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Dedicated to the Commemoration of my Friend and Colleague
Dr. Manfred GAILHOFER (6.1.1936-3.7.2009)
[see Phyton 49 (2): 313–320]

Anther and Anthesis in *Pararchidendron pruinosum* (*Mimosaceae-Ingeae*)

By

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With 19 Figures

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Summary

TEPPNER H. 2010. Anther and anthesis in *Pararchidendron pruinosum* (*Mimosaceae-Ingeae*). – Phyton (Horn, Austria) 50(1): 91–108, with 19 figures.

In pseudo-umbels of *Parachidendron pruinosum* (BENTH.) NIELSEN the flowers normally open successively during 3–4 days. The individual flowers, with corollas 4.5–5 mm in length, last five or six days in anthesis. The 22–28 stamens (8–14 mm long) form a brush, white on the first two or three days, then turning cream or light ochre-brown. Each of the two locules of a theca is divided transversally by a parenchymatous septum and the locule-halves contain one 16-grained, acalymmated polyad each. Anther wall anatomy and filament insertion are also considered.

Zusammenfassung

TEPPNER H. 2010. Anther and anthesis in *Pararchidendron pruinosum* (*Mimosaceae-Ingeae*). [Anthere und Anthese von *Pararchidendron pruinosum* (*Mimosaceae-Ingeae*)]. – Phyton (Horn, Austria) 50 (1): 91–108, mit 19 Abbildungen.

Die Blüten einer Scheindolde von *Pararchidendron pruinosum* (BENTH.) NIELSEN öffnen sich sukzessive, meist innerhalb von 3–4 Tagen. Eine Einzelblüte verweilt fünf oder sechs Tage in Anthese. Die Krone ist ca. 4,5–5,0 mm lang. Die Stamina (22–28;

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8–14 mm lang) bilden einen Pinsel, mit weißen Filamenten an den ersten zwei oder drei Tagen, die sich dann nach gelblich oder hell ocker-braun umfärben. Jedes der beiden Lokulamente einer Theka ist durch ein parenchymatisches Septum quer geteilt. Die Lokulamenthälften enthalen je eine acalymmate Polyade aus je 16 Pollenkörnern. Anatomie der Antheren und Filament-Ansatz sind ebenfalls berücksichtigt.

1. Introduction

Parachidendron pruinosum (BENTH.) NIELSEN var. *junghuhnianum* (BENTH.) NIELSEN was investigated as part of my interest in structure and function of the flowers and anthers of *Mimosaceae*, especially *Ingeae* (PRENNER & TEPPNER 2005, TEPPNER 2007a, 2007b, TEPPNER & STABENTHEINER 2006, 2007). This tree species grows wild in Malesia, and was observed flowering in the Botanic Garden in Graz (Fig. 1–5). Other than species accounts in floras (for e. g. NIELSEN & al. 1984, NIELSEN 1992: 145–148, COWAN 1998: 39–40) and SEM-figures of the anthers (TUCKER 1996: 242), apparently nothing has been published about this subject.

2. Material and Methods

Pararchidendron pruinosum (BENTH.) NIELSEN var. *junghuhnianum* (BENTH.) NIELSEN [det. H. TEPPNER May 27, 2009, using NIELSEN 1992 and COWAN 1998]. Grown in the temperate greenhouse (May – September in the open) of the Botanic Garden of the Institute of Plant Sciences, University of Graz, Austria, Europe. – Origin: Apparently purchased from the seed trade, but insufficient labelling obscures the species' original accession [received as *Abarema grandiflora* (SOLAND. ex BENTH) KOSTERM.], sown 1998 or earlier, two young trees, one flowering in 2008 for the first time.

The flowers were observed between May 24 and June 15, 2009 in the open (Fig. 1–5), during a rainy period under a roof. Umbels or single flowers were taken to the laboratory and studied with a Wild M38 dissecting microscope. Photos were taken with an Exakta VX 1000 with a Steinheil Macro-Quinon objective.

Flower buds (Fig. 1, 2) were fixed in ethanol:chloroform:acetic acid 5:3:1 and stained with a 45% aceto-carmine solution by standard methods (e. g. DARLINGTON & LA COUR 1963, SHARMA & SHARMA 1965). The anthers were then dissected on a slide in a drop of acetic acid. Buds of 2.3–4.0 mm in length were investigated. The smallest buds contained postmeiotic polyads with the exine layer developed, whereas the largest buds examined were matured nearly to the point of opening of the corolla. For dissections, observations and photos were made with a 'Zeiss Photomikroskop III', along with an 'Agfapan APX 100 professional' film. The negatives were scanned with CanoScan 8800F and the images were edited with Adobe Photoshop CS3.

Abbreviations used in the figures:

en endothecium
ep epidermis
m middle layer (2–3 layered)
s septum
t tapetum
tm tapetal membrane

Fig. 1. *Pararchidendron pruinosum* var. *junghuhnianum*, end of a twig with a pair and a single inflorescence in leaf axils. Leaf bipinnate with alternate leaflets.

Fig. 2. *Pararchidendron pruinosum*, detail of the twig end in Fig. 1.

