

THE MORPHOLOGY AND TAXONOMY OF *CYCADOLEPIS JENKINSIANA* AND *ZAMITES RECTA* FROM THE LOWER CRETACEOUS KIRKWOOD FORMATION OF SOUTH AFRICA

by

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ABSTRACT

Cycadolepis jenkinsiana, a bennettitalean scale-leaf, is shown to have had two types of venation, is shown not to be covered by hairs as had previously been thought and has a strong association with *Zamites recta*, the most common vegetative leaf species to be found in the Kirkwood Formation of the Algoa Basin. The morphology of *Zamites recta* is reasonably clear and this species has definite affinities with the Bennettitales based on its gross morphology and a single microscopic character, i.e. sinuous epidermal cell walls of the pinnae. *Zamites morrisii* is shown to be only a variant of the better represented *Z. recta*. Two of the previously described species of *Zamites*, *Z. rubidgei* and *Z. africana* are excluded from *Zamites*.

INTRODUCTION

Four species of *Zamites* were reported from near Geelhoutboom, Cape Province in the Uitenhage series by Seward (1903) who based his work on specimens described earlier by Tate (1867) and new material collected for him. With his work as a background and more specimens now available from this locality, it is clear that only one morphological species, *Zamites recta* (Tate) Seward, is recognizable in the Kirkwood Formation. One species, *Zamites africana* (Tate) Seward, should be excluded from the genus *Zamites* particularly because of the form of its pinna base and mode of attachment to the rachis. A second of the four species, *Zamites rubidgei* (Tate) Seward, is based on a single incomplete specimen, which shows only five parallel tapering leaves or pinnae but with no distinctive structure by which it could be assigned with confidence to any genus. Of the two remaining species, *Zamites morrisii* (Tate) Seward and *Zamites recta*, the latter has nomenclatural priority due to its occurring first in the treatment of Tate (1867). This paper will outline the reasons for combining the two species into one more comprehensive species and review the morphology of the leaves and their association with a bennettitalean scale leaf *Cycadolepis jenkinsiana* (Tate) Seward which occurs exclusively with them.

The large scale leaves of *Cycadolepis jenkinsiana* (Tate) Seward form a conspicuous, if numerically minor, portion of the flora from the Kirkwood Formation of the Algoa Basin. *Cycadolepis* here is used in the broadest sense following the diagnosis as amended by Harris (1953, 1969). The morphological features of these scale leaves require amplification since the study by Seward (1903) seems inadequate in his interpretation of the pattern of veins on the leaf surface.

SYSTEMATIC PALAEOBOTANY

Order Bennettitales

Genus: *Cycadolepis* Saporta, 1875 (emend. Harris, 1953)

Species: *Cycadolepis jenkinsiana* (Tate) Seward, 1903
(Figures 1, 2)

Synonymy

Cyclopteris jenkinsiana Tate 1867, p. 146, Plate 6, Figure 4

Diagnosis emended

Scale-leaves, ovate to orbicular; margin entire; base truncate; apex obtuse; surface with midrib which may extend to apex; larger veins numerous, 2 mm apart, forking, curving from base to margin with occasional anastomoses; smaller veins between larger, generally parallel with large veins, irregularly anastomosing, 2-10 mm; cuticle thick with occasional sinuous walled cells; stomata not seen.

Locality

Specimens utilized in this study were collected from the Kirkwood Formation 3/4 km west of Dunbrody Station on the west-facing cliff of the Bezuidenhout's River, 14 km east of Kirkwood, Cape Province, South Africa. The illustrated specimens are held in the type collection of the Bernard Price Institute for Palaeontological Research of the University of the Witwatersrand, Johannesburg and catalogued under their BPI (Pal) PB numbers. Other specimens are catalogued with their accession code 276.

