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VASCULAR BUNDLES IN PALM STEMS—THEIR BIBLIOGRAPHIC EVOLUTION

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HAMLET might well have referred to palms when he spoke of "things both rank and gross in nature." Perhaps no other members of the vegetable kingdom have discouraged study because of their size, complexity, and general unwieldiness. In addition palms are predominantly tropical in their distribution. Because of this combination they have been relatively neglected by a science which has developed in north temperate countries and with dimensions which have become confined within limits set by a herbarium sheet. This was not always so, however. Although obvious practical difficulties attend the study of palms, their central position in an understanding of the morphology of angiosperms was clearly appreciated by botanists of the early nineteenth century.

> A minute anatomical examination of the palms is of especial importance in regard to the anatomy and physiology of plants, because the characters of the monocotyledons are most clearly exhibited in them, and they therefore afford the most favorable means of acquiring satisfactory ideas of the structure and growth of this great class of plants (Hugo von Mohl, 1849).

In this grasp of essentials early observers recognized three basic growth forms amongst arborescent plants, represented respectively by an oak, a palm, and a tree fern, and there was no attempt to subdivide botanical science into artificial and independent disciplines. Growth, development, structure and function were all given equal consideration.

It is interesting to realize also that some of these observers, notably von Mohl, had a better understanding of the construction of palms than of dicotyledonous trees. This unbalance was rapidly restored when the behavior of the cambium in hardwoods and conifers was properly interpreted. These trees, however, were available to all botanists; palms to few. This situation is emphasized by the experience of Mirbel who, directed by the French Academy of Sciences to investigate the date palm, had difficulty in procuring material even in North Africa. Von Mohl's statement is still viable today. In view of the failure of modern investigators to build on the accurate work of early observers, who can say what misconceptions in our appreciation of monocotyledonous morphology exist today? Obvious bias results when specialized forms like grasses, sedges, and lilies are studied because they are accessible and amenable to study by routine techniques whereas other forms are neglected because they are bulky and inaccessible.

Some indication of the dearth of knowledge in this field was given by our recent quantitative analysis of the vascular anatomy of a small palm, *Rhapis excelsa,* by means of ciné photography (Zimmermann and Tomlinson, 1965). In doing so we discovered considerable discrepancies between our scale diagrams (fig. 3) of the course of vascular bundles, based on direct observation, and those in modern textbooks (fig. 2), never to scale, purporting to illustrate the same thing. It may be argued that *Rhapis,* being a diminutive palm is exceptional, but we have considerable supplementary evidence to show that *Rhapis* is indeed a model for all palms. A ready explanation for this discrepancy was discovered when we followed the history of textbook diagrams. Quite clearly they had "evolved." This evolutionary process could be traced from a few early ones, based on careful and accurate observation, but incomplete, to several subsequent ones copied from the prime sources but elaborated by authors who had no first-hand knowledge of the subject. A few elementary errors became magnified and so distorted the real situation. Only direct observation could detect and correct these errors but the problem of the palm stem no longer occupied a central position in botanical science and the magnitude of the task discouraged the undertaking. The difficulties are quite obvious. Dissection of mature bundles ruptures delicate vascular connections. Bundles are commonly juxtaposed accidentally, especially when they are crowded, but superficial examination cannot show whether there is vascular continuity or not. The problem is therefore a microscopical one,

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but palm stems are too bulky to be handled by routine botanical microprocedures.

There seemed to be a moral in this history which is quite applicable to modern investigators, so we present a brief summary of our bibliographic investigation showing as far as we can be sure the wrong steps taken and the reason for them. It is an evolutionary history better documented and with a more reliable time-scale than most "phylogenies." Historical interrelationships are illustrated diagramamtically in figure 1.

