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***Inga feuillei* (Mimosaceae-Ingeae): Anther Opening and Polyad Presentation**

By

Herwig TEPPNER*) and Edith STABENTHEINER**)

With 50 Figures

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Key words: *Inga feuillei*, *Ingeae*, *Leguminosae*, *Mimosaceae*, *Mimosoideae*. – Anther, anther opening, anther septation, anthesis, filament isthmus, floral ecology, morphology, pollen presentation, polyads. – Environmental scanning electron microscopy.

Summary

TEPPNER H. & STABENTHEINER E. 2006. *Inga feuillei* (Mimosaceae-Ingeae): Anther opening and polyad presentation. – *Phyton* (Horn, Austria) 46 (1): 141 – 158, with 50 figures. – English with German summary.

The development of anthers in the opening flowers of *Inga feuillei* DC. (*Mimosaceae-Ingeae*) was investigated with the help of stereo microscopy and environmental scanning electron microscopy (ESEM) and documented with photos. The two thecae sit far apart on a massive connective and have transverse septa by parenchymatous tissue. The filament inserts in an ellipsoid attachment zone on the dorsal side of the anther with a narrow isthmus, its apex dehydrates and the cells collapse during the anther opening. The latter starts with a slit along the whole stonium. The theca valves strongly fold basally inwards, the adjacent (central) parts of the valves become flat and port the polyads; the margin of the valves shrivels and bend back. So, finally, four flat bulges with two polyads each are exposed in a rubber stamp-like manner. The polyads have two different faces and are covered with a thin layer of pollenkitt. The opening process of the anthers lasts for $1/2 - 1\frac{1}{2}$ hours and occurs in the afternoon. The flowers are usually open for one night, the preceding

*) Pens. Univ.-Prof. Dr. Herwig TEPPNER, Institute of Plant Sciences, Division of Systematics and Geobotany, Karl-Franzens University Graz, Holteigasse 6, A-8010 Graz, Austria, Europe; e-mail: herwig.teppner@uni-graz.at

**) Ass.-Prof. Dr. Edith STABENTHEINER, Institute of Plant Sciences, Division of Plant Physiology, Karl-Franzens University Graz, Schubertstrasse 51, A-8010 Graz, Austria, Europe; e-mail: edith.stabentheiner@uni-graz.at

afternoon and the following morning. Sphingids and noctuids are most probably the normal pollinators.

Zusammenfassung

TEPPNER H. & STABENTHEINER E. 2006. *Inga feuillei* (Mimosaceae-Ingae): Antheren-Öffnung und Polyaden-Präsentation. – *Phyton* (Horn, Austria) 46 (1): 141 – 158, mit 50 Abbildungen. – Englisch mit deutscher Zusammenfassung.

Die Entwicklung der Antheren in den sich öffnenden Blüten von *Inga feuillei* DC. (Mimosaceae-Ingae) wurde mit Hilfe von Stereolupe und REM verfolgt und durch Photos dokumentiert. Die beiden Theken sitzen weit getrennt auf einem massiven Konnektiv und sind durch Parenchym quer septiert. In einer ovalen Anheftungszone am Rücken der Anthere sitzt das Filament mit einem schmalen Isthmus an, dessen Apex während des Antheren-Öffnens austrocknet und kollabiert. Der Öffnungsprozeß beginnt mit einem Spalt entlang des ganzen Stomiums. Die Theka-Valven falten sich an ihrer Basis stark einwärts, die angrenzenden (zentralen) Teile der Valven werden flach und tragen die Polyaden. Der Rand der Valven schrumpft und krümmt sich zurück. So sind schließlich vier oben ebene Wülste mit je zwei Polyaden emporgehoben und bilden insgesamt eine stempelförmige Struktur. Die Polyaden haben zwei verschieden gestaltete Flächen und sind von einer dünnen Schicht Pollenkitt überzogen. Die Blüten sind meist für eine Nacht, den vorhergehenden Nachmittag und den folgenden Vormittag offen. Schwärmer und Eulen dürften die normalen Besucher sein.

1. Introduction

In *Ingae* and as well as in *Mimosaceae* as a whole, anther opening and pollen presentation have become features of interest in characterization of taxa. HERNANDEZ 1986 and GUINET & HERNANDEZ 1989 used such characteristics for the delimitation of the new genus *Zapoteca* from *Calliandra*. PRENNER & TEPPNER 2005 described *Calliandra angustifolia*. HUGHES 1997 (among other things) discusses open anthers in *Leucaena* (*Mimoseae*) and KENRICK & KNOX 1979 those of *Acacia* (*Acacieae*).

According to LEWIS & RIO ACRE 2005 the *Inga* alliance (10 genera) is a core group of *Ingae*. Thus it would be of interest to know its anthers in more detail and to provide a basis for comparison with other genera, especially *Calliandra*. The short description and the low magnification image in TEPPNER 1998 are not sufficient for this purpose. According to the monograph of PENNINGTON 1997 *Inga* comprises c. 300 species (a number of imperfectly known taxa included). A discussion of the age of speciation within *Inga* was initiated by BERMINGHAM & DICK 2001 and RICHARDSON & al. 2001.

Inga feuillei DC. (a variety with fruits hairy at the dorsal and ventral dilatation), is being cultivated at the botanic garden since 1979. Five trees were planted in the division for Andean plants in the entrance hall of the new greenhouse complex of the Institut für Pflanzenwissenschaften in Graz in 1995. The trees have now a DBH (diameter at breast height) of 10 –

20 cm. *I. feuillei* has been described and reviewed in a previous paper (TEPPNER 1998).

2. Material and Methods

Seeds were purchased in Lima, Peru, on June 12, 1979, H. TEPPNER 79/428 & K. KEPLINGER, and were sown few days later in the cool greenhouse in Graz. The treelets were c. 3 m high, when planted 1995 in the new greenhouse of the Institute of Plant Sciences of the University in Graz (Austria, Europe).

Anthesis was observed on intact inflorescences directly on the trees. In addition, cut inflorescences were watered and investigated in the laboratory using a stereomicroscope (Wild M 3B) and the environmental scanning electron microscope (ESEM). Flower buds of cut inflorescences also open on the second and third day approx. at normal time, thus one can assume that on the first day the timing of anthesis is the same as on the intact trees. This is also in accordance with the experience on the trees.