Fig. 3. *Pararchidendron pruinosum*, view of the top of an umbel in early anthesis. Buds, flowers starting to open, first-day flowers (with diverging filaments, mainly above and at the right side) and second-day flowers on the left (filaments straight and nearly parallel), corolla lobes straight. – All filaments white. One style marked with an arrow. – Scale bar equal 1 cm.

Fig. 4. *Pararchidendron pruinosum*, third-day flowers, the filaments coloured light ochre, filaments and styles predominantly straight, corolla lobes diverging. – Three styles marked with arrows.

Fig. 5. *Pararchidendron pruinosum*, the majority of flowers of the umbel at the end of anthesis (filaments diverging), three flowers at the right side after anthesis (filaments withered and pendent).

3. Anther

In flower buds of c. 2.3–2.4 mm in length the anthers are approximately full-sized and the last stages of anther development can be investigated. In buds of c. 3.5–4.0 mm the anthers are nearly ripe and still included on coiled filaments in the corolla; the anthers are c. 0.25 mm long, 0.40–0.45 mm wide and 0.30–0.35 mm thick (Fig. 6, 9). The connective is very strongly developed, like a massive cushion of approximately the same thickness in the entire width of the anther (Fig. 9) and forms a thick bulge on the apical end (Fig. 7). The attachment zone joining this bulge is formed of smooth epidermal cells with a slightly bulged cell surface; as a part of the filament it includes the end of the vasculature (Fig. 7, 8). Isthmus- and normal filament-epidermis are structured in the usual manner for the *Mimosaceae* (Fig. 7, 8; Teppner & Stabentheiner 2006, 2007, 2010).

The epidermal cells of the connective are strongly bulged (papillose), those of the valves to a lesser extent; both possess a ribbed surface discernible as sharp ridges in optical sections. The epidermal cells are smooth along the stomium suture (Fig. 15, 16), which splits open over the shoulders to the base of the valves to both ends of the anther (as usual in *Mimosaceae*) (Fig. 9).

The endothecium cells are at first wider than high or ± isodiametric and are filled with strongly light-refracting contents (Fig. 11–13). Later the cells become radially elongated and transparent (Fig. 14), and soon the characteristic thickenings appear: radial ribs (acute distally, Fig. 19) and basal plates (Manning & Stirton 1994: 145). The endothecial thickenings are lacking along the stomium. In the outer valve of a theca the thickenings are developed over the base a little inward just under the polyad, whereas in the inner valves the thickenings reach only the base of the valve. Above the septum near the stomium no thickenings are developed.

The middle layer consists of two or three cellbeds (Fig. 11–14). After the secretion of the tapetal membrane with orbicules, the tapetum is still intact (Fig. 11–14, as usual in *Mimosaceae*).

A theca consists of two locules. Each locule is divided by a parenchymatous, transversal septum into two locule-halves which contain one acalymmated polyad of 16 pollen grains each. In the centre, at the thinnest point, the septum consists of four to six cell layers. Most likely, the two faces of the flat polyads do not significantly differ, but the applied methods are not suited to detect minor differences. The adherence between the grains of a polyad is not very strong, so the polyads are easily damaged during the preparation.

4. Floral Morphology and Anthesis

The partial inflorescences of *Pararchidendron pruinosum* are long-pedunculate pseudo-umbels (also called umbels or corymbs; Fig. 1–5),

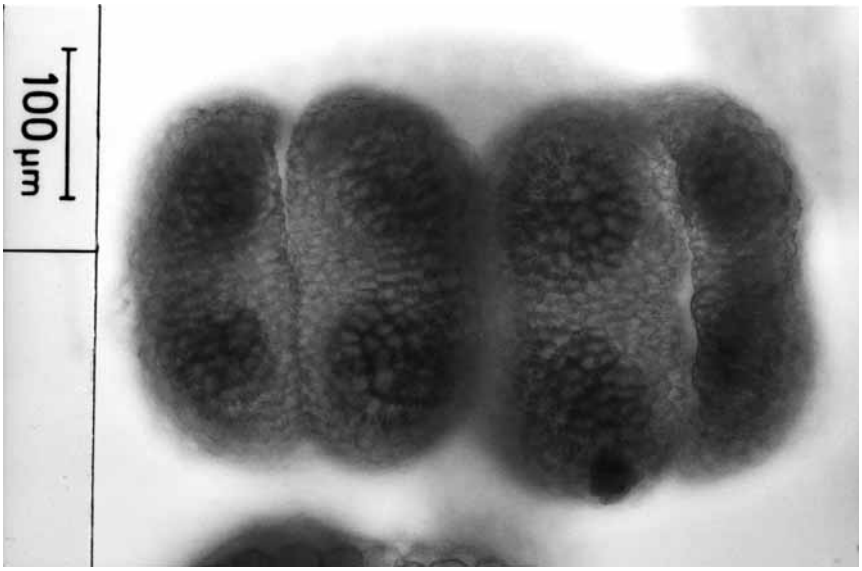

Fig. 6. *Pararchidendron pruinosum*, whole anther, ventral side, optical plane at the height of the stomium, the latter openend slightly by the pressure of the cover slip. Apical bulge out of the optical plane. Bud length 4.0 mm.

c. 3.5–5.5 × 2 cm, which occur singly or paired on reduced brachyblasts in leaf axils (as in the scheme for *Abarema jupunba*, in GRIMES 1992: 147 and 1999: 321) and consist of c. 15–50 flowers on c. 3.5–5.0 mm long pedicels in the axils of small bracts (thin, c. 0.5–1.0 mm long, without glands).