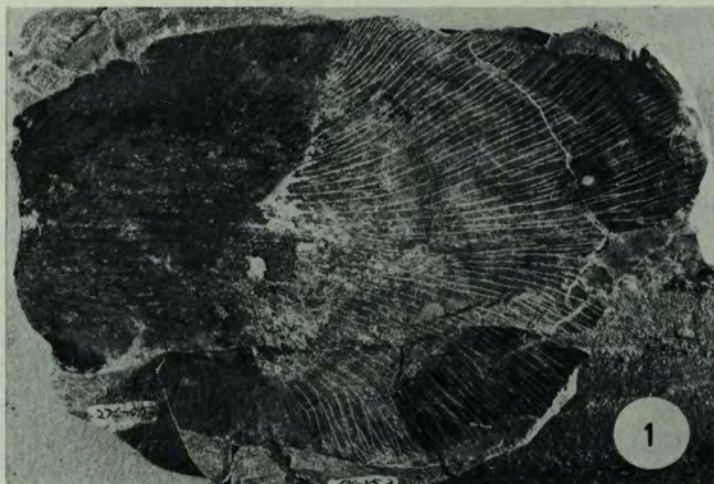


Figure 1. *Cycadolepis jenkinsiana*. PB 313 $\times 0,6$. A single nearly complete leaf.

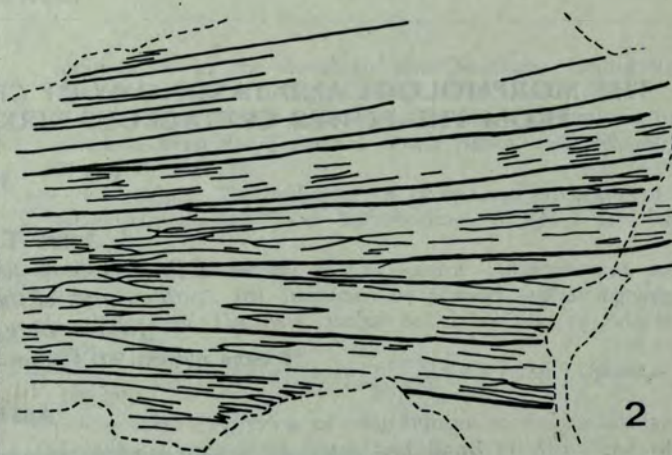


Figure 2. *Cycadolepis jenkinsiana*. PB 314 $\times 3$. Line drawing of minor vein pattern.

Description

Complete specimens of this scale leaf measure up to 13,5 cm long by 12 cm or more wide; most are broadest about half way along the length of the leaf. The margin is entire and without ornamentation. The base is one-third of the total width of the leaf and shows no evidence of a petiole. A large number of sub-parallel veins enter the base about 1 to 1,5 mm apart. Specimen PB 313 (fig. 1) has 22 veins across a width of 4,0 cm. The veins nearest the mid-line are essentially straight, paralleling the midvein; those entering the base nearer the margin arch gently outward and curve to become perpendicular to the margin in the proximal half of the leaf, but the angle with the margin is less for those ending in the distal portion (fig. 1). These veins end blindly near the margin. The midvein is of a complex nature. It seems to be composed of a central bundle of veins similar to those which occur in the laminar portion of the leaf. Smaller lamina veins do not seem to branch off this midvein but rather arise from the repeated forking of those which enter the lamina independently at the leaf base. This midvein may not have been a vein at all but a strand of supporting tissue. Veins which traverse the lamina dichotomize repeatedly but at irregular intervals to near the margin; then at about 1 to 2 cm from the margin each vein dichotomizes several times and the spaces between them become quite small. Anastomoses are rare, usually only seen at isolated intervals across the leaf (fig. 1). The specimen (PB 313) shown in Figure 1 has only 6 anastomoses visible on its surface.

The smaller veins which lie between the larger are very fine and generally parallel the larger veins. They fork and fuse frequently and irregularly; some cross connections between these fine veins are perpendicular to the vein courses, others more oblique or even acute. In areas where the larger veins are distant there may be 6 to 10 veins between the larger (fig. 2). Occasionally the smaller veins are seen to arise at an acute angle from the larger veins (fig. 2).