For an overview of the internal structure of the anther, longitudinal and transversal manual cuts in water were used.

Time scale is indicated in CET (Central European normal time).

For ESEM investigations fresh anthers were mounted on aluminum stubs using C-impregnated double sided tape and investigated without any further preparation using a Philips XL 30 ESEM scanning electron microscope (FEI), using the following conditions: 0.8–0.9 torr chamber pressure, 9 mm working distance, 20 kv acceleration voltage, LFGSED (large field gaseous secondary electron detector).

For the observation of the opening process, fully ripe but still closed anthers from opening flowers were inserted into the chamber of the ESEM; after a few minutes opening of the anthers began.

3. Results

3.1. Anthesis

Flowers within a spike open, beginning from the base, acropetally (Fig. 1). Anthesis of all flowers of a day is nearly synchronous. The start of anthesis, the opening of the valvate corolla lobes, takes place between 10:00 – 13:00 hours. The hank of anthers and coiled filaments appears (Fig. 5 and 6). The longitudinal axis of the anther is \pm parallel to the longitudinal axis of the (apical part of the) filament, which lies in a flat longitudinal depression on the dorsal side of the anther (Fig. 6, compare Fig. 12 and 13). The filaments extend progressively and the anthers slowly start to turn in a position perpendicular to the filaments. At c. 16:00 usually, the opening of the anthers begins (only few single anthers open earlier, from 15:00). The filaments are coiled to nearly straight and greenish in the distal part, surpassing the tips of the corolla by c. 1.0–1.5 cm. Till 17:00 opening has progressed, in a part of anthers polyads are exposed, the filaments are more or less straight but still greenish and not of full length; the position of anthers is more or less oblique. When the filaments become straight, between 17:00 and 18:00, the nectar secretion starts but remain low in the

first 2–3 hours (up to 1–3 mm high, one-sided between ovary and filaments). At 18:00 nearly all anthers are open and the polyads exposed, nevertheless, not all anthers are in the final horizontal position and the filaments are still a little greenish at their tips. Thus, the full presentation of the polyads and the beginning of nectar secretion take place before the duskfall. In full darkness, at c. 19:00–20:00, the opening process seems to be finished: the filaments are extended to their final length (surpassing the corolla tips for 2.0–2.5 cm), are white and the anthers are perpendicular to the filaments (Fig. 2 and 42). The process from the first splitting of the corolla lobes up to the presentation of the polyads lasts for 3–4 hours, the anther opening itself usually for c. $\frac{1}{2}$ to 1 or $1\frac{1}{2}$ hours. The time span needed in the ESEM lies in the same dimension. Anthesis is accompanied by a weak but distinct and characteristic odour (night and day, with varying intensity) which may be described as perfume-like when fresh and a little strong when fading. The anthers persist on the withered and dry filaments.

Anthesis of a single flower lasts for one night in Peru. The same is true for our greenhouse in c. June to August (day length 14–16 hours), where wilting of the filaments takes place between 9:00–11:00 of the next morning. In September (day length 12–13 hours) fading of the filaments begins at c. 20:00–21:00 on the day after the opening day and they are distinctly withered at 23:00–24:00. Under cooler conditions in November opening of the flowers occurs later, anthers open just in the night (after 21:00) and withering takes place in the morning of the third day.

3.2. Some Notes on Flower Morphology

Calyx length measures c. 10–13 mm, the corolla c. (13–)20–24 mm, the fully developed filaments c. 40–45 mm (Fig. 2 and 3); their basal part is fused into a tube shorter than the corolla, c. 12–17 mm long (Fig. 3 and 7), and forming a stemozone of c. 2.0–4.0 mm (Fig. 7). The numbers of stamens varies between (75–)100–120 per flower (Fig. 2 and 3).

The thecae and the locules, respectively, are partitioned by a transversal septum of parenchymatous tissue. In the centre of the locule the septum is thin, 1–2-layered, towards the periphery it dilates to 5–7 layers (compare ENDRESS & STUMPF 1991: 253, DNYANSAGAR 1954 and ENGLER 1876: 275–291 for other *Mimosaceae*). So an anther consists of two thecae, four locules and eight locule halves with one polyad each (diagram and discussion of terminology in PRENNER & TEPPNER 2005: 270, 272, 279–280). As well known for the longitudinal septum (e.g., KEIJZER 1987: 489, 490, 492), this transversal septum is also dissolved during late developmental stages in the flower bud. The remains of the peripheral cells of the transversal septum appear on the valves as bulges (e.g., Fig. 35, 41, 45) dilated like a gusset towards the valve margin (Fig. 33). In the depth of the locules

the 'cross' of the remains of the longitudinal and the transversal septum can be seen (e.g., Fig. 37 and 47). Here the cellular structure of the septa can be clearly recognized.

The nectary is a circular, shallowly ten-lobed bulge, c. 0.6–1.0 mm high, adnate for its whole length to the stemonozone (Fig. 7). The inner diameter near the base of the nectar room measures c. 2.0 mm. The nectar fills the whole tube, but also flowers without nectar may occur sporadically, in spite of the presence of a nectary. Nectar access is very narrow, the entrance is completely closed by filaments and style, thus access is possible between the filaments only. It is relatively easy to put a needle (up to 1.0 mm in diameter) between the filaments to the nectar but not thicker objects, e.g., the tip of a small forceps. The gynoeceum is 1 (often 2-, rarely 3-)carpellate (Fig. 3, 7 and 4). Male flowers with a small carpellodium (c. 2.0 mm long) may occur along with the hermaphrodite ones.

3.3. Anthers, Filament Attachment Zone and Isthmus

The closed anthers (Fig. 8–13) measure c. 0.5 mm in length \times 0.7 mm in width. A massive cushion-like connective holds the two thecae. The apical end of the anther (connective) is a little rounded, the basal one a little emarginated. The epidermal cells form shortly conical, ribbed papillae. The distinct stomium passes along the whole length, over the shoulders of the anthers up to the connective (Fig. 8 and 10).