Flower bud initials are formed apparently in winter under short-day conditions, then the flowering period lasts from late May into June under local climatic conditions [6–12°C in the night, 13–26 (–30)°C during the day, day length ca. 15–16 hours).

The flowers are usually 5-merous, hermaphroditic, and with hardly discernible odour. The calyx is c. 1.5–1.8 mm long, this length including the c. 0.4–0.5 mm long, free, triangular lobes. The exterior of the calyx is short appressed-hairy. The corolla is 4.5–5.0 mm long, including the 1.0–1.2 mm long lobes, which are at first erect, later reflexed. Fine, appressed, short hairs occur on the outer corolla surface, and patent hairs occur on the lobe margins. The stamens are 22–28 in number and 8–14 mm long, at first white, later turning to cream or light ochre-brown (sometimes called orange in the literature), filaments united into a tube in basalmost, c. 2.0–2.8 mm. The connection of the filaments to the corolla (corolla-filament-tube or stemonozone) is very short (c. 0.1 mm, maximally 0.15 mm). The anthers are perpendicular to the filament. The discus-bulge around the gynophore is c. 0.5–1.0 mm in diameter and 0.2 mm high. The gynophore is c. 1.1–

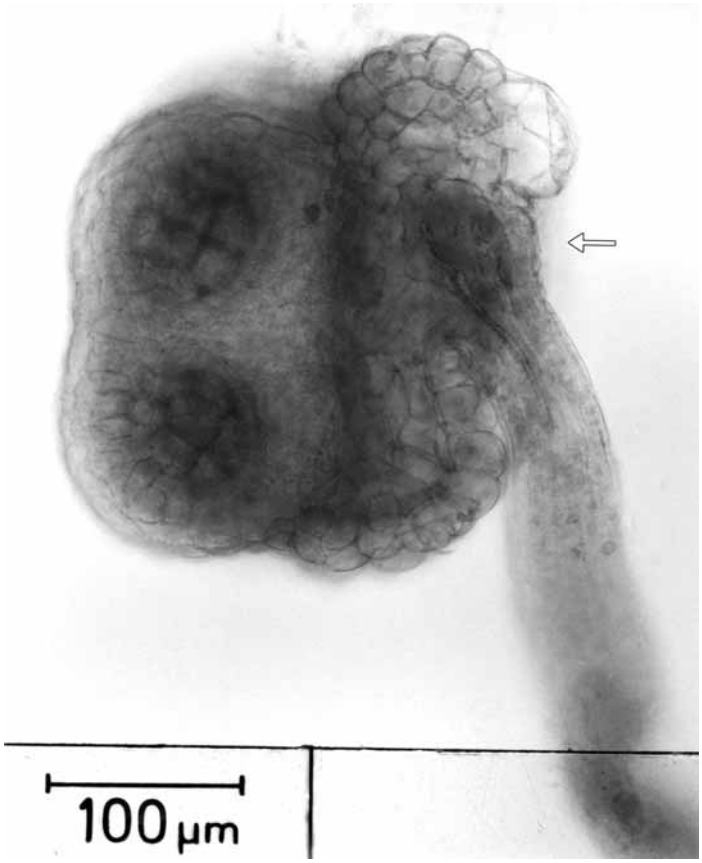

Fig. 7. *Pararchidendron pruinosum*, anther split longitudinally, the portion connecting to the filament in side view, the theca on the left, the connective with the apical bulge on the right, the filament inserts below at this bulge. – The group of minutely bulged epidermal cells in the upper part of the isthmus of the filament is called attachment zone (arrow). – Bud length 2.4 mm. – For details see Fig. 8 and 11).

1.4 mm and the ovary c. 1.6–1.8 mm long. The style is c. 8.0–9.0 mm, and is slightly thicker and stiffer than the filaments (Fig 3, 4). The tip of the style is cylindric and truncate, with the stigma positioned in a terminal flat depression, ± covered in stigmatic fluid. Nectar is extruded by the disc in small amounts or it may fill the space between the filaments up to the base of the ovary.

Flower opening starts in a portion of buds in an inflorescence successively during the day (not synchronous) and begins with clefts between the corolla lobes and the stretching and elongation of the filaments (Fig. 3, Teppner & Stabentheiner 2010: Fig. 1). The filaments in these early stages

