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GRØNLANDS GEOLOGISKE UNDERSØGELSE Bulletin No. 98

# FOSSIL PICRODENDROID FRUIT FROM THE UPPER DANIAN OF NÛGSSUAQ, WEST GREENLAND

BY

B. ESKE KOCH

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WITH 11 FIGURES IN THE TEXT, AND 24 PLATES

> KØBENHAVN 1972

#### GRØNLANDS GEOLOGISKE UNDERSØGELSE

#### The Geological Survey of Greenland

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#### Abstract

Rosenkrantzia picrodendroides n.gen. et n.sp., based on 47 specimens of fossil fruit in very good preservation, is described. The fruit was a nut (or drupe), with a thick pericarp of primitive anatomy. It is l-locular, containing one fully developed seed; about half of the specimens also contain remnants of a second aborted seed. The seed is pendulous from an apical placenta, and has a long longitudinal raphe. Hilum is distal, chalaza basal. The original ovary can be reconstructed: l-locular with min. two ovules, pendulous from the distal placenta, anatropous. The fully developed seed consists mainly of two thick, interfolded cotyledons with no distinct endosperm.

The taxonomical investigation includes a study of fruits of two of the recent *Picrodendron* species. A phylogenetic conclusion is advanced which supports the position of the Picrodendraceae in the order Juglandales.

The taxonomic position of *Rosenkrantzia* appears to lie somewhere between the Cupuliferae (*Quercus* group) and Juglandales, or in palaeontological terms, between the *Dryophyllum* and *Dewalquea* groups.

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Fig. 1. Map showing a section of northern West Greenland with the localities which are mentioned in the text. 1: Scaphitesnæsen. 2: big section, Qaersutjægerdal. 3: big section, Agatkløft.

## INTRODUCTION

This publication describes fossil fruits collected from Upper Danian localities in the interior of Nûgssuaq.

Since 1946 expeditions to Nûgssuaq led by Professor A. ROSEN-KRANTZ, under the auspices of the Geological Survey of Greenland, have studied the geology and palaeontology of the region. Agatdalen in central Nûgssuaq proved to be of special interest, its rich fossiliferous localities making it a stratigraphical key area for the Senonian and Danian of West Greenland (textfig. 1). Well-preserved fossil fruits were collected by Professor A. ROSENKRANTZ and his colleagues during their extensive collecting of marine fossils from the Upper Danian deltaic deposits of the Agatdal Formation. As a participant in some of these expeditions the author had the opportunity to concentrate on collecting fossil plants, and in the summer of 1956 in particular a good collection of fossil fruits was made at Scaphitesnæsen (textfig. 1).

The deposits of the Agatdal Formation, consisting of deltaic and interdigitating marine beds in Agatdalen, were first assigned by Professor A. ROSENKRANTZ (KOCH, 1963) to the Lower Paleocene. Hence, the first part of the author's studies on the fossil flora on Agatdalen was published under the heading: 'Fossil plants from the Lower Paleocene ......'. Marine fossils are abundant and from a study of the molluscs the age was modified to Upper Danian (ROSENKRANTZ, 1970). Because of the geographical position, isolated from areas with synchronous deposits, stratigraphic correlation is difficult and it is complicated by the current discussion on the Cretaceous-Tertiary boundary and the position of the Danian. During the discussions on the Cretaceous-Tertiary boundary ROSENKRANTZ often expressed the opinion that the Danian ought to be accepted as the lowermost Tertiary so that little is in reality changed and in fact the plants discussed here lived just on the threshold of the Tertiary.



Fig. 2. Rosenkrantzia picrodendroides n. gen. et n. sp. Central length-section: n: calcified nucellus with reproduction of the cotyledonous structure. p: pericarp. s: stylar base. t: testa.

4:1. GGU no. 9249.41. Loc. Scaphitesnæsen.

Косн phot.

### ROSENKRANTZIA

n. gen.

#### Diagnosis

Fossil fruit with a thick pericarp differentiated into 3 layers: exo-, meso- and endocarp. The dominating layer is the mesocarp consisting of a dense sclerenchyma, enclosing 12 eustelic conducting strands, leading longitudinally from the petiole to the distal end. Fruit 1-locular containing 1 fully developed seed; in many cases the remnants of a second, aborted seed is present. Placenta apical; seed(s) pendulous and with long raphe. Hilum and chalaza at opposite ends of the seed, hilum distal, chalaza basal. The original ovary was 1-locular, placenta distal with min. 2 anatropous, pendulous ovules.

The seed consists mainly of two thick interfolded cotyledons, no distinct endosperm.

# ROSENKRANTZIA PICRODENDROIDES n. gen. et n. sp.

Holotypus: Specimen GGU no. 9249.14 (cut into 9 thin sections). Locus typicus: Scaphitesnæsen, Turritellakløft.

Stratum typicum: The beds of Turritellakløft Member (ROSENKRANTZ in Koch, 1959, 75–78), exposed in the Scaphitesnæsen locality, Turritellakløft. Upper Danian; beds which are equivalent to part of the *Macclintockia* Zone (Koch, 1963).

#### Diagnosis

A fossil fruit, subglobose varying between ellipsoid and ovoid. Dimensions varying between the following extremes: axial length: 2.0-3.0 cm; maximum diameter in cross-sections: 1.8-2.5 cm.

Short petiole with abscission scar. Surface-sculpture of 12 stout, longitudinal ribs consisting of wood fibres. Distal stylar papilla. Thick pericarp (endocarp?) of 3 layers, the middle layer being the major one, consisting of stout sclerenchymatic tissue, enclosing 12 large, excentric, eustelic conducting structures, situated inside the wood fibre strands of the ribs. In the symmetry plane of the fruit, at the inner border of the pericarp is a single concentric funicular strand which leads from the petiolar region to the distal end where it enters the placenta and continues into the funiculus.

Fruit 1-locular. Ovary had 2 ovules of which only one matured. Relics of the aborted seed may be left in the locule at the side along the funicular strand, leaving a longitudinal sinus in the mature seed. Accordingly, the mature seed varies in shape: oblong-guttiform with or without a more or less distinct longitudinal sinus; accordingly the cross-section is subcircular-cordate. Seed with thin 2-layered testa; seed derives from a pendulous, anatropous ovule. Hilum distal. Raphe preserved on testa, flat and wide, leading from distal to proximal end of the seed in its symmetry plane. Chalaza proximal, slightly excentric. From chalaza 15 testal strands diverge, leading longitudinally to the distal end of the seed. 2 intimately folded cotyledons dominate nucellus. The axes of the cotyledonous folds are parallel to the axes of the seed. No endosperm.

# Quantitative foundation of the study

The study is based on 47 fossil fruits of this species from the Upper Danian Agatdal Formation in Agatdalen (textfig. 1). Most specimens were collected at Scaphitesnæsen in the Turritellakløft canyon; a few specimens are from Qaersutjægerdal, most of which are fragments.

The collection consists of 24 relatively complete fruits, 18 complete seeds and 5 segments of the pericarp.

#### State of preservation

The Scaphitesnæsen locality is situated near a fault which separates the Upper Danian of the northern interior end of Agatdalen from the Senonian deposits of the southern lower part of the valley. The fossiliferous fine-grained sandstone is strongly shattered and intensely jointed. A precipitate of siderite in crystalline aggregates plays an important role as an infilling in the joints and is a characteristic coating on the rock specimens and fossils. Accordingly, the majority of the fossils from Scaphitesnæsen have suffered deformation (pl. 1, fig. 1). The fossils of the small collection from the Qaersutjægerdal valley (1 complete fruit (pl. 1, fig. 4, pl. 14, fig. 1), 1 complete seed (pl. 14, fig. 1) and 5 segments of the pericarp (pl. 10, figs 3, 6)) are well-preserved and undeformed.

