

# *Parapodocarpus* gen. nov. and its implications for interpreting the ovulate organ in the Podocarpaceae

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The systematic position of Podocarpaceae has been open to question because the extant taxa in this family were thought to lack organized cones, and there were no well-defined bracts and scales in their ovulate cones. A new genus, *Parapodocarpus* gen. nov., is established based upon the bract-scale complexes, which are found either isolated or attached to an axis. The morphology and anatomy of the bract-scale complexes were examined using an SEM and paraffin sections under optical microscope, respectively. The fossil bract-scale complexes are similar to those of extant Podocarpaceae in their early development. These fossils are important in the systematics of Podocarpaceae because they have structures that can be interpreted as scales and bracts, with the bract enclosing most of the scale. A new interpretation of the spatial relationship between the bract and scale is proposed, allowing a closer relationship between Podocarpaceae and other coniferous families (e.g., Pinaceae, Araucariaceae). This interpretation broadens applicability of the bract-scale complex concept proposed by Florin.

**Key-words**— Podocarpaceae, Bract, Scale, Ovulate cone, Fossil, Cretaceous.

## INTRODUCTION

THE extant Podocarpaceae are mainly a Southern Hemisphere family with some elements in the Northern Hemisphere (Kelch, 1997; Hill & Brodribb, 1999), divided into 8 to 19 genera by different taxonomists (Cheng *et al.*, 1978; Fu *et al.*, 1999; Hill & Brodribb, 1999; Quinn & Price, 2003). The genus *Podocarpus* is very diversified and includes over 90 species (De Laubenfels, 1985). The Podocarpaceae are restricted primarily to rainforest or wet montane environments where they compete efficiently with angiosperms (Hill & Brodribb, 1999). The history of Podocarpaceae can be traced back to the Triassic (Yao *et al.*, 1997; Hill & Brodribb, 1999) or even possibly to the Permian (Yao *et al.*, 2000), consisting primarily of Southern Hemisphere records (Jurassic<sup>+</sup> Vishnu-Mittre, 1957; Bose & Maheshwari, 1974; Jurassic, Townrow, 1967a,b; Triassic, Anderson, 1978; Tertiary, Wells & Hill, 1989; Triassic, Meyer-Berthaud & Taylor, 1991; Triassic, Yao *et al.*, 1993; Pleistocene, Jordan, 1995) and a few Northern Hemisphere records (Recent, Sharp 1946; Eocene, Dilcher 1969; Cretaceous, Krassilov 1974; Triassic, Zhou 1983; Jurassic, Reymanowna, 1987; Recent, Contreras-Medina *et al.*, 2006). Such a distribution might suggest a "Gondwanan" origin (Kelch, 1997). The Cenozoic records of

Podocarpaceae are extensive in the Southern Hemisphere, which demonstrates a high diversity and widespread distribution of the family in the past (Hill & Brodribb, 1999). Although many vegetative organs are found in the fossil record (Hill & Carpenter, 1991; Jordan, 1995; Axsmith, *et al.*, 1998), only a few reproductive organs are reported (Zhou, 1983; Reymanowna, 1987; Axsmith *et al.*, 1998; Hill & Brodribb, 1999).

In this paper, a Lower Cretaceous (late Albian) occurrence of podocarpaceous ovulate organs in the Northern Hemisphere (Kansas, USA) is presented. The well-preserved bract-scale complexes are found either isolated or attached to an axis in the Dakota Formation. Characters of these bract-scale complexes appear to bridge the morphological gap between Podocarpaceae and other conifer families.

## MATERIAL AND METHODS

The Dakota Formation consists of sediments deposited during the late Albian and early Cenomanian (Brenner *et al.*, 2000) along the margins of the Western Interior Seaway in North America. These sediments are widely distributed from New Mexico and Arizona all the way northeast to Iowa and Minnesota.