The construction around the filament attachment seems to be very complicated. The filament is diminished at its apex and forms a narrow isthmus (Fig. 12–15). This is responsible for the versatility of the anthers. Its epidermis consists of c. twenty rows of shortly cylindrical cells (Fig. 15). The attachment zone lies in a depression on the dorsal side of the anther, is elliptical and divided by the small filament insertion point unequally. The larger apical part, is covered by shortly papillate cells with smooth or partially striate cuticle. The very small basally directed area on the other side of the filament shows small cells but otherwise similar to the other epidermal cells (Fig. 14 and 15). During the maturation of the anthers in the afternoon, the isthmus- and attachment zone-cells change dramatically: they collapse, apparently by dehydration. The collapsing in the filament isthmus begins in the epidermis directly at the anther (Fig. 16 and 17), progresses successively (Fig. 18–22) and finally, in the evening, the whole apical half of the isthmus is collapsed (Fig. 23). The cells of the attachment zone, especially of the larger apical field can collapse more (Fig. 19–21) or less (Fig. 22–23). If the turgescence of these cells should be responsible for the longitudinal, erect original position of the anthers, then the loss of turgor may be the cause for the bending of the anther in the position perpendicular to the filament.

3.4. Anther Opening and Polyad Presentation

The opening process is presented here for three anthers in different positions: The view of the basal end of the anther (Fig. 11, 24 and 25), of the apical end from a little above (Fig. 26–35) and of the inner (ventral) side from above (Fig. 36–41). It begins with the appearance of a slit through the stomium (Fig. 11), practically simultaneously along the whole length. The bending back of the theca walls follows (Fig. 24, 26 and 36). The theca valves are sharply folded inward at their very base (e.g., Fig. 25, 27, 31 and 37). The sides, a little arched by the volume of the polyads, bend back, and this zone which bears the polyads becomes more and more flat (e.g., Fig. 27–35, 38–41). Finally the ends of this zone are a little bent down (e.g., Fig. 35, 41 and 42). The margin of the theca valves crumples further back and shrivels (e.g., Fig. 34, 35 and 42–46). So the polyads appear elevated. Practically, a longitudinal bulge with a flat upper side is formed inward in each valve and the four bulges of an anther lie in one plane, approximately. The end sectors of the bulges bear the polyads and, as a whole, the anther forms a rubber stamp-like structure at the end of the opening process (Fig. 42).

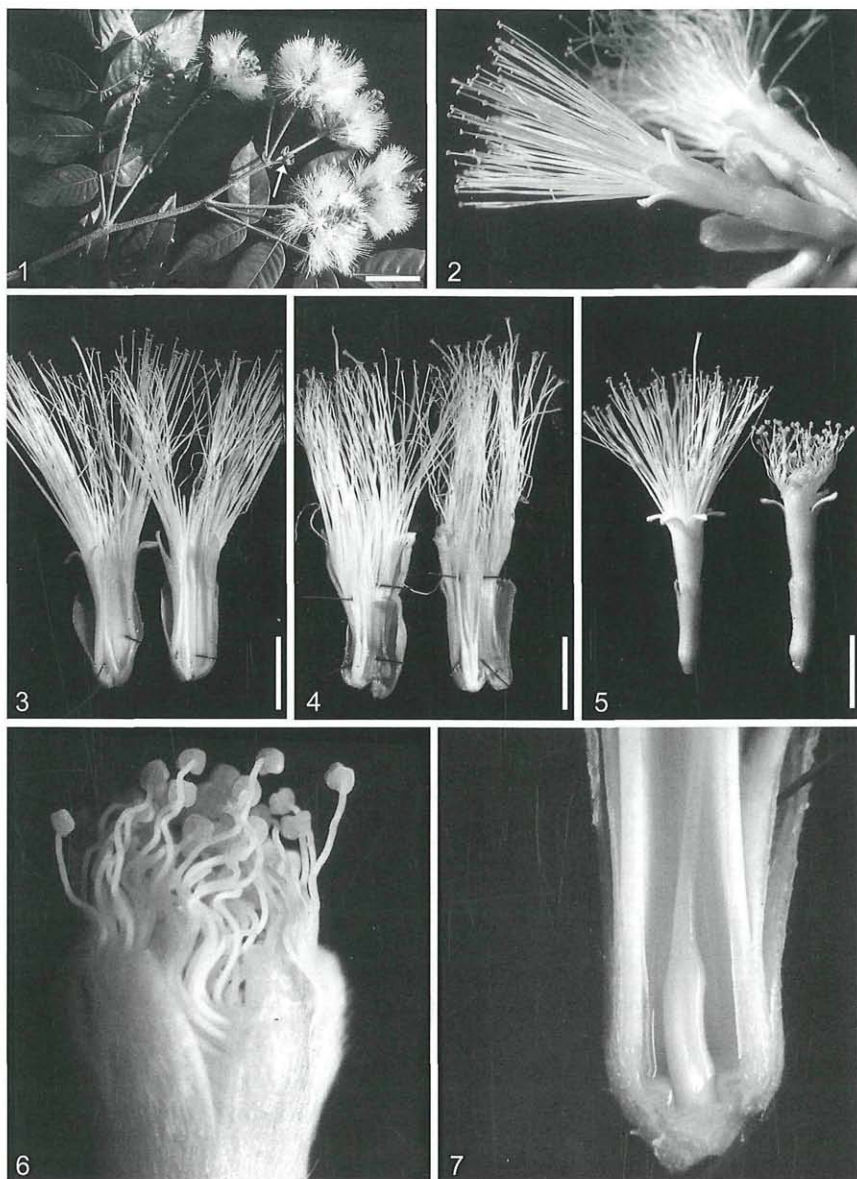
If the thecae of an anther do not open synchronously, the inner walls can overlap (Fig. 25 and 31) and eventually a polyad can be wedged in.

The remains of the transversal septum form a distinct bulge on the valves (e.g., Fig. 33). In the open anther the 'cross' of this transversal bulge with the remains of the longitudinal septum can be seen (e.g., Fig. 35, 36–41 and 47). No tapetal membrane nor other sporopollenin structures were observed in the locules around the polyads.