The strong pericarp (endocarp?) is preserved as a combination of incoaling and mineralization (textfig. 2). Originally the pericarp (endocarp?) consisted mainly of sclerenchymatic tissue (pl. 9, figs 1-3), i.e. a

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strongly lignified structure which to a wide extent has been incoaled during diagenesis. This coal structure has been consolidated by calcite that fills the cell lumina, fissures and pores left by disintegration and other interstices. The testa of the seed has normally been incoaled (textfig. 2, t) and is preserved in the same way. The less resistant tissues, being originally a more permeable structure, were replaced by calcite, i.e. preserved in mineralization. Hence, the nucellus is wholly calcified (textfig. 2, n). In some cases the entire nucellus is reproduced in calcite and even the cotyledon structure in outline (textfig. 2, n). In some cases parts of the nucellus have been dissolved before fossilization and the hollows left are partly filled with druses of calcite (pl. 2, figs 1-4; pl. 3, fig. 1).

A few compressions of pericarp segments have been found which are referred to this species.

## Description of the fossil structure

The shape of the fossil fruit in question varies between subglobular, ellipsoid and ovoid. The length axis of the biggest specimen is about 3 cm long (a half cm remnant of the petiole not included) (pl. 1, 4; pl. 14, fig. 1). The diameter of the maximum cross-section is 2.1-2.5 cm. The dimensions of the smallest specimens are 2.5 cm and 1.8-2.0 respectively. It is difficult exactly to state the proportions of the original fruit, because most specimens have suffered deformation. Hence the original shape can only be estimated from an evaluation of the total material. The fruit of *Rosenkrantzia picrodendroides* seems to have been ovoid with the axial proportions varying between the values 4:3:3 and 3:2:2 (textfig. 3) (pl. 1, figs 1-3).

#### Petiole

The fossil fruit has a 0.5 cm long, thick, cylindrical petiole (pl. 1, fig. 4). It ends in a concave abscission scar (pl. 1, fig. 5). On the scar is a prominent central dot in the position of the conducting strand. From this point 4 (?) ribs radiate, each one reaching a smaller, peripheral dot which is interpreted as a scar after an interrupted peripheral fibre strand. On the specimen GGU no. 35264 three dots can be observed, but judging from their position we must expect a fourth one which has been disturbed during the collection or preparation of the fossil.

#### Pericarp

The surface of the pericarp has 12 strong, longitudinal ribs (pl. 1, fig. 1B). On a single big specimen some ribs bifurcate, but, whether this



Fig. 3. Rosenkrantzia picrodendroides n.gen. et n. sp. General presentation of fossils: 1: specimen not worn (ribs preserved), compressed. 2: worn (rolled) and uncompressed specimen. 3: corroded specimen. 4: specimen not worn (ribs preserved), uncompressed.

1:1. GGU no. 1: 11705.1 2: 11705.11 3: 9249.31 4: 9249.16 Loc. Scaphitesnæsen.

is an original feature or one produced during deformation of the fruit cannot be determined. The specimen in question is somewhat flattened owing to deformation.

The pericarp is thick and makes up one fifth of the diameter of the fruit in central cross-sections (pl. 2, figs 2-3).

In the cross-sections of the pericarp 3 layers can be distinguished which, in this paper, tentatively are referred to as exo-, meso- and endocarp (pl. 2, fig. 4; pl. 3, fig. 1). This does not involve an interpretation or proof concerning the origin of these layers; but the terms are used provisionally for the practical purpose of concise description. The author is well aware that the present fossil fruit can be interpreted either as a remnant of a drupe with or without remnants left of the epicarp, or as a nut. The author has not solved this problem even though he is tempted to reject the latter possibility.

#### Exocarp

Of the 3 pericarpal layers the exterior one is massive and strongly incoaled (textfig. 2; pl. 3, fig. 3). Consequently it is opaque and has not revealed any cell structure by normal methods. Investigation in reflected light of a polished surface with the Ultrapak system of Leitz showed a lamellar structure conforming with the surface of the fruit which no doubt derives from a layered cellular structure. In the following discussion this layer is referred to as the exocarp.

#### Mesocarp

Next follows a thick pericarpal layer which tentatively is referred to as the mesocarp (pl. 2, fig. 4; pl. 3, fig. 1).

This layer consists of a massive sclerenchymatic tissue containing 12 large, eustelic conducting structures (pl. 3, figs 1–2). These stelar structures and the intervening areas of sclerenchymatic ground-tissue are equally wide and regularily scattered. The conducting structures are synchronous with the pericarpal ribs.

The conducting structures of the mesocarp are well-preserved (mineralized) revealing anatomical details. It is well illustrated by the type specimen (pl. 2, fig. 3; pl. 3, fig. 3) which has been cut into a series of thin sections. Of these the 3-4 central ones demonstrate the anatomy of the pericarpal conducting structures well (pl. 3, fig. 3). These structures will be described in detail:

The eustelic conducting structures (pl. 3, fig. 2) have a large central pith surrounded by a varying number of conducting strands (16) 15–10 (9) of which far the largest one is situated near the outer periphery of the mesocarp (centrifugal); the strands diminish in a centripetal direction; i.e. the smallest are found near to the inner margin of the mesocarp opposite to the larger strand. Hence, the eustelic structure is excentric in centrifugal direction. This is emphasized by the fact that the cross-section of the conducting structure is elliptical with the longest axis in radial direction. Centrifugally the conducting structures are protected by a solid tissue of very thick-walled wood-fibres (pl. 3, figs 2–3). In cross-section this massive tissue forms a crescent with its convexity in centrifugal direction. This crescent makes up the bulk of the ribs of the pericarp, and covers about  $60^{\circ}$  of the eustelic structure.

The large central pith consists of rather thick-walled cells with simple bordered pits. (pl. 3, figs 2-3; pl. 5, figs 1, 3; pl. 6, fig. 1).

The conducting strands, except the large peripheral one, are equidimensional with somewhat varying and irregular circumference (pl. 3, figs 2-3; pl. 7, fig. 2). The largest, peripheral strand is, in the best preserved cross-sections, broad, fan-shaped, expanding centrifugally (pl. 6, fig. 2). In the centripetal point of this structure we find the oldest vessels (protoxylem). From this point unicellular-bicellular rows of vessels radiate centrifugally, while new rows are successively intercalated (pl. 7, fig. 1). The tissue between these wedges of vessels presumably consisted of thin-walled cells, the walls of which are only suggested in the calcite by what may be the mid-lamella. The author interpretes this tissue as the phloem. The outermost, i.e. centrifugal, convex zone of the fan-shaped strand consists of similar tissue. Outside, in the cross-sections, is found a zone of small, round cells with better preserved, somewhat thicker walls.

In the longitudinal sections we find, peripheral in the conducting structure, remnants of long, very thin-walled, badly preserved cells in the shape of sieve-tubes (pl. 8, fig. 1). In length-section through the large, centrifugal strand the innermost vessels prove to be the oldest (pl. 8, fig. 1 at the top). They show clear evidence of stretching during the growth of the structure. Hence, the spiral thickenings are irregular and steeply inclined contrary to those of the outermost vessels, i.e. the younger vessels with low pitch and close spiral thickenings.

The smaller strands of the stelar circle (pl. 7, fig. 2) have a centripetal part consisting of screw-vessels and centrifugally more thin-walled cells with round lumen when seen in cross-section. In length-sections (pl. 8, fig. 2) the latter are long and parenchymatic, but so badly preserved that they cannot be proved to be sieve-tubes, which is only indicated by their position.

Centrifugally, outside the conducting eustelic structures, we find, as mentioned before, a crescent shaped area (pl. 3, fig. 3) of very thickwalled cells (pl. 4, figs 1-2) as seen in cross-section. In length-sections this tissue proves to consist of long, prosenchymatic cells, i.e. wood-fibres (pl. 5, fig. 2). These fibres are very thick-walled and have small lumina.

Around the eustelic conducting structure we often find groups of small sclereides, especially well developed centrifugally. The tissues around the conducting structure have often suffered strong deformation but can generally be identified as sclereidic tissue.

Between the conducting structures we find mesocarpal sectors of about the same width of a strongly incoaled substance (pl. 2; pl. 3, fig. 1). These areas have been studied in exceptionally thin cross- and lengthsections and prove to consist of very thick-walled sclereides (pl. 9). In this sclereidic ground tissue scattered areas are found consisting of compressed cells with thinner walls. The author has not solved the problem of whether this is a primary or a secondary structure. The author is tempted to accept the latter possibility and connect it with the deformation to which the fruits have been subjected.