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<sup>\*</sup>now considered early Cretaceous (Tiwari & Tripathi, 1995; Banerji & Jana, 1998)

The fossil material reported here was collected from a Dakota Formation outcrop near Blackwolf (38°43'52"N, 98°22'13"W, Plate 1), Ellsworth County, Kansas, USA during the summers of 1999 and 2000. The sediments are considered Late Albian (Brenner *et al.*, 2000). Samples were collected from organic rich claystone and clayey sandstone. The samples were macerated in filtered tap water for more than one week. Mechanical agitation was required for some of the more resistant samples. After maceration, the samples were filtered using a USA Standard Testing Sieve No. 35 (mesh size of 0.5 mm). Then the samples were dried under low heat, cleaned with 20% hydrochloric acid (HCl), then with 49% hydrofluoric acid (HF), washed and dried. The specimens reported here were picked out for study from the samples using a dissecting microscope.

The specimens for scanning electron microscopy (SEM) were coated with gold-palladium in a sputter at least four times to ensure they were well-coated, then viewed using a Hitachi S-570 or S-4000 FE SEM. Photographs were taken using a Nikon camera with TMax 100 film, or in digital mode. After SEM observation, one specimen (Plate 2, Figs 2g-m) was processed using HNO<sub>3</sub>, embedded in paraffin and sectioned at intervals of 16 µm (Johansen, 1940; Jensen, 1962).

Samples of *Podocarpus nerrifolius* Don and *Nageia nagi* (Thunb.) Kuntze were collected from Hangzhou, Zhejiang Province in China in 1993-1994. They were fixed, embedded in paraffin, sectioned and then observed under a Leitz microscope.

### SYSTEMATIC DESCRIPTION

Class - Pinopsida

Order - Pinales

Family – Podocarpaceae Endlicher, 1847

Genus — *Parapodocarpus* Wang *et* Dilcher gen. nov.

*Type species* - *Parapodocarpus kansensis* Wang *et* Dilcher sp. nov.

*Diagnosis*: Bract-scale complex spatulate. Scale for the most part enclosed by a bract, exposed adaxially only in depression close to tip of the bract, with micropyle directed more or less towards the bract tip.

*Etymology*: “Para-” similar to, “-podocarpus” extant genus in Podocarpaceae.

*Remarks*: The immature nature of *Parapodocarpus* is presumed due to the lack of a seed, and its similarity to the ovulate organ of podocarps in their early stages. In *Nageia nagi* (Plate-3, Fig. a; Li, 1995, Plate XVIII, Fig. 1) and *Podocarpus nerrifolius* (Plate-3, Fig. b; Li, 1995, Plate XVI, Fig. 2), the megaspore mother cell occurs about 10 cells under the nucellus surface, and is characterized by surrounding smaller cells with denser cytoplasm. A similar situation is seen in a comparable position in *Parapodocarpus*: a cluster of

cells with dense cellular contents (Plate 2, Fig. j, central dark material), which is distinct from other surrounding tissues, are embedded in the scale tissue just below the bottom of the distal cavity within the micropyle. This kind of dense cellular contents does not occur in other portions of the specimen (Plate 2, Figs k, m; sect. 9). Therefore, we think that the bract-scale complexes are immature and so it is not surprising that no seed is found in these fossils. Early development of ovulate organs in extant podocarps (such as *Acmopyle pancheri* (Brongn. & Gris.) Pilg., Figs. 2G&H in Mill *et al.*, 2001; *Podocarpus elatus*, Figs 52-53 in Tomlinson & Takaso, 2002) are very similar in general morphology to that in the fossils described here (Plate 2, Figs e-h).

Anatomically, there is no separation between the bract and scale in the proximal portion of the bract-scale complex (Plate 2, Fig. m: sects. 8-11), but there is a distinct separation in the distal portion of the complex (Plate 2, Fig. m: sects. 3-6).

