

PADGETTIA, A NEW GENUS BASED ON FERTILE NEUROPTEROID FOLIAGE FROM THE PERMIAN OF TEXAS*

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AS Permian floras become increasingly well-known, it becomes more apparent that the Permian period produced many peculiar plant forms that defy close comparison with plants of the present. *Padgettia*, the new genus to be described here, is represented by one of these morphologically anomalous types of plants.

The material upon which this account is based was found in an assemblage of plant compressions collected in 1939 by Charles B. Read, U.S. Geological Survey, at a locality "approximately 2 miles northwest of Padgett", in Young County, Texas, (U.S.G.S. Palaeobotanical Locality Number 8967). According to the geological map of Young County (Plummer and Fuqua, 1937), outcrops in that area lie within the Lower Permian Moran formation of the Wichita group, at an undetermined distance above the Dothan limestone of former usage.

The abundant plant remains are preserved in a fine-grained, dark grey shale with well-developed fissility. In some specimens the preservation is so fine that epidermal cell patterns are visible under high magnification; in most specimens, however, only a very thin film of dark brown carbonaceous matter remains, which presents a fairly sharp colour contrast with the shale matrix.

The plant assemblage is fairly diverse, containing representatives of *Cordaites*, *Bowmanites*, *Sphenophyllum*, *Pecopteris*, *Sphenopteris*, *Odontopteris*, and *Padgettia*. Although the Pueblo formation, which underlies the Moran, is known to contain *Callipteris*, this Permian "guide" fossil is not recognizable in the Padgett collection. *Padgettia* seems to have dominated the florule, and on the basis of more than fifty fertile pinnules, its known features are diagnosed as follows:

Padgettia readi n. gen. and sp.

Combined Diagnosis — Plants with large neuropteroid pinnules; pinnules bearing one

to several adnate, seed-like fructifications, probably imbedded in the lamina, aligned parallel to the venation on either side of the midrib.

Fronds at least once pinnate; pinnules apparently isophyllous, long (12 cm. or more) and relatively narrow (to 3 cm. wide) with entire margins and cordate bases, the laminae tapering gently to acute apices. Pinnule midribs to 3 mm. wide, finely striated; lateral veins closely spaced, departing decurrently at an angle of approximately 30 degrees, arching to meet pinnule margins nearly perpendicularly, usually forking once within a short distance of the midrib.

Fructifications ovoid, elliptical or pyriform, from 2.5 to 9.0 mm. long and 2.0 to 5.0 mm. wide, usually borne one or two, occasionally several to a pinnule, being evenly spaced in the latter instances. Fructifications oriented lengthwise along decurrence of lateral veins, with broadest ends toward pinnule midrib, some in contact with midribs, and apparently attached to laminae or imbedded in them throughout their length; apices of some fructifications extended as either broad or constricted "beaks", terminating truncately at pinnule margins.

Holotype — U.S.N.M. 41165 a and b (counterparts): figures 3 and 4.

Description of the Material — The Padgett collection contains nearly a hundred seedlike fructifications, distributed among 52 pinnules. Most of the fertile pinnules, which in the sterile form have a decidedly neuropteroid appearance, have only one fructification each, but 12 have 2 each, 7 have 3 or more, and one small pinnule fragment, 3 cm. long and 1.7 cm. wide, has 7. The holotype, the counterparts of which are shown in Figs. 3 and 4, is an incomplete pinnule 6 cm. long and 2 cm. wide, with 8 fructifications. Sterile pinnules apparently do not differ from fertile ones in regard to size, outline or venation.

The fructifications are all flattened to the extent that they create hardly any relief on

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the leaf surface; in this flattened condition they are mostly ovoid or pyriform. There is no evidence of pedicellate attachment. Most specimens occur on the laminar area between the midrib and pinnule margin, but a few have their basal ends in contact with the midrib; none of these, however, extend from one side of the midrib to the other.