#### Picrodendroid Fruit

#### Endocarp

The innermost layer of the pericarp, tentatively called the endocarp, consists of a rather incoaled, compressed tissue (pl. 10, fig. 1). The endocarpal tissues consist of relatively thin-walled (?), parenchymatic cells which have been compressed in radial direction, so that the radial walls are compressed into folds. In this condition the cells show tangential orientation. They may have been cork cells.

Innermost in the endocarpical layer we find a big conducting strand which in cross-section is oval and with concentric structure (pl. 10, figs 1-2). It is situated in the symmetry plane of the fruit which bisects the aborted seed and the corresponding sinus of the fully developed seed. In the cross-sections these structures and the strand in question are located on the same side of the fruit. The strand represents the placental strand leading from the petiolar region of the fruit into its distal end where it enters the conical placenta.

### **Dehiscence** mechanism

From the same beds of the Agatdal Formation in which the fossil fruits were found the author received a few specimens of what he interprets as detached pericarpal valves (pl. 10, figs 3, 6). They are flattened by compression. Flattening must be the normal geological consequence when a valved organic structure, softened by disintegrative agents, has been subject to the load of the overlying sediments. The valves are preserved as compressions and have regular and smooth margins. The shape is that of a regular sphaerical dihedron. The surface of one specimen shows 3 longitudinal well-preserved ribs (pl. 10, fig. 3) like those on the pericarp of the entire fruits; another specimen has worn remnants of similar ribs (pl. 10, fig. 6). The structure, size and shape of the specimens agree with the pericarp of the fruit of *Rosenkrantzia picrodendroides* considering the compressions as a quarter of the total pericarp. Consequently the pericarp of *Rosenkrantzia picrodendroides* might have dehisced by 4 valves.

The smooth and regular margin of the specimens might lead one to suppose an active dehiscence. The strong incoaling of the pericarp of the fruits and the many secondary cracks have obscured the possible supporting evidence. A few of the fossils (GGU nos. 9249.5 & 9249.30), which have been forced open, presumably during collection, may present supporting clues. The pericarp has opened in two equal parts along smooth surfaces suggesting pre-existing fissures or some other kind of dehiscence mechanism (pl. 10, fig. 5). Two pairs of thin ribs at right angles on the distal end of the pericarp indicates the zones of weakness (pl. 10, fig. 4).

#### Seed

The fully developed seed is oblong-guttiform (pl. 11, fig. 2; pl. 13, fig. 1) with some variation (pl. 13, figs 2-3). The base is rounded; from the middle it narrows in the distal direction and terminates in a papilla (the 'stylar base'). Many specimens have a longitudinal sinus (pl. 14, figs 1B, 1C, 1D) opposed by a corresponding blunt ridge. In cross-section these seeds have a more or less obvious triangular-cordate shape (pl. 13, fig. 2; pl. 14, figs 1B-C).

The ripe fruit contains one fully developed seed. In many cases it also contains the remnants of an aborted seed (pl. 16, figs 2-3).

In the cross-sections the sinus proves to fit to the remaining structure of the displaced second seed.

The seed is surrounded by a rather thin, but massive testa (textfig. 2, t; pl. 2, fig. 4; pl. 10, fig. 1; pl. 17, fig. 1).

#### Testa

The testa consists of two layers, as can be recognized on the best preserved specimens (pl. 11, figs 1, 3). The exterior layer is thick, making up five-sixth of the testa, and consists of cork tissue of thick-walled, flat cells with tangential orientation, arranged in lamellae conforming with the surface of the seed (pl. 11, fig. 4). In most specimens the cork cells seem to be somewhat compressed in radial direction.

The interior thin layer consists of small cells (pl. 11, figs 1, 3), the walls of which presumably were less resistant because in most specimens this tissue is totally or partly dissolved. In no cases were the cells of this tissue sufficiently well preserved to allow a reasonable description.

The testa contains 16 conducting strands. Only one cross-section (GGU no. 11705.3) is so complete that the author was able to count them. Of these 15 are normal testal traces (pl. 12, figs 1, 3) and the remaining very wide strand is the raphe (pl. 12, fig. 2). Two of the normal traces are so near to each other that it was difficult to determine whether the structure should be interpreted as one or two. A non-conducting bridge of tissue in the middle of the structure is to the author the conclusive evidence for suggesting two.

The testal traces are situated exteriorly in the outer testal layer (consisting of cork tissue) and are only separated from the testal surface by a delicate lamina of incoaled matter (pl. 12, fig. 3). This lamina coats the testa of the entire seed. The lack of any visible structure prevents an interpretation of this lamina. It might be a functional cuticle.

Most of the tissue of the testal traces consists of conducting cells with spiral thickenings.

#### Nucellus

The entirely calcified nucellus (pl. 14) has not revealed any detectable remnants of an endosperm. On the contrary, the entire nucellus seems to consist of two strongly folded and interfolded laminar structures, interpreted as the cotyledons. Normally, no cellular tissues of the cotyledons are preserved but the fissures between the cotyledons are left in the calcite presenting a very good model of the structure (pl. 14, fig. 3) (textfig. 4). This can be observed on polished sections and thin sections as



Fig. 4. Rosenkrantzia picrodendroides n.gen. et n.sp. Central cross-section of a seed. The cotyledonous structure drawn from a polished surface. The textural pattern of the calcite druses makes the background.

×4. GGU no. 9249.58. Loc. Scaphitesnæsen.

G. Jørgensen del.

well as on the surface of the calcified nucellar body which in many cases has been found lying loose in the fruit, or has been collected separately in the field. Hence, we can in that way observe a folded pattern (pl. 14, figs 1B, 2) on the rounded base of the isolated nucellar body. At the basal periphery this interfolded structure disentangles into a number of length fissures leading towards the distal end (pl. 14, figs 1A, 1D, 1E). According to these observations the cross-sections show the folded structure, and the length-sections, except in the basal region, have a simple cotyledonous structure of subparallel 'ribbons' in the axial direction (textfig. 2; pl. 2, figs 1A, 1B). Hence, the cotyledons are interfolded in a rather simple manner with the axis of the folds parallel to the length axis of the seed.

In the thin sections ghosty rectangular cells have been occasionally observed supporting the author's interpretation, the cells proving the organic origin of the structure (pl. 13, fig. 4; pl. 15, fig. 1). Fungal hyphae in these structures (pl. 15, fig. 2) bear witness to the normal way of disintegration which has obscured the cell aggregate before the calcification fixed the structure.

#### Abortive ovule

Besides the fully developed seed, there are remnants of an abortive one in several of the investigated specimens (pl. 16, figs 2-3). It has been observed in the cross-sections as well as in the length-sections. In some of the remaining fossils, X-ray photographs have revealed the same structure. It seems that about half of the specimens demonstrate this phenomenon. This judgement rests upon the number of seeds which show a sinus (see p. 14), those cut into thin sections and the X-ray photographs (pl. 16, figs 4-5) of entire specimens which were left untouched. Evidence from 26 specimens gave 13 with and 13 without abortive structure.

In cross-section the abortive structure appears like a calcite lens fitting into the sinus of the complete seed (pl. 16, fig. 2). The sinus found in some of the seeds in this way can be explained as a consequence of the competition between the two ovules. No original cellular structures are preserved in the calcite lens, but incoaled matter is included in the calcite aggregate (pl. 16, fig. 1). No distinct testa which can be proved to belong to the aborted seed has been detected. But, incoaled remnants of cellular tissue have been found forced into the structure that is now represented by the calcite lens. In one case the author found the testa of the fully developed seed with one of its enclosed conducting traces deformed into a few ridges that extend into the abortive structure (pl. 16, fig. 6). This obviously bears witness to a kind of stress and indicates that the abortive structure at that time was sufficiently flexible to suffer plastic deformation. A deformation by exterior forces would have introduced deformation of the cells with folding of the cell walls parallel to the compression. The 'folded' structure in question would in that case have been introduced by lateral pressure with a corresponding deformation of the cells and reduction of the cellular lumina.

But there is no folding of the cell walls and no compression of the cellular lumina in the deformed testal trace; there is a tendency for some of the cells to be orientated parallel to the surface of the 'folds' but without reasonable relation to the intensity of the 'folds'. Besides, big undeformed cells are scattered through the pattern. In the opinion of the author this merely indicated growth deformation in a structure consisting of living cells which expanded by growth under resistance.