The configuration and morphology of the fossils described here also suggest some similarities to mature female reproductive organs of Ginkgoales. In *Parapodocarpus*, the circular configuration of the micropyle (Plate 2, Figs b, f-i) and the surrounding tissue are similar to the seed scar and collar of Ginkgoales at first sight, but in Ginkgoales the seed scar is larger (3-8.5 mm, UF0901; Zhou & Zheng, 2003; Zheng & Zhou, 2004) with two bundle traces entering the ovule (Carothers, 1907). In addition, the seed scar area and collar are terminal in Ginkgoales, not lateral as in *Parapodocarpus* (Plate 2, Figs a-h) and extant Podocarpaceae. The ovulate scales in the fossils are situated on the adaxial of the bract or compressed as if lateral, as in Podocarpaceae; but the ovulate organs of Ginkgoaceae are terminal (Takaso, 1980), usually with one fertile ovule (Crane *et al.*, 1990). Based on above comparisons, we think it unlikely that the fossils are related to Ginkgoales.

*Species* - *Parapodocarpus kansensis* Wang *et* Dilcher sp. nov.

Plate 2, Figs a-m; Text-Fig. 1, a-d.

*Diagnosis*: Bract-scale complex spatulate. Scale enclosed in a bract, and exposed only in an elliptical or rounded triangular depression on the adaxial surface in the distal portion of the bract. Bract with narrow, round or keeled proximal portion and the distal portion enlarged, surrounding and enclosing the scale.

Number of specimens examined: 5.

Specimen numbers: UF15719-44002, UF15719-44003, UF15719-44004, UF15719-44005, UF15719-44006.

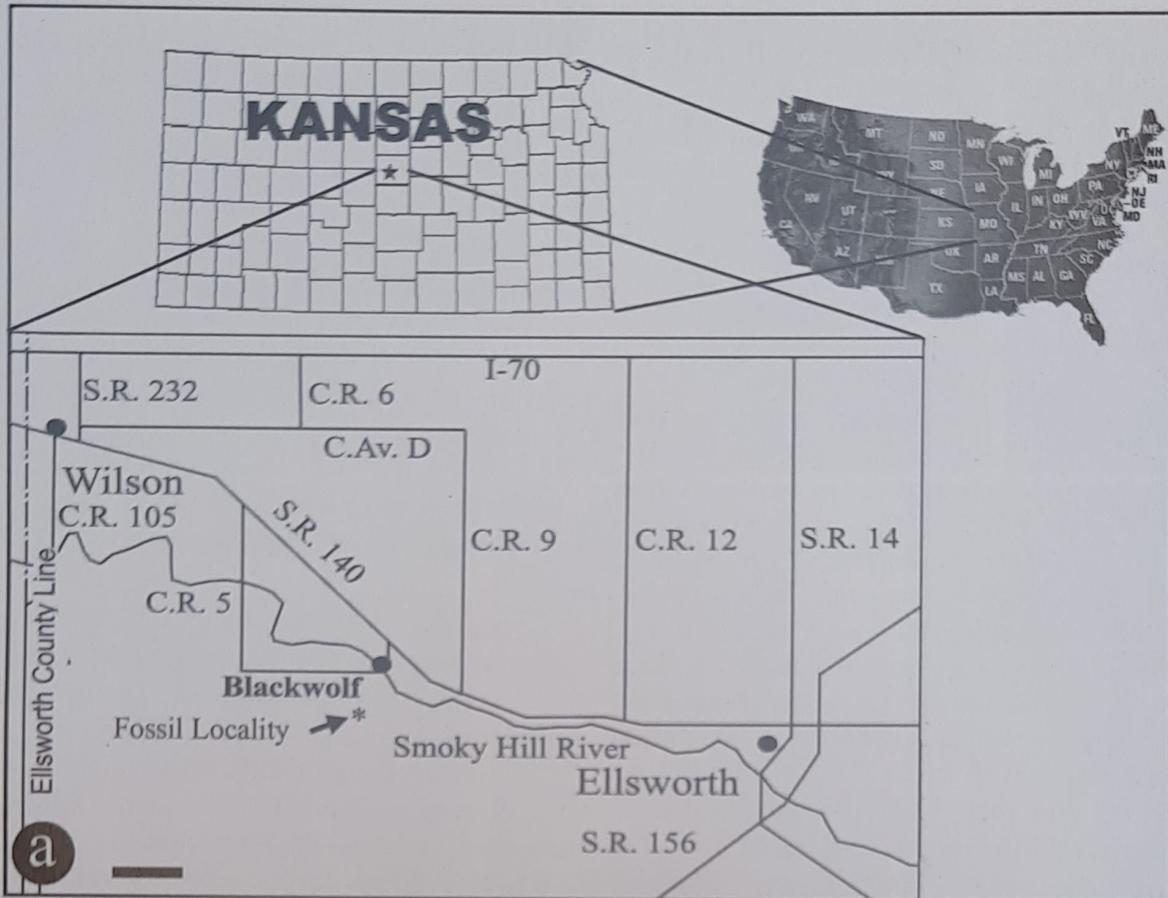
*Etymology*: The specific epithet “kansensis” signifies the origin of the specimen, the state of Kansas.

