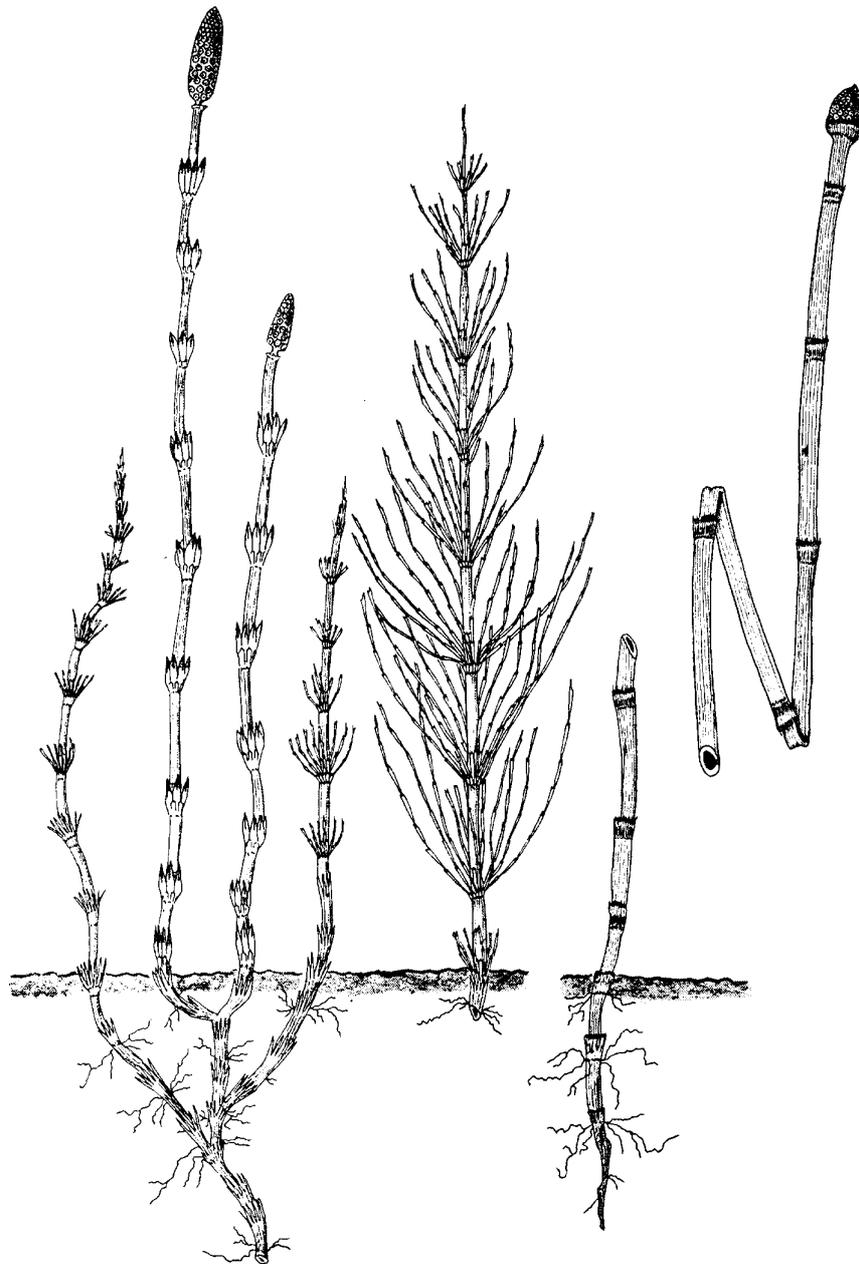
## Distribution and taxonomy of Genus *Equisetum*