The cuticle of these leaves is very poorly preserved and the matrix surface is coarse and has not yielded adequate surface replicas for SEM preparations. Many small fragments of the cuticle have been mounted for optical examination and the only structure seen is an occasional impression of a thick very sinuous anticlinal wall.

Stomata were apparently very widely scattered, as occasional nearly circular holes of uniform size appear in the cuticle but nothing of their structure is preserved.

Discussion

The original attribution of this group of scale leaves to Saporta's (1874) genus was based entirely upon the macroscopic features of the leaves (Seward, 1903). Seward (1895) had enlarged Saporta's genus to include petiole bases and isolated scales which may have been fertile but which have lost evidence of either pollen- or megaspore-bearing structures. Later when the more precise taxonomic distinctions between the Cycadales and Bennettitales based on cuticular morphology became apparent, the diagnosis of *Cycadolepis* was restricted to those scale leaves of this general form having syndetocheilic stomata and restricted to the Bennettitales (Harris, 1953).

The Kirkwood specimens can be attributed to the Bennettitales only on two grounds: first, the sinuous walls of the epidermal cells as shown by their cuticular remains and, second, their restricted appearance with *Zamites recta* and no other bennettitalean leaf at this locality. These are not sufficient criteria to allow a dogmatic attribution of these leaves to *Cycadolepis*, but at least they give some evidence for the choice of the genus.

Our more recently collected specimens from Be-zuidenhout's River locality near Dunbrody Station certainly belong to the same taxon as those described and illustrated by Seward (1903).

There is one interpretation based on the newly collected specimens which differs considerably from

that of Seward (1903). He interpreted the fine dark lines between the major veins as a ramentum of anastomosing or at least overlapping hairs. This seems unlikely for several reasons: the consistently parallel orientation of the network, its anastomosing character and the length of the individual members which make up the reticulum (fig. 2).

All of these taken together seem to indicate a network of small veins rather than a surface covered with long and very unusual epidermal hairs. It is possible that the larger structures were not conducting tissue but a ramifying series of supportive strands of sclerenchymatous or collenchymatous nature, with the fine network representing the veins.

The state of preservation does not allow other identification of the cell types which make up the two networks which would be necessary to distinguish between conductive or supportive tissues. It is also possible that the larger structures were complex fibrovascular bundles having both types of tissue and serving the combined function of support and conduction.

At present *Cycadolepis jenkinsiana* must stand as a possible bennettitalean scale-leaf with a complex and unusual surface pattern of two distinct types of branching and anastomosing fibrous networks.

Genus: *Zamites* Brongniart, 1828

Species: *Zamites recta* (Tate) Seward, 1903 (figs. 3, 4).

Synonymy

Palaeozamia (*Otozamites*) *recta* Tate, 1867. p. 144, Plate 5, Figure 7a, b.

Palaeozamia (*Podozamites*) *morrisii* Tate 1867. p. 145, Plate 5, Figure 4.

Zamites morrisii (Tate) Seward, 1903. p. 25, Plate 5, Figure 4.

Diagnosis emended. Compound frond, lanceolate, up to 60 cm in length; apex acute; pinnae attached to upper surface of rachis, opposite or alternate; lanceolate, margin entire, base contracted, truncate,

with callosity or thickening on upper surface at point of attachment to rachis, apex acute; veins sub-parallel from base, or spreading slightly, 10 per mm; rachis woody, with hexagonal raised scars at point of pinna abscission; petiole not represented; cuticle thick, with impressions of sinuous anticlinal wall thickenings.

Locality

Kirkwood Formation, 3/4 km west of Dunbrody Station on west-facing cliff of Bezuidenhout's River, Cape Province, South Africa.