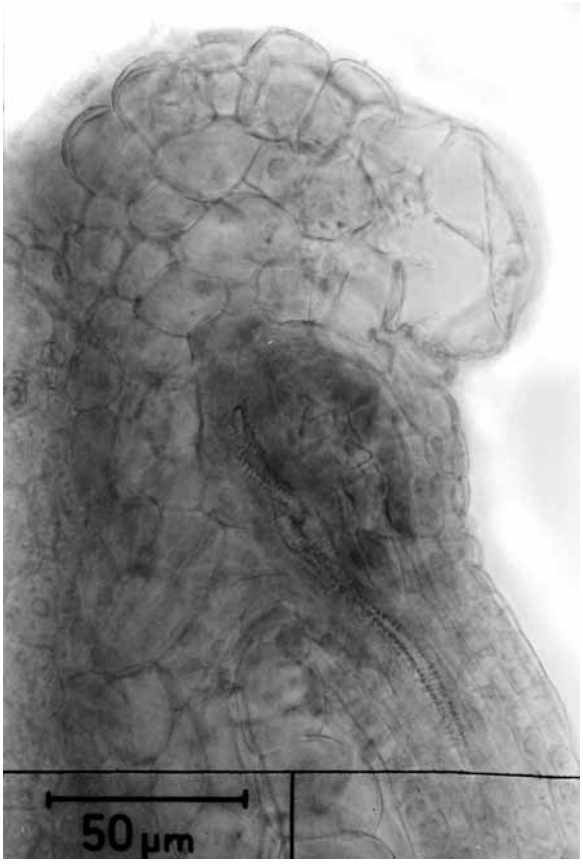

Fig. 8. *Pararchidendron pruinosum*, detail of Fig. 7, apical bulge of the connective, isthmus and attachment zone of the filament, as well as the end of the vascular bundle.

of expansion and release, form a more or less coiled bundle, and 0–3 anthers may open at this time. The straightening of the coiled filaments begins at the top (distally) and progresses to the base. Thus, in an intermediate stage with distally straight and basally bent filaments the stamens of a flower appear irregularly diverging. Fully stretched filaments forming a narrow brush are reached at the end of the first or on the second day and are firstly white (Fig. 2, Fig. 3, left). At this time c. half, or as many as all of the anthers are opened (for the opening process itself see Teppner & Stabentheiner 2010). The styles remain slightly bent at this time (Fig. 3), and are usually a little shorter than the filaments, bearing stigmatic fluid in the apical cavity (see also Teppner & Stabentheiner 2010). On the third or fourth day the colour of the filaments changes to cream or a light ochre-

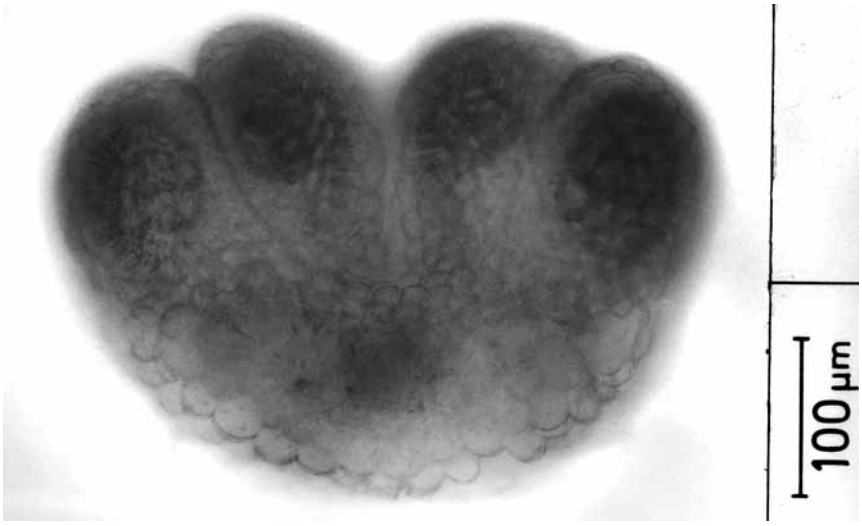

Fig. 9. *Pararchidendron pruinosum*, view of the distal end of an anther, optical section near the distal end of the anther. The stomium lies in a furrow and reaches up to the base of the valves. – Bud length 2.8 mm.

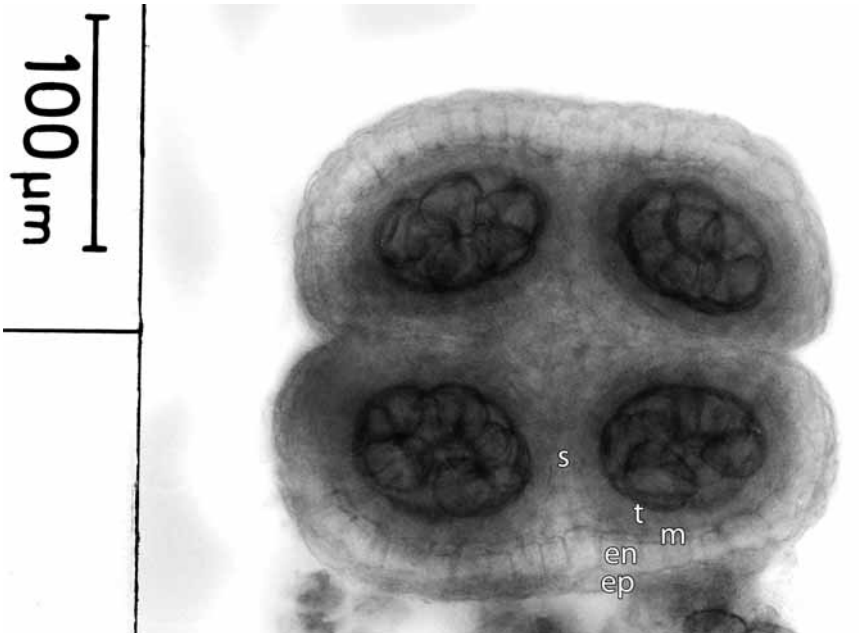

Fig. 10. *Pararchidendron pruinosum*, a theca in optical, longitudinal section, two locules partitioned by a parenchymatous septum, one polyad in each locule half. – Bud length 2.3 mm.

