

# Gynoecium, fruit and seed structure of Paullinieae (Sapindaceae)

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Despite an emphasis on fruit characters in Paullinieae taxonomy, few detailed morphological and anatomical studies of the gynoecia, fruits and seeds exist. The aims of the present study were (1) to provide a detailed documentation of gynoecium, fruit and seed structure and ontogeny in selected Paullinieae taxa; (2) to determine whether the gynoecium, seed and seedling provide additional characters of systematic value within the tribe; and (3) to relate the structural findings to mechanisms of fruit dehiscence and dispersal within these taxa. Newly described characters of systematic value within Paullinieae are shape and surface of the obturator, type of pollen tube transmitting tract, indumentum of the inner and outer surface of the carpels, ovary wall anatomy, aril anatomy, pseudo-hilum form, seedling germination mode and structure of first leaves. The fruits of *Paullinia* are septifragal, and conspicuous colour contrasts between the pericarp, aril and seed in most species of this genus are suggestive of a bird dispersal syndrome. Interestingly, it appears that relatively minor structural changes are associated with switches to rodent dispersal in *Paullinia sphaerocarpa* and water dispersal in *P. clathrata* and *P. hystrix*. Anemochorous fruits are septifragal (*Cardiospermum* and *Urvillea*) or schizocarpic (*Houssayanthus*, *Lophostigma*, *Serjania*). They are structurally similar and *Cardiospermum* with septifragal capsules may also show septicial dehiscence. © 2005 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2005, 147, 159–189.

**ADDITIONAL KEYWORDS:** *Cardiospermum* – fruit biology – gynoecium and fruit morphology – *Paullinia* – *Serjania* – *Urvillea*.

## INTRODUCTION

### PAULLINIEAE – A POORLY KNOWN TRIBE OF SAPINDACEAE

In recent years, biodiversity research has gained increased attention both within and outside the scientific community, mainly because of the awareness that vast areas of natural habitats, predominantly in the tropics, are rapidly being lost. A central objective of biodiversity research is species inventory, a task that involves detailed morphological study to allow for identification and classification. Such research lays the foundations for further systematic, ecological, evolutionary and applied research.

Large groups of tropical plants are still poorly known and among such groups are the mainly Neotropical liana of the tribe Paullinieae (six genera/430 spe-

cies; Sapindaceae). Considerable research has been done on the biology and systematics of Sapindaceae from Australasia (Leenhouts, 1967; Leenhouts & Vente, 1982; Reynolds & West, 1985; Adema, 1991; van Welzen, 1991; van Welzen, Piskaut & Windadri, 1992; Adema & van der Ham, 1993; Adema, Leenhouts & van Welzen, 1994; Etman, 1994), yet less is known about the Neotropical taxa. In recent years many new taxa have been described from tropical America (e.g. Ferrucci & Acevedo-Rodríguez, 1997; Somner & Ferrucci, 1997; Acevedo-Rodríguez, 1998, 2003; Acevedo-Rodríguez & Ferrucci, 2002; Weckerle & Reynel, 2003). These new taxa have been distinguished primarily on the basis of fruit morphology. Few detailed studies of fruit and seed structure exist, and even fewer studies have attempted to relate differences in these structures to differences in dispersal biology (Weckerle & Rutishauser, 2003). The Paullinieae display a high diversity of fruit and seed morphology, and so are particularly ripe for such a study.

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The most comprehensive studies involving morphological and anatomical characters of Paullinieae were conducted by Radlkofer over one hundred years ago (Radlkofer, 1875, 1886, 1895a, b). In addition to vegetative and floral characters, he provided information on the shape of fruits and seeds as well as the indumentum and anatomy of the pericarp (e.g. Radlkofer, 1895a). His generic and infrageneric classification of, for example, *Paullinia* is mainly based on pericarp characters. Because Radlkofer mainly investigated herbarium material, detailed analyses of gynoecium characters, aril structure and fruit dehiscence were not possible. In 1993, Acevedo-Rodríguez published revisions of two Paullinieae groups: one section of *Serjania* (Acevedo-Rodríguez, 1993a) and the genus *Lophostigma* (Acevedo-Rodríguez, 1993b). The sections of *Serjania* as defined by Radlkofer (1875) and Acevedo-Rodríguez (1993a) are based chiefly on fruit morphology.

Macromorphological descriptions of Paullinieae can be found in floras (e.g. Macbride, 1956; Croat, 1976; Reitz, 1980; Ferrucci, 1991) and in the dissertation of Beck (1991a) regarding the generic limits in the tribe. Palynological studies are provided by Muller & Leenhouts (1976), Ferrucci & Anzotégui (1993) and van der Ham & Tomlik (1994).

The aims of the present study were (1) to provide a detailed documentation of gynoecium, fruit and seed structure and ontogeny in selected Paullinieae taxa; (2) to determine whether the gynoecium, seed and seedling provide additional characters of systematic value within the tribe; and (3) to relate the structural findings to mechanisms of fruit dehiscence and dispersal within these taxa.

#### DISTRIBUTION OF PAULLINIEAE AND MORPHOLOGICAL BACKGROUND

The almost exclusively neotropical Paullinieae harbour most of the sapindaceous climbers and comprise the species-rich genera *Serjania* (220 spp.) and *Paullinia* (180 spp.), and the small genera *Cardiospermum* (14 spp.), *Houssayanthus* (three spp.), *Lophostigma* (two spp.) and *Urvillea* (17 spp.) (Radlkofer, 1933; Ferrucci, 1987). A few species of *Cardiospermum* show a pantropical distribution. *Paullinia pinnata* L. is the only member of its genus occurring in America as well as in tropical Africa and Madagascar (Irvine, 1961). The species-rich genera *Paullinia* and *Serjania* form woody lianas. There is some overlap in the distribution of *Paullinia* and *Serjania*, but the vast majority of *Paullinia* species occupy humid dense tropical forests, especially in Amazonia, whereas the anemochorous *Serjania* occurs in drier areas, along forest edges and in weedy and disturbed areas (Acevedo, 1993a). In the latter habitats the more herbaceous *Urvillea* and *Car-*

*diospermum* also occur. All genera bear spirally arranged, imparipinnately compound leaves with stipules. The pinnate leaves are often five-foliolate, but may vary from three-foliolate (*Urvillea*) to multifoliolate.

Paullinieae are characterized by unisexual, obliquely monosymmetric flowers with four to five sepals, four petals with basal appendages, and two to four cushion-like extrastaminal nectaries. Male flowers have eight functional stamens and a rudimentary pistil whereas female flowers show (besides indehiscent anthers) a three-carpellate gynoecium with a single ovule per carpel. The plants are monoecious (rarely dioecious; C. S. Weckerle, pers. observ.). The genera and species are separated mainly by fruit characters. *Houssayanthus*, *Lophostigma* and *Serjania* are characterized by schizocarpic fruits with winged (samaroid) mericarps, *Cardiospermum* and *Urvillea* by papery, inflated capsules, and *Paullinia* by capsules.

Usually the capsules in *Paullinia* contain dark seeds that are partly or completely enveloped by a translucent or white 'aril-like structure'. Use of the term 'aril-like structure' in *Paullinia* and other Sapindaceae is inconsistent and disputable (e.g. Radlkofer, 1878, 1895b; van der Pijl, 1957; Corner, 1976; Werker, 1997). Avoiding these terminological problems the terms 'aril' and 'sarcotesta' are used here with the following definitions suited for Sapindaceae: 'sarcotesta' for fleshy layers that are produced by the entire seed surface (testa), 'aril' for the usually fleshy and white outgrowths that are produced by certain regions of the seed surface. The testa region to which the aril is attached we term 'pseudo-hilum', consistent with van der Pijl (1957). The term 'hilum', referring to the scar-like mark on a seed where it was inserted, is not used in our paper. The shiny dark seed coat, which may be partially enveloped by the aril, will be labelled as 'dry testa'.