3.5. Polyads

The roundish to elliptic polyads are 32-celled. The inner (= upper or exposed) side of the polyad (e.g., Fig., 36–46) and the outer (= lower or adherent) side (Fig. 48 and 49) show distinct differences: on the upper side the pollen grains are arched evenly, whereas on the lower side the bulge is flattened (Fig. 50). Furthermore the upper side of the polyad (contiguous to the longitudinal septum of the developing anther) is more or less in a single plane, whereas the lower side is arched (Fig. 50), what can be seen through the theca wall already (e.g., Fig. 8, 26 and 37). The polyads are covered by a thin layer of pollenkitt which can be seen in the optical section of the

Fig. 1–7. *Inga feuillei*. Fig. 1. A twig with axillary inflorescences (spikes), in part crowded at the end. Arrow: end of the shoot axis. – Fig. 2. One flower in anthesis (length c. 4.3 cm) and two withered ones. – Fig. 3. Two flowers in late anthesis with G 1, split longitudinally. – Fig. 4. Two flowers at the day after anthesis, one with G 2, the other (right) with G 3, split longitudinally. – Fig. 5. One flower in late anthesis,



the other after the begin of opening, 15:20 CET on September 8. – Fig. 6. Developing anthers, shortly after the start of the opening of the corolla, c. 14:20 on September 18. Anthers on the longest filaments c. 5 mm above the tips of the corolla lobes. – Fig. 7. Flower cut longitudinally. Calyx and corolla bent sideward (right) for showing the stemozone (c. 2.8 mm). Maximal height of the nectary c. 0.7 mm. Ovary c. 3.5 mm long. – Scale bars in Fig. 1: 5 cm, in Fig. 3-5: 1 cm.

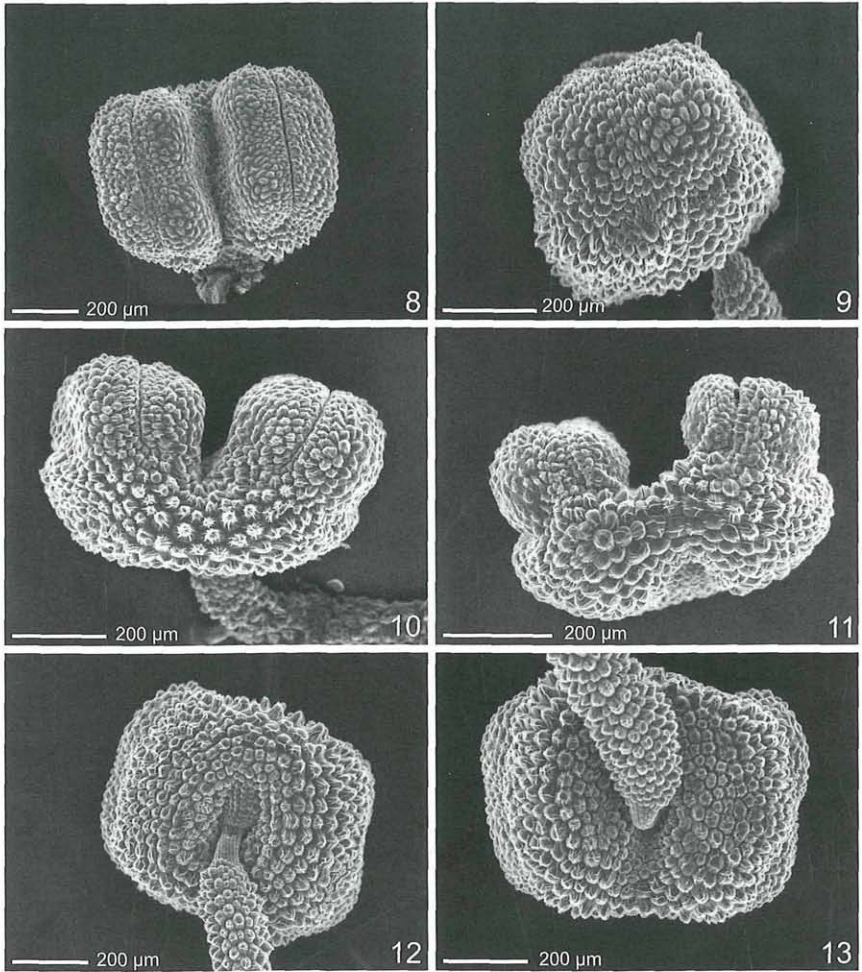


Fig. 8–13. *Inga feuillei*, closed anthers from opening flower buds. – Fig. 8. Ventral side, apex above. – Fig. 9. Side view, apex on the left side. – Fig. 10. View of the apical end. – Fig. 11. The basal end. In the right theca opening has started. – Fig. 12. Dorsal side, filament in normal position in the depression. – Fig. 13. Dorsal side, same orientation as Fig. 12, but filament bent upward, to show the depression.

polyad in the light microscope. Sometimes a small amount can be recognized in the ESEM (Fig. 30, 33 and 34). The tip of a needle usually is not sufficient to remove a polyad by adhesion from the anther, but with the side of a needle the plane of contact is of appropriate size. On a finger-tip or on a slide or cover slip the polyads adhere very well.

4. Discussion

4.1. Morphology

Inga stamens show characteristic features which are common in *Mimosaceae*: long and coiled filaments in the bud stage enclosed in the corolla and extending during anthesis; glabrous filaments; narrow isthmus at the apex of the filaments (TUCKER 1996: 238); papillate epidermis. The tip of the anther (connective) has no effiguration as in many *Mimosaceae*, but at least the tip is rounded. The dehiscence suture extends over both shoulders of the thecae (ENDRESS & STUMPF 1991: 253).

From the few figures of open anthers in the literature (e.g., *Acacia* ENDRESS 1996: 282, *Zapoteca* GUINET & HERNANDEZ 1989: 9, *Calliandra* PRENNER & TEPPNER 2005: 279) it seems, that a longitudinal bulge formed from the theca valve by inward folding, should be common in *Mimosaceae* (and other angiosperms). The peculiar feature in *Inga* is the exposed part of this bulge, which becomes nearly plane, so that the polyads can usually adhere with a large part of their face. A somewhat similar situation seems to occur in *Zapoteca*, but the figures in GUINET & HERNANDEZ 1989: 9 and HERNANDEZ 1990: 228 give the impression, that the longitudinal bulge is not flat and the polyads adhere with a smaller part of their face only. Longitudinal and transversal septum are largely dissolved before opening; this phenomenon, in general terms, is discussed in KEJZER 1987: 489–492.