The author has found no remnants of a septal structure which might indicate that the calcite lens is the filling of a second displaced locule of an originally 2-locular ovary (cf. *Picrodendron* p. 24).

#### **Pendulous** ovule

The fully developed seed has evolved from a pendulous ovule with slightly excentric placentation at the top of the locule. In this region the

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short, free funiculus can be recognized in one of the central lengthsections of specimen GGU no. 9249.41 (textfig. 2; pl. 17, figs 1-2).

#### **Placental strand**

By combined study of the cross- and length-sections the course of the placental strand can be located. This strand commences in the petiolar strand. Basally it enters the endocarp in the symmetry plane of the fruit, i.e. just outside the middle of the sinus of the fully developed seed and just outside the middle of the calcite lens, which the author interpretes as an abortive structure and even vis-a-vis the raphe of the seed. The placental strand continues longitudinally just inside the interior surface of the pericarp. The strand is strong, centric and in cross-section it is oval with the cells arranged in radial rows. The central cells are disintegrated. The majority of the strand consists of conducting tissue of strong elements. The conducting tissue is surrounded by a tissue which should be interpreted as wood parenchyma the cells of which have multiseriate bordered pits on the radial walls (cf. lengthsection of specimen GGU no. 9249.17, section no. 1). The strand can be traced into the distal end of the fruit (cf. the series of cross-sections of the type specimen e.g. pl. 2, fig. 3 and the length-section no. 1 of specimen GGU no. 9249.17) where it enters the placenta. In the length-section of specimen GGU no. 9249.17 we find the placental strand entering this region, and on pl. 18, figs 1-3 we observe the placental strand in the placenta.

#### Placenta

In length-section the placenta is a triangular area situated below the remains of the stylus i.e. a cross-section of a conical placental structure, situated between the pericarp and the seed in the distal end of the fruit (pl. 17, fig. 1, R).

In the placenta the funicular strand is surrounded by a thick coat of parenchymatic tissue (wood-parenchyma?).

#### **Funiculus**

The continuation of the parenchymatic coat of the placental conducting strand has been observed to be in direct contact with the testa of the distal part of the seed. This means that the free funiculus has been observed (pl. 17, fig. 1, F; fig. 2, F). From the placental region, the funicular strand can be traced backwards into the placenta and into the pericarp of the distal end of the fruit in one of the lateral sections.

Hence, the seed is obviously pendulous, derived from a pendulous ovule.

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#### Raphe and chalaza: anatropous ovule

The seed seems to have evolved from an anatropous ovule. One of the conducting traces of the testa is more than twice as wide as the normal ones (pl. 12, fig. 2) (pl. 12, fig. 1) (pl. 13, figs 1A, 1C). In cross-sections of the entire fruit it is situated just inside the pericarpal placental strand, in the symmetry plane. From the funiculus it runs into the testa where it proceeds in an exterior position to the base of the seed. Basally it termi-



Fig. 5. Rosenkrantzia picrodendroides n.gen. et n.sp. The chalaza end of the seed. C: chalaza. T: testal traces converging into chalaza, where the superimposed raphe (R) ends. (see pl. 13, fig. 1 B).

×5. GGU no. 9249.22. Loc. Scaphitesnæsen.

nates in the slightly excentric point from where the normal testal traces diverge: the chalaza (pl. 11, fig. 2; pl. 13, fig. 1B-C). Hence, the large testal trace is interpreted as the raphe.

On one of the fossil seeds (specimen GGU no. 9249.22) the normal traces as well as the supposed raphean strand are seen as longitudinal ribbons leading from pole to pole. The normal traces converge basally into chalaza and the supposed raphe stretches like a tongue over the point of divergence (the chalaza) of the normal traces, and partly covers some of the testal traces (textfig. 5; pl. 13, fig. 1B). This supports the interpretation that the large testal trace is the raphe. Unfortunately, damage to the testa in the chalaza region of this fossil (9249.22) means that the direct contact between raphe and testal traces at the chalaza can only be observed for a few of the traces.

The excentricity of the chalaza (pl. 11, fig. 2) may support the idea of the aborted seed referred to above. In an originally l-seeded, l-locular fruit the chalaza may be expected to be in a central position.

# X-RAY PHOTOGRAPHIC TECHNIQUE

X-ray photography was used for estimating the percentage of fossils which have traces of an aborted second seed in the locus (pl. 16, figs 4-5). The first experiments were made several years ago in the X-ray laboratory of the Dentological Highschool of Aarhus. Later, when X-ray photographic equipment was installed in the Sedimentological Laboratory of the Geological Institute, Aarhus University, the work was continued here. The method depends on the fact that the absorption of X-rays differs greatly for coal and calcite. Hence, the incoaled structure of the pericarp and the testa can be separated from the calcified nucellus and in well-preserved specimens even the aborted seed can be detected. In this way it was possible to detect the aborted seed in a few entire or nearly entire specimens without using the much more complicated and destructive process of cutting them into thin sections.

The method has proved to be useful and has been employed on quite a few other fossil seed species under investigation by the Section of Palaeobotany, Geological Institute of Aarhus University (Koch, 1972) (Koch & FRIEDRICH, in press).

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# DISCUSSION

The excellent state of preservation and the abundance of fossils has made possible a detailed description and revealed a number of diagnostic characters. A systematic position on an evolutionary line between the Cupuliferae and Juglandales is indicated. A certain phylogenetic relation to the family Picrodendraceae may be inferred. This family belongs, in the opinion of HUTCHINSON (1959, pp. 196–197), to the Order Juglandales. ENGLER'S 'Syllabus der Pflanzenfamilien' (ENGLER & MELCHIOR, 1964) makes *Picrodendron* a member of the Rutales (see section on *Picrodendron* below).

# Summary of diagnostic characters of the fruit of *Rosenkrantzia picrodendroides*

The fruit has a thick pericarp consisting of heavy sclerenchymatic tissue which contains 12 longitudinal eustelic conducting strands (primitive). A dehiscence mechanism (with 4 valves) is suggested. The pericarp is differentiated into endo-, meso- and exocarp. The fruit is l-locular with one ripe seed, the seed consisting mainly of two intimately folded cotyledons surrounded by a relatively thin but solid testa. The ovary originally contained at least 2 ovules, of which only one ripened. The ovules are pendulous from the top of the locule and anatropous.

# Systematic relationship

Rosenkrantzia picrodendroides was either a nut or a drupe, l-locular with 1 (-2?) seeds. Seed contains 2 folded cotyledons and seems to be without any distinctive endosperm. It thus seems reasonable to turn to the Juglandales to look for possible relatives. The erect and orthotropous ovule of the members of the Juglandaceae present an obvious difference. However, the fruit of *Picrodendron* (Picrodendraceae) has 2 anatropous ovules per locule. The resemblance of *Rosenkrantzia picrodendroides* to the single locus of the fruit of *Picrodendron* is obvious.



Fig. 6. Picrodendron baccatum (L) KRUG et URBAN. Branch with pistillate flowers and fruit. Reproduced after SMALL 1917, pl. 204.

# Picrodendron (Jamaica Walnut)

(textfigs 6-7)

This genus is only found in the Caribbean region. Three species are recognized: *P. baccatum* (L) KRUG & URBAN on Jamaica; *P. macrocarpum* (A. RICHARD) BRITTON (BRITTON, 1906) on Cuba and the Bahamas; and *P. medium* SMALL (SMALL, 1917) on Santo Domingo.





Fig. 7. Picrodendron baccatum (L) KRUG et URBAN. Branch with staminate inflorescences and isolated units. Reproduced from SMALL, 1917, pl. 203.

According to SMALL (1912) we owe the first reference to the Jamaica Walnut to SLOANE (1695). The tree was regarded as a walnut. Accordingly LINNAEUS (1759, p. 1272) retained it in the genus Juglans (J. baccata). PLANCHON (1846) described the Jamaica Walnut under the generic name *Picrodendron* and referred it to the family Simaroubaceae. BENTHAM & HOOKER (*P. arborum*) (1862, p. 315) and ENGLER & PRANTL (1896, p. 230) retained it in the family Simaroubaceae.