Most of the fructifications occur nearer to the base than the tip of the pinnule. Their orientation conforms closely with the angle of decurrence of the lateral veins, so that the fructifications are typically situated with their long axes directed apically at a wide angle to the midrib, with their broadest ends toward the midrib. Where several fructifications are present on the same side of the midrib, they tend to be approximately evenly spaced and, as shown in Figs. 3 and 4, they may also occur in opposite pairs.

Although not all of the fructifications extend as far as the pinnule margin, many have beak-like apical prolongations that extend as far as, but not beyond, the pinnule margin. The beak may be narrow and constricted, giving the fructification its pear—or urnlike outline, or it may continue unstricted to the pinnule margin as an extension of the greatest width of the fructification.

The outline of the fructification is delimited by a more or less pronounced furrow—evidently a compression border—in the matrix. This surrounds a small, flat, lens-like body of sediment that can be flaked off to expose the opposite side of the specimen; this obviously represents the filling by sediment of an originally hollow structure on the pinnule. Some of the furrows are filled with fusinized carbonaceous matter, suggesting that the original structure had considerable substance; some specimens are almost completely covered by a thin film of coal, but others lack this, having lost it to their counterparts when the matrix was split.

No spores or cuticular remains were found in any of the fructifications, although several specimens were sacrificed for matrix dispersal and examination of residues; nor was it possible to determine definitely whether the fructifications were borne on the lower or upper surface of the pinnule, although they generally appear to have been on the lower surface.

The degree of frond division is not known because only one specimen was found with two pinnules attached to an ultimate rachis.

It is likely, however, that the frond was at least bipinnately compound.

Interpretation—The problem of morphological interpretation of the fertile pinnules of *Padgettia* has been discussed with various colleagues, and although the possibility that the ovoid objects represent abnormalities of unknown origin has been considered, the consensus favors their interpretation as fructifications. My personal opinion is that *Padgettia* is a pteridosperm, and that the pinnules described here are the ovuliferous parts. Reasons for this interpretation are:

1. The presence in the Padgett collection of a large number of the ovoid objects, and their complete restriction to one species of plants in this reasonably diverse flora, seems convincing evidence that they constitute a natural growth feature of the pinnules.

2. The strict conformity of the long axes of the objects with the decurrence of the lateral veins of the supporting pinnules indicates a preferential orientation along the ultimate vascular strands, as in linear fern sori. In addition to this feature, the relatively even spacing and opposite pairing in the few observable instances are also suggestive of reproductive structures rather than pathological effects, insect damage, or other artificially induced abnormalities.

3. Their shape is seed-like and their size is comparable to that of any number of the smaller pteridospermous seeds. They are too large for microsporangia or isoporangia, and there is no evidence to indicate that they are multisporangiate sori.

The most unusual and perhaps morphologically most significant aspect of the seeds is the manner in which their apical ends are truncated exactly at the pinnule margins. Had the seeds been pedicellate or, if sessile, had they been attached only at their basal ends, it is unlikely that their apical ends would have coincided exactly with the pinnule margins in all instances. The marginal truncation of the seeds thus suggests that they were imbedded within the lamina and as the seeds matured, slits opened along the pinnule margins to permit access of pollen to the micropyles and shedding of the matured seeds from the sporophylls. The compressed "beaks" would thus represent the fossilized avenue of access between the seeds and the outside of the sporophylls.

Further support of this interpretation lies in the evidence of complete sessility or adnation of the seeds as demonstrated by their

consistently decurrent alignment. Had the seeds been stalked or incompletely attached to the lamina, some of them certainly would have been preserved in other positions relative to the lateral veins.