Early accounts of palm stem anatomy up till 1876 were based on direct observation. During this phase many essential features were correctly observed, notably by von Mohl (1824–1849). Other authors whose work belongs to this period include Desfontaines (1798), Meneghini (1836), Lestiboudois (1840), Mirbel (1843–1844), Karsten (1847), Nägeli (1858). Historical surveys are given by Branner (1884) and Monoyer (1925), both of whom were among the very few later investigators to examine palm stems at first hand. Branner clearly grasped the essential features of palm-stem structure and development, as is indicated below. In the hands of these observers

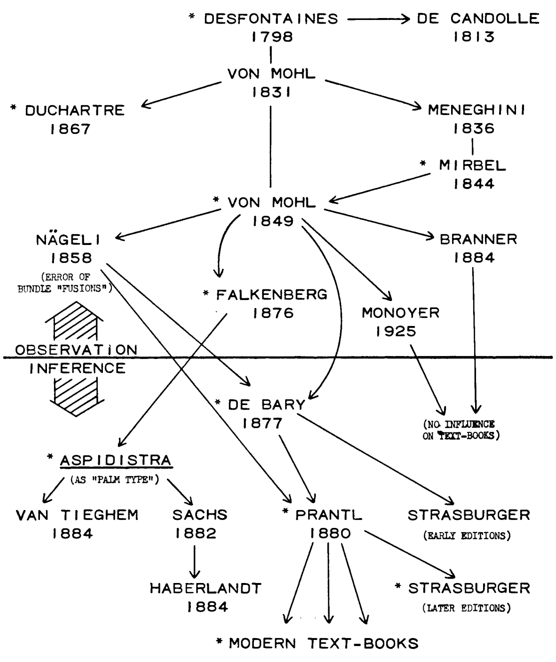

FIG. 1. Genealogy of diagrams illustrating the course of vascular bundles in palm stems. Publications marked with an asterisk are illustrated in fig. 2. We are indebted to Miss Anne Bellinger for the construction of figs. 1 and 2.

the subject progressed. The publication of Falkenberg's *Comparative Investigations of the Structure of the Vegetative Organs in Monocotyledons* (1876) marks the watershed. Subsequently interest in the subject declined, too early to prevent errors being incorporated in textbooks, especially de Bary's influential *Comparative Anatomy.* Falkenberg's monograph gave emphasis to a theoretical entity, the "palm-type" of vascular construction, based on what can now be seen to be insubstantial evidence. De Bary's textbook of 1877 makes no reference to Falkenberg's work which is unfortunate, a careful reading of Falkenberg's text might have saved de Bary from propagating a source of error. Diagrams in subsequent textbooks seem largely progeny from these two parental sources. One difficulty in our bibliographic investigation has been that diagrams are often reproduced without acknowledgment of their source. Nevertheless, genealogies can usually be traced because of simple errors which, like a family stigma, have unwittingly persisted (fig. 2). Followed in this way some diagrams in modern textbooks are of the fifth or sixth generation.

BEFORE VON MOHL

Because the accuracy of his observations exceeds those of his contemporaries, Hugo von Mohl's work provides a convenient base line. His predecessors recognized that the conducting tissues in palm stems were isolated strands, crowded at the periphery, less congested at the center with a distinct narrow cortical region surrounding the central cylinder. Desfontaines (1798) had given birth to the idea that the peripheral bundles were old, the central young. New bundles appeared in the stem center connected to each new leaf so that there was a constant outward displacement of older by newer bundles with a resulting peripheral congestion. It was suggested that all bundles ran to the base of the stem. This wholly ingenious idea was seized upon by de Candolle (1813) as a basis for distinguishing monocotyledons with such endogenous vascular bundles from dicotyledons in which they were exogenous. Although invalidated by von Mohl's demonstration that bundles crossed over each other this idea is still historically significant because it demonstrates that taxonomists of the period were willing to accord major significance to features of growth and development. Mirbel's scheme of 1844, in which vascular bundles were shown to extend from one side of the stem to the other and so cross over in a different way, was also regarded as vitiating Desfontaines' concept because such an arrangement could not develop by endogenous growth. We ourselves have interpreted Mirbel's observation as being the result of representing the helical path traced by the central bundles, a feature well recognized by early workers, in a single plane (Zimmermann and Tomlinson, 1965: p. 171). Nägeli, who drew attention to this helix, seems also to have appreciated that vascular bundles in a helix could develop by endogenous growth.