*Holotype*: UF15719-44002, Plate 2, Figs a, b.

*Locality*: Blackwolf, Ellsworth County, Kansas.

*Age*: Late Albian, Lower Cretaceous.

*Stratigraphic position*: The Dakota Formation.



## PLATE -1

Figures a, b: Geographic position of the fossil locality in Kansas, USA.

a: A map of the United States with the state of Kansas enlarged to show the vicinity of the fossil locality.

b: A view of the outcrop near Blackwolf. The outcrop is located in Ellsworth County, Kansas (38°43'52"N, 98°22'13"W). Bar = 2.58 km.

**Repository:** The Paleobotanical and Palynological Collection, Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA.

**Description:** Fragment of an ovulate organ, width >2.9 mm (Plate 2, Fig. a), consisting of bract-scale complexes attached to an axis (Plate 2, Fig. a) or isolated (Plate 2, Figs c-e, h). Axis width about 0.26 mm (Plate 2, Fig. a). Bract-scale complex more or less spatulate (Plate 2, Figs a, c, e, g, h), 2.3-3.6 mm long, 0.5-0.6 mm thick, about 0.2-0.3 mm wide at the base and up to 0.8-1 mm wide at the tip (Plate 2, Figs a, c-e, g, h). Tip of the bract slightly hooded and arching over the scale. Scale inserted on the adaxial surface of the bract (Plate 2, Figs a, c-e, g, h). Part of the scale composed of parenchyma tissue (Plate 2, Fig. k), mostly enclosed in the keeled bract (Plate 2, Figs k, m: sects. 9, 10; Text-Fig. 1, d), exposed only in a semi-elliptical or round triangular depression formed by the distal portion of the bract. Micropyle more or less erect or pointing slightly toward the tip of the bract (Plate 2, Figs a-g). Possible megaspore deeply embedded in the scale tissue beneath the bottom of the micropylar cavity, composed of cells smaller than the surrounding ones with dense cellular contents (Plate 2, Figs j, m; sects. 7-8). A cavity in the distal portion of scale, with an opening 40-70  $\mu\text{m}$  in diameter (Plate 2, Figs b, f, g, i), thickened at the tip (Plate 2, Fig i). Fine striations on the surfaces of the cone axis and bract-scale complexes (Plate 2, Figs a, e, g, h).

**Extant Material:** For comparative analyses with extant podocarps, the premature ovulate organs of *Nageia nagi* (Plate-3, Fig. a) and *Podocarpus nerrifolius* (Plate-3, Fig. b) were

longitudinally sectioned. These sections clearly show, by following the continuity of the similar tissues, that the scale is sandwiched between the bract tissues (Plate-3, Figs a-c). The megaspore mother cell is seen beneath the dome situated on the bottom of the micropylar cavity (Plate-3, Figs a-b).