The ovules of Sapindaceae are campylotropous, crassinucellar and bitegmic. In most Sapindaceae, no clear distinction between placenta and funicle is possible. We follow the terminology of Corner (1976), who describes similar ovules as shortly and thick funiculate (see Discussion: 'Ovules').

#### SYSTEMATIC BACKGROUND

Pantropical Sapindaceae (140 genera/1800 species) are by far the largest family of the order Sapindales (Judd *et al.*, 2002). Molecular analyses restrict the order to the following six major families: Anacardiaceae, Burseraceae, Meliaceae, Rutaceae, Sapindaceae (including Aceraceae and Hippocastanaceae) and Simaroubaceae (Gadek *et al.*, 1996; Chase, Morton & Kallunki, 1999; Savolainen *et al.*, 2000a; Soltis

*et al.*, 2000). Radlkofer's (1933, 1934) classification of Sapindaceae is still widely used. He distinguished two subfamilies according to ovule number per locule. These are currently known as Sapindoideae with one ovule, and Dodonaeoideae with two or rarely more ovules. Recent studies generally accept the two subfamilies. Dodonaeoideae are often described as a paraphyletic group, an assemblage of relictual taxa, and Sapindoideae as a more homogeneous and derived group. In phylogenetic analyses based on *rbcL* (Savolainen *et al.*, 2000a), Dodonaeoideae, Aceraceae and Hippocastanaceae, all containing two ovules per locule, are basal in Sapindaceae. A basal position had been assumed earlier by Muller & Leenhouts (1976). Two ovules therefore seem to be the plesiomorphic state for Sapindaceae.

The sapindoid tribes Paullinieae and Thouinieae are considered as most derived, presumably closely related to Cupanieae (Muller & Leenhouts, 1976; Acevedo, 1993a; Judd, Sanders & Donoghue, 1994; van der Ham & Tomlik, 1994). Molecular analyses based on *rbcL* confirm these suggestions (Klaassen, 1999; Savolainen *et al.*, 2000b). A preliminary cladistic analysis based on morphological characters restricts Paullinieae to two major clades (Acevedo-Rodríguez, 1993a). One is the 'Serjania group' comprising the schizocarpic genera *Serjania*, *Houssayanthus* and *Lophostigma*, and the other clade ('Paullinia group') consists of the mainly septifragal genera *Paullinia*, *Cardiospermum* and *Urvillea*.

## MATERIAL AND METHODS

Morphological studies were carried out on living and fixed material of the taxa listed in Table 1. Flowers as well as young and mature fruits of *Paullinia*, *Serjania*, *Cardiospermum* and *Urvillea* were collected during a field trip in Peru (2000). Fruit biology of these taxa was observed in the field and two to five seedlings of each species were grown from seeds in Peru. The living material was fixed in 70% EthOH. *Paullinia* aff. *caloptera* was determined according to the isotype Spruce 1488 (NY).

For structural analysis of the gynoecium at least three samples of each species were examined. For *Paullinia obovata*, however, only one gynoecium was available. Fruit morphology is based on more than ten fruits per species.

For sectioning, the ovaries and young fruits were embedded in Kulzer's Technovit (2-hydroxyethyl methacrylate) under normal conditions as described by Igersheim (1993) and Igersheim & Cichocki (1996), or in UV light, and then sectioned at 5 µm with a Microm HM 355 microtome and a conventional microtome knife type C or D. Mucilaginous secretions of pectic nature were identified with ruthenium red (Gerlach, 1984). For contrast enhancement, ruthenium red staining was post-stained with toluidine blue (Weber & Igersheim, 1994). The sections were mounted in Histomount. Mature fruits and seeds were sectioned by hand with razor blades.

**Table 1.** Species examined for the morphological studies

Taxa	Section*	Collection data
<i>Paullinia alata</i> G. Don	I	Weckerle & Igersheim 000309-2/1, 000310-1/5, 000527-1/2, 010117-1/1, 010206-1/1; Peru; MOL, Z
<i>Paullinia clavigera</i> Schtdl.	I	Weckerle & Igersheim 000527-1/3, 000604-2/3, 000604-2/4, 000409-1/2, 010113-1/2, 010207-1/2; Peru; MOL, Z
<i>Paullinia obovata</i> (Ruiz & Pav.) Pers.	I	Weckerle & Igersheim 000315, 2/1, 000316-2/1, 000318-3/1, 000329-1/1, 000330-2/1, 000331-2/1, 000404-1/5, 000405-1/4, 000410-1/1, 000527-1/4, 000531-1/6, 000707-1/1, 000710-1/6, 000718-2/1, 010112-1/1, 010112-1/2, 010115-1/2, 010116-1/2, 010128-1/1, 010202-1/1, 010202-1/2; Peru; MOL, Z
<i>Paullinia pachycarpa</i> Benth.	IV	Weckerle & Igersheim 000318-2/1, 000414-1/3, 000415, 1/1, 000417, 1/1, 000418-1/1, 000307-1/1; Peru; MOL, Z
<i>Paullinia</i> aff. <i>caloptera</i> Radlk.	XII	Weckerle & Igersheim 000406-1/2, 010118-1/1, 010118-1/2; Peru; MOL, Z
<i>Paullinia dasystachya</i> Radlk.	XII	Weckerle & Igersheim 000409-1/1, 010111-1/1, 010117-1/2; Peru; MOL, Z
<i>Cardiospermum halicacabum</i> L.		Weckerle & Igersheim 000316-1/1, 000710-1/3; Peru; MOL, Z
<i>Serjania altissima</i> (Poepp.) Radlk.		Weckerle & Igersheim 000407-1/2, 000702-1/4, 000719-1/7; Peru; MOL, Z
<i>Urvillea ulmacea</i> Kunth		Weckerle & Igersheim 000703-1/6, 000705-1/3, 000705-1/6, 000711-1/1, 000719-1/4, 000719-1/6; Peru; MOL, Z

\*Radlkofer (1895a) divided *Paullinia* into 13 sections, mainly based on fruit morphology. Section numbers of the *Paullinia* spp. are given following Radlkofer (1895a) and Beck (1991b). Section I. *Paullinia* (syn. *Neurotoechus*); Section IV. *Pachytoechus*; Section XII. *Caloptilon*.

For scanning electron microscopy (SEM) studies, the specimens were dehydrated in an ethanol series and acetone, critical point dried and sputter-coated with gold. Ovaries densely covered with hairs were pre-treated with osmium tetroxide. All light microscope (LM) micrographs were taken using an Olympus BX50 microscope and a digital AxioCam HRC (Zeiss) camera.

All permanent slides of the microtome sections are deposited at the Institute of Systematic Botany of the University of Zurich (Z).

## RESULTS

### *PAULLINIA ALATA* G. DON

Lianas of tropical Central and South America. The mature intertwined stems are composed of one central and three peripheral steles. Leaves are five-foliolate with winged petiole and rachis. Inflorescences are cauliflorous, fasciculate thyrses, evenly distributed along stems (Figs 1, 2). New inflorescences are formed on the same stem sites.