Description

A large number of incomplete fronds of *Zamites recta* are now known, but none of these is complete at its base so no specimen has been obtained with a petiole. The most proximal leaflets are also unknown. Seward (1903) estimated that the fronds of *Zamites recta* were up to 60 cm in length but this is an unsupported suggestion. Pinnae of *Z. recta* range from quite small, less than 3 cm long near the apex of the frond to 7 cm long from wider portions of the leaf. Pinnae range in shape from nearly straight to markedly falcate but all have the characteristic vein pattern and relatively obvious constriction at the base of the pinna. The rachis as shown by Seward (1903) has very prominent ribbed cushions where individual pinnae have abscised naturally or been torn away. The veins which enter through the constricted point of attachment of the pinnae bifurcate and spread to occupy evenly the entire width of the pinnae (fig. 3). Beyond the near basal region they run nearly parallel to the margins of the pinna and do not fork or anastomose further. Near the apex of the pinna the veins may be slightly closer together but generally run directly to the margin and end blindly there.

Cuticle fragments have been macerated from a single specimen of *Zamites recta* (fig. 4) but show very little structure except for occasional sinuousities as



Figure 3. *Zamites recta*. PB 315 \times 1.5. Portion of frond showing pinna bases and venation.

Figure 4. *Zamites recta*. PB 316. \times 1.5. Portion of frond with complete pinna.

are found in almost all bennettitalean leaf cuticles. No other cuticular structure is visible and surface replicas of impression specimens have failed to provide any further information on the cell pattern of the pinnae or rachis.

Discussion

Typical *Zamites recta* comprises the bulk of both Seward's material and that collected recently. *Zamites morrisii* was known only from a single specimen which appeared to be smaller and to represent only a slight variant of the general pattern of the pinnae of *Z. recta*. The range of variation in *Zamites recta* is sufficient to include *Z. morrisii* easily and the relatively broader form of the pinnae of *Z. morrisii* is found in larger specimens of *Z. recta*.

Zamites africana is clearly distinct from *Zamites*. The pinnae are not constricted at their point of attachment to the rachis and the proximal basal margin is decurrent on the rachis where it seems continuous with the distal margin of the adjacent pinna (Seward, 1903). This form of leaf would better be classified as *Pterophyllum* if the pinnae are set laterally on the rachis as they seem to be in Seward's Plate 5, Figure 3. This is assuming that they are bennettitalean and do not belong to the Cycadales.

Zamites rubidgei is known only from five large (13.5 cm long × 1 cm wide) leaf fragments with parallel veins lying on a single block of shale (Seward, 1903). Neither the apex nor base is shown in any of the five fragments. With so little data to work with, no convincing classification is possible.

Frankel (1960) has reported the occurrence of both *Zamites recta* and *Zamites rubidgei* from the Lower Cretaceous rocks along the Umfolosi River in Natal. His illustration of *Zamites recta* (fig. 4) appears very similar to Seward's *Zamites africana* with laterally

attached broad-based pinnae of the *Pterophyllum* type. The illustrated specimen of *Zamites rubidgei* (plate 35, fig. 2) is more like *Zamites recta* as it is defined now. The original *Z. rubidgei* had not sufficient taxonomic characters present to justify its erection as a separate species and the Umfolosi specimens are better preserved and more complete than the type specimen of *Z. rubidgei*. It is best to include these as representatives of the most completely known species whose characters they match than to refer them to an ill-defined species thus creating two equivalent species with the same morphology.

Seward listed several species of *Zamites* known from other Mesozoic localities which resemble *Z. recta*. The most closely allied species seems to be, as Seward (1903) mentioned, *Zamites gigas* (L. and H.) Morris from the Jurassic of Yorkshire. This is a very well-defined species of *Zamites* which has recently been studied extensively in its macro- and microscopic morphology (Harris, 1969). The South African specimens have unfortunately not sufficiently well preserved cuticle for a close comparison with *Z. gigas*, but appear in general to fit very close to the English species within the genus. It is interesting to note that Harris (1969), in his taxonomic treatment of *Z. gigas*, lists nine species of *Zamites* which are similar to *Z. gigas* but have no known cuticle, including four of the six species used by Seward (1903) in his comparisons with *Z. recta*, but Harris does not include *Z. recta*.

The association with scale leaves assigned by Seward to *Cycadolepis jenkinsiana* is a strong one. No other known species of bennettitalean foliage leaf occurs with the scale-leaves at any of the Kirkwood Formation plant fossil localities.

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