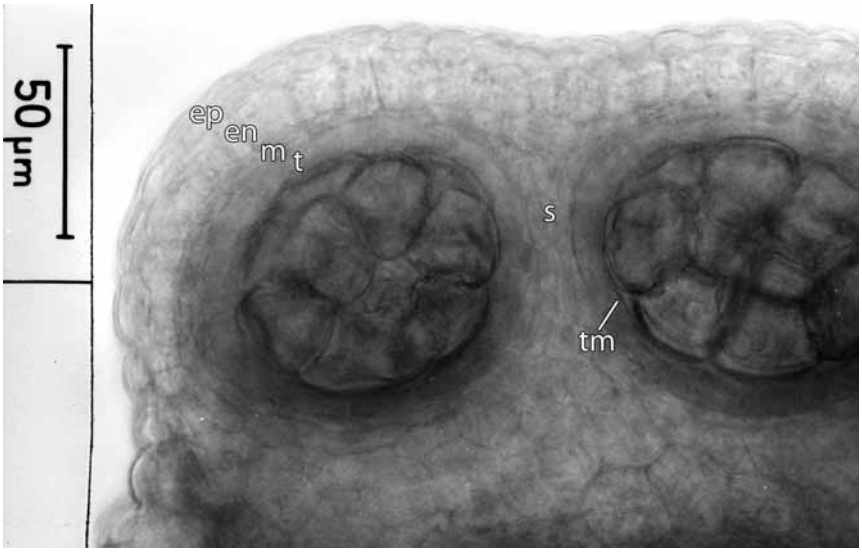

Fig. 11. *Pararchidendron pruinosum*, detail of the locule in Fig. 7, optical, longitudinal section, endothecium cells with globular content, m two-layered, septum with 4–5 layers in the central part.

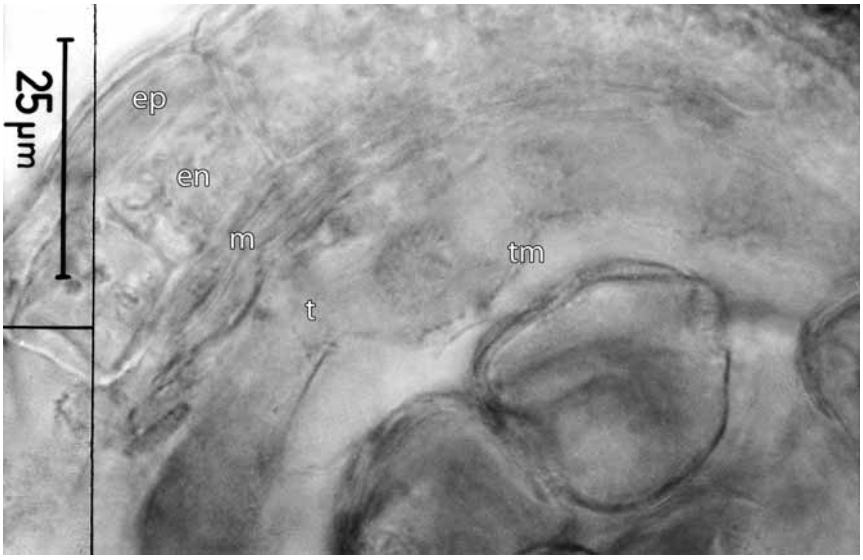

Fig. 12. *Pararchidendron pruinosum*, optical, longitudinal section through locule wall and polyad, endothecium cells with globular content, m three-layered. – Bud length 2.3 mm.

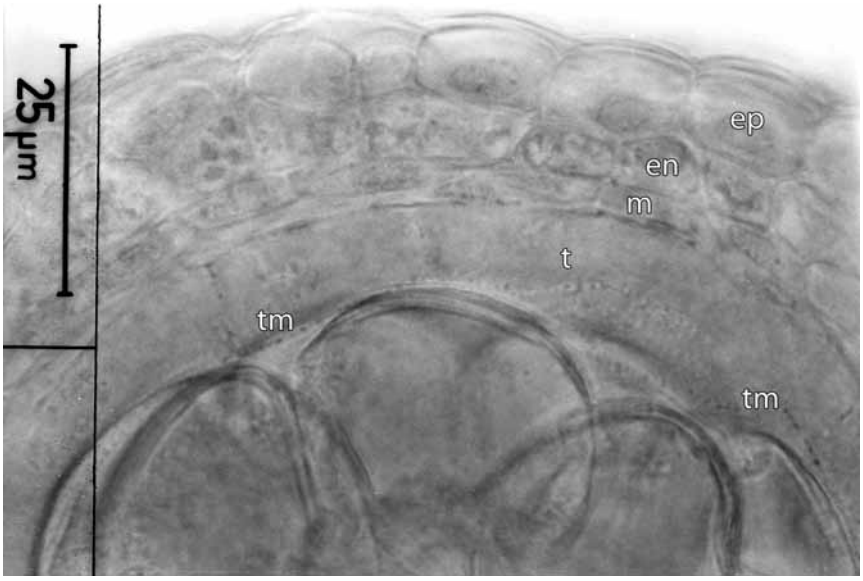

Fig. 13. *Pararchidendron pruinosum*, other part of the same locule as in Fig. 12, optical, longitudinal section through locule wall and polyad.