#### *Gynoecium at anthesis*

The superior, tricarpellate gynoecium consists of a slightly three-angled to nearly spherical ovary with a diameter of 2 mm or less. The three papillate stigmas are slightly longer than the style (Figs 25, 26). The ovary is synascidiate for approximately half of its length, i.e. up to the upper level of ovule insertion (border between obturator and ovule; Fig. 31A, B), and symplicate up to the three stigmas (Fig. 31C). The pollen tube transmitting tract (PTTT) forms a canal in the style and upper part of the ovary. It is filled with secretion and lined with one cell layer, which produces hair-like cells protruding into the centre of the canal. Dorsal and synlateral vascular bundles are present. In addition, a network of secondary lateral vascular bundles is formed, surrounded by numerous inconspicuous bundles and laticiferous cells (Fig. 31A–C). Each locule is provided with an inner hypodermal layer with oxalate crystals (druses) (Fig. 32).

One median ovule per locule is present. Ovules are campylotropous, crassinucellate and bitegmic. They fit tightly into the locules (Fig. 31C) and are c. 0.6 mm long including the obturator. The inner integument is five cells thick, the outer one six. The micropyle is formed by the inner integument and is covered with secretion (Figs 27, 28). The ovules are erect or ascending, with the micropyle directed downwards. An obturator is formed at the micropylar side of the funicle (Figs 27, 28). It has approximately the same length as the ovule, and the surface is conspicuously papillate and secretory. A single vascular bundle enters the obturator and continues to the chalaza ('pachychalaza'

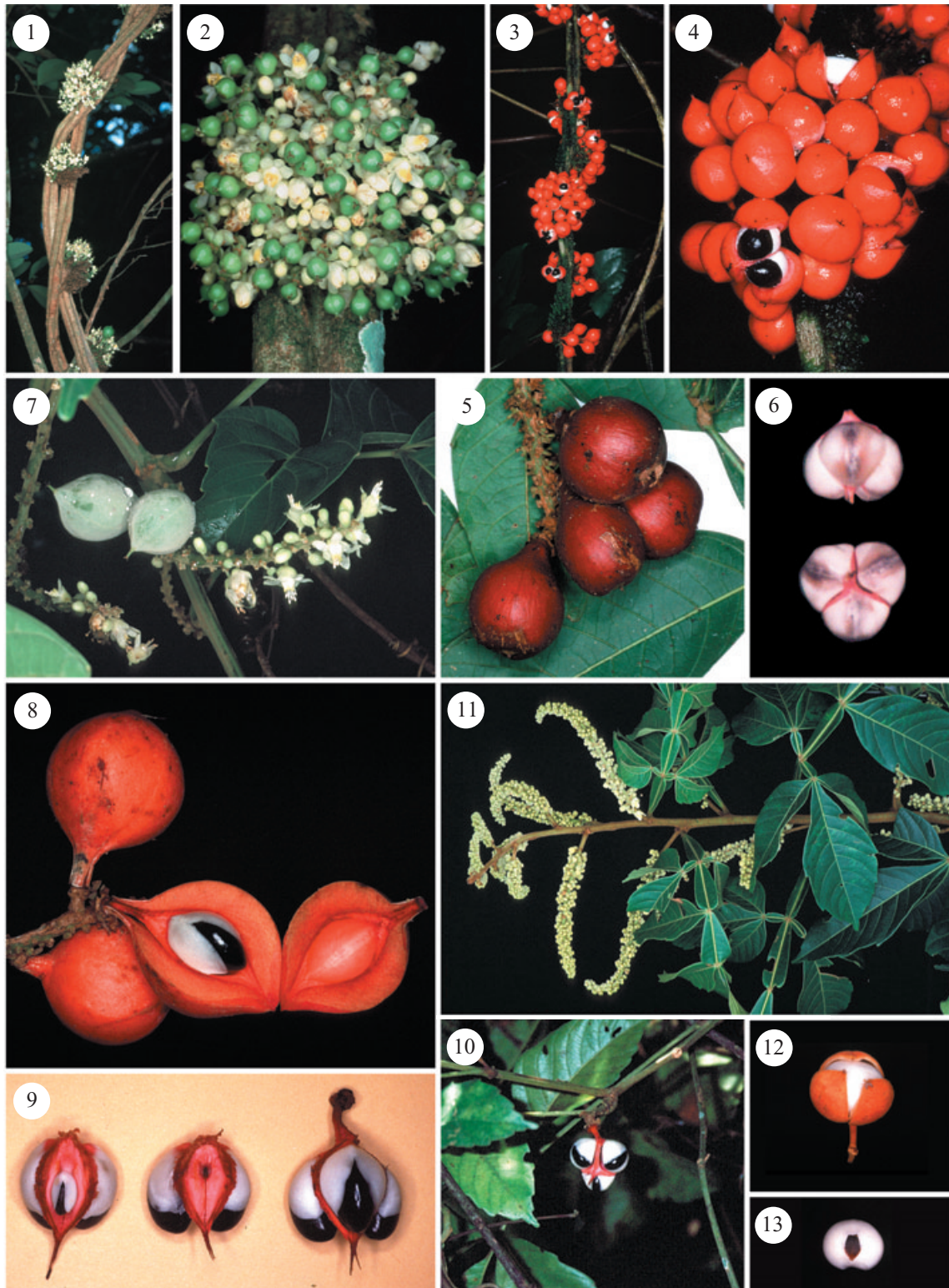
after Corner, 1976), where it branches. Below the obturator few unicellular hairs are found on the placenta. Their number increases during seed development (Fig. 29).