Present day *Equisetum* species are naturally distributed throughout much of the world, although they are notably absent from Australia and New Zealand ( Scagel et al., 1984 ) and from the islands of the central Pacific, Indian, and South Atlantic islands (Schaffner, 1930 ). The diversity of species increases from the equator to the temperate zone in the northern hemisphere, whereas there are only four species in the Southern Hemisphere ( Hauke, 1963 ; Hauke, 1978 ). The present day species of the genus *Equisetum* are divided into two distinct subgenera: subgenus *Equisetum* , with eight species and subgenus *Hippochaete*, with seven species. There are several primary differences between the two subgenera. Species in subgenus *Equisetum* have stomata that are flush with the epidermal surface, whereas members of the subgenus *Hippochaete* have stomata that are sunken below the epidermal surface. The stems of the subgenus *Equisetum* are short-lived, relatively soft, and tend to be regularly branched, whereas the stems of the subgenus *Hippochaete* , with few exceptions, tend to be long-lived, hard, fibrous, and unbranched or irregularly branched ( Hauke, 1963 ; Hauke, 1969a ). In addition, four of the species of the subgenus *Equisetum* demonstrate stem dimorphism between non-photosynthetic, unbranched, coniferous stems and photosynthetic, branched, vegetative stems ( Hauke, 1978 ). No such dimorphism occurs in the subgenus *Hippochaete* ( Hauke, 1963 ). Although the chromosome number (n=108) is the same for all *Equisetum* species, the subgenus *Hippochaete* has larger chromosomes than those of subgenus *Equisetum* ( Hauke, 1978 ).



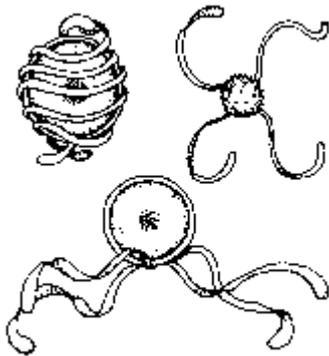
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as far south as Argentina (approximately 40° South latitude) ( Hauke, 1963 ). The subgenus *Equisetum* contains the species commonly known as "horsetails." The eight species of this group are *E. arvense* , *E. pratense* , *E. sylvaticum* , *E. fluviatile* , *E. palustre* , *E. bogotense* , *E. diffusum* , and *E. telmateia* . The species in this group tend to be regularly branched and hence can resemble bushy horse tails. Certain members of this subgenus are found from 80° North latitude to 40° South latitude. Only one species of this subgenus, the diminutive *E. bogotense* of Central and South America, has a range that extends to the Southern Hemisphere. The other seven species of this group are found in the Northern Hemisphere ( Hauke, 1963 ). Most species of subgenus *Equisetum* are temperate, with a few extending their ranges into the subtropics and only *E. bogotense* ranging into the tropics. The aerial stems of all of these species, except for *E. bogotense* and *E. diffusum*, (the two most southerly species), are annual ( Hauke, 1978 ).



## *Ecology and reproductive biology of Genus Equisetum*

**Equisetum** species grow in wet places such as moist woods, ditches, wetlands, and in road fill where sufficient groundwater is available. Rhizomatous clonal growth is a universal feature of the genus and is very important in its ecology and its ability to utilize ground water. A single rhizome system may cover hundreds of square feet ( Hauke, 1963 ). The rhizomes penetrate to soil depths of four meters in some circumstances ( Page, 1997 ). This deep rhizome growth gives the plants the ability to survive environmental disturbances such as plowing, burial, fire and drought. The extensive rhizome system also allows the *Equisetum* plants to supply themselves with water and mineral nutrients from deep underground and hence allows them to grow in habitats, such as road fill, which appear dry on the surface ( Hauke, 1966 ). A remarkable characteristic of *Equisetum* species is