The *Ingeae*-stamens most similar to *Inga feuillei* figured with details in the literature are *Albizia julibrissin* and *Archidendron vaillantii* (ENDRESS & STUMPF 1991: 250, 252), *Pararchidendron pruinosum* and *Calliandra houstoniana* (TUCKER 1996: 242). Isthmus details are not discernible in these figures, so comparisons are not possible. For *Gasteria verrucosa* (*Asphodelaceae*) dehydration of the filament tip is mentioned in KEJZER 1987: 490. SCHMID 1976 discusses the importance of changes in the filament structure for interruption of water transport as one possible support of desiccation of anthers. Such changes might be caused in the vessels by the very quick elongation of the filaments. We do not know, if the collapsing of the cells at the isthmus apex is also important in this connection. Some *Mimosaceae* abscise and shed the anthers, *Inga* and others do not. Therefore, abscission and shedding of anthers is not a necessary or logical consequence of a narrow isthmus.

From the few species, in which the nectary is better documented, the nectary adnated to the stemozone in *I. vera* WILLD. subsp. *affinis* (DC.)

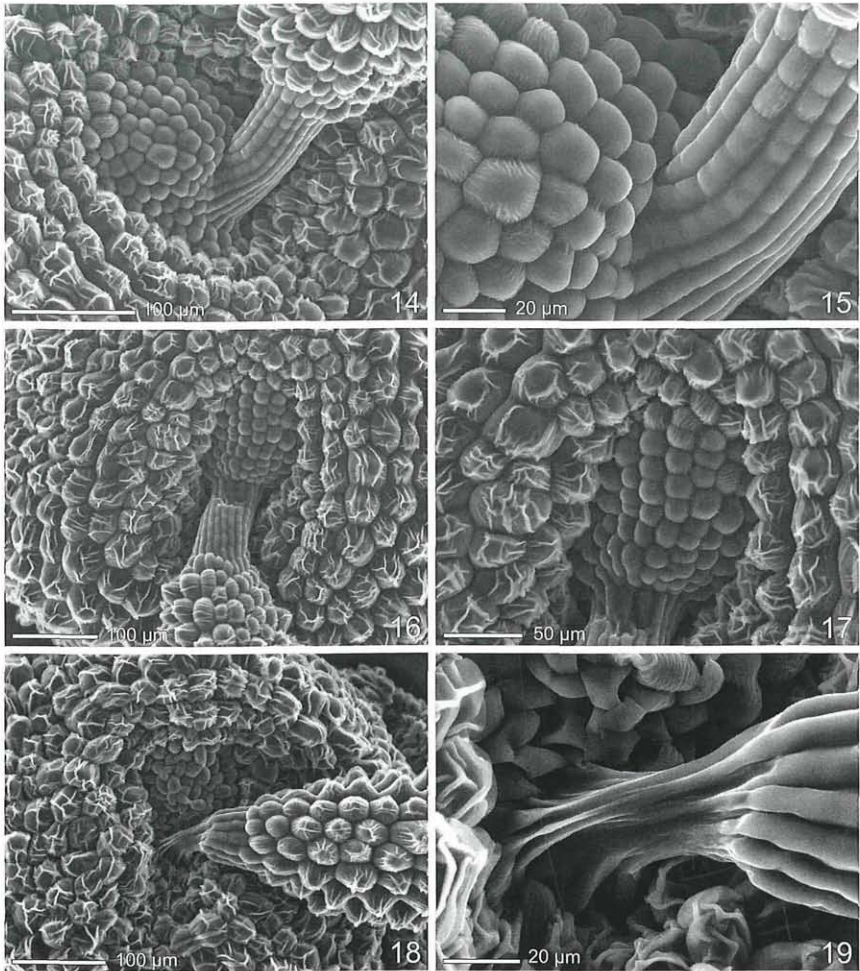


Fig. 14–19. *Inga feuillei*, filament attachment zone and isthmus. – Fig. 14. Fresh anther soon after the start of the opening of the corolla. Filament bent sideward to show the whole attachment zone. Apical part left and the small basal part right. – Fig. 15. Detail from Fig. 14. – Fig. 16. Detail from Fig. 12. The filament in the original position in the basal depression. On the isthmus the first cells collapsed. – Fig. 17. Detail from Fig. 16. – Fig. 18. Open anther at c. 19:30, filament bent sideward. Dehydration of the isthmus progressed, attachment zone cells also collapsing. – Fig. 19. Detail from Fig. 18.

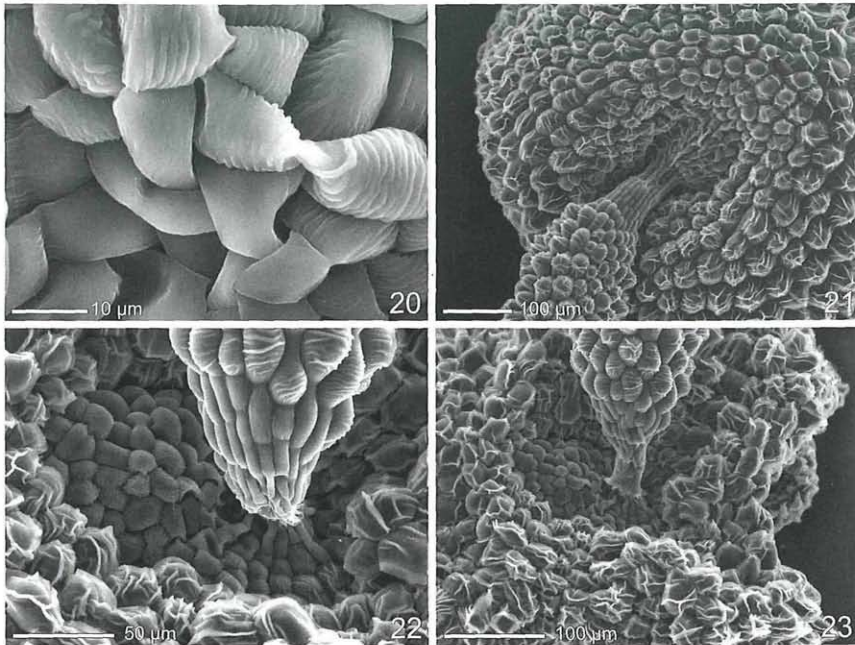


Fig. 20–23. *Inga feuillei*, filament attachment zone and isthmus. – Fig. 20. Open anther from Fig. 18 and 19, shrivelled cells of the apical part of the attachment zone. – Fig. 21. Anther of Fig. 16 and 17, c. 40 minutes later, at c. 14:30, drying up progressed. – Fig. 22. and 23. Open anther, filament bent sideward, apical part of the attachment zone left. Two different stages of progressed drying up. Fig. 22 at c. 19:00, Fig. 23 c. twenty minutes later.