In his paper on the Jamaica Walnut, SMALL (1917) regarded the *Picrodendron* species as representative of a line of development between the walnuts and oaks. He created the family Picrodendraceae. CRONQUIST (1944) argued for the exclusion of *Picrodendron* from the Simaroubaceae and accepted the erection of a separate family, the Picrodendraceae.

ENGLER'S 'Syllabus der Pflanzenfamilien' (ENGLER & MELCHIOR, 1964, p. 268) retained the family Picrodendraceae and placed it in the Rutales, but pointed out its uncertain systematic position.

HUTCHINSON (1959, pp. 196-197) placed the genus *Picrodendron* in the order Juglandales and retained it in the family Picrodendraceae.

The 3 species of *Picrodendron* are much alike. They differ slightly in the shape of leaflets, length of petiole, size and shape of the fruit (drupe) and the thickness of the endocarp.

The similarity of the fruit of the 3 species makes it possible to give a generalized description which will be satisfactory for our purpose.

According to the cited publications and the author's observations the fruit of *Picrodendron* can be described as follows:

The fruits of *Picrodendron* have been described as a drupe with 2 loculi (pl. 18, fig. 4). The shape varies from globular-ovoid to oval. Length of the drupe 1.5-2.5 cm (pl. 18, fig. 4). The pericarp is thick, 1.5-2 mm in the drupe of *P. baccatum*. The 2 remaining species have an obviously thicker pericarp. The pericarp (pl. 19, fig. 3; pl. 20) consists of an exterior, thin, fleshy epicarp which on dried specimens is resistant owing to a thick epiderm and sclerenchymatic fibres. The endocarp (the 'stone') is very hard and consists mainly of very thick-walled wood-fibres; thus, a peripheral layer of fibres with longitudinal orientation surrounds a thick inner layer of fibres with radial orientation. This inner layer contains many longitudinal conducting strands of thick-walled units which are intercalated in the fabric of the fibre tissue, the fibres giving way for the strand by curving around it. Consequently, the fibres show a somewhat winding course, and interiorly they assume a tangential orientation. The epicarp is consequently thin and the endocarp thick.

On the dry specimens at the author's disposal, the surface is seen to be divided into 4 segments by 4 weak longitudinal ribs, having corresponding structure in the endocarp. Where they join in the distal and proximals ends, these ribs are at right angles to each other. One set corresponds to the septum. The latter pair of ribs corresponds to a radial zone of the pericarp of fibres of special appearence (pl. 19, fig. 3), presumably belonging to a rudimentary dehiscense mechanism. (According to HUTCHINSON (1959, pp. 196–197) the fruit is indehiscent). If the author's phylogenetic model, which is presented below and which is founded upon an interpretation of the *Picrodendron* fruit, is correct, then this seam of the pericarp may be the seam of fusion of the carpel.

The septal pair of ribs corresponds to a radial pericarpal zone (fissure) of different structure which is a direct continuation of the septal structure. During the production of thin sections the pericarp easily opened along this structure (pl. 19, fig. 2).



Fig. 8. *Picrodendron baccatum* (L) KRUG et URBAN. Sketch of cross-section of a fruit (see pl. 19, fig. 3). A—A: septum. E: endocarp. N: nucellus. P: epicarp. S: septal strand. Dotted: empty space. Remarkable is the continuation of the epicarp (black) into the septum to constitute its middle layer in which the centric conducting strand is found. ×5.

The ovary contained 2 ovules in each locus. Of these 4 ovules only one developed to a seed, the remaining ones aborted. Thus, the ripe fruit contains one seed. The empty locus has been superseded by the ripe seed, the septa being displaced to the periphery except at both ends of the fruit where relics of the second locus are left (pl. 18, fig. 4; pl. 19, fig. 1).

The seed consists mainly of the thick, folded cotyledons.

The septum is a relatively thick 3-layered structure with the placental conducting strand in an axial position, embedded in the middle layer (textfig. 8; pl. 19, fig. 3; pl. 20, figs 1-2).

During the investigation of *Picrodendron* fruits the author found the relationship between septum and pericarp especially interesting (pl. 20). The supposed rudimentary pericarpal dehiscence-zone which corresponds with the septum proves to be a continuation of the middle septal layer. Centrifugally it joins the epicarp of which it appears to be

a direct continuation. The epicarp as well as the middle septal layer consists of a mucilaginous tissue of thin-walled cells. Hence, the epicarpal tissue crosses the endocarp like a thin more or less continuous laver and it continues into the septa to constitute its middle layer. In the dried ripe specimens this tissue is rather disintegrated but seems to have consisted of very thin-walled cells. The outer layers of the septum are continuations of the endocarp of the two halves of the 'stone', consisting of thickwalled fibres and scattered conducting tissue. The placental conducting strand is found in an axial position, embedded in the middle layer of the septum. In the fruit of *Picrodendron baccatum* the septal strand is concentric in cross-section with a central circular area of somewhat diffuse structure like a pith (pl. 21, fig. 2). The author assumes that this is what JARDIN (1901, p. 302) called 'une large lacune mucilagineuse' in his description of the petiole of the Picrodendron leaf. The surrounding xvlem cylinder consists of radiating rows of conducting units, separated into wedges by distinct uniseriate rays. The petiolar strand of the leaf of Picrodendron baccatum is a nearly identical structure, which the author also has studied (cf. pl. 21, fig. 1). In Picrodendron macrocarpum we found the septal strand bilateral in central cross-sections. The xylem cylinder is biparted by the pith which cuts through the whole structure (pl. 22).

# **Phylogenetic interpretation**

These observations support the author's interpretation of the *Picrodendron* fruit as a double structure homologous with a syncarpium consisting of 2 fruits, originally each with 2 ovules in the ovary. This structure may have evolved from 2 free fruits of a pair which during a long evolution have been joined into one carpical structure in the recent *Picrodendron* species. In a series of sketches (textfigs 9-10) the author has tried to visualize this evolution in a generalized theoretical representation.

The consequence of the author's interpretation of the construction of the septum of the *Picrodendron* fruit and its relation to the pericarpal layers is that its ancestor produced a syncarp of two fruits (textfigs 9 and 10) or inflorescence units (textfigs 9 and 10) consisting of two fruits. These fruits derived from ovaries with 2 ovules and consequently contained one or two seeds each. The main change concerns the placentation which is apical (pseudoapical provided that the author's theory is correct) in the *Picrodendron* fruit but proximal in this theoretical ancestor. Instead of a syncarp we can alternatively imagine (cf. textfigs 9 and 10) an inflorescence of two fruits or of pairs of fruits with the cited number of seeds, but still with proximal placentation. We might name this theoretical ancestral construction: 'the *Eo-Picrodendron* tribe' to account

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Fig. 9. A theoretical model of the evolution of the fruit of *Picrodendron*, based on generalized sketches of cross-sections of the fruits. A: *Picrodendron*. B: the immediate predecessor which might be referred to the Picrodendraceae. C: '*Eo-Picrodendron*', near to the Juglandaceae. (cf. textfig. 10).

for the theoretical variation of a possible group of related ancestors. Obviously this conclusion brings *Picrodendron* into a closer phylogenetic relationship with the Juglandales (the Juglandaceae). This becomes especially striking if we accept an ovary with orthotropous ovules among the ancestral variants.



Fig. 10. A theoretical model of the evolution of the fruit of *Picrodendron*, based on generalized sketches of length-sections of the fruits (a parallel to the representation of textfig. 9). A: *Picrodendron*. B: The immediate predecessor. C: *'Eo-Picrodendron*'.

Nevertheless, the concept of SMALL (1917) claiming that the Picrodendraceae belong to a line of evolution in the interregnum between the



Fig. 11. Rosenkrantzia picrodendroides n.gen. et n.sp. A theoretical sketch demonstrating the possible systematic position of the genus Rosenkrantzia. Some possible phylogenetic relationships are proposed based upon the theoretical reconstructions of the predecessors of Rosenkrantzia (i.e. 'Eo-Rosenkrantzia') and Picrodendron (i.e. 'Eo-Picrodendron'); connecting lines have been omitted because a variety of possibilities exist.