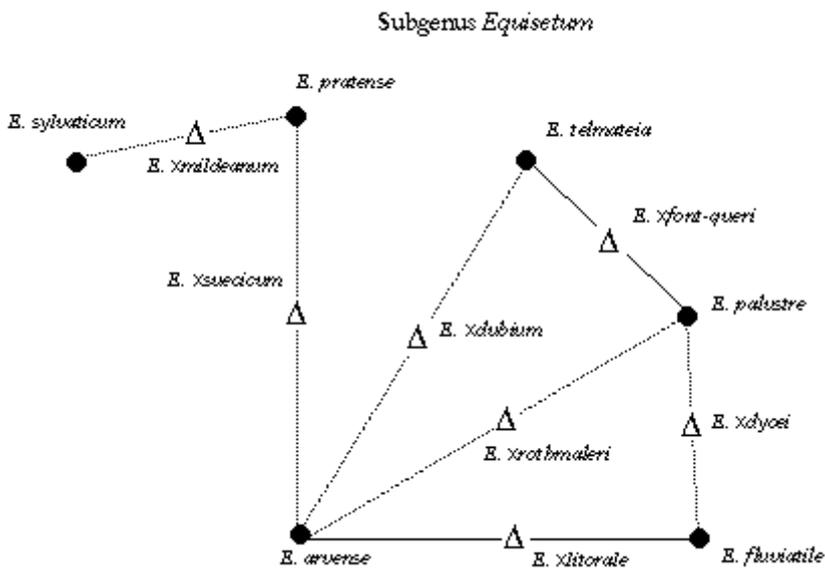


their ability to take up and accumulate silicon in their tissues. This element appears to

be necessary for growth. Silica accumulates on the epidermis of the plants, giving the epidermis a rough texture ( Parsons and Cuthbertson, 1992 ). This characteristic is probably very important in explaining the seeming absence of insect and fungus interactions with horsetails ( Hauke, 1969a ). Recent research on the protective value of silica seems to indicate that silica solutions when applied to plants can provide effective protection from fungal diseases and from insect attack. This would explain why gardeners have long used horsetail extract to protect plants against pathogens and predators ( Quarles, 1995 ). As in other pteridophytes, sexual

dispersal in *Equisetum* occurs by means of spores. *Equisetum* spores are green, spherical, and have thin spore walls ( Hauke, 1963 ). Each *Equisetum* spore has four unique strap-like structures called elaters ( hapters ) attached to the spore surface at a common point. These elaters are hygroscopic (i.e. they expand and contract with changes in humidity) and probably function to help disperse the spores (Hauke, 1963). *Equisetum* spores are short-lived and can germinate within 24 hours of release from the cone. After 5-17 days, depending on humidity, they are no longer capable of germination ( Hauke, 1963 ). In nontropical species (the majority of *Equisetum* ), the spores are produced over a short period of time during the growing season ( Duckett, 1985 ). *Equisetum* gametophytes appear to require a substrate of recently exposed bare mud in order to become established ( Duckett and Duckett,1980 ). Like pioneer species, they rapidly attain sexual maturity and are adversely affected by competition from bryophytes and vascular plants ( Duckett and Duckett, 1980 ; Duckett, 1985 ). The resulting inefficiency of spore germination and gametophyte reproduction in non-pioneer situations probably limits gene flow and leads the high degree of genetic divergence found between *Equisetum* populations ( Korpelainen and Kolkkala, 1996 ). Therefore, sexual reproduction in *Equisetum* is limited to rather narrow ecological conditions and this limits the dispersal ability of *Equisetum* via spores.