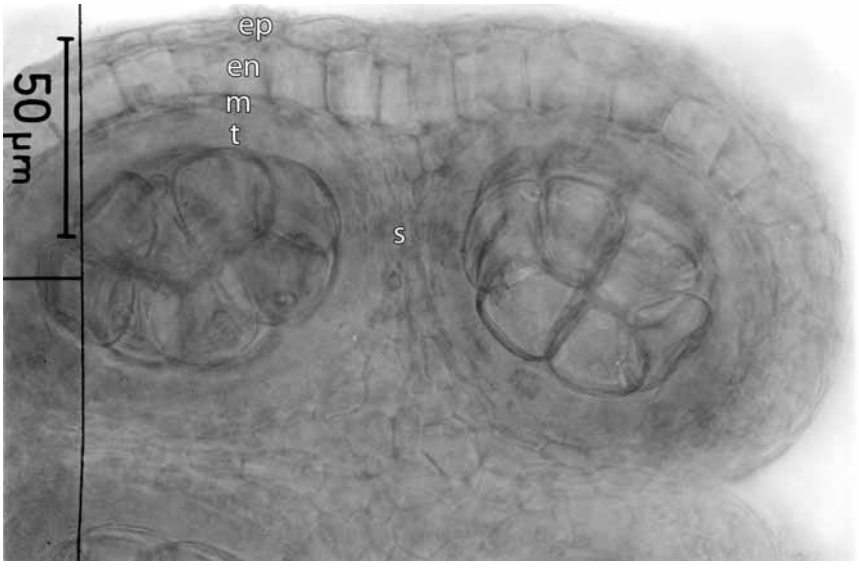

Fig. 14. *Pararchidendron pruinosum*, locule in optical, longitudinal section, stage a little later than in Fig. 11–13, endothecium cells with homogenous content. – Bud length 2.3 mm.

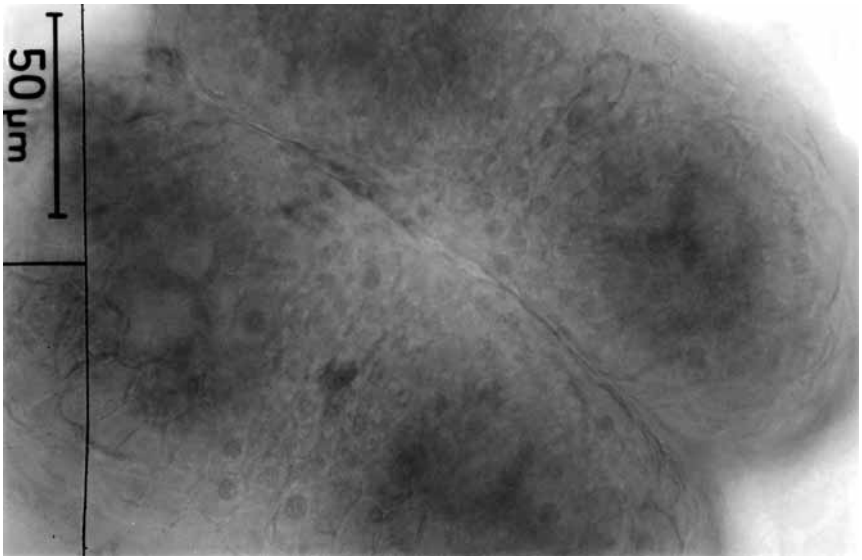

Fig. 15. *Pararchidendron pruinosum*, theca from above (ventral side), stomium in the optical plane, remaining wall (mainly endothecium) in optical section. Endothecium still without thickenings. Polyads out of the optical plane. Stomium opened slightly in the centre by the pressure of the cover slip. – Bud length 2.3 mm.

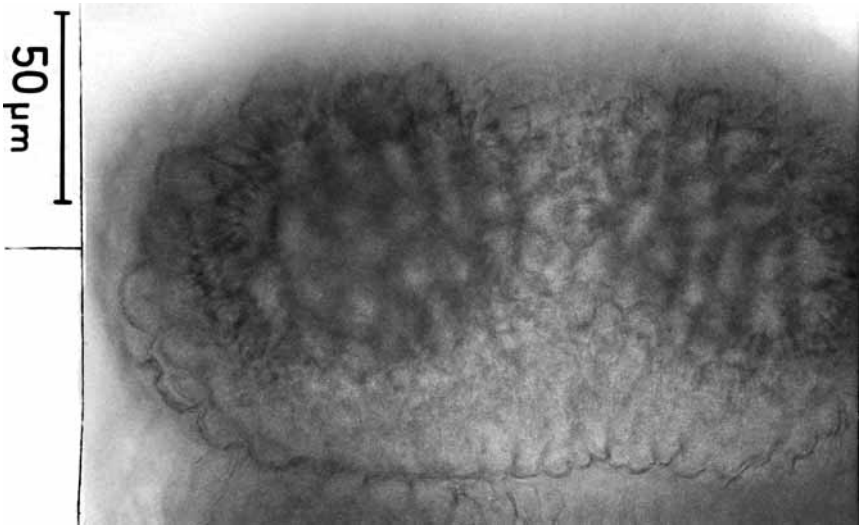

Fig. 16. *Pararchidendron pruinosum*, stomium of a theca in surface view (epidermal cells), endothecial cells with thickenings in optical section, polyads out of the optical plane. In the center, above the septum (between the polyads), cells with thickenings more distant from the stomium than in the subterminal parts of the valve. – Bud length 2.8 mm.