HUGO VON MOHL

The section *De palmarum structura* contributed by von Mohl to volume 1 of Martius' monumental *Historia naturalis palmarum* was published in 1831 although the whole volume is dated 1824. He later (1849) modified his views somewhat in the light of Mirbel's and other criticism. Von Mohl showed the essential course of palm bundles as a "double curve" (strictly the direction of bundles after entry from the leaf changing twice), the upper part in which the bundles were in obvious contact with the leaves, being obliquely towards the stem center, the lower part extending over a much longer distance and almost parallel to the long axis of the stem but gradually approaching the periphery again. He also recognized that the bewildering variety in anatomical structure of bundles seen in a single section of the stem could be explained by variation throughout the length of a single bundle over and over again. He built up a picture of this variation from a study of the bundles cut at a single level and according to his notion of the general course of the bundles. He supplemented this with a study of single bundles, presumably dissected from a stem. Von Mohl's achievement is notable because he apparently had only dried specimens or at the most young ones, presumably supplied by Martius. This probably accounts for his failure to record raphides, which are abundant in palm stems. Presumably, as Karsten points out, they decomposed in his dried specimens. Von Mohl also recognized that for descriptive purposes it was immaterial whether the bundles were traced upwards or downwards, and chose to describe their pathway when traced in a downward direction. According to Branner this was, however, crucial, because in doing so von Mohl missed the essential continuity of vascular bundles throughout the stem which Branner himself clearly recognized and which we have more recently confirmed. The connections are tenuous and it is not surprising that in his dissections von Mohl overlooked them.

Von Mohl thus left one fundamental feature unexplained. How is vascular continuity between separate vascular bundles maintained? All diagrams hitherto had shown independent bundles. This would mean that there is no direct vascular pathway from root to leaf. Desfontaines and Mirbel did show this continuity because in their diagrams all vascular bundles proceed to the base of the stem, but entirely overlooking the relatively constant number of vascular bundles in a palm stem, not a decreasing number upwards. (In detailed fact there are fewer vascular bundles at the base than the apex.) Von Mohl recognized these physiological difficulties but his explanation is unsatisfactory. His earliest account (1831) is obscure. He knew that the bundles could not all run to the base of the stem. His scheme envisages a gradual tapering of bundles in the congested periphery of the stem. They could either end blindly or "blend" with adjacent bundles. The fibrous system of the cortex was believed to represent these basal extensions. In this way the basal extremity of each persistent bundle was thought to make no significant contribution to the diameter of the uniformly cylindrical stem. Several later investigators, notably Schacht, Nägeli, and Falkenberg, paid especial attention to the origin of cortical bundles and discovered in fact that they were continuous with small fibrous bundles of the leaf base and that central bundles never passed into the cortex when followed in a downward direction. In reply to later criticism by his contemporaries he (1849) was more firm about their blind ending in a basipetal direction. Any physiological difficulties about lack of vascular continuity were dismissed by von Mohl because similar blind ending bundles were known to exist in dicotyledons. A transference of sap from one bundle to another across a parenchymatous gap was envisaged. This begging of the question was to continue so that even Haberlandt (1914: p. 383), was to regard the continuity of vascular bundles as of "minor importance." *Dracaena,* in which the base of the stem was thickened, was equated by von Mohl to a palm in which the bundles did not taper in a basal direction; the secondary vascular bundles, which are now known to originate from a secondary cambium, were regarded as the basal continuation of distal leaf traces.

Despite these deficiencies von Mohl had grasped essentials. He could not do more because of the limited material he had to work with. The stage was set for an extension of von Mohl's observations. This was not to be so, however.

