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TAXONOMIC CONSIDERATIONS FOR CARBONIFEROUS COALIFIED COMPRESSION EQUISETALEAN STROBILI¹

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ABSTRACT

Equisetalean strobili normally are encountered as disarticulated organs. This condition has necessitated the creation of 12 form genera to accommodate the various morphological architectures and anatomical configurations. Taxonomically useful characteristics, which are discernable in permineralized specimens, are rarely distinguishable in coalified compressions due to their destruction during diagenesis and coalification. Therefore, genera established on the position of sporangiophore-trace origin, such as *Schimperia* Remy and Remy, are untenable when dealing with coalified compressions. Although the two largest genera of strobili, *Calamostachys* Schimper and *Palaeostachya* Weiss, may be synonymous, it is proposed that these form genera be retained when dealing with coalified compression specimens. Each genus provides a particular architectural concept for specimens which may not be assignable to the species level. *Calamostachys* and *Palaeostachya* are highly overspeciated genera. It is suggested that characteristics necessary to delimit new species include bract height, degree of bract fusion, disposition of bracts, bract : sporangiophore ratio, number of sporangia per sporangiophore, and sexual status.

CARBONIFEROUS EQUISETALEAN FRUCTIFICATIONS (sensu Good, 1975) are often encountered as coalified compressions and permineralizations. Natural affinities of these strobili often can be established when coalified compressions are found in attachment to stems, but commonly these reproductive structures are found as isolated organs. Since parental form genera were originally described and diagnosed from coalified compression specimens, even when structurally preserved strobili are found in attachment to a parental stem, it is very difficult to determine the parent plant accurately. Therefore, these problems have necessitated the establishment of numerous form genera to accommodate the various morphological configurations of disarticulated strobili.

Identification of coalified compression equisetalean strobili is difficult when the fructifications have been laterally compressed during diagenesis. Normally, coalification of the tissue accompanies lateral compression and this tends to obscure the detail necessary for delimitation to genus, and more often, to species. This condition has resulted in an artificial classification system (Arnold, 1958; Good, 1975). Criteria used for the separation of genera have been the position of sporangiophore

insertion and the number of sporangia per sporangiophore. Insertion of the sporangiophore may occur along any portion of the strobilus axis from immediately above to immediately below and partially fused with the bract whorl. Sporangia may number 1–4 per sporangiophore head. Criteria utilized to separate species have included cone size, internodal distance, bract length, bract number, sporangiophore number, and spore characteristics.

Twelve genera have been established based upon the position of sporangiophore insertion. *Palaeostachya* Weiss (1876), *Huttonia* Sternberg (1837), and *Weissistachys* Rothwell and Taylor (1971) are differentiated by the oblique insertion of the sporangiophores above the bract whorl. Good (1975) notes that although this condition is usually termed axillary, when sporangiophores are inserted between adjacent bracts of a whorl, they are, thus, not positioned in the bract axil. *Palaeostachya* bears four sporangia per sporangiophore head, whereas *Weissistachys* possesses only two sporangia per sporangiophore and the distal end of the sporangiophores are fused into a narrow undulating ridge. *Huttonia* has been described as *Palaeostachya*-like (Stur, 1887), and Browne (1927) transferred this monotypic genus to *Palaeostachya*. Nemejc (1950) demonstrated the oblique insertion of the sporangiophore above a highly fused bract whorl. He retains these strobili within *Huttonia*, because nowhere in the sectioned specimens he ex-

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amined were the number of sporangia discernable.

Perpendicular sporangiophore insertion at the middle of the internode is considered as the most delimiting characteristic of *Calamostachys* Schimper (1869). However, this mode of insertion is also characteristic of *Calamocarpon* Baxter (1963) and *Schimperia* Remy and Remy (1975). Four sporangia are attached to the sporangiophore in each genus, but *Calamocarpon* is reported to possess a single large functional megaspore within each megasporangium. Remy and Remy (1975) transferred *Calamostachys binneyana* (Carruthers) Schimper to a new genus, *Schimperia*, which is characterized by sporangiophore insertion at a node.

Four genera have been erected in which the sporangiophore is inserted either within the upper third of the internode, immediately below the bract whorl, or partially fused with the bract whorl. *Mazostachys* Kosanke (1955) was described from an authentically cemented specimen from above the Colchester (No. 2) coal (Mazon Creek). Sporangioophore insertion is directly below the bract whorl and each sporangiophore possesses only two sporangia. *Cingularia* Weiss (1870) and *Metacalamostachys* Hirmer (1927) were established for fructifications which display sporangiophore insertion directly below the bract whorl and possess, respectively, four sporangia and one sporangium per sporangiophore head. Good (1975) creates a new genus, *Pendulostachys*, for fructifications where the basal portion of the sporangiophore stalk is fused to the lower surface of the bract disc above. Four sporangia are attached to the sporangiophore head, and the sporangiophore stalk and sporangia are oriented parallel to the strobilus axis.