III

Cupuliferae (Quercus group) and Juglandales is still valid. The 'Eo-Picrodendron tribe' might be found in or near to the well-known Dewalquea group. On the other hand, the Rosenkrantzia fruit becomes less closely related to Picrodendron than could be expected at the first glance. Rosenkrantzia has apical placentation and might resemble one locus of the Picrodendron fruit regarding this character as well as by the existence of 2 anatropous ovules in the ovary of both of them. When the 'Eo-Picrodendron tribe' turns out to have a proximal placenta this resemblance can only be apparent.

The rather complicated fruit of *Rosenkrantzia* with its apical placenta needs a long placental strand. If we retrospectively imagine a reduction of this strand, this leads to an ancestral type with proximal placentation. This 'Eo-Rosenkrantzia' is not necessarily involved in the '*Eo-Picrodendron* tribe', but a varying degree of resemblance and phylogenetic relationship can be imagined. Here we have exhausted the possibilities of the basic observations and speculations.

The impression must be that *Rosenkrantzia* is also situated on a phylogenetic line between the Cupuliferae (*Quercus* group) and the Juglandales, *Dryophyllum* and *Dewalquea* respectively.

The Fagales have pendulous ovules and axial placentation, a variation of ovary structures not remote from the structure of the ovary inferred for the *Rosenkrantzia* fruit. The primitive pericarp seems to make *Rosenkrantzia* an ancestral type, possibly with a phylogenetic position within or related to the *Dryophyllum* group. The author has tried to visualize his ideas concerning the theoretical systematic relationships in the generalized sketch of textfig. 11. The author is well aware that this is a construction made by a palaeobotanist with his specialized experience. It is the author's hope that experienced botanists will also feel tempted to analyze the problem.

## Conclusion

From the above discussion the author's phylogenetic conclusion must be that *Rosenkrantzia picrodendroides* n.gen. et n.sp. is on an evolutionary line between the Cupuliferae and Juglandales.

The study on the *Picrodendron* fruits justifies the placing of *Rosenkrantzia* in a systematic position with some relation to, but not within, the family Picrodendraceae.

# RELATED FOSSIL SPECIES

In connection with this discussion some of the other form species of the Agatdal Formation and the synchronous Upper Atanikerdluk Formation may be relevant.

Dicotylophyllum bellum (KOCH, 1963, p. 66 and pl. 23, fig. 2 of this paper) is a palmately compound leaf with 3 (-5) leaflets and an extremely long petiole. It closely resembles the leaves of the *Picrodendron* species (pl. 23, fig. 1). Like the fruits of *Rosenkrantzia* the *Dicotylophyllum bellum* leaves are common in the collections from the Upper Danian (previously Lower Paleocene) of Nûgssuaq (KOCH, 1963). Until now no criteria supplementary to those determined macroscopically by KOCH (1963) have been found. A study of the epidermal structures has yet to be made. Even a male inflorescence from Atanikerdluk (pl. 24) revealing a stout axis with irregularly spread globular staminate heads much resembles the similar androus structures of the *Picrodendron* species (cf. *Picrodendron baccatum*, textfig. 7). This fossil structure will be described by the present author in a separate paper.

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Dr. A. SKOVSTED (Botanical Museum of the University of Copenhagen) placed at the author's disposal the collections in his care and obtained a number of new specimens. Dr. V. R. JAMES, Superintendent of Royal Botanic Gardens, Kingston, Jamaica, and Dr. E. LELAND WEBBER, Director of the Chicago Natural History Museum, kindly provided specimens of the fruit of Picrodendron. Dr. E. RATJEN and Dr. T. TROEST (Dentological Highschool, Aarhus) and Professor GUNNAR LARSEN (Geological Institute, University of Aarhus) facilitated the experiments with X-ray photography by placing their laboratories at the author's disposal. Konservator C. HALKIER (Mineralogical Museum of the University of Copenhagen), has contributed a number of excellent photographs and much valued advice. Dr. W. L. FRIEDRICH (Section of Palaeobotany, Geological Institute, Aarhus University) has assisted the author in many ways, especially by improving a method for the preparation of sections of the very hard fruits of Picrodendron. The author expresses his gratitude for this help and for stimulating discussions. The photographer of the author's laboratory, Mr. JOHN SOMMER, has undertaken a wide range of experimental photography to solve the problems in illustrating this paper. Dr. A. R. LORD was kind enough to read and correct the manuscript. The author expresses his sincere thanks for all this help.

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# PLATES

The depicted samples and details from thin sections are all referred to a label number of the Geological Survey of Greenland (GGU). The reference between label no. and locality is as follows:

Loc. Scaphitesnæsen, Turritellakløft (loc. 1 on textfig. 1): GGU no. 9249, 11705, 11977.

Loc. big section, Qaersutjægerdal (loc. 2 on textfig. 1): GGU no. 8174, 11711, 35264.

Unless otherwise stated the photographs are the work of the author.

The depicted specimens will be kept in the National Type Collection of the Mineralogical Museum, University of Copenhagen.

Rosenkrantzia picrodendroides n.gen. et n.sp.

- Fig. 1 A The same compressed specimen as pl. 1, fig. 1 B. Axial view from basal end. Central abscission scar of the petiole visible. 1:1. GGU no. 11705.1. Loc. Scaphitesnæsen.
- Fig. 1 B Compressed but well-preserved fruit seen from the direction of compression. Pericarpal ribs. 1:1. GGU no. 11705.1. Loc. Scaphitesnæsen.
- Fig. 1 C The same compressed specimen as pl. 1, fig. 1 B. Axial view from distal end. Central stylar scar. 1:1. GGU no. 11705.1. Loc. Scaphitesnæsen.
- Fig. 2 Fruit on bedding-plane in sandstone. Pericarp partly removed. 1:1. GGU no. 8174.1. Loc. Qaersutiægerdal.
- Fig. 3 A Worn specimen, uncompressed. Side view. Pericarpal ribs worn off exposing the underlying strands. 1:1. GGU no. 11705.11. Loc. Scaphitesnæsen.
- Fig. 3 B The same worn specimen as in pl. 1, fig. 3 A. Axial view from proximal end. 1:1. GGU no. 11705.11. Loc. Scaphitesnæsen.
- Fig. 4 Fruit in sandstone, opened along the length-section, and nucellus removed. View into the cavity which is lined by testa (light, reflecting). Pericarp in cross-section. Proximally the stout petiole in cross-section with conducting strand. The impression of the abscission scar is left as a small separate structure in the shape of a dome. Ca. x 2. GGU no. 35264. Loc. Qaersutjægerdal. J. SOMMER photo.
- Fig. 5 Basal end of the fossil of pl. 1, fig. 4. Abscission scar is left as an impression (negative). A: abscission scar. B: pericarp. C: testa. D: petiole. x 4. GGU no. 35264. Loc. Qaersutjægerdal.

J. SOMMER photo.

PLATE 1.



1 A





1 C



2



3 A



3 B





Rosenkrantzia picrodendroides n.gen. et n.sp.

Fig. 1 A Central length-section through a whole fruit. Thick pericarp enclosing a fully developed seed with surrounding testa and a nucellus dominated by the cotyledonous structures. Distally the funiculus adheres to the testa below the triangular placenta region, beyond which is the stylar base.

2:1. GGU no. 9249.41. Loc. Scaphitesnæsen.

- Fig. 1 B The same specimen as pl. 2, fig. 1 A. The seed is cut exactly along its median plane and shows its distal papilla. (cf. textfig. 2).
  2:1. GGU no. 9249.41. Loc. Scaphitesnæsen.
- Fig. 2 Central cross-section of fruit with general view of pericarpal strands. Pericarp somewhat worn and dissolved on one side, well-preserved on the opposite side, (up). The seed is without a sinus. A hollow shows that the nucellus was partly dissolved before fossilization. 2:1. GGU no. 11705.3. Loc. Scaphitesnæsen.
- Fig. 3 Central cross-section of fruit. General view of pericarp and its strands. Seed with sinus and corresponding structure deriving from abortive seed.

2:1. GGU no. 9249.14, cross-section 7. Loc. Scaphitesnæsen.

Fig. 4 Half central length-section of fruit, demonstrating the pericarpal layers: A: exocarp. B: mesocarp. C: endocarp. Innermost follow testa (t) and nucellus (n).
4:1. GGU no. 9249.41. Loc. Scaphitesnæsen.