AFTER VON MOHL; THE DEVELOPMENT OF THE "PALM-TYPE" CONCEPT

Falkenberg studied *Chamaedorea,* a diminutive palm. There is some confusion because his text describes *C. schiedeana* although his illustration (fig. 2H) refers to *C. elatior,* a species which Nägeli had described earlier with the additional comment that these two species differed in several features. It is difficult to grasp the significance of Falkenberg's observations in view of the fact that he studied only the seedling axis (a one-year-old plant). It may be that his diagram (fig. 2H) is based on earlier observation. Essentially it corresponds to von Mohl's (fig. 2C) with added detail showing that different bundles from a single leaf penetrate into the central cylinder in varying degrees, a difference we have emphasized by referring to them as major, intermediate, and minor bundles (Zimmermann and Tomlinson, 1965), although realizing that there is no sharp distinction between these categories. Nägeli, however, had already pointed out this difference. De Bary's two diagrams make no pretense of first-hand knowledge: one (fig. 2D, his fig. 117) is based on von Mohl; the other (fig. 2E, his fig. 118) introduces the needless sophistication of a hypothetical distichous scheme with dorsal (major) and ventral (minor) bundles. This does emphasize the difference between dorsal and ventral bundles but, however, overlooks the great rarity of a distichous leaf arrangement in palms and that no investigator had examined these few distichous palms. In this respect Falkenberg's diagram is more realistic than de Bary's because major and minor bundles can indeed proceed along much the same radius into the leaf. De Bary also emphasizes a major error in tentatively uniting the basal extremities of two vascular bundles in his fig. 118 (fig. 2E). Neither von Mohl nor Falkenberg had illustrated this fusion. They both concluded that the bundles ended blindly toward the base of the stem, Falkenberg much more emphatically than von Mohl. Von Mohl remarked about the possibility of such unions—"they run . . . to the base of the stem, or terminate, after a course of variable length, in other vascular bundles, becoming blended with them" (English translation, 1849: p. 8). Later von Mohl had returned to this same point in commenting on Mirbel's failure to describe clearly the ultimate fate of the bundles when traced basipetally.

> Neither have I, as already observed, been able to make out this point with certainty. . . . It is probable, therefore, that the majority of the vascular bundles terminate blindly in the cellular tissue beneath the rind. This assumption . . . . (English translation, 1849: p. 90.)

Von Mohl had carefully distinguished what he observed from what he inferred so that it is certain that he never observed the fusion which de Bary's diagrams implied.

Falkenberg discused this point in detail, emphasizing that the only fusions of physiological significance were those in which continuity of vascular tissue occurred.

> Von einer wirklichen Vereinigung zweier Fibrovasalstränge kann nur dann die Rede sein, wenn die Gefässe und Cambiformzellen eines Stranges in direktem Zusammenhang stehen und dieses liess sich bei *Ch. Schiedeana,* niemals an der Peripherie des Centralcylinders, wohl aber in seinem inneren Theile beobachten.

The latter reference to fusions in the center of the stem was the only one Falkenberg made to bundle unions and he makes no further comment. It should again be noted that Falkenberg examined only the seedling axis. Otherwise, occasional forkings had been recorded, by Lestiboudois (1840), Karsten (1847: p. 99), and by Schacht, but not as the regular system now known to exist(fig. 3). The only later author to consider the physiological implications of von Mohl's scheme was Monoyer (1925) and his diagram shows bundle interconnections. Nevertheless, his strands end blindly below and his diagram is difficult to reconcile with the *Raphis* scheme unless one regards it as vastly out of scale and his interconnections as our "bridges." To what extent his diagram reflects distinctive features of the palm, *Arecastrum romanzoffianum,* he studied, we do not know.

The only record of direct observation of basal fusions at the periphery of the central cylinder is in Nägeli's text. After confirming von Mohl's observation on the course of bundles and, briefly, the changes in structure throughout a bundle, Nägeli (1858: p. 132) goes on to describe their ultimate fate: "Wenn der von oben nach unten gehende Strang dicht innerhalb der Rinde angelangt ist, so vereinigt er sich mit einem andern, der ihm gerade zunächst liegt." Moreover, Nägeli denies the presence of any regular bundle fusions in the stem center. "Im Marke dagegen mangeln