**Remarks:** Only a portion of the female reproductive structure is preserved. The fragmental axis, less than 1.5 mm long (Plate 2, Fig. a), may be a part of a lax cone composed of multiple bract-scale complexes. Such cones have been found in extinct *Mehtaia* (Vishnu-Mittre, 1957, Plate 6, Fig. 37), and extant podocarps (Stiles, 1912; Gibbs, 1912; Tomlinson, 1992). In the fossils presented here, the apical region of the scale has a central cavity with a circular opening (Plate 2, Figs b, f-i), distinct from the semicircular abscission zone with resin canals after the seed falls off in extant podocarps (UF1156; Mill *et al.*, 2001).

An opening is formed on the tip of the scale with a non-radial symmetrical configuration. In this paper we interpret this opening as the micropyle based on comparison with its counterpart in extant podocarps (Bierhorst, 1971, Fig. 25-13A; Mill *et al.*, 2001, Figs 2G&H; Tomlinson & Takaso, 2002, Figs 52-53, especially in Fig. 53; and Plate-3). The distal margin of the micropyle is apparently narrower than the proximal margin, with left and right sides symmetrical (Plate 2, Figs b, f, g; Text-Fig.1, a, b). This configuration implies that the micropyle points to the distal portion of the bract. Anatomical data is based on one specimen (UF15719-44006) that was serially sectioned.



## PLATE -2

Figures a-m: *Parapodocarpus kansensis* gen. et. sp. nov.

a: Bract-scale complex attached to a cone axis. Note the sturdy basal portion of the complex. Holotype. UF15719-44002. b: Detailed view of Fig. a showing a micropyle. Note the asymmetrical configuration of the micropyle where the distal margin is much narrower than the lateral and proximal margins. c: Oblique view of an isolated bract-scale complex with an unknown structure (arrow). UF15719-44003. d: Lateral view of a bract-scale complex. Note the hood (arrow) formed by a bract at the tip, and a relatively slender basal portion (also see Text-Fig.1). UF15719-44004. e: Adaxial view of a bract-scale complex. Note the pointed apex, sturdy basal portion (also see Text-Fig.1), and the scale in an elliptical depression of the bract. The rectangular region is magnified in Fig. f. f: Detailed view of Fig. e showing the micropyle. Scale apical configuration is similar to Fig. b. Note that the scale is in an elliptical depression of the bract. Paratype. UF15719-44005. g-m. Bract-scale complex with anatomy shown. UF15719-44006. g: Detailed view of Fig. h showing the micropyle. Scale apical configuration is similar to Fig. b. Note that the scale is situated in the round triangular hood formed by bract (also see Text-Fig.1). h: Adaxial view of an isolated bract-scale complex. Note the slender and twisting basal portion of the complex (also see Text-Fig.1). The bars on the left margin mark the positions of sections shown in Fig. m. i: Longitudinal cross section of the micropyle of the specimen in Fig. h. Note the thickening around the micropyle. This portion of the scale fell off during  $\text{HNO}_3$  processing, so it is shown separately, rather than in connection with other portions of the scale in Fig. m. j: Transverse section across the megaspore region in the specimen shown in Fig. h. Note the dense cellular content and thin walls of the cells, compared with Fig. k. This is a detailed view of Fig. m: section 8. For magnification, refer to the bar in Fig. k. k: Transverse section across the position below the megaspore region in the specimen in Fig. h. Note the thin wall tissue and very little cellular content, compared with Fig. j. This is a detailed view of Fig. m: section 9. l: Top view of the bract-scale complex in Fig. h. Note the hood completely eclipsing the scale so only the bract is visible. m: Serial transverse sections of the specimen shown in Fig. h. Sections 1-11 show the cross view of the specimen from top to bottom, as marked in Fig. h. Note that the mainly thick-walled tissue of the bract enclosing the mainly thin-walled tissue of the scale in the proximal half of the bract-scale complex, and that there is a keel (arrow in Fig. m: section 9) on the abaxial side (left side) of the bract. Section 8 is the one cutting across the position of the megaspore region in the complex. Also keep in mind that the tip portion of the scale (micropyle), which fell off during processing, is missing in these sections. These are sections No. 36, 55, 63, 74, 77, 79, 80, 82, 84, 110 and 165, respectively, from a total of 187 sections, and their positions are marked in Fig. h. The sections are from Slide a (58 sections), Slide b (59 sections), Slide c (35 sections) and Slide d (35 sections). Figs a-h, l are SEM pictures, others are light microscopy. Scale bars for Figs a, c, d, e, h = 1 mm; Figs b, f, j, k = 0.1mm; Fig. g, l = 0.5 mm; Fig. i = 0.2 mm; Fig. m = 0.4 mm. os = scale, br = bract, ca = cone axis.