#### *Fruit and seed development*

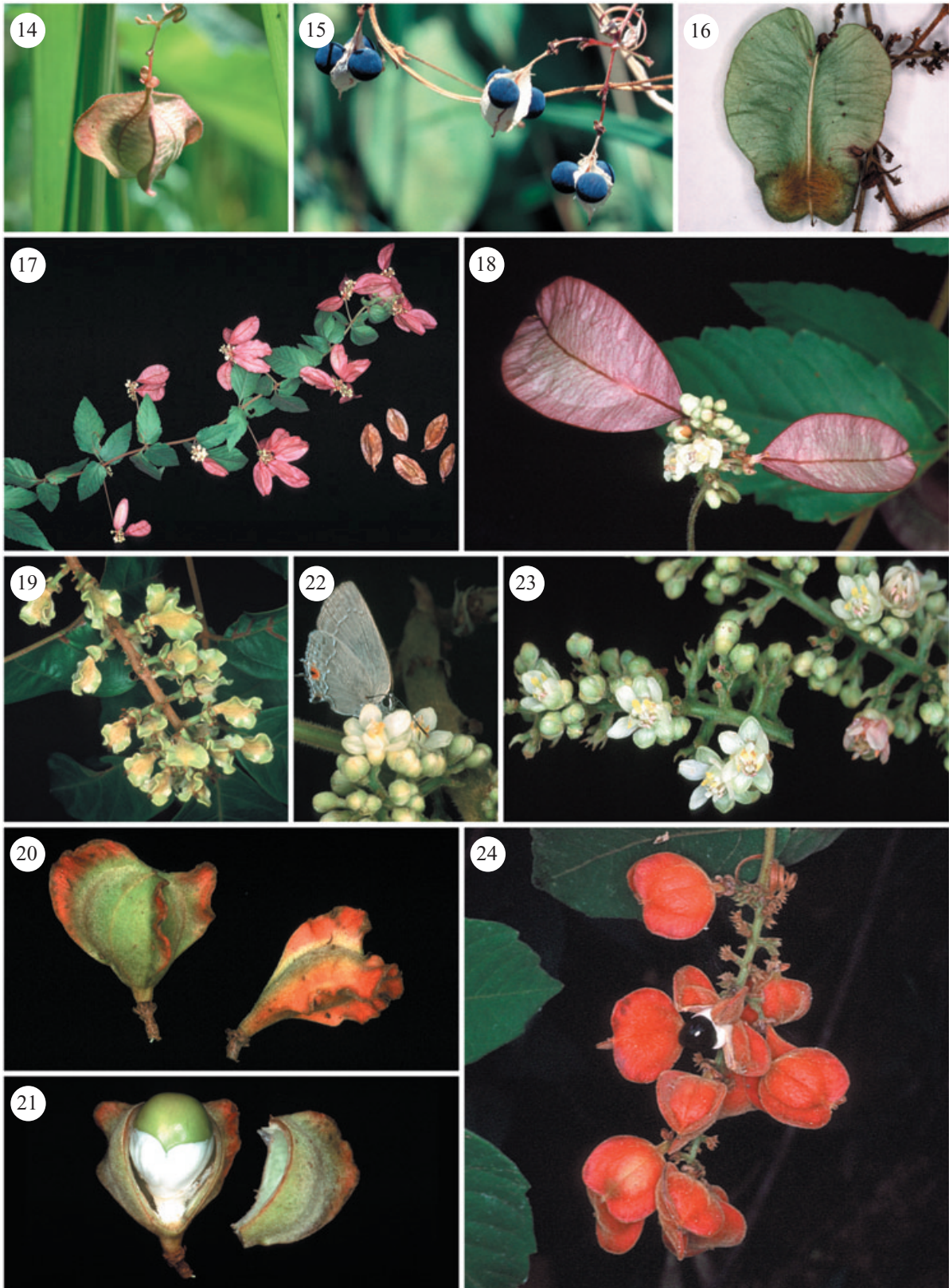
After anthesis the pericarp grows earlier than the seeds. Thus in fruits with nearly mature size the seeds may still be rather small. In young fruits, sclerenchyma sheaths are differentiated around the numerous inconspicuous bundles of the gynoecium wall. They are arranged in the exocarp and along the future dehiscence line between the septifragal carpels (similar to *P. clavigera*, cf. Fig. 33). If mature fruits are dried, these peripheral sclerenchyma bundles become visible as small longitudinal ridges on the fruit surface, a character considered by Radlkofer (1895a) as important for his classification of *Paullinia*. The mesocarp consists of parenchyma cells that form large intercellular spaces, especially inside the inner ring of conspicuous vascular bundles. The mature fruit is 1.5–2.2 cm long, including the slender stipe, and 1–1.8 cm wide (Fig. 31D). The shiny red pericarp has a diameter of c. 1 mm (measured in the dorsal region of the carpel in the middle of the fruit; Fig. 31E) and a glabrous surface. The capsule is septifragal with dehiscence lines characterized by closely arranged, small cells. After dehiscence shiny black seeds surrounded by a white aril are displayed, forming a conspicuous contrast with the persistent red capsule valves (Figs 3, 4).

There are one to three seeds per fruit, developing out of the three ovules. In the mature seeds two testa regions may be distinguished depending on the position of the aril: (1) the testa to which the white aril is attached is called 'pseudo-hilum' (van der Pijl, 1957) – after removal of the aril it is visible as a light brown region of specific shape (Fig. 31H–J: shaded in grey); (2) the shiny dark testa region which is partly enveloped by the aril is called 'dry testa' (Fig. 31F–J: indicated in black).

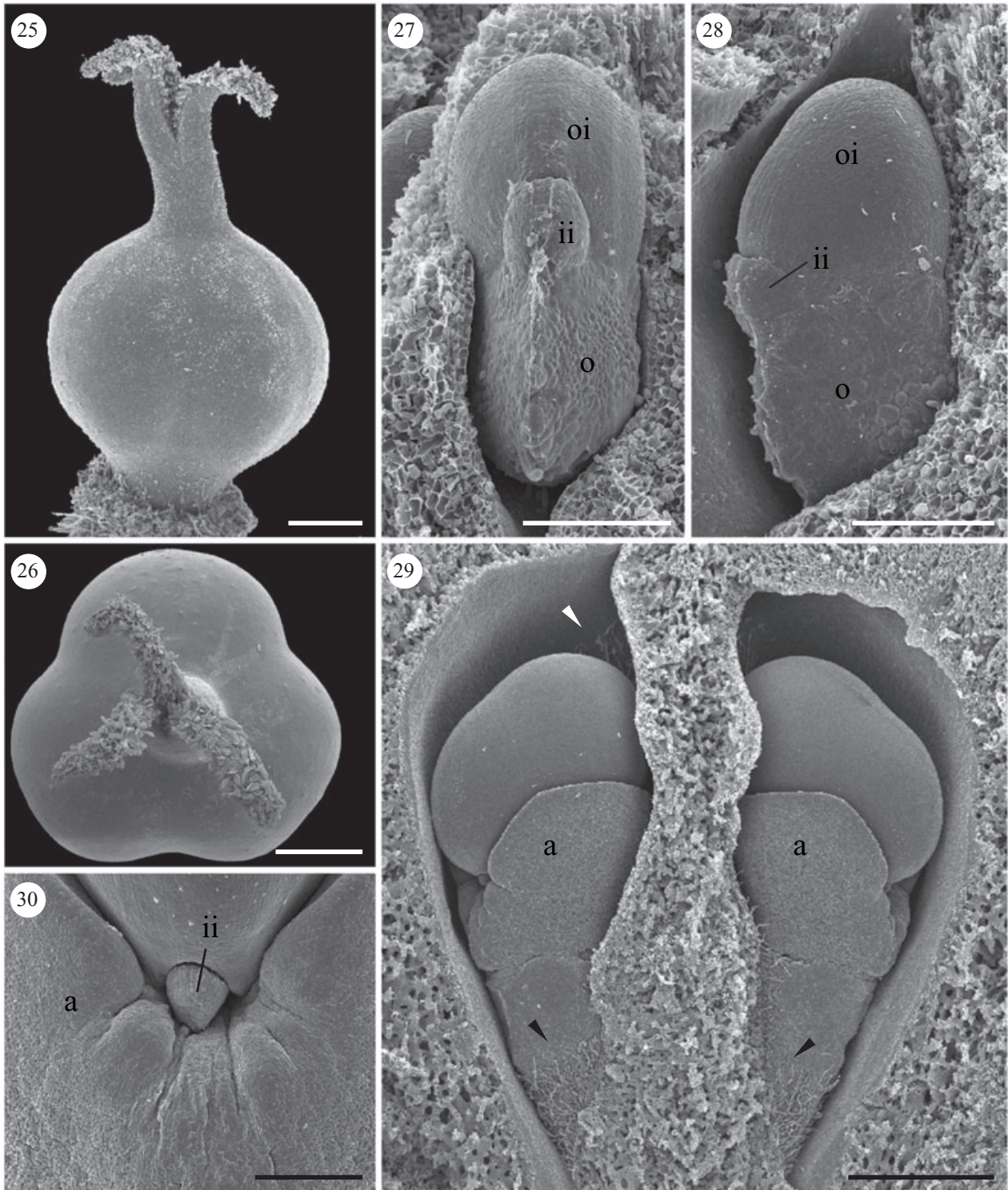
The aril is initiated after fertilization. The young seed has a dense vascular net in the chalazal region. The basal parts of the chalaza (i.e. ovule insertion area) as well as the outer integument contribute to the development of the aril. The young aril forms two lobes, which are united on the adaxial side (Figs 29, 30). In the mature seed the two aril lobes envelop the dry testa for a few millimetres (Fig. 31F, G). The aril tissue consists of large spherical cells with starch. Most cells are tanniferous. The pseudo-hilum, which also forms two lobes (Fig. 31H–J), consists of small, sclerified cells. The dry testa is c. 150 µm thick and made up of tanniferous, thick-walled, compressed cells. The columnar epidermal cells with thickened anticlinal walls are 25–30 µm high, with a stellate outline.