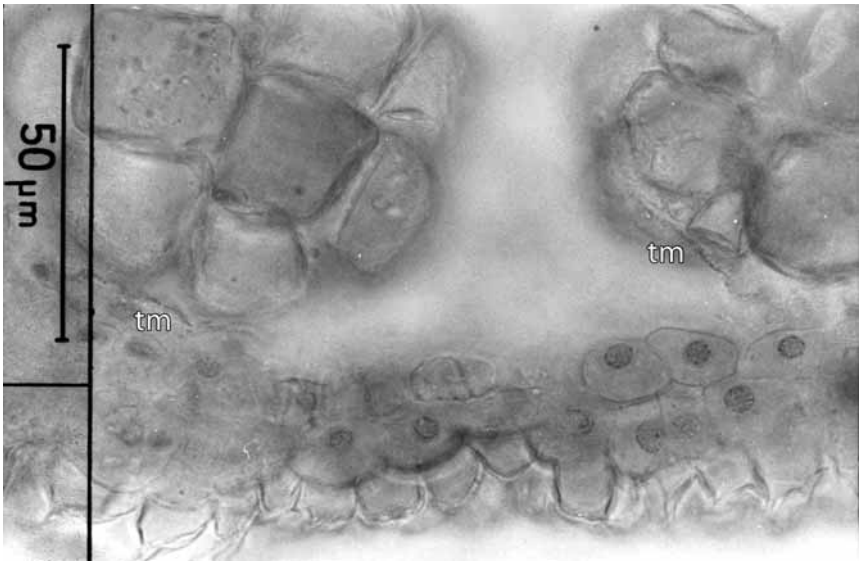

Fig. 17. *Pararchidendron pruinosum*, theca split longitudinally, central part of a locule, the septum already dissolved in its centre. – Bud length 3.5 mm.

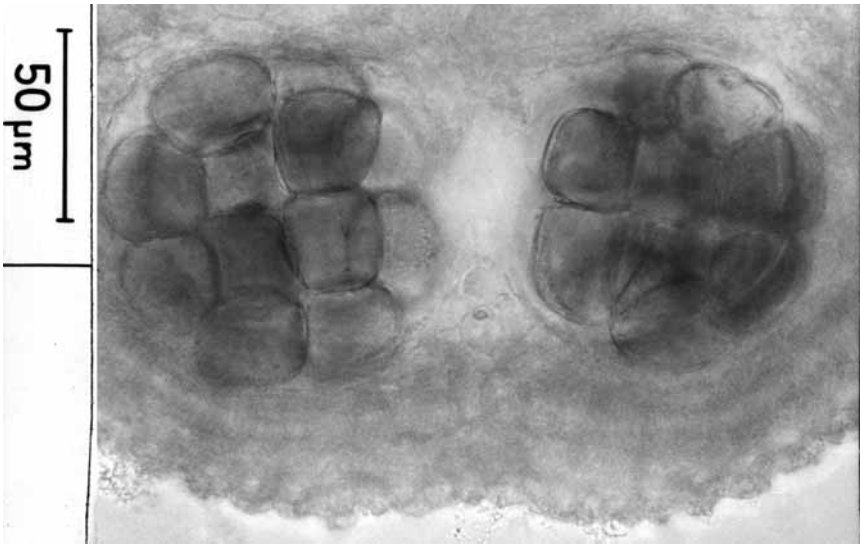

Fig. 18. *Pararchidendron pruinosum*, optical longitudinal section through a locule, septum dissolved in the centre. – Bud length 4.0 mm.

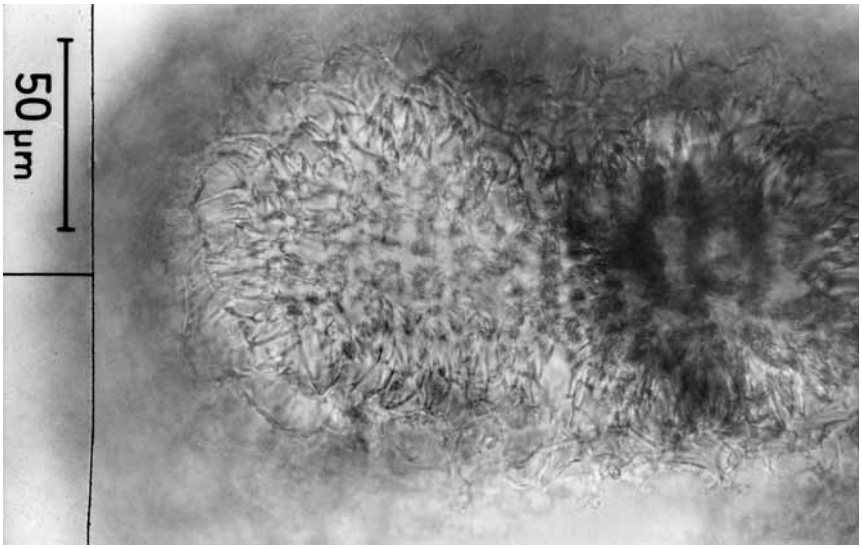

Fig. 19. *Pararchidendron pruinosum*, locule in one half (left) without, in the other (right) with a polyad, optical section through the endothecium. Endothecial thickenings in optical section in the centre of the locule-halves, at the periphery more or less in side view. – Bud length 4.0 mm.