Another point worthy of consideration is the relationship between size of seeds and development of the apical beak. The smallest seeds are unbeaked, while the best developed beaks occur on the largest seeds, suggesting that all seeds did not mature at once, and that the beak was not developed until the seed had matured to the pollination stage, when a point of pollen entry became necessary. It seems probable that these sporophylls were shed and covered by sediment after the seeds had been pollinated and dropped from their foliar envelopes, for the presence in most specimens of a small lens-like flake of sediment is evidence that these were hollow structures when buried in the mud. This would largely explain the absence of a megaspore membrane or seed cuticle in the larger specimens; the smaller ones, on the other hand, may have been preserved before cutinization of parts was sufficiently advanced for satisfactory preservation.

In the absence of the direct evidence necessary for incontrovertible establishment of these structures as seeds — the presence of a megaspore membrane — two alternative interpretations must be admitted, although neither of these appeals to me. If, on one hand, the *Padgettia* fronds are to be regarded as pteridospermous microsporophylls, they are structurally unique among the Paleozoic pteridosperms, for the male organs of those plants — in so far as they are known — are all elaminal, synangial structures of considerable size and complexity; the probability of homology between sporophylls of *Padgettia* and certain of Halle's (1929) seed-bearing foliage from the Permian of China (in particular, fronds of *Emplectopteris triangularis*) strikes me as a much stronger one. On the other hand, interpretation of *Padgettia* as an isosporous fern would limit comparison to one with the modern Ophioglossaceae, particularly *Ophioglossum*, whose sporangia are regarded as being imbedded in foliar tissue (EAMES, 1936, p. 121). It is conceivable that a form-like *Padgettia*, through reduction of intersporangial lamina and contraction of the pinnule rachis, eventually produced a fertile spike like that of *Ophioglossum*. However, such an evolutionary process cannot be demonstrated on the basis of the available evidence.

Discussion — The taxonomic implications of *Padgettia* are important, because in its sterile state a pinnule of this plant is indistinguishable from *Neuropteris* foliage. In leaf shape and venation, *Padgettia readi* bears a close resemblance to *Neuropteris permiana* Sellards (1908), from the Permian of Kansas, and the two species would possibly be regarded as conspecific if the fructifications of the Padgett material were not known. It must be pointed out, of course, that Sellards' material may ultimately prove to belong to *Padgettia* rather than to *Neuropteris*, should its fructification ever become known; the evidence on hand, however, does not warrant the taxonomic recombination.

On the basis of the great morphological difference of the fructification of *Padgettia* from any known neuropterid fructification, assignment of the Padgett material to *Neuropteris* would be justifiable only from the standpoint of sterile foliar morphology. Such a taxonomic choice would involve disregard of the strong probability of foliar homeomorphy and would effect an unreasonable extension of the circumscription of *Neuropteris*. Seed attachment has been demonstrated for the type species, *N. heterophylla* Brongniart (see KIDSTON, 1904) as well as for *N. obliqua* Brongniart (KIDSTON & JONGMANS, 1911) and *N. schlehani* (JONGMANS, 1954). In those species, the seeds are large, pachytestoid bodies that terminate naked extensions of the pinna rachis, with only one seed borne on any single rachis. Moreover, the male fructification of *N. schlehani* has been shown by Jongmans (1954) to be a large whittleseyan campanulum, so that even if there were evidence for interpreting the pinnules of *Padgettia* as microsporophyllar, there would still be no basis for identifying them with *Neuropteris*.

Mention should be made of two other examples of presumably fertile neuropteroid foliage that may be more closely related to *Padgettia* than to *Neuropteris*. Chodat (1908, p. 404, 405) briefly described a specimen of *Neuropteris auriculata* Brongniart, from the Stephanian of France, which bore several samaroid "sporospermes" with "more or less flattened indusia". Chodat's description and illustrations are somewhat less than adequate, so that suitable comparisons with *Padgettia* are not possible; however, it seems likely that the structures reported by Chodat are more similar to the megasporophylls of

Padgettia than to the known female fructifications of *Neuropteris*.