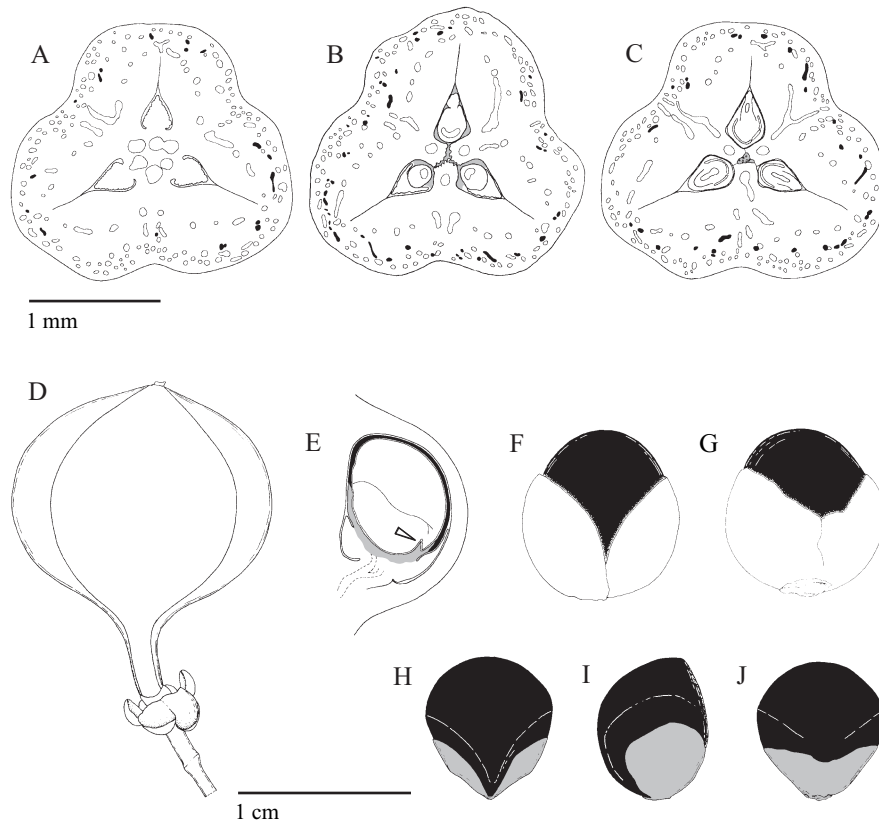
**Figures 1–13.** Flowers, fruits and seeds of *Paullinia* species. Figs 1–4. *P. alata*. Figs 5, 6. *P. clavigera*. Figs 7–10. *P. obovata*. Figs 11–13. *P. pachycarpa*.



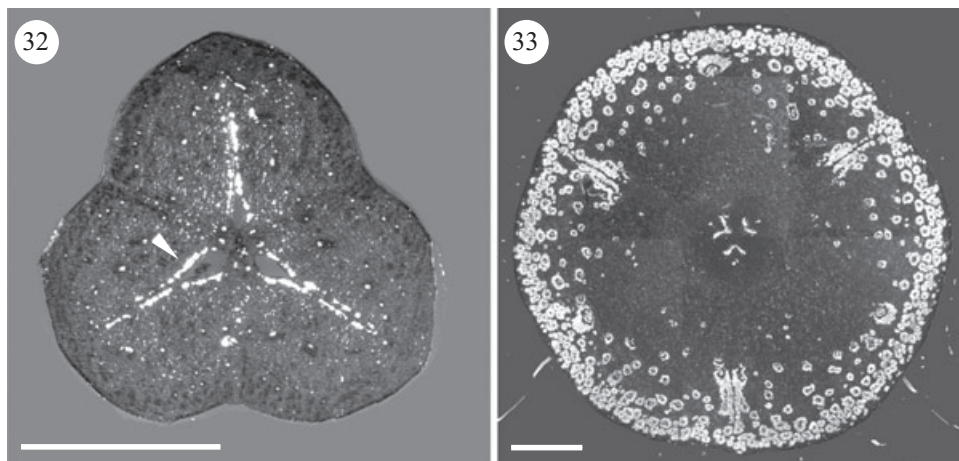
**Figures 14–24.** Flowers, fruits and seeds of Paullinieae species. Figs 14–15. *Cardiospermum halicacabum*. Fig. 16. *Serjania altissima*. Figs 17–18. *Urvillea ulmacea*. Figs 19–21. *Paullinia* aff. *caloptera*. Figs 22–24. *P. dasystachya*.



**Figures 25–30.** *Paullinia alata*. Figs 25–28. Dissected female flower shortly after anthesis. Fig. 25. Gynoecium from the side. Scale bar = 500  $\mu\text{m}$ . Fig. 26. Gynoecium with stigmatic region, from above. Scale bar = 500  $\mu\text{m}$ . Fig. 27. Abaxial view of ovule with prominent obturator. Scale bar = 200  $\mu\text{m}$ . Fig. 28. Ovule from the side. Scale bar = 200  $\mu\text{m}$ . Figs 29–30. Seed development. Fig. 29. Immature seeds from the side with developing aril; arrowheads point at hairs within the locules. Scale bar = 1  $\mu\text{m}$ . Fig. 30. Same object, close-up of micropylar region. Scale bar = 200  $\mu\text{m}$ . Abbreviations: a, aril; ii, inner integument; o, obturator; oi, outer integument.



**Figure 31.** *Paullinia alata*. A–C, TS of gynoecium, slightly postanthetic. Vascular bundles indicated with thin lines. Laticiferous cells indicated in black. Secretion of pollen tube transmitting tract (PTTT) shaded in grey. A, level of obturator, synascidiate zone. B, level just above ovule insertion, beginning of symplicate zone. C, symplicate zone. D–J, mature fruit and seeds. Pseudo-hilum shaded in grey. Dry testa indicated in black. D, fruit. E, longitudinal section of seed and pericarp; arrowhead points at ‘radicle-pocket’. F, G, seed with aril, abaxial view and adaxial view. H–J, seed with detached aril, abaxial view, side view, adaxial view.



**Figures 32–33.** *Paullinia alata* and *P. clavigera*. Scale bars = 1 mm. Fig. 32. *P. alata* transverse section of gynoecium shortly after anthesis; arrowhead points at inner hypodermal cell layer with oxalate crystals (bright). Fig. 33. *P. clavigera* TS of young fruit, showing numerous vascular bundles provided with sclerenchyma sheaths (bright). Photographs taken with polarized light.



The mature seeds are nearly spherical, with a diameter of 0.8–1.1 cm including the aril (Fig. 31F, G). The radicle is separated from the cotyledons by a partial septum, which is called ‘radicle-pocket’ by Corner (1976) (Fig. 31E).