brown. In the early phase of the colour change a small percentage of anthers (estimated less than 5%) may be still closed. Soon all anthers open, the initially connivent or erect corolla lobes bend outward somewhat and the styles turn more or less straight, becoming as long as or, usually, becoming slightly longer than the filaments (Fig. 4). All these changes may indicate the change from a functionally male or hemaphrodite stage to a female stage of the flower.

By the fifth or sixth day of anthesis, the filaments become somewhat irregularly diverging once more (Fig. 5), which may mark the end of anthesis. From the seventh day onward, in a portion of the styles the apical annulus around the stigma or the stigma itself may become brown (others remain white up to the time the flower is shed). Often 1–2 polyads were observed in the stigmatic cavity, but it remains unclear if this is caused by movements of styles and stamens or by the manipulation of the flowers during observation and preparations. For some days more, the filaments appear fully turgid. However, by the 11th day onward usually, wilting becomes evident, either as the apical half or third of the filament bends downward or, as the filaments wither from drying (Fig. 5, right side). At this time (sometimes as early as the eighth day), the nectar is reabsorbed. From the 12th day on, non-pollinated flowers begin to drop off (abscission at the base of the pedicel).

According to the above mentioned interpretation, anthesis of an individual flower lasts for five or six days. Because the flowers of an umbel open on successive days, anthesis of a whole umbel is usually c. 8–9 days. Flowers still present from c. the 15th day onward are successfully pollinated and have the potential to set fruit.

Pararchidendron is clearly self fertile, though it was not possible to discern whether it is self-pollinating or whether vectors (i.e., insects) are required to trigger fertilization. During sporadic observations during the day no flower visitors were observed on the *P. pruinosum* flowers in the garden.

5. Discussion

Pararchidendron (with a single species and four varieties: Nielsen & al. 1984: 79–84, Nielsen 1992: 145–148) is a member of the tribe *Ingeae*. Modern results on the generic affinities within *Ingeae*, unfortunately not sufficient to resolve clearly these affinities, are summarized in Lewis & Rico Arce 2005: 193–195. By this reconstruction, *Pararchidendron* together with the American *Hydrochorea* and *Abarema* form the *Abarema* alliance within the core *Ingeae*. Brown 2008: 38 criticizes this inclusion of *Pararchidendron* in the *Abarema* alliance. In Brown & al. 2008: 742 *Pararchidendron* appears in a clade of "Australian & SE Asian *Ingeae*" together with three species of a non-monophyletic genus *Archidendron*, and the genera *Paraserianthes, Archidendropsis* and *Wallaceodendron*. Living material of *Archidendron* was not accessible for the present study. From the figures of the androeceum (showing only minimal details of the anthers) of *Archidendron lucyi* in van Heel 1993: 553 and *A. vaillantii* in Endress 1996: 109 and the anther in Endress & Stumpf 1991: 252 the connective seems to be of usual size for *Mimosaceae*, is not so wide as in *Pararchidendron* and the apical bulge is less prominent, and is therefore not so close to *Pararchidendron* in this regard. According to my observations of flowers of some frequently cultivated *Ingeae* the closest similarities to *Pararchidendron* occur with *Pithecellobium dulce* (Roxb.) Benth. and *Albizia julibrissin* Durazz. (two figures of anthers in Endress & Stumpf 1991: 250). I hope to describe this in forthcoming papers.

Owing to the very gradual transition from anthesis to postanthesis it is very difficult to estimate the duration of anthesis. Even the conservative estimate as above gives a duration of five or six days. This is very long for *Ingeae* and *Mimosaceae* as a whole. Regarding the wilting of filaments as marking the end of anthesis (in the sense of capability of pollination followed by fertilization) would give a duration of c. 11 days, this is highly improbable because sometimes even in flowers dropping off filaments may be turgescent and stigmas white. Under natural conditions, with daily rainfalls alternating with hot sunny phases, the transition of anthesis to

post-anthesis events may be more pronounced. Observation of pollinators within the range of natural distribution, either in nature or in cultivated settings, would also be of interest. From the successive opening of flowers and anthers during the daylight hours, I would expect diurnal visitors at least in part.

The structure of the anther is essentially comparable to other *Ingeae* with 8-, 16- or 32-grained polyads such as *Albizia* (YAMASAKI 1956), *Paraserianthes* (ENGLER 1876), *Inga* (TEPPNER 2007b) and *Acacieae* (ROSANOFF 1866, ENGLER 1876, NEWMANN 1933). Each locule is divided into two locule-halves by a septum of parenchymatous tissue, containing one polyad (surrounded by the tapetal membrane) each.

6. Acknowledgements

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