In the event that a specimen does not exhibit sufficient detail that would allow it to be assigned to any of the above taxa, two genera have been established to accommodate these forms. *Macrostachya* Schimper (1869) and *Paracalamostachys* Weiss (1884) were created, respectively, for large and small strobili in which the manner of sporangiophore insertion is unknown. When this relationship is established, specimens are normally reassigned to either *Calamostachys* or *Palaeastachya*.

Weissistachys, *Huttonia*, *Calamocarpon*, *Schimperia* and *Pendulostachys* are monotypic. Two species are recognized within *Cingularia* and *Metacalamostachys*, whereas *Mazostachys* is known from the description of three species. The majority of known equisetalean fructifications have been assigned to either *Palaeastachya* (21 species) or *Calamostachys* (62 species).

In order to delimit *Palaeastachya dircei* Gastaldo (1981) from the recognized forms of equisetalean strobili, species characteristics in all the genera were compiled for comparison. A number of taxa within *Palaeastachya* and *Calamostachys* were encountered which either did not fit the accepted generic diagnosis or were established on insufficient data. The purpose of this paper is to recognize the discrepant taxa which do not fit the presently accepted generic diagnoses, and to establish criteria necessary to erect new species within the strobilus complex based upon the study of *P. dircei*.

OBSERVATIONS—Six species within *Calamostachys* are reported to possess sporangiophore insertion in a position other than in the middle of the internode. *Calamostachys germanica* Weiss (Abbott, 1968) and *C. calathifera* Weiss (1884) have been described as possessing perpendicularly inserted sporangiophores below the midpoint of the internode. Abbott (1968) created two species, *C. minuta* and *C. recurvata*, which exhibit sporangiophores originating in the upper third, above the middle, and lower third, below the middle, of the internode respectively. In addition, *C. recurvata* was reported to possess a sporangiophore that was ascending in character, and appears to be obliquely inserted. Abbott (1968, p. 17) remarks that this configuration "makes it appear close to a *Palaeastachya*," but does not discuss her reasons for assigning these specimens to *Calamostachys*. Stockmans and Williere (1953) have erected three species of *Calamostachys* from the Namurian of Belgium which exhibit a sporangiophore origin in the lower third of the internode. *Calamostachys laxa* Stockmans and Williere (1953; pl. XLV, fig. 3–4) appears to demonstrate sporangiophore insertion within the lower third of the internode, and the sporangiophore may be oblique. A radical departure from the perpendicular sporangiophore insertion is evident in the description and figures of *C. magloniensis* Stockmans and Williere. This species demonstrates oblique sporangiophore insertion in the lower third of the internode (Stockmans and Williere, 1953; pl. XXIII, fig. 6, 6a). Although *C. sabiensis* Stockmans and Williere is described as possessing obliquely inserted sporangiophores within the lower third of the internodal region, their figures (pl. XXIII, fig. 8, 8a) do not conform to their description.

Remy and Remy (1975) established *Calamostachys spicata* var. *eimeri* based upon specimens from the Saxonian (upper Rotlie-

gend) of the Nahe-area in Germany. This form demonstrates a peculiar intermediate sporangiophore configuration between *Calamostachys* and *Palaeostachya*. The proximally disposed sporangiophores appear perpendicular to the strobilus axis, whereas the distally disposed sporangiophores are obliquely inserted within the lower third of the internodal area. An ontogenetic scheme is proposed for the evolution of the *Calamostachys* organization from the *Palaeostachya* organization. This has allowed Remy and Remy (1975) to reduce *Calamostachys* to its original content.

Good (1975) recognized that *Calamostachys bisporangiata* Abbott (1968) does not conform to the accepted generic diagnosis. As the name implies, only two sporangia are found in attachment to the sporangiophore. The perpendicularly inserted sporangiophore is located at the midpoint of the internode and is distinctly *Calamostachys*-like, but the reduced number of sporangia is inconsistent with the present concept of the genus. Good (1975) believes that this species may be a *Mazostachys*.

All presently recognized *Palaeostachya* strobili conform to the accepted position for origin of the sporangiophore, but three species have been described as possessing only two sporangia per sporangiophore (Gastaldo, 1981, table 1). Matthew (1906) erected *Palaeostachya acicularis* from the Little River Group of southern New Brunswick in which the sporangiophore is described as bearing "a double spore case (or a single spiral case attached by its back to the stalk)." The illustration is a line drawing which shows a longitudinal view of the specimen, and the recognition of two sporangia per sporangiophore is most likely due to the exposure of the fructification, rather than to the actual condition. *Palaeostachya paucibracteata* von Sandberger (1866) is also described from a fructification exposed in longitudinal view, and also represents a limited aspect of exposure. If a longitudinal exposure of *P. dircei* (Gastaldo, 1981, fig. 6) was the only aspect of the strobilus considered, a bisporangiate configuration may have been incorrectly interpreted.