T.D. PENN. (HOC 1990: 248) seems to be the most similar to *I. feuillei*, to some extent also *I. edulis* MART. (HOC 1990: 248). According to ANCIBOR 1969 *I. uruguensis* HOOK. & ARN. (included in *I. vera* subsp. *affinis* in PENNINGTON 1997: 716) shows a nectary like *I. feuillei* but no stemonozone, whereas in the figure in HOC 1990: 252 a stemonozone is drawn and the nectary is very prominent, forming a hollow cylinder adnate to the stemonozone basally. These are inconsistencies, which remain to be clarified.

The characteristics of the 32-celled, acalymmated polyads lie within the known scope (HOC 1985, 1990: 240, SORSA 1969, NIEZGODA & al. 1983, BARTH 1965). The polyads of some *Inga* species are called disymmetric and of plane-convex shape in lateral view (HOC 1985). Disymmetry, i.e., two perpendicular symmetry planes are possible along the longest and the shortest axis of the polyad faces, is also seen in *I. feuillei*. A plane parallel to the polyad faces (i.e., in lateral view) gives no mirror-images, here the polyad of *I. feuillei* is asymmetric. The shape is plane-convex or nearly so in *I. feuillei* (plane above: Fig. 50).

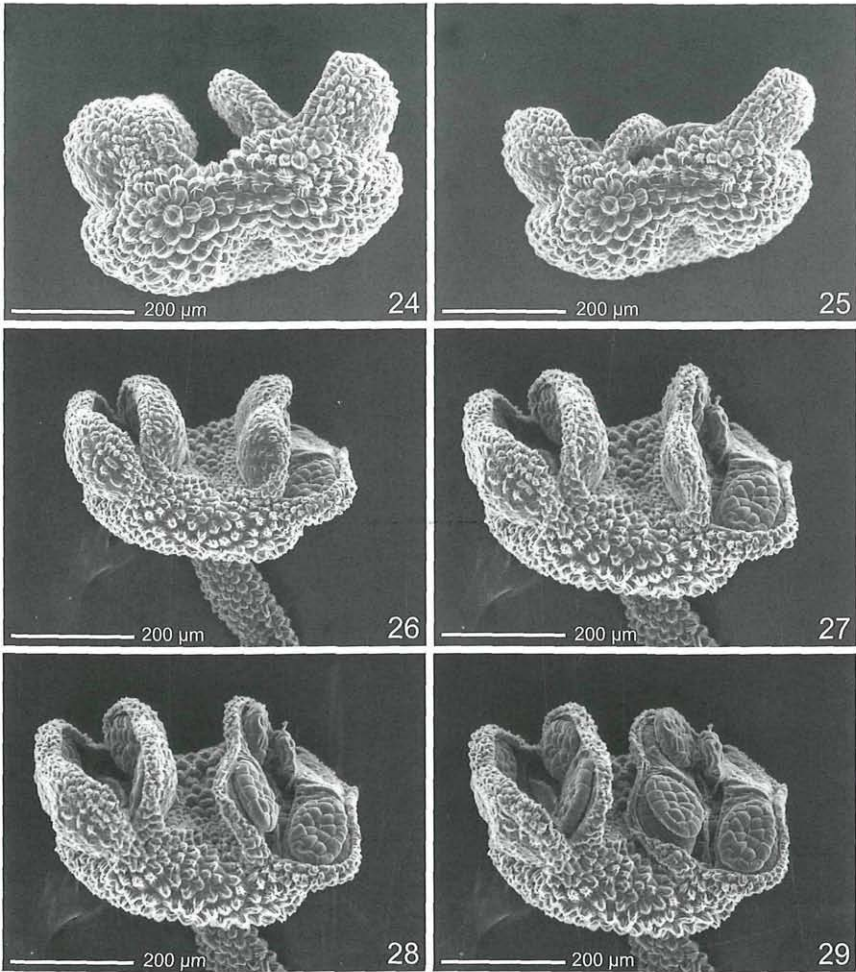


Fig. 24–25. *Inga feuillei*, anther begins to open, view of the basal end. The two thecae behave not fully synchronous (previous stage in Fig. 11).

Fig. 26–29. A sequence of c. the first half of the opening process, viewed from a little above to the apical end of the anther (continuation in Fig. 30–35). – Theca valves fold sharply inward at their very base and valves bent back. Polyads stick on the theca valves. A degenerated polyad is wedged-in at the base of the right locule.