#### Germination and seedling

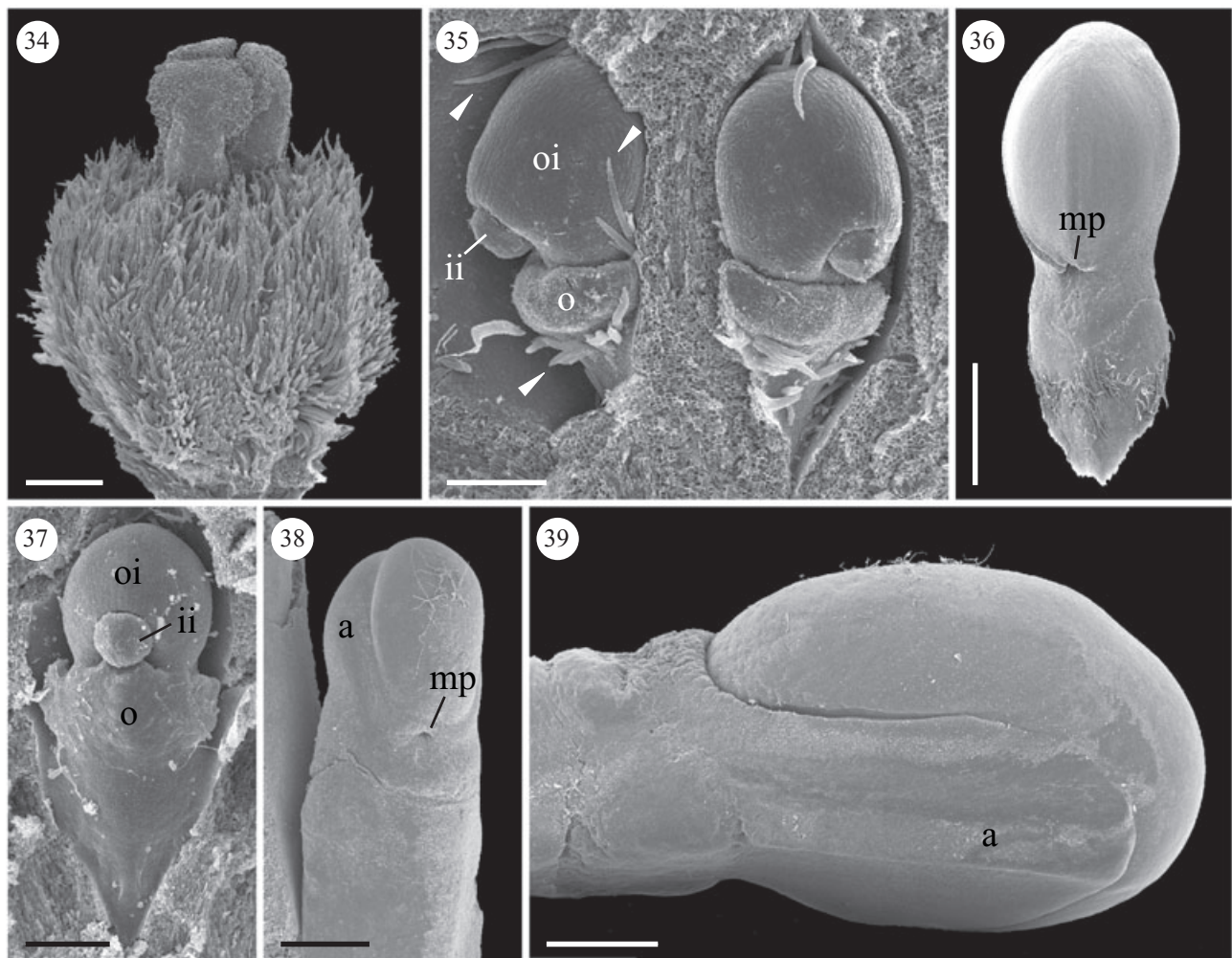
Germination is hypogeal; the cotyledons remain enclosed in the testa. Seeds germinate after 9–19 days. Germination ability is lost as soon as seeds have dried up. At least the first four leaves are reddish and simple, the petioles are winged. The first two seedling leaves are opposite, the following leaves change to spiral phyllotaxis.

#### *PAULLINIA CLAVIGERA* SCHLTDL.

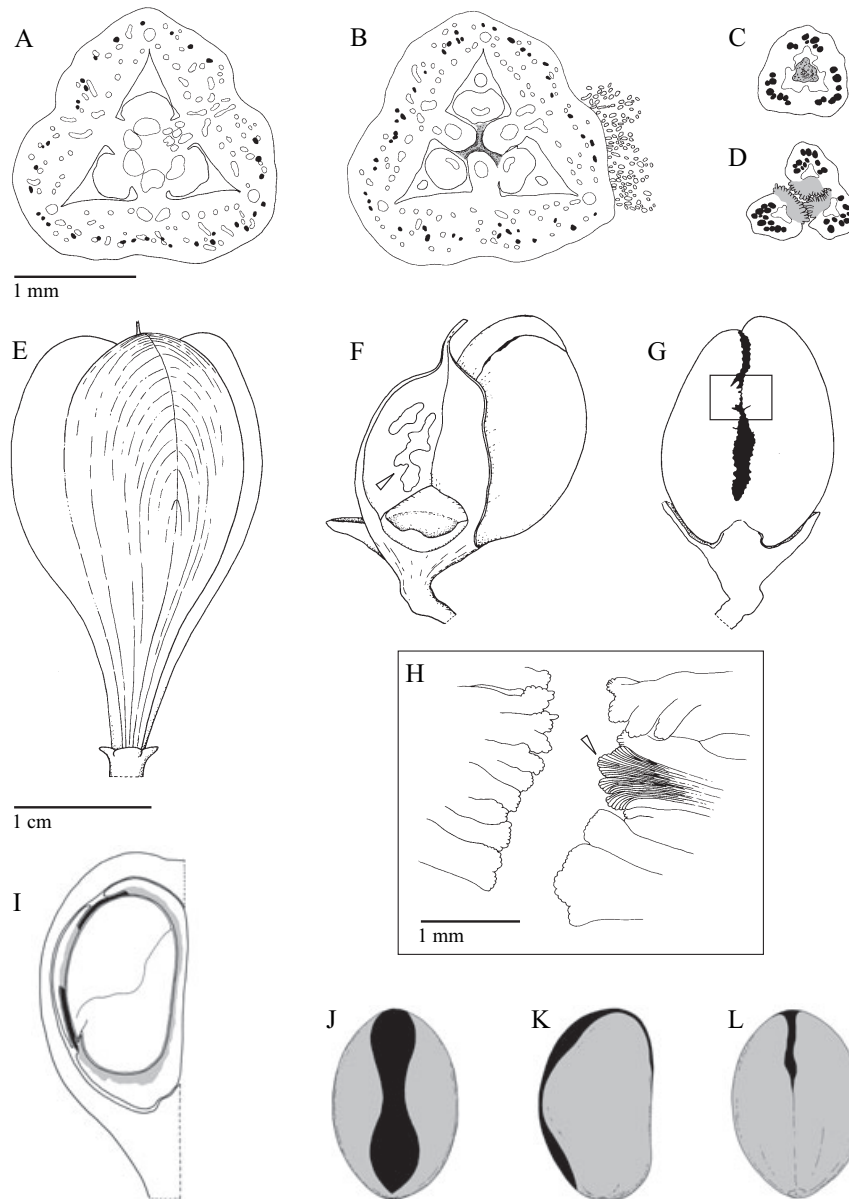
The woody lianas occur in tropical Central and South America. The mature stems contain one stele. Leaves are five-foliolate pinnate with winged petiole and rachis. Inflorescences are axillary thyrses with conspicuous elongate, deciduous bracts.