Abbott (1968) describes *Palaeostachya aperta* (Lesquereux) Abbott originally assigned to *Asterophyllites aperta* Lesquereux (1858). The strobilus is very large and composed of alternating whorls of bracts and sporangiophores, but each sporangiophore bears only two sporangia. Abbott noted that this specimen did not fit within the circumscription of the "valid" taxa assigned to *Palaeostachya*.

Species delimitation within *Palaeostachya* and *Calamostachys* is dependent upon the

available histological and morphological characters. Rarely are coalified compression specimens also permineralized. Therefore, structural characters utilized to separate anatomically preserved specimens cannot be used when attempting to delimit coalified compressions. It has been demonstrated that most species erected within *Palaeostachya* have been created with less than sufficient data to justify their specific status (Gastaldo, 1981). The same condition of overspeciation is true in *Calamostachys*. A suite of 16 morphological characters which may be utilized in order to separate coalified compression species has been published (Gastaldo, 1981) as a guide for future referral.

DISCUSSION—Good (1975) concludes that *Calamostachys* and *Palaeostachya*, which are based solely upon sporangium insertion and sporangium number, are badly defined and probably represent artificial genera. Arnold (1958) discusses the generic concept of *Calamostachys* and states that the ultimate validity of sporangiophore position as a generic character will depend upon the discovery of intermediate forms. The discovery of *Calamostachys spicata* var. *eimeri* (Remy and Remy, 1975) is indeed an intermediate form. The morphological variation described and illustrated for *C. spicata* var. *eimeri* allows the synonymy of *Palaeostachya* with *Calamostachys*. Remy and Remy (1975) note that both genera possess sporangiophore traces originating slightly above the bract trace and ascending into the sporangiophore stalk. *Schimperia* is created to accommodate those permineralized strobili with perpendicularly inserted sporangiophores at the midpoint of the internode, and which possess vascular traces originating at the same locus as the sporangiophore. This separation of strobili based upon the point of sporangiophore-trace origin is more complex than it may appear. For example, *Calamocarpon* exhibits a similar origin for the sporangiophore trace as *Schimperia* (Good, 1975), although Leisman and Bucher (1971) report the origin of the sporangiophore trace in their material as slightly above the bract trace. *Palaeostachya decacnema* Delevoryas (1955) is reported to have its sporangiophore traces depart from the cone axis midway between bract nodes and descend to the point of sporangiophore insertion. If the reason behind the separation of *Schimperia* were applied to these taxa, at least two new genera could be established based upon the differences in sporangiophore origin and accompanying characteristics. Unfortunately, this system of classification based upon anatomical features is untenable for coalified

compressions. There appears to be no way in which to differentiate specimens that may be representative of *Schimperia* from *Calamostachys* unless permineralized equivalents have been described.

Equisetalean fructifications have most often been found in association with sterile portions of other equisetalean form genera, but rarely are these strobili found attached. It is not known whether the different strobilar form genera of the *Palaeostachya*-type, *Calamostachys*-type, *C. spicata* var. *eimeri*-type, and the *Schimperia*-type were borne upon distinctly different parental plants or upon closely related vegetation. Since our knowledge of parental affinities is quite incomplete (features that are possible taxonomic criteria for separating strobili apparently vary within and between established genera), the present system of generic classification appears to be the only workable solution to the problem. Therefore, it is suggested that the angle at which the sporangiophore is inserted and the number of sporangia per sporangiophore be used as the criteria necessary for assignment of coalified compression specimens to either *Calamostachys* or *Palaeostachya*. It is recommended also that specimens with do not clearly exhibit either or both of these characters be assigned to *Macrostachya* or *Paracalamostachys*.

It is possible that *C. spicata* var. *eimeri* is an isolated geographic variant in the population of equisetalean strobili. Remy and Remy (1975) use this specimen as the basis of an architectural scheme to derive a *Calamostachys* strobilus from a *Palaeostachya* strobilus by means of phyletic gradualism. If phyletic gradualism were the mechanism responsible for the development of this intermediate form, this architectural scheme should be encountered in much older strata. *Palaeostachya* and *Calamostachys* are recognized from Namurian deposits, but no specimen collected, to date, from the Lower Pennsylvanian and its equivalents has demonstrated the morphological configuration of *C. spicata* var. *eimeri*. If this transitional form developed during the proposed ontogenetic scheme which separated the *Calamostachys*-type strobilus, it would have to have been a long-ranging form (Namurian-Upper Permian) and should have been previously collected. If additional forms are not recognized in older deposits or outside of this particular region, the theory of punctuated equilibrium would suggest that *C. spicata* var. *eimeri* was a momentary genetic mutant existing contemporaneously with the remainder of the strobilus population. *Calamostachys spicata* var. *eimeri* should be presently regarded as a geo-

graphically and stratigraphically enigmatic form until additional specimens are collected and identified from localities and horizons outside of the Nahe-area.