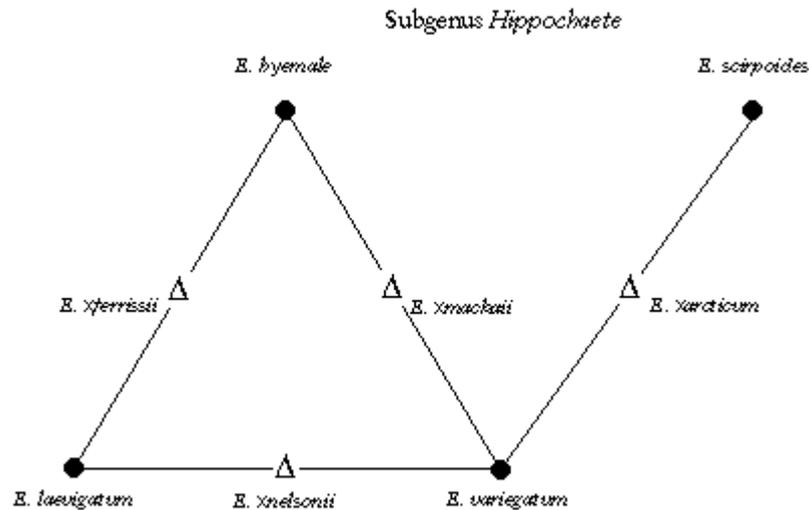
## *Equisetum*



The uniform chromosome number throughout the genus ( $n = 108$ ) facilitates hybridization between *Equisetum* species (Scagel et al., 1984). Hybridization is also favored by the relatively narrow ecological requirements of gametophytes which encourages the formation of mixed populations of gametophytes on suitable sites (Hauke, 1978). These mixed populations increase the probability of cross fertilization between gametophytes of different, but compatible, species. In areas where environmental conditions are especially conducive to spore

germination and gametophyte establishment, *Equisetum* hybrids are particularly frequent and widespread. In Britain and Ireland, for example, *Equisetum* hybrids are particularly successful (Page, 1985). This success appears to be due primarily to the moist temperate oceanic climate and relatively low competition from other plants, conditions which favor both gametophyte and sporophyte generations of *Equisetum* (Page, 1985). *Equisetum* hybridization is especially frequent within the subgenus *Hippochaete* where five common hybrids are known. Within the subgenus *Equisetum*, there is only one common hybrid (Hauke, 1978). There are many more known hybrids within each subgenus, but these hybrids tend to be much less common (Hauke, 1978). No hybrids between the two subgenera have yet been reported and this adds further evidence that the two subgenera are naturally distinct (Krahulec et al., 1996). *Equisetum* species have a remarkable ability to reproduce vegetatively. This helps to compensate for the inefficiency of spore reproduction. An extensive rhizome system allows *Equisetum* species to rapidly colonize disturbed areas (Hauke, 1963). This ability gives *Equisetum* a distinct advantage over species requiring seed establishment or which have slow-growing rhizomes (Hauke, 1969a). For instance, the widespread creation of roadside ditches in America has created significant new habitat for some *Equisetum* species. This is because the soil in ditch habitats tends to be moist and the rhizomatous growth of *Equisetum* species allows them to survive and thrive under the conditions of sediment accumulation that are characteristic of ditches (Rutz and Farrar, 1984). The ability of *Equisetum* to survive and spread in areas of heavy sediment accumulation was dramatically demonstrated after the 1912 eruption of Katmai Volcano in Alaska. In studies of vegetational recovery from the volcanic tephra (ash and silt) deposited by this eruption, *E. arvense* was found to be the most successful herb. It was able to penetrate as much as one meter of tephra, more than any other herbaceous species, and colonize large areas via rapid rhizomatous growth (Bilderback, 1987). The remarkable ability of *Equisetum* to prosper under disturbed conditions was also demonstrated after the eruption of Mount St. Helens in 1980 when *Equisetum* formed almost monotypic stands in the newly deposited tephra (Rothwell, 1996). The deep rhizome system of *Equisetum* also allows these plants to survive fire and rapidly recolonize burned-over sites (Beasleigh and Yarranton, 1974). It is probable that the vigorous and extensive rhizomatous habit of *Equisetum* has been very important to the long term survival and spread of the genus (Hauke, 1969a).