#### *Gynoecium at anthesis*

The gynoecium is similar to that in *Paullinia alata*, but the ovary is covered with unicellular hairs (Fig. 34). The inner surface seems to be postgenitally united up to the stigmas (Fig. 40A–D). The PTTT is massive, i.e. it consists of cells with mucilaginous cell walls. Vascularization is similar to *P. alata*. The ovary wall is provided with numerous laticiferous cells,



**Figures 34–39.** *Paullinia clavigera* and *P. obovata*. Figs 34–36. *P. clavigera* Figs 34, 35. Dissected female flower shortly before anthesis. Fig. 34. Gynoecium from the side. Scale bar = 500  $\mu$ m. Fig. 35. Ovules (one per locule) from the side; arrowheads point at hairs within locule. Scale bar = 200  $\mu$ m. Fig. 36. Seed development. Abaxial view of immature seed. Scale bar = 1 mm. Figs 37–39. *Paullinia obovata*. Fig. 37. Anthetic female flower. Abaxial view of ovule. Scale bar = 200  $\mu$ m. Figs 38, 39. Seed development. Fig. 38. Immature seed from the side. Scale bar = 1 mm. Fig. 39. Further developed seed from the side with ear-like aril. Scale bar = 1 mm. Abbreviations: a, aril; ii, inner integument; mp, micropylar region; o, obturator; oi, outer integument.



**Figure 40.** *Paullinia clavigera*. A–D, TS of gynoecium just before anthesis. Vascular bundles indicated with thin lines. Laticiferous cells indicated in black. Secretion of pollen tube transmitting tract (PTTT) shaded in grey. A, level of obturator, synascidiate zone. B, level just above ovule insertion, beginning of symplicate zone. C, style. D, stigma. E–L, mature fruit and seeds. Pseudo-hilum shaded in grey. Dry testa indicated in black. E, fruit. F, loop-holed septum (two seeds removed); arrowhead points at loop-holes. G, seed with aril, abaxial view. H, close-up of lobed aril margin (see rectangle in G); arrowhead points at extensively elongate cells. J–L, seed with detached aril, abaxial view, side view, and adaxial view, respectively.

which are conspicuous in the style and stigma (Fig. 40A–D). Unlike in *P. alata*, the inner hypodermis of the locules does not contain oxalate crystals. Unicellular hairs are found along the inner epidermis and on the placenta (Fig. 35).

The ovules are c. 0.6 mm long including the obturator. The inner integument is four or five cells thick, the outer seven or eight. The cell walls of the inner integ-

ument are slightly swollen in the micropylar region. The obturator is one-third as long as the ovule; its surface is mucilaginous and therefore secretory.

#### *Fruit and seed development*

The pericarp develops in a very similar way as that in *Paullinia alata*, although the mature fruits have different shapes and sizes. In *P. clavigera* the capsules

are pear-shaped, 2.0–3.2 cm long, including the stipe, and 1.9–2.2 cm wide. The mature pericarp 1–1.5 mm thick (Fig. 40I), dark red and glabrous (Fig. 5). The peripheral sclerenchyma bundles, which are formed during fruit development (Fig. 33) appear as small ridges on the mature fruit surface, curved towards the dorsal line of the carpels (Fig. 40E). After dehiscence the three capsule valves fall off and reveal the seeds, which are almost completely enveloped by a translucent white aril (Figs 6, 40G). The seeds are separated from each other by a pale pink septum, which is very thin and partly provided with loop-holes (Fig. 40F).

One to three seeds per fruit develop. Development of the aril begins in the basal parts of the chalaza and the outer integument with the differentiation of relatively large, spherical, tanniferous cells. Two shallow lobes on both sides of the micropyle are formed, which enlarge to the top of the seed during seed development as in *P. obovata* (Fig. 39). The mature aril consists of extensively elongate cells (Fig. 40H). No starch could be detected. In the mature seed the pseudo-hilum forms two lobes, which are united on the funicular side at least up to the middle of the seed. The dry testa area is dumbbell-shaped on the abaxial side and forms a narrow strap on the adaxial side (Fig. 40J–L). The dry testa is anatomically similar to *P. alata*; it is *c.* 460 µm thick and the columnar epidermal cells are *c.* 150 µm high. The mature seeds are ellipsoidal, 1.1–2.0 cm long and 1.0–1.4 cm wide including the aril (Fig. 40G).

#### *Germination and seedling*

Germination is comparable with that in *P. alata*. *Paullinia clavigera* differs only in longer petioles of the first opposite seedling leaves.

#### *PAULLINIA OBOVATA* (RUIZ & PAV.) PERS.

The woody lianas occur in western Amazonia. The mature stems contain one stele. Leaves are five-foliolate, petiole and rachis are unwinged. Elongate inflorescences (thyrses) with triangular, deciduous bracts arise from foliage leaf axils (Fig. 7).

#### *Gynoecium at anthesis*

The gynoecium is similar to that in *Paullinia alata*; however, the ovary is covered with short and often pluricellular glandular hairs. The PTTT forms a canal filled with secretion and lined with one cell layer, which produces hair-like cells protruding into the centre of the canal (Fig. 41A–C). Vascularization is similar to that in *P. alata*. The ovary wall is provided with numerous laticiferous cells (Fig. 41A–C). The hypodermis of the locules contains oxalate crystals (druses); the inner epidermis is glabrous.

The ovules are *c.* 0.6 mm long including the obturator. The inner integument is five cells thick, the outer

seven or eight. The obturator is slightly shorter than the ovule, its surface is mucilaginous and therefore secretory (Fig. 37).

#### *Fruit and seed development*

The pericarp develops in a similar way as in *Paullinia alata*. The mature fruits are fusiform to obovate, 2.5–9 cm long, including the stipe, and 1.5–3.5 cm wide (Fig. 41D). The mature pericarp is 4–6 mm thick (Fig. 41E), shiny red or yellow, glabrous to puberulous (Fig. 8). After dehiscence the capsule valves fall off and reveal the seeds, which are partly enveloped by a white aril. The seeds are separated by a red septum (Figs 9, 10).

Two or three seeds per fruit develop. Development of the aril is similar to that in *P. clavigera*. In the young aril spherical tanniferous cells are filled with starch. Two lobes on both sides of the micropyle are formed, enlarging to the top of the seed (Figs 38, 39). The tanniferous aril cells elongate during seed maturation, but to a lesser extent than in *P. clavigera*. In the mature seed the pseudo-hilum forms two lobes, which cover approximately half to three-quarters of the seed (Fig. 41G–I). The dry testa region is anatomically similar to *P. alata*. It is *c.* 400 µm thick, with the columnar epidermal cells *c.* 100 µm long. The mature seeds are ellipsoid to ovoid in adaxial view and broadly ellipsoid in side view. They are 1.8–2.5 cm long and 1.3–1.6 cm wide including the aril (Fig. 41F).

#### *Germination and seedling*

Germination is comparable with that in *Paullinia alata*. Seeds germinated after 4–14 days. The first opposite seedling leaves are often trifoliolate.

#### *PAULLINIA PACHYCARPA* BENTH.

The species is found in Amazonia. The mature stems contain one stele. Leaves are three- to nine-jugate, with the basal leaflet pairs being trifoliolate or bipinnate-ternate (Fig. 11); petiole and rachis are winged. Inflorescences are axillary thyrses.