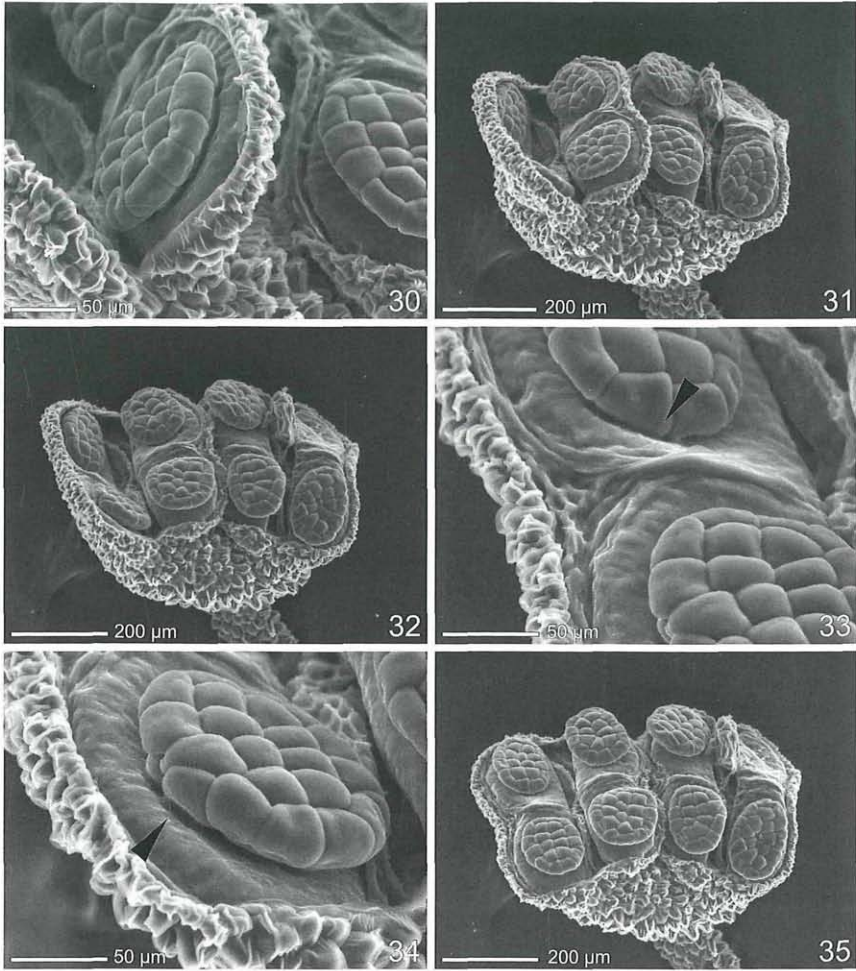


Fig. 30–35. *Inga feuillei*, stages of c. the second half of the opening process of an anther, continuation from Fig. 26–29. – Fig. 30. Apical half of the inner valves of the two adjacent thecae, with their adhering polyads. – Fig. 31 and 32. Progress of opening, in the right theca the valves flat already. – Fig. 33. Central part of a valve with the bulge from the transversal septum, dilated ventrally (left). Arrow: pollenkitt. – Fig. 34. Margin of the valve below the nearly flat longitudinal bulge already. Pollenkitt (arrow) between valve and polyad. – Fig. 35. Opening completed, all four flat bulges nearly in the same plane, exposing the polyads. – Time span between Fig. 26 and 35: c. 45 minutes.

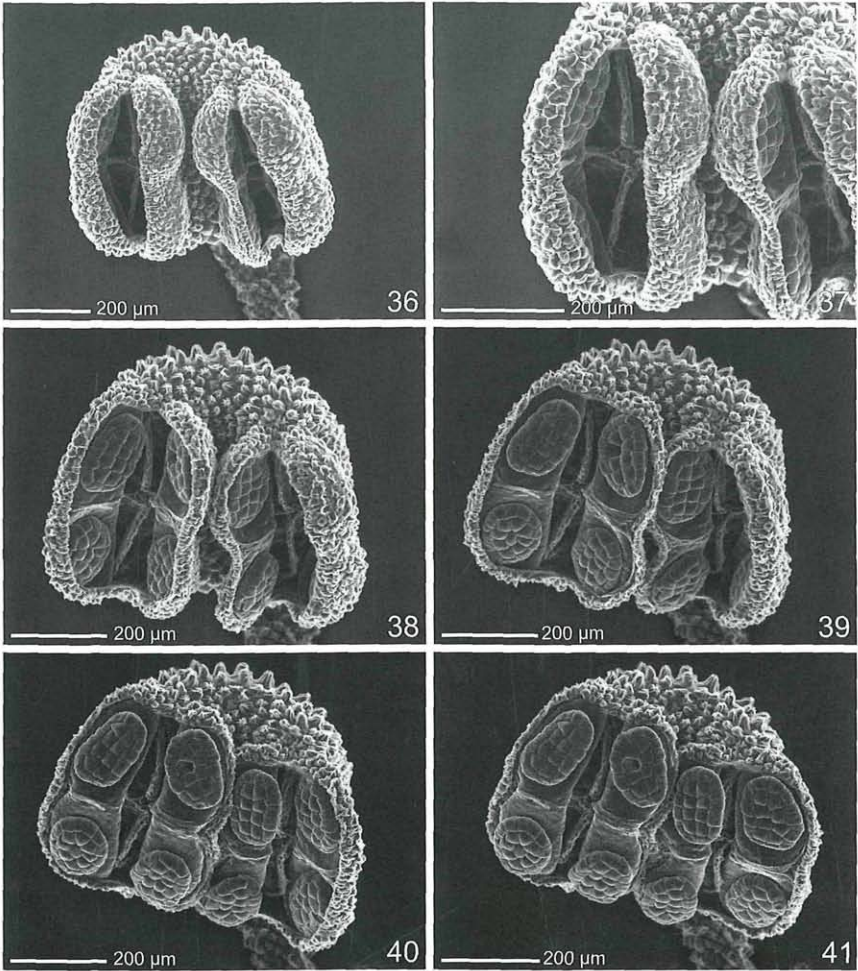


Fig. 36–41. *Inga feuillei*, opening anther from above, apical end above. Polyads adhere to the backwards-bending valves and the remains of the longitudinal septum crossed by the transversal septum become visible in the bottom of the thecae. The space at the bottom of the theca becomes narrower progressively by the strong inward folding of the very base of the theca valves. Finally (Fig. 41) all bulges with their polyads nearly in the same plane. – Time span between Fig. 36 and 41: c. 45 minutes.