1 A







1 B



- Fig. 1 Half central cross-section of fruit demonstrating the pericarpal layers: A: exocarp. B: mesocarp with eustelic strands. C: endocarp. Innermost follow testa (t) and nucellus (n).
  4:1. GGU no. 11705.3. Loc. Scaphitesnæsen.
- Fig. 2 Cross-section: General view of an eustelic strand of the pericarp. Centrifugally it is protected by the crescent-shaped fibre strand of a pericarpal rib. Inside follows the large, centrifugal, fan-shaped trace of the strand. The other smaller traces are arranged in an oval around the central pith.
  x 44. GGU no. 9249.14, cross-section 7.
- Fig. 3 Cross-section of exocarp and mesocarp: Exteriorly the black, opaque exocarpal zone of a rib can be seen. Next the crescent-shaped wood-fibre strand of the rib. Interiorly follows the eustelic strand, with its large pith. (Corresponding length-section of pith on pl. 5, fig. 1).
  x 44. GGU no. 9249.14, cross-section 5.







- Fig. 1 Cross-section of wood-fibre strand of a pericarpal rib. Interiorly follows the corresponding fan-shaped trace. (cf. pl. 6, fig. 2). x 156. GGU no. 9249.14, cross-section 5.
- Fig. 2 Cross-section of wood-fibres of a pericarpal rib. Corresponding lengthsection on pl. 5, fig. 2. x 312. GGU no. 9249.14, cross-section 5.





- Fig. 1 Radial length-section of a fruit through the outer part of its pericarp tangential to one of the eustelic strands of the mesocarp. To the right the opaque exocarpal layer, next the wood-fibre strand of the rib and to the left the large pith and part of one of the smaller traces. x 44. GGU no. 9249.17, central length-section.
- Fig. 2 Length-section of wood-fibres of a pericarpal rib. Corresponding cross-section on pl. 4, fig. 2.
  x 312. GGU no. 9249.17, length-section.
- Fig. 3 Length-section through pith of eustelic mesocarpal strand. To the right wood-fibres of the corresponding pericarpal rib. x 156. GGU no. 9249.17.







Rosenkrantzia picrodendroides n.gen. et n.sp.

- Fig. 1 Parenchymatic, thick-walled cells of the pith of an eustelic strand seen in cross-section (cf. pl. 3, figs 2-3).
  x 500. GGU no. 9249.14, cross-section 7.
- Fig. 2 Cross-section of fan-shaped conducting trace of a mesocarpal eustelic strand. Radial rows of vessels of which the innermost are uniseriate. In centrifugal direction the rows of vessels expand into bi-, tri- or tetraseriate. Alternating with the rows of vessels are mono-, biseriate or even polyseriate rows of phloem cells, which also tend to form a peripheral sheet.

x 156. GGU no. 9249.14, cross-section 5.



Rosenkrantzia picrodendroides n.gen. et n.sp.

Fig. 1 Details of cross-section of the fan-shaped conducting trace of a mesocarpal eustelic strand. Radiating monoseriate rows of vessels dividing in the centrifugal direction into bi-, tetra- or polyseriate aggregates. Alternating phloem tissue. (Corresponding length-section on pl. 8, fig. 1).

x 312. GGU no. 9249.14, cross-section 5.

Fig. 2 Cross-section through small lateral trace of mesocarpal eustelic strand partly surrounded by the pericarpal ground tissue of sclereids. (Corresponding length-section on pl. 8, fig. 2).
x 312. GGU no. 9249.14, cross-section 5.



- Fig. 1 Length-section through the big centrifugal trace of mesocarpal eustelic strand. Vessels and sieve tubes. The top corresponds to the inner side. (Corresponding cross-section on pl. 7, fig. 1).
  x 312. GGU no. 9249.41, length-section 3.
- Fig. 2 Length-section through small lateral trace of mesocarpal eustelic strand. Vessels and sieve tubes. (Corresponding cross-section on pl. 7, fig. 2. x 312. GGU no. 9249.41, length-section 1.







- Fig. 1 Exocarpium (black zone on right) and mesocarpal ground tissue of sclereids in cross-section. x 44. GGU no. 11705.3, cross-section 6.
- Fig. 2 Length-section through mesocarpal ground tissue of sclereids. (Corresponding cross-section on pl. 9, fig. 3). x 312. GGU no. 9249.17.
- Fig. 3 Cross-section through mesocarpal ground-tissue of sclereids. (Corresponding length-section on pl. 9, fig. 2). x 312. GGU no. 11705.3, cross-section 6.





Rosenkrantzia picrodendroides n.gen. et n.sp.

- Fig. 1 Cross-section through the endocarp (E) with the placental strand (S) near the inner surface of the pericarp. Testa (T) with raphe (R) and calcified nucellus (N). x 44. GGU no. 11705.3, central cross-section.
- Fig. 2 The placental strand in cross-section (cf. pl. 10. fig. 1). x 156. GGU no. 11705.3, central cross-section.
- Fig. 3 Well-preserved detached pericarpal valve with 3 ribs. 1:1. GGU no. 11711.1. Loc. Qaersutjægerdal.
- Fig. 4 Oblique view from distal end of a fruit with one half of the pericarp left. The other half has been separated along a longitudinal median section leaving the cross-section of the pericarp as a smooth surface. The opening has followed blunt ridges of the distal surface of which one running downwards is preserved. A similar ridge at 90° to the scar of dehiscence is seen pointing to the right.

x 2.5. GGU no. 9249.30. Loc. Scaphitesnæsen.

Fig. 5 Fruit with one half of pericarp removed, presumably broken along dehiscence fissure leaving a smooth cross-section of the pericarp (note the pericarp on right side).

1:1. GGU no. 9249.5. Loc. Scaphitesnæsen.

Fig. 6 Detached pericarpal valve. Corroded specimen. Traces of 3 ribs remain. 1:1. GGU no. 11711.2. Loc. Qaersutjægerdal.

















Rosenkrantzia picrodendroides n.gen. et n.sp.

Fig. 1 Length-section through the 2-layered testa. O: outer layer, I: inner layer.

x 156. GGU no. 9249.41, half central length-section.

- Fig. 2 Seed with almost complete testa (distal fragment lacking). Longitudinal bands correspond to the testal traces which converge towards the slightly excentric chalaza region. 5:2. GGU no. 9249.22. Loc. Scaphitesnæsen.
- Fig. 3 Testa (TT) with testal trace (t. t.) in length-section. x 156. GGU no. 9249.41 (Central length-section no. 2).
- Fig. 4 Cross-section through testa (T) and the endocarp (E). The outermost testal layer with its thick-walled cells (cork cells) is preserved. The innermost layer has been dissolved. x 156. GGU no. 9249.14, cross-section 5.



- Fig. 1 Cross-section through testa (T) with a testal trace. Exteriorly the endocarp (E) and interiorly the nucellus (N). x 44. GGU no. 11705.3, central cross-section.
- Fig. 2 Cross-section through testa (T) with raphe (R). Exteriorly the endocarp (E) with the placental strand and interiorly the nucellus (N).
  x 44. GGU no. 11705.3, central cross-section.
- Fig. 3 Testa (T) with testal trace in cross-section. E: endocarp. x 156. GGU no. 11705.3, central cross-section.









Rosenkrantzia picrodendroides n.gen. et n.sp.

Fig. 1 A Seed with testal impression of the raphe (R) and testal traces. Excentric chalaza.

5:2. GGU no. 9249.22. Loc. Scaphitesnæsen.

- Fig. 1 B The chalaza region of a seed. The narrow testal traces are covered by the wide raphe (R), (cf. textfig. 5). 5:2. GGU no. 9249.22. Loc. Scaphitesnæsen.
- Fig. 1 C Seed in oblique view from the chalaza region: Raphe (R) and testal traces covered by the raphe strand in chalaza.
  5:2. GGU no. 9249.22. Loc. Scaphitesnæsen.
- Fig. 2 Seeds with more or less fragmentary testa. Basal view. Scale in mm. Ca. 1:1.

Upper from left: GGU no. 11705.8 Loc. Scaphitesnæsen. GGU no. 9249.34 Loc. Scaphitesnæsen. GGU no. 35264 Loc. Qaersutjægerdal. Lower from left: GGU no. 9249.39 Loc. Scaphitesnæsen. GGU no. 11977.1 Loc. Scaphitesnæsen. GGU no. 9249.42 Loc. Scaphitesnæsen.