Species delimitation of coalified compression species within *Palaeostachya*, and hence other strobilar genera, should be approached cautiously. Presently, species appear to be based upon cone size, internodal distance, bract length, bract number, and sporangiophore number, even though taxa have been erected with considerably less than this amount of data (Gastaldo, 1981). Strobilus size does not appear to be a valid criterion except when distinguishing a very large cone from a small cone. The majority of cones which have been recognized are about the same in overall dimensions, and could be population variants if other criteria were not assessed. Size of the strobilus may vary depending upon the physiological environment (nutrient abundance or deficiency) and genetic preprogramming resulting in normal population variance. Distinguishing morphologically similar fructifications based solely upon size should not be done. The same may be stated about the use of internodal distance as a delimiting character. This feature is probably correlated with absolute cone size. As can be seen in the taxa erected within *Palaeostachya*, the cones that are similar in size exhibit the same range in internodal distances (Gastaldo, 1981, table 1). In addition, it is not known if, upon maturation of the strobilus, the axis elongates, as in the living genus *Equisetum*. If there is an elongation of the cone axis during the final stages of maturation, two specimens collected at different stages of maturation would appear very different.

Bract length, which represents the height to which the bracts ascend vertically, appears to be a criterion that is useful in separating species and is probably related to the reproductive strategy of the strobilus. Those species possessing bracts that enclosed a number of supra-adjacent whorls of bracts and sporangiophores provided a greater degree of protection to the developing sporangia than those that enclosed a single supra-adjacent whorl. In addition, those species which exhibit alternating superposed whorls of bracts, such as *Palaeostachya dircei*, appear imbricated and probably retained this condition until maturation.

Another character which is used to differentiate species is the number of bracts per whorl. This character appears to vary within a single cone as one examines the bracts in the lower and upper portion of the fructification. In addition, this character has been shown to

vary within different specimens of the same species (Good, 1975). Most species described are based upon very few specimens, and in most cases upon a single specimen, and this cannot possibly demonstrate the bract variation within the population.

The ratio of bracts to sporangiophores, degree of fusion of bracts, number of sporangia and sexual status (homospory or heterospory), though, appear to be consistent characters within populations of equisetalean strobili, and should be utilized as delimiting characters. Good (1975) studied large populations of a few permineralized equisetalean strobili and discussed their variability with respect to certain morphological characters. Large populations of many equisetalean strobili need to be examined in order to establish whether these characters are consistent or variable within a large number of species.

CONCLUSIONS—Coalified compression equisetalean strobili pose specific problems when attempting to assign them to a taxonomic rank. Diagenesis often obscures the detail necessary to place them within a generic, and more often, a specific taxon. Details preserved in permineralized specimens are rarely available in coalified compressions. Although sporangiophore-trace origin and configuration have been considered to be taxonomically and phylogenetically important, this characteristic is not always consistent, and is unavailable when dealing with coalified compressions. Therefore, classification schemes based upon differences in anatomical configuration are untenable. Although *Calamostachys spicata* var. *eimeri* exhibits morphological features of *Palaeostachya* and *Calamostachys*, it has not been encountered outside of the holotype locality. It may, therefore, represent an isolated geographical and stratigraphical population variant. Until additional forms are recognized outside of the Nahe-area, it would be premature to utilize it as the basis for synonymizing *Calamostachys* and *Palaeostachya*. Equisetalean cone specimens are often encountered which are identifiable only at the generic level, and the established form genera are convenient taxa which allow the author a more precise definition of the specimens. Although it is recognized that these strobilar form genera, and possibly all cone form genera, may be synonymous, it is proposed that the present system of classification, based upon the insertion of the sporangiophore and number of sporangia, be retained.

Many species have been erected upon a minimal amount of information, and often the

delimiting characteristics are unfixed when a population of strobili is examined. Characters that are highly variable include cone size, internodal distance, and bract number, and should not be used to separate new species. The characters deemed necessary to erect a new species include bract height, the degree of bract fusion, the disposition of the bracts (superposed or alternate), bract : sporangiophore ratio, number of sporangia per sporangiophore, and sexual status of the fructification.

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