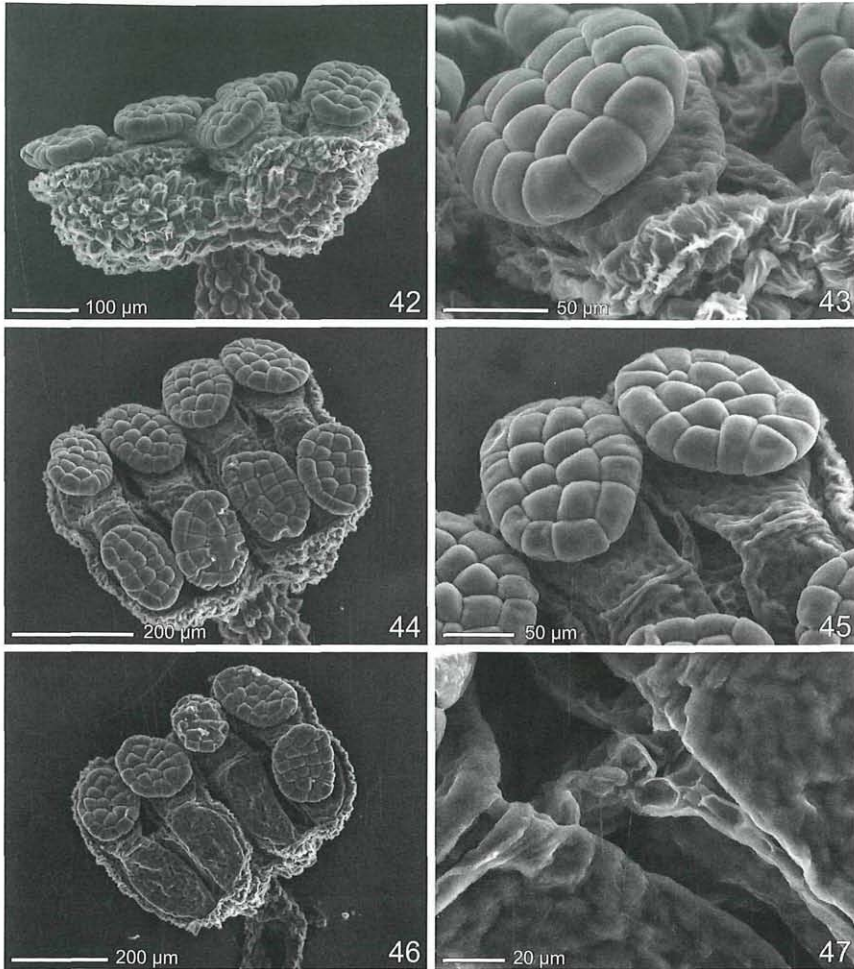


Fig. 42–47. *Inga feuillei*, open anthers after the anthesis night, on the next morning, thus the surface of the longitudinal bulges shrivelled. – Fig. 42. View of the basal end. – Fig. 43. Detail from Fig. 42. – Fig. 44. View from above. – Fig. 45. Detail from Fig. 44. – Fig. 46. View from above, one polyad degenerated, three polyads removed artificially for showing the plane surfaces of the longitudinal bulges. – Fig. 47. Detail from Fig. 46, showing the cross of the remains of the longitudinal septum with the transversal one.

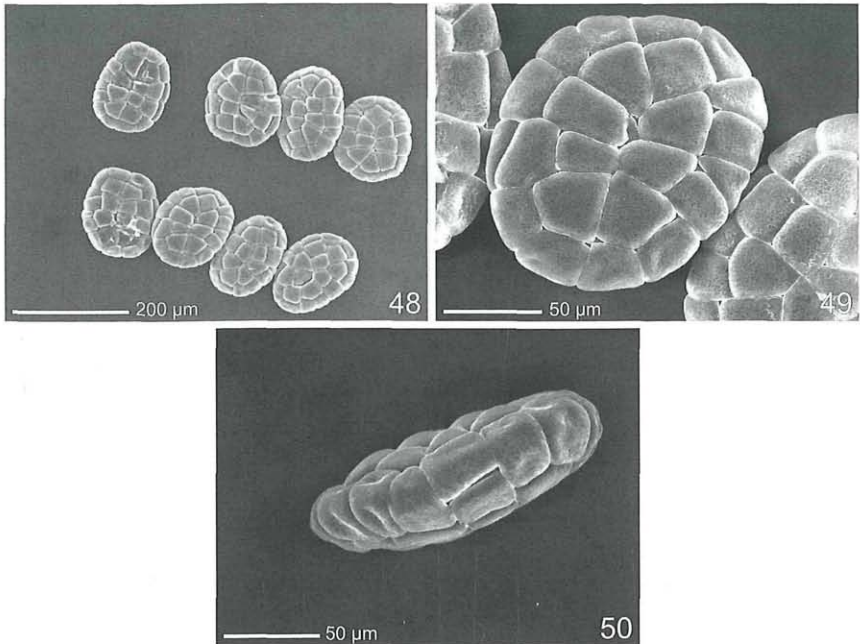


Fig. 48–49. *Inga feuillei*, under side (= outer or adherent side) of the polyads. – Fig. 48. All eight polyads of one anther „stamped“ onto the viscid tape of the stub. One polyad a little shifted during the preparation. – Fig. 49. Detail of Fig. 48. Fig. 50. A polyad in lateral view, differences in the arching of the surface of the pollen grains between upper and lower side.

4.2. Flower Ecology

Phenology of flowering with respect to seasonality as well as to flower opening and duration is highly variable in the genus. KOPTUR 1983a,b observed in seven species of *Inga* in Costa Rica. She reports nocturnal or day and night anthesis, opening in the morning, the afternoon or continuously etc. and a duration of flowers between 5 and 21 hours; nectar production starts when filaments are fully extended; in *I. feuillei* this was a little earlier. The nectar composition of eight species is discussed in KOPTUR 1994 (freshly secreted nectar is sucrose-dominated).

A wide range of pollinators is possible in *Inga* species depending, among others, on the time of anthesis. Nocturnal flowers may be visited by sphingids, noctuids and bats, whereas, when daytime is also involved, hummingbirds, butterflies, bees etc. may be visitors as well (e.g., KOPTUR 1983a,b, 1984: 1133–1134, SALAS 1974, VOGEL 1968: 579–581, HETHAUS & al. 1975, HABER & al. 1981). In *I. feuillei* the size of the flowers, the mainly nocturnal nectar production and the narrow access to the nectar makes

sphingids and noctuids as pollinators probable, which were observed as to be effective pollinators in the greenhouse (TEPPNER 1998: 41–42). In our greenhouse we had colonies of bumblebees (*Bombus terrestris*, *B. haematurus*) who collected the floral and extrafloral nectar and caused some accidental pollinations. To what extent other visitors of *I. feuillei* are involved in the natural environment in the afternoon and in the morning, is not known.

5. Acknowledgements

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