#### *Gynoecium at anthesis*

The ovary is *c.* 2 mm long and 1.6 mm wide. The surface is covered mainly with unicellular hairs, in addition to a few pluricellular glandular hairs (Figs 42, 43). The ovary is synascidiate for approximately half of its length (Fig. 49A). At the base of the symplicate region the PTTT forms a canal filled with secretion, the outline is conspicuously papillate; higher up the canal becomes very narrow, made up of only one cell layer (Fig. 49B, C). The secondary lateral bundles form an almost continuous band with the dorsal bundles. Synlateral vascular bundles are present. The outer part of the ovary wall is provided with abundant

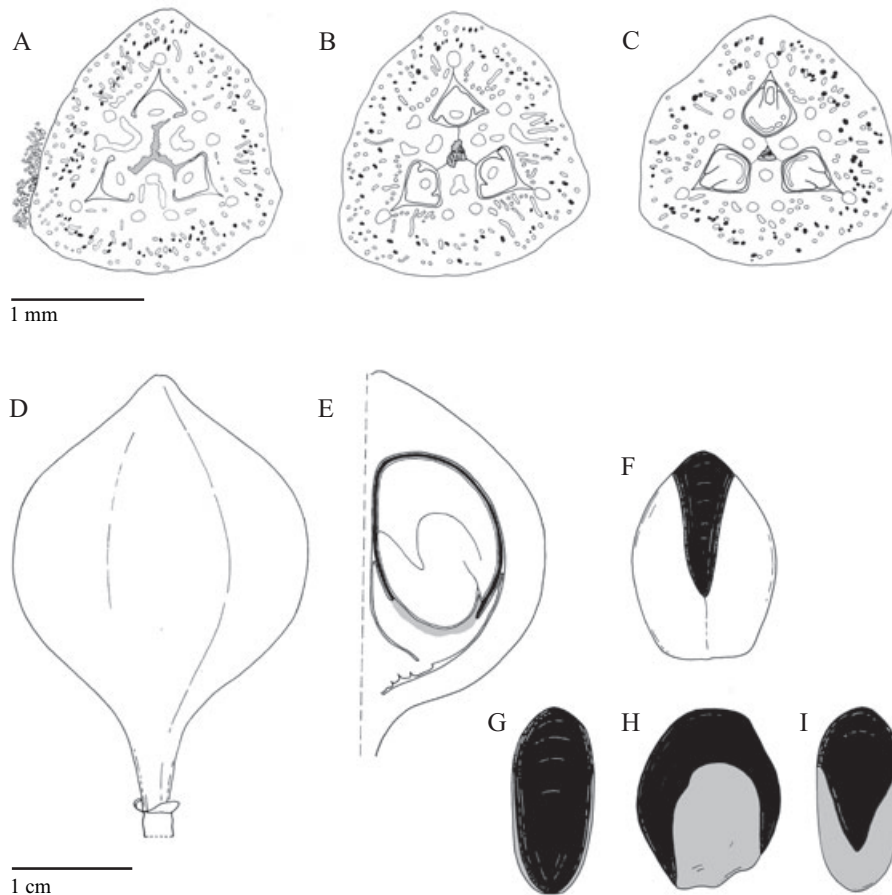
laticiferous cells (Fig. 49A–C). The inner hypodermis of the locules does not contain oxalate crystals. The inner epidermis is glabrous.

The ovules are c. 0.5 mm long including the obturator (Figs 44, 45). The tissue of the inner integument is slightly mucilaginous in the micropylar region. The inner and the outer integument are five cells thick each. The obturator is approximately one-third to half as long as the ovule, it fits tightly into the basal part of

the locule (Fig. 49A). Its surface is papillate, mucilaginous and therefore secretory.

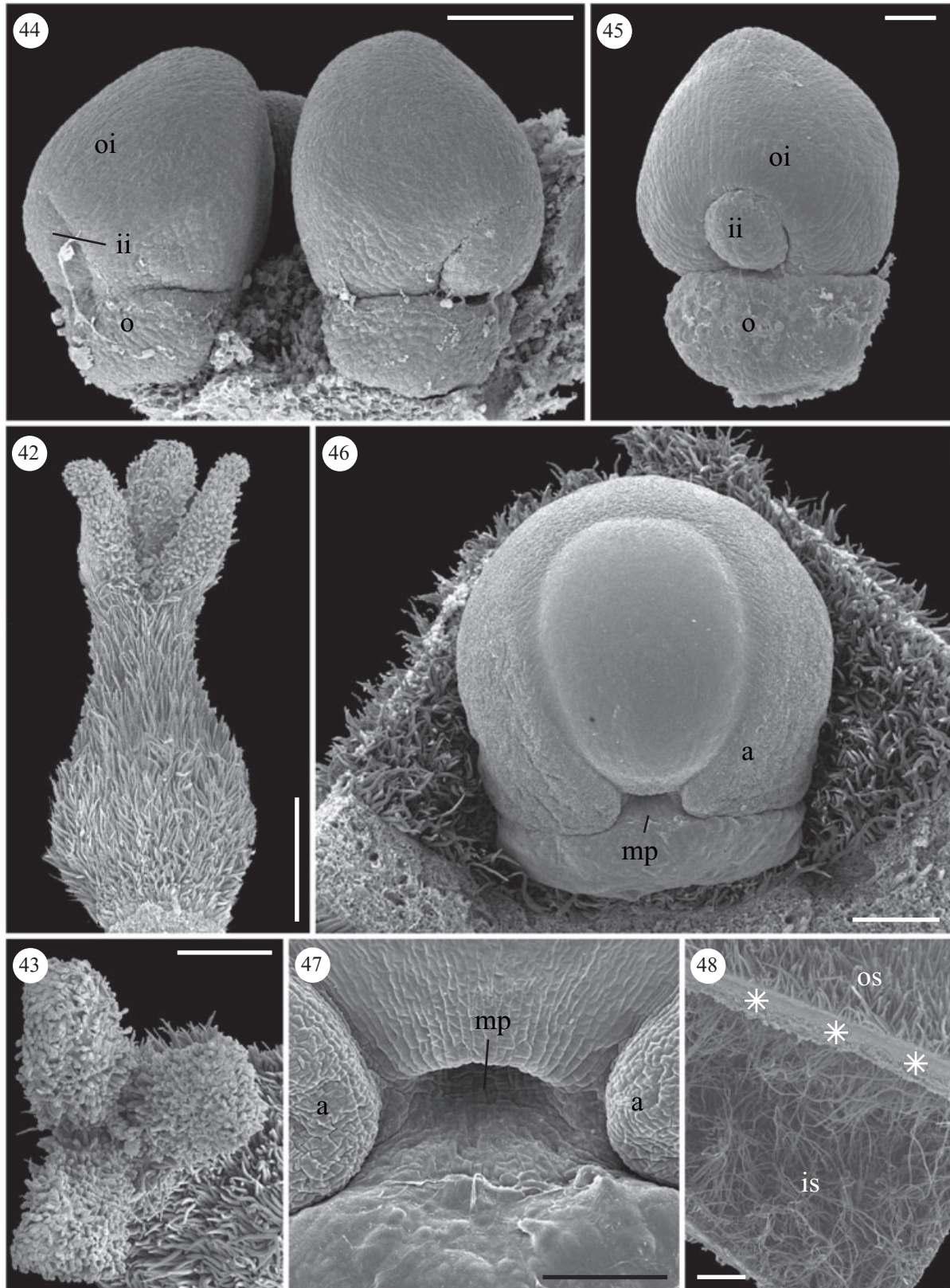
#### *Fruit and seed development*