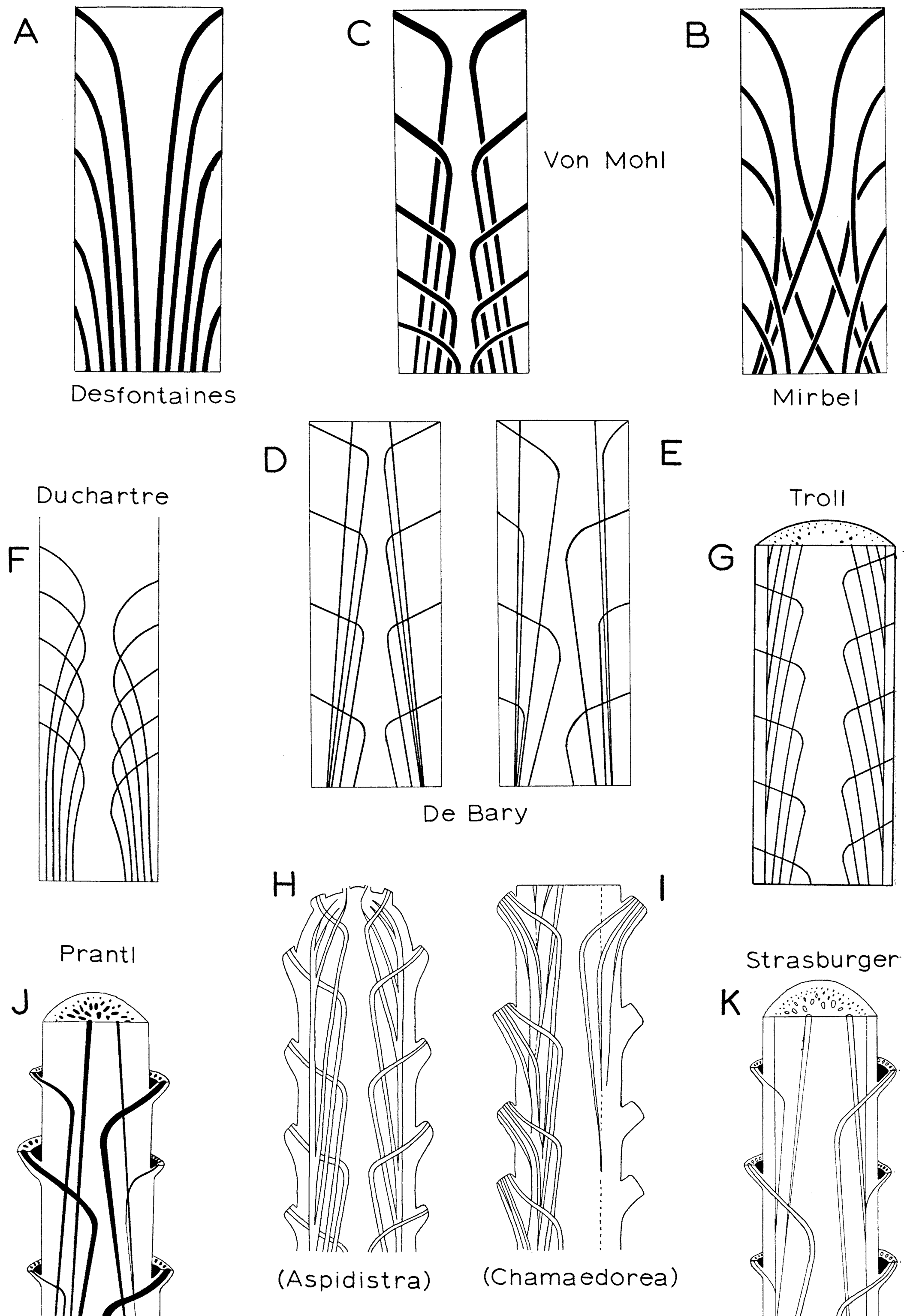

FIG. 2. Textbook and other diagrams, representing hypothetical course of vascular bundles in palm stems (*cf.* fig. 3). A–C redrawn from Monoyer (1925). D–K redrawn to standard size from publications indicated. For comparative details see text.

bei *Chamaedorea,* wie es Mohl für die übrigen Palmen angiebt, die Vereinigungen (oder Verzweigungen) der Stränge beinahe gänzlich." Possibly Nägeli overlooked the splitting of the leaf trace, which we know from our own observations on *Chamaedorea* occurs in the major bundles in the center of the stem, because he examined serial sections close to the shoot apex. In such leaf traces differentiation of xylem in the branch bundles may have been incomplete. Schacht seems to have seen them, possibly because he examined older material. Such speculation serves no useful purpose, however.