Fig. 3 Seeds with more or less fragmentary testa. Side view. Scale in mm. 9:10.

Upper from left: GGU no. 35264 Loc. Qaersutjægerdal. GGU no. 11977.1 Loc. Scaphitesnæsen. GGU no. 9249.34 Loc. Scaphitesnæsen. Lower from left: GGU no. 9249.39 Loc. Scaphitesnæsen. GGU no. 9249.22 Loc. Scaphitesnæsen. GGU no. 11705.8 Loc. Scaphitesnæsen.

Fig. 4 Length-section through peripheral tissues of seed. C: cellular structure of cotyledon with epiderm and cuticle. T: testa.
 x 312. GGU no. 9249.17.



1 A



1 B



1 C









- Fig. 1 A Seed with partly removed testa and fissures of cotyledonous structure on the calcified nucellus. Side view. 5:2. GGU no. 35264. Loc. Qaersutjægerdal.
- Fig. 1 B Calcified nucellar structure with sinus seen from the proximal end (chalaza region). Folded cotyledonous structure. 5:2 GGU no. 35264. Loc. Qaersutjægerdal.
- Fig. 1 C Calcified nucellar structure seen from the distal end (hilum region) with the distal papilla. 5:2 GGU no. 35264. Loc. Qaersutjægerdal.
- Fig. 1 D Calcified nucellar structure in side view. Sinus and fissures of cotyledonous structure parallel to the axis of the seed. 5:2. GGU no. 35264. Loc. Qaersutjægerdal.
- Fig. 1 E Seed with partly removed testa and fissures of cotyledonous structure on the calcified nucellus. View from side opposite to sinus. 5:2 GGU no. 35264. Loc. Qaersutjægerdal.
- Fig. 2 Calcified nucellar structure without sinus seen from the proximal end (chalaza region). Folded cotyledonous structure. 5:2. GGU no. 9249.39. Loc. Scaphitesnæsen.
- Fig. 3 Central polished cross-section of seed with testa and calcified nucellus with 2 interfolded cotyledons (cf. textfig. 4).
  5:2. GGU no. 9249.58. Loc. Scaphitesnæsen.





1 B



2



1 C



3





1 D

- Fig. 1 Length-section through periphery of seed. N: nucellus with cell-structure of cotyledon and epiderm with cuticle. T: testa with conducting trace. E: endocarp.
  x 156. GGU no. 9249.17, central length-section.
- Fig. 2 Length-section through peripheral tissues of seed. The cotyledonous
  - tissue dissolved by fungal attack. Fungal hyphae orientated according to the cellular structure. N: nucellus. e: epidermal zone. E: endocarp.
    - x 312. GGU no. 9249.17.



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Rosenkrantzia picrodendroides n.gen. et n.sp.

- Fig. 1 Cross-section through calcified aborted seed structure (S). The structure has been recrystallized and so devoid of original cellular structures. Incoaled remnants are seen. Endocarp (E) with placental strand (P). x 44. GGU no. 9249.14, cross-section 5.
- Fig. 2 Central cross-section through a fruit with pericarp, a fully developed seed and a lens-shaped aborted seed.
  2:1. GGU no. 9249.14, cross-section 7. Loc. Scaphitesnæsen.
- Fig. 3 Central length-section of fruit with pericarp, a fully developed seed and a lens-shaped aborted seed. The structure is somewhat disturbed by a micro-fault.

2:1 GGU no. 9249.17, central length-section. Loc. Scaphitesnæsen.

Fig. 4 X-ray photographic cross-section of a fruit with remnants of an aborted seed which appears as a narrow lens at the upper periphery of the fully developed seed (black central region). The pericarp strands stand out as a ring of black spots.

x 2. GGU no. 9249.31. Loc. Scaphitesnæsen. J. WINTHER X-ray photo.

Fig. 5 X-ray photographic cross-section of a fruit with remnants of an aborted seed seen as a narrow lens at the upper periphery of the fully developed seed (black central region). The pericarpal strands stand out as a ring

of black spots. x 1. GGU no. 9249.31. Loc. Scaphitesnæsen.

J. WINTHER X-ray photo.

Fig. 6 Remnants of testa (T) of the fully developed seed with testal trace deformed by growth into the aborted seed (A). x 156. GGU no. 9249.14, cross-section 7.



Rosenkrantzia picrodendroides n.gen. et n.sp.

- Fig. 1 Distal end of central length-section of fruit with funiculus (F), nucellus (N), pericarp (P) placental region with funicular strand in cross-section (R), stylar base (S) and testa (T).
  - 6:1. GGU no. 9249.41, central length-section. Loc. Scaphitesnæsen.
- Fig. 2 Remnants of funiculus (F) adhering to testa (T) P: placenta. N: nucellus. Length-section.

x 44. GGU no. 9249.41, central length-section.



Rosenkrantzia picrodendroides n.gen. et n.sp.

- Fig. 1 Conducting tissue of funicular strand in the placental region. Tissue in strongly incoaled condition.
   x 312. GGU no. 9249.41, central length-section.
- Fig. 2 Length-section through the placental region: Cross-section through funicular strand in strongly incoaled condition.
   x 312. GGU no. 9249.41, central length-section.
- Fig. 3 Length-section through funicular strand in the placental region. Tissue in strongly incoaled condition.
   x 156. GGU no. 9249.41, central length-section.

Picrodendron baccatum (L) KRUG et URBAN:

Fig. 4 Fruits seen from the base, in lateral view and in cross-section.
x 1.5. Loc. Braeton to Rodney's Lookout, St. Catherine, Jamaica. Coll.
R. D. GIBBS (Herb. C. D. ADAMS 9395). 6/4-1961.




2





Picrodendron baccatum (L) KRUG et URBAN:

Fig. 1 Fruit cut open by cross-section, with the seed removed. The displaced septum with its central conducting strand is visible. x 3. Loc. see pl. 18, fig. 4.

J. SOMMER photo.

Fig. 2 Central cross-section of fruit. During preparation of the section by grinding the two halves easily separated along the middle layer of the septum and its continuation across the pericarp (see p. 20). x 3. Loc. see pl. 18, fig. 4.

J. SOMMER photo.

Picrodendron macrocarpum (A. RICHARD) BRITTON

Fig. 3 Cross-section of fruit. x 5. Loc. see pl. 18, fig. 4.

J. SOMMER photo.





Picrodendron baccatum (L) KRUG et URBAN:

Figs. 1-2 Thin sections showing the pericarp with the departing septum (S). The central septal layer continues through the endocarp (E) into the epicarpium (e). (Central cross-sections). x 26. Loc. see pl. 18, fig. 4.



Picrodendron baccatum (L) KRUG et URBAN:

- Fig. 1 Cross-section of leaf petiole. x 52.
- Fig. 2 Cross-section of septal strand of the fruit. Central septal strand in the surrounding septal tissues. M: middle septal layer (homologous with epicarp; E: outer layer (homologous with endocarp). x 94.





Picrodendron macrocarpum (A. RICHARD) BRITTON:

- Fig. 1 Cross-section through the septum of a fruit: bilateral septal strand in the septal tissues. M: middle septal layer (homologous with the epicarp), E: outer fibrous layers (homologous with the endocarp). x 94.
- Fig. 2 Cross-section through bilateral septal strand in the surrounding tissues. x 188.



Picrodendron baccatum (L) KRUG et URBAN

Fig. 1 Typical leaf: trilobate with long petiole 1:1. Loc. Great Goat Island, Jamaica, collected 17.7. 1906.

Dicotylophyllum bellum (HEER) SEWARD & CONWAY

Fig. 2 Typical leaf, (cf. KocH, 1963).

1:1. GGU no. 35492. Loc. Kangersôq, Nûgssuaq, West Greenland.

C. HALKIER photo.



Undetermined staminate inflorescence.

- Fig. 1 The entire staminate inflorescence. Impression in clay-ironstone. (see p. 30) Coll. Min. Mus. Copenhagen, Atanikerdluk H. B. 1865. West Greenland.
- Fig. 2 The entire staminate inflorescence. Cast produced from the fossil of pl. 24, fig. 1. 1:1.