Scale tissue is mainly composed of parenchyma, extending from megaspore region to the base of the bract-scale complex (Plate 2, Figs k, m; sects. 9-11). It can be rationally assumed that the parenchyma tissue continues into the cone axis, although it is not preserved in this specimen.

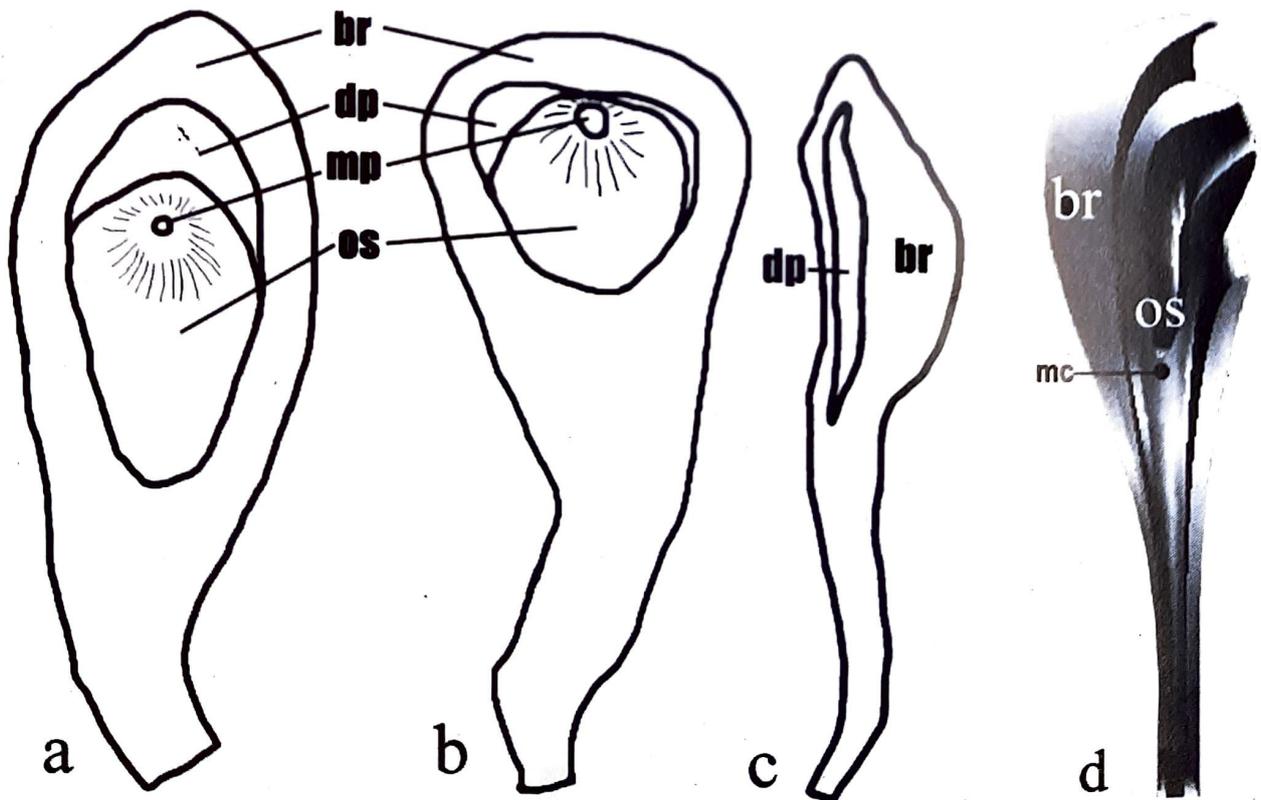
The micropyle of UF15719-44006 became detached when processed with nitric acid, so it was sectioned separately (Plate 2, Fig. i). There is one small structure (UF15719-44003; Plate 2, Fig. c, arrow) that might be an aborted bract-scale complex, a sterile bract, a tip of the cone axis, or other undetermined structure.