Falkenberg's monograph has been regarded consistently as a basic source of information in comparative studies of the monocotyledonous axis. From our own studies of *Rhapis, Chamaedorea,* and other palms, we now know that Falkenberg's text and illustration analyze the palm stem, at best, incompletely. Nevertheless, Falkenberg compared a number of other monocotyledons with *Chamaedorea,* all of which he designated plants with a "palm-type" of vascular bundle distribution (*e.g.*, fig. 2I). He established a number of other contrasted "types." De Bary's approach was very similar. The central position of palms in an understanding of monocotyledons generally was then maintained, as earlier botanists would have wished, but all on incomplete or even incorrect evidence. To what extent Falkenberg's other vascular analyses will prove to be deficient can only await their re-examination. It is an unfortunate matter of history that with Falkenberg and de Bary the "palm-type" concept was established and accepted uncritically.

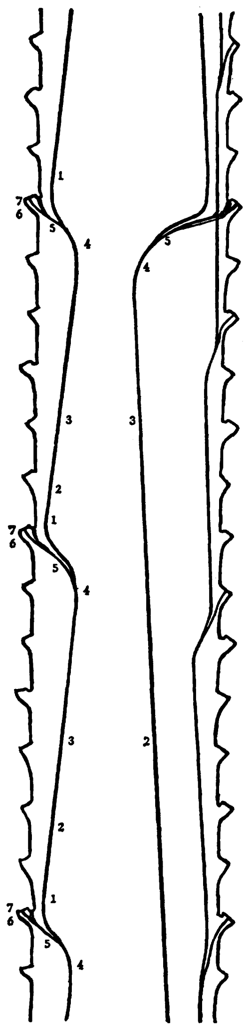

FIG. 3. Course of vascular bundles in stem of the palm *Rhapis excelsa* (after Zimmermann and Tomlinson, 1965). Drawn to scale, horizontal scale 4 × vertical scale. The helical course of the bundles is not represented.

TEXTBOOK DIAGRAMS

Only one textbook illustration, that of Duchartre (1867), seems to be derived directly from von Mohl (fig. 1, 2F). Otherwise, Falkenberg and de Bary may be recognized as secondary, if misleading sources. We can now see how other textbook diagrams have been derived from them. In introducing a false sense of realism into their diagrams subsequent writers have continued a tradition begun by de Bary. In order to produce a pattern with geometrical symmetry, the tentative linkage included by de Bary became incorporated gradually as an essential feature of diagrams. Principles of symmetry do indeed govern real palm stems, but not those that govern their evolution on paper. The ultimate extension of these principles "established" by de Bary is shown most clearly in Troll's textbook (1948) in which all bundles are linked by a continuous peripheral commissure (fig. 2K). Furthermore, the legend to this figure describes it as representing a "so-called palm-type, for example *Zea mays*" which is quite misleading. This looks as if it is derived initially from de Bary's figure 117. De Bary's other diagram (his fig. 118) was reproduced without modification, *e.g.,* in the early editions of Strasburger's *Textbook of Botany* (1894) but not in later ones. The most vigorous offshoot was undoubtedly a redrawn diagram in Prantl's *Textbook of Botany* (6th ed., 1886: p. 61) with a false attempt at reality (fig.