Fontaine and White (1880, p. 47, 48, Pl. 8, Figs. 7, 8, 8a) figured seemingly fertile pinules of *Neuropteris hirsuta* Lesquereux from "20 ft. below the Pittsburg coal" near Bellaire, Ohio. The fruiting bodies were "linear-elliptical sori, $4\frac{1}{2}$ mm. long and 1 mm. wide at the middle . . . normally placed in groups of four, the sorus nearest the base of the pinnule being situated near the middle of the lamina . . . each succeeding sorus of the group approaching nearer to the midrib, until the last one comes quite close to it, thus forming rows, each containing 4 sori, and each row inclined toward the midrib". These were interpreted as fern sori, comparable to those of *Scolopendrium vulgare*, although individual sporangia are neither described nor distinguishable in the illustrations. If these are actually fructifications, they resemble much more closely those of *Padgettia* than those of any species of *Neuropteris* and add significantly to the already demonstrable artificiality of *Neuropteris*. Unfortunately the Fontaine and White material is no longer available, so that first-hand examination is not possible.

The evolutionary significance of *Padgettia* might well be evaluated in relation to Halle's (1929, p. 18-22) well-known comments on the position of pteridospermous seeds in relation to the fronds on which they were borne. Although only a few instances of demonstrable connection between seed and leaf were then known, Halle pointed out that the older Carboniferous examples consisted of terminal seeds on much reduced foliar segments. Younger Carboniferous forms showed a trend toward increased proximity of seed to lamina and decreased heterophylly. Finally, the majority of known Permian examples produced seeds neither terminally nor marginally but actually attached to the surface of either the lamina or rachis of apparently unreduced foliar segments. Thus, even though there are still few examples to com-

pare, the time-morphology relationships of the known ones are sufficiently striking that it is not unreasonable to postulate that evolution of pteridospermous seed position underwent a Bowerian "phyletic slide", analogous to that entailed in the evolution of fern fructifications, the terminal position of the oldest seeds reflecting the terminal position of the ancestral psilophytic sporangium.

It is of interest to regard *Padgettia* in the light of such an evolutionary process, for it may be that *Padgettia* represents a stage in evolving seed position even more advanced than the Permian forms reported by Halle. Having migrated from the termini of naked rachises to the surface of an unmodified lamina, furtherance of the tendency toward increased proximity of seeds to foliar lamina eventually might have resulted in actual embedment of the seed within foliar mesophyll. How this was accomplished, what the ecological or evolutionary advantage of such a modification could have been, and what the subsequent stages in such an evolutionary process were are difficult questions, but the possibility of such a sequence is supported to some degree by the age relationships of the fossils involved.

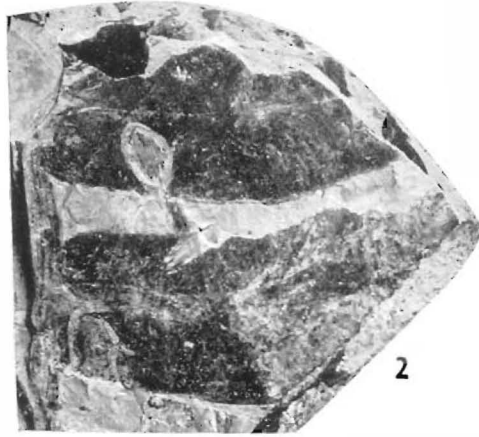
The question of affinity of *Padgettia* to other Paleozoic plants with neuropterid foliage is one that must await discovery of many more pertinent specimens. Perhaps the close resemblance between the pinnules of *Padgettia* and foliage of *Neuropteris* is only another example of homeomorphic evolution and no genetic relationship is involved. On the other hand, it is possible that *Padgettia* represents a late stage in a neuropterid evolutionary sequence that began in such Carboniferous forms as *Neuropteris heterophylla*, with the evidence of a lineal relationship being retained only in the form of the pinnules. The latter alternative would, of course, necessitate a drastic reduction of seed size, concomitant with the "phyletic slide" and eventual embedment of the seeds within the pinnules.