## DISCUSSION

*Parapodocarpus* has the scale attached on the adaxial surface of the bract, and the bract encloses the scale for the most part (Plate 2, Fig. m; Text-Fig. 1, d; Plate-3, Figs a-c). As in Plate 2, Fig. m: sects. 4-5, the scale is surrounded or enclosed by the keeled bract. This spatial relationship between scale and bract has not previously been reported for fossil or extant conifers. However, similar situations have been documented (although not explicitly stated) in *Nageia nagi* (Plate-3, Fig. a; Li, 1995, Plate XVIII, Figs 1-5), *Podocarpus nerrifolius* (Plate-

3, Fig. b; Li, 1995, Plate XVI, Fig., 2), *Acmopyle pancheri* (Mill *et al.*, 2001, Figs 2G&H), *Podocarpus elatus* (Tomlinson & Takaso, 2002, Figs 52-53), and *Dacrydium araucarioides* (Bierhorst, 1971, Fig. 25-13A). In *Nageia nagi* and *Podocarpus nerrifolius*, the continuation of similar tissue type suggests that the scale tissue is sandwiched between those of the bract. The bract ("adaxial bract", Tomlinson & Takaso, 2002, Fig. 49) in *Podocarpus elatus* tends to enclose the scale, which appears inserted onto the adaxial surface of the bract (Bierhorst, 1971, Fig. 25-13A; Mill *et al.*, 2001, Figs 2G&H; Tomlinson & Takaso, 2002, Figs 52-53, especially in Fig. 53). In *Parapodocarpus*, the bract and scale are not completely fused (Plate 2, Fig. m: sects. 3-8). In extant Podocarpaceae, fusion is so complete that the distinction between scale and bract is not discernable. This fusion has caused such confusion in the interpretation of the nature, morphology, and anatomy of the scale and bract that Tomlinson *et al.*, (1989) and Tomlinson & Takaso (2002) claimed that *Phyllocladus* in Podocarpaceae lacked an ovuliferous scale.

Florin (1944) suggested that the scale in Podocarpaceae was derived from a short shoot, and its fusion with the bract gave rise to the unique configuration of the bract-scale complex



Text-Fig. 1

a-d: Sketches and reconstruction of the bract-scale complexes.

a, b and c: Sketches of isolated bract-scale complexes shown in Plate-2, Figs e, h, d.

d: An idealized sketch of the longitudinal section of the bract-scale complex, showing the spatial relationship between the bract and scale. Note the megaspore region. br = bract; dp = depression formed by bract; mc = megaspore region; mp = micropyle; os = scale.

in Podocarpaceae, although how this came about was never elaborated.

Based on evidence presented, we propose that the bract in Podocarpaceae enclosed the scale in its axil and fused with its basal portion. The distinction between the bract and scale in the extant elements has been obscured due to the fusion, but the distinction can still be seen in the early podocarps (i.e. *Parapodocarpus*), especially in the distal portion (Plate 2, Fig. m: sects. 4-5).