2G). Because of this, it is a favorite of writers of modern textbooks, often reproduced at third or fourth hand. In later editions of Strasburger's textbook, for example, it replaces the earlier diagram, appearing first in the fifth English edition of 1921. Comparison of Prantl's original figure (fig. 2G) with later diagrams in modern textbooks (fig. 2J) shows the addition of a continuous series of peripheral fusions. We have been unable to trace the exact origin of these additions. Clearly, however, there has been "descent with modifications."

A curious feature of other textbooks has been the use of Falkenberg's diagram of *Aspidistra elatior* (fig. 2I) to illustrate the "palm-type." This appears, for example, in van Tieghem's *Textbook of Botany* of 1884, correctly cited. In other publications, *e.g.,* Sachs (1882), Haberlandt (1884), it is simply cited as an example of the "palm-type" without the information that it is not of a palm. This is a very misleading representation since any pretense of knowledge of the actual disposition of bundles in palm stems is discussed in favor of a hypothetical generalization.

BRANNER'S NEGLECTED CONTRIBUTION

Amidst all this confusion into which the study of the anatomy of palm stems had degenerated at the end of the nineteenth century there had appeared a paper which extended von Mohl's observations but which was completely disregarded. Essential features of the distribution of vascular bundles in palm stems and a rational attempt at a developmental interpretation had been published by Branner (1884). J. C. Branner, an American geologist, had studied living palms in Brazil and carried out more first-hand observations than any investigator before or since. His results, clearly set against the historical background of early work, were published in the *Proceedings* of the American Philosophical Society. His observations, though they contradicted textbook diagrams proliferating in this era, were disregarded. This neglect cannot be ascribed entirely to the chauvinism of European botanists, because the article is listed in modern bibliographies, but probably is the result of Branner's failure to produce a neat and ordered diagram of the type which found favor in the eyes of textbook writers. Branner was also concerned more with demonstrating how the vascular system develops than its construction, which seemed so clear to him. On this he is quite unequivocable (Branner, 1884: p. 466):

> Beginning at the base of the palm trunk, a bundle is traceable into a frond, at the base of which it branches; the stem division gradually approaches the centre of the stem, and there curves sharply outwards to connect with another frond, and so, curving in and out, it connects with frond scars and spadices from base to apex.

Branner had access to virtually unlimited material, but no better technical methods than his contemporaries. The reason for his success and the reason he was so far ahead of his contemporaries to the extent that they neglected him is that he approached the problem developmentally, studying the course of bundles upwards in the direction of growth of the palm stem. Developmental aspects had not been entirely neglected by earlier workers; they had been discussed by von Mohl, but development and construction had never been continuously associated. Unfortunately, Branner's detailed account deals with the mechanics of development in a way which is not readily comprehended and it is probably for this reason that it has been consistently ignored. Subsequently, with the exception of Monoyer's and our own investigations, no first-hand study has been carried out and textbook errors have propagated in a distinctly unhealthy way.

CONCLUSIONS

This article is not intended as an attack on textbooks merely because we have the benefit of a hindsight denied other authors. It is quite possible that our historical interpretation is wrong, but at least it is based on some first-hand familiarity with the anatomy of palm stems. It is appreciated that the writer of a text merely collates information without necessarily verifying it, least of all when this is an especially lengthy undertaking. But a textbook does give a false impression if it presents all information as assured facts, although this impression may rest more in the mind of the student reader than an author. A measure of the excellence of a textbook, nevertheless, might be the extent to which it encourages critical thinking. The present history shows the danger of preferring hypothetical inference to direct observation. Descriptive plant anatomy is a fundamental discipline with a long history. Its practitioners today are few. A greater number of students and research workers rely on second-hand information. Uncritical acceptance of this can be dangerous. Fundamental concepts can only be established with certainty if they are constantly re-examined; otherwise they degenerate into dogmas which it becomes heresy to challenge. Plant anatomy has the reputation of being an aspect of botany which is fully "worked out" and any tendency to orthodoxy in thinking will only encourage this naive notion. The history of knowledge of the palm stem which we have traced is a good example of how much more the direct investigator can still learn about an elementary subject. Only if a constant attack on basic concepts is permitted and even encouraged will plant anatomy survive as a vital discipline.

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