REFERENCES

- CHODAT, R. (1908). Les ptéropsides des temps Paléozoïques, Etude critique. *Arch. des sci. physiques et naturelles*. 26(10): 394-416.
- EAMES, A. J. (1936). Morphology of vascular plants. Lower groups (Psilophytales to Filicales). McGraw-Hill Book Co, New York and London.
- FONTAINE, W. M. & WHITE, I. C. (1880). The Permian or Upper Carboniferous flora of West Virginia and S.W. Pennsylvania. *Second Geol. Surv. Pennsylvania: Rept. of Progress*.
- HALLE, T. G. (1929). Some seed-bearing pteridosperms from the Permian of China. *Kungl. Svenska Vetensk. Handl. 3rd series*. 6(8): 3-24.



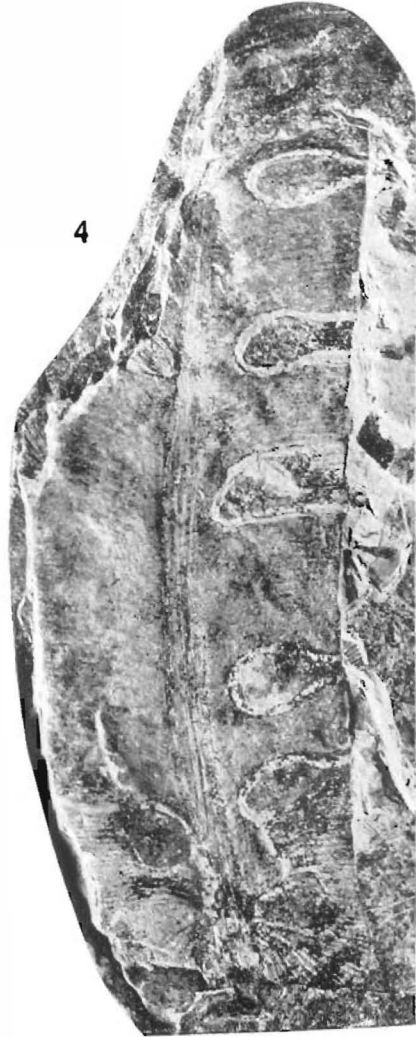
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- JONGMANS, W. J. (1954). Contribution to the knowledge of the flora of seam Girondelle (lower part of the Westphalian A). Part 1. *Mededel. Geol. Stichting*. Ser. C-III. **1**(4): 5-16.
- KIDSTON, ROBERT (1904). On the fructification of *Neuropteris heterophylla*, Brongniart. *Phil. Trans. Roy. Soc. London*. Ser. B. **197**: 1-5.
- KIDSTON, ROBERT & JONGMANS, W. J. (1911). Sur la fructification de *Neuropteris obliqua* Bgt. *Arch. Neerl. des Sci. Exactes et Nat.* ser. IIIB. **1**: 25.
- PLUMMER, F. B. & FUGUA, H. B. (1937). Geologic map of Young County, Texas. *Univ. Texas, Bur. Econ. Geol. Map* (1930), revised 1937.
- SELLARDS, E. H. (1908). Fossil plants of the Upper Paleozoic of Kansas. *Univ. Geol. Surv. Kansas*. Special report on oil and gas. **9**: 586-00.

EXPLANATION OF PLATE I

1. Portion of pinnule of *Padgettia readi* showing midrib at right, pinnule margin at left, and one fructification with apex extending to margin. $\times 4$.

2. Portions of two pinnules attached to ultimate rachis. Note two fructifications, one near base of

each pinnule, both directed toward bottom of photograph. $\times 2$.

3, 4. Counterparts of holotype, showing attachment of several fructifications. Note truncation of beaks at pinnule margins. $\times 2$. Fig. 3: U.S.N.M. 41165a; Fig. 4: 41165b.