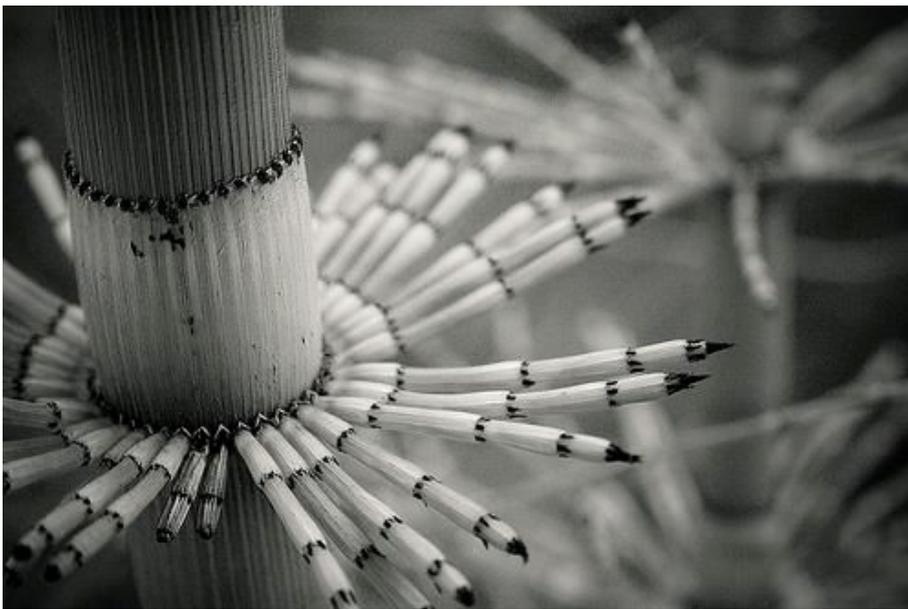
## *Equisetum*



**Fragmentation** of rhizomes and stems allows *Equisetum* to disperse readily in suitable habitats where there is sufficient moisture. Even the aerial stem fragments can sprout and form new colonies (Wagner and Hammitt, 1970; Schaffner, 1931; Praeger, 1934). Hence, vegetative reproduction allows *Equisetum* clones to persist and spread even in the absence of sexual reproduction (Hauke, 1963). Vegetative reproduction probably accounts for the widespread occurrence and persistence of common *Equisetum* hybrids even where one or both of the parents are absent (Hauke, 1963). This is because hybrids are generally sterile and hence are without means of sexual reproduction. The rhizome system of a vigorous hybrid clone theoretically has the ability to maintain dense colonies within limited areas for long periods. Fragmentation and transport of rhizomes and stems then has the potential to disperse the clone from the site of the original hybridization (Hauke, 1963). This would account for the abundance of *Equisetum* hybrids even if hybridization is a relatively uncommon occurrence (Hauke, 1963). The distribution and ecology of the giant *Equisetum* species of the American tropics, *E. giganteum* and *E. myriochaetum*, and *E. x schaffneri* provides another interesting case study in the importance of vegetative persistence of hybrids in the genus. These three species are largely confined to the upper elevations between 150 and 3000 meters. *Equisetum giganteum* is a giant species which grows up to 5 m in height. It is the most widespread horsetail in Latin America, ranging from Guatemala to Brazil, Argentina and Chile as well as on Hispaniola, Jamaica and Cuba (Hauke 1969a; Hauke, 1963). *Equisetum myriochaetum* is also a giant species and is known to grow to 8 m in height. *Equisetum myriochaetum* has a more limited range and is distributed from southern Mexico to Peru (Hauke, 1963). There is also a widespread hybrid, *E. x schaffneri*, between these two giant horsetails which ranges from Mexico to Peru (Hauke, 1963). Although *E. x schaffneri* is sterile, it persists via vegetative reproduction and may form large colonies (Hauke, 1967). This hybrid is found throughout the region of overlap between its parent species, but it is also found in Mexico, where *E. giganteum* is not known to occur, and in Venezuela, where *E. myriochaetum* is not known to occur. This unexpectedly extensive distribution may be due to vegetative dispersal or to the production of an occasional, rare, viable spore (Hauke, 1963). Viable spores have been observed for other *Equisetum* subg. *Hippochaete* hybrids (Krahulec et al., 1996), so this hypothesis appears plausible. *Equisetum x schaffneri* once again demonstrates the remarkable frequency and persistence of *Equisetum* hybrids.

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