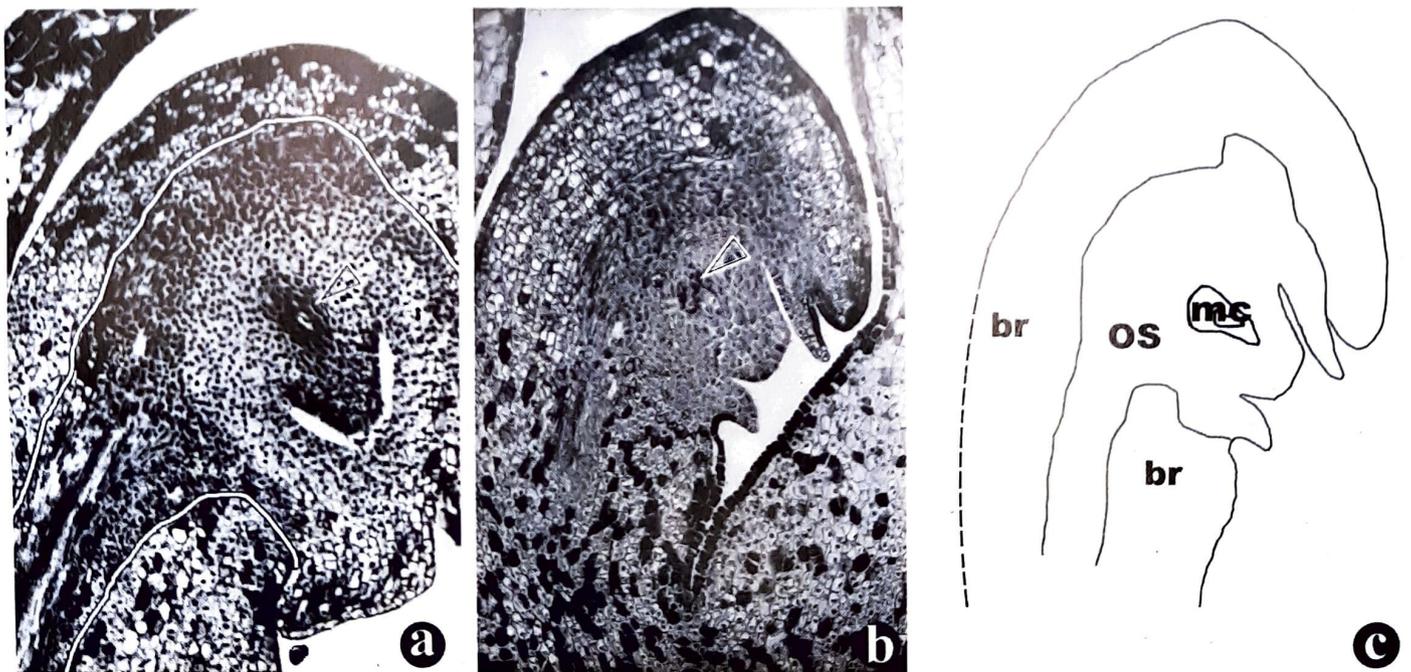
The fact that the epimatium appears later in the ontogeny of the bract-scale complex in extant Podocarpaceae (Stoffberg, 1991) implies that the epimatium is a relatively novel structure in Podocarpaceae, as Tomlinson *et al.* (1989) and Tomlinson (1992) suggested. Epimatium could be well taken as a modification of the distal portion of the scale (Florin, 1944; Vishnu-Mittre, 1957; De Laubenfels, 1992). This is in agreement with the lack of epimatium in *Parapodocarpus*.

The bract-scale complex is a diagnostic feature in conifers even though it could not be applied to the Podocarpaceae satisfactorily. Now with the evidence from the fossils, the ovulate organ of the Podocarpaceae can be interpreted as a bract-scale complex wherein the bract encloses most of the

scale leaving the apical portion exposed for pollination. This helps to bridge the gap between the Podocarpaceae and other conifer families.

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#### PLATE -3

Figures a-c: Longitudinal sections of bract-scale complexes of extant podocarps, showing relationship between bract and scale. a: A longitudinal section of a bract-scale of *Nageia nagi* at the time of megaspore genesis. Note the dark central cells around the megaspore mother cell (arrow) and the borders between different tissue types (white-black line). b: A longitudinal section of a bract-scale of *Podocarpus neriifolius*. Note the megaspore region (arrow), different tissue types and their spatial relationship. c: Sketch of Fig. b. Note the scale sandwiched between the tissues of the bract. For abbreviations, see Text-Fig.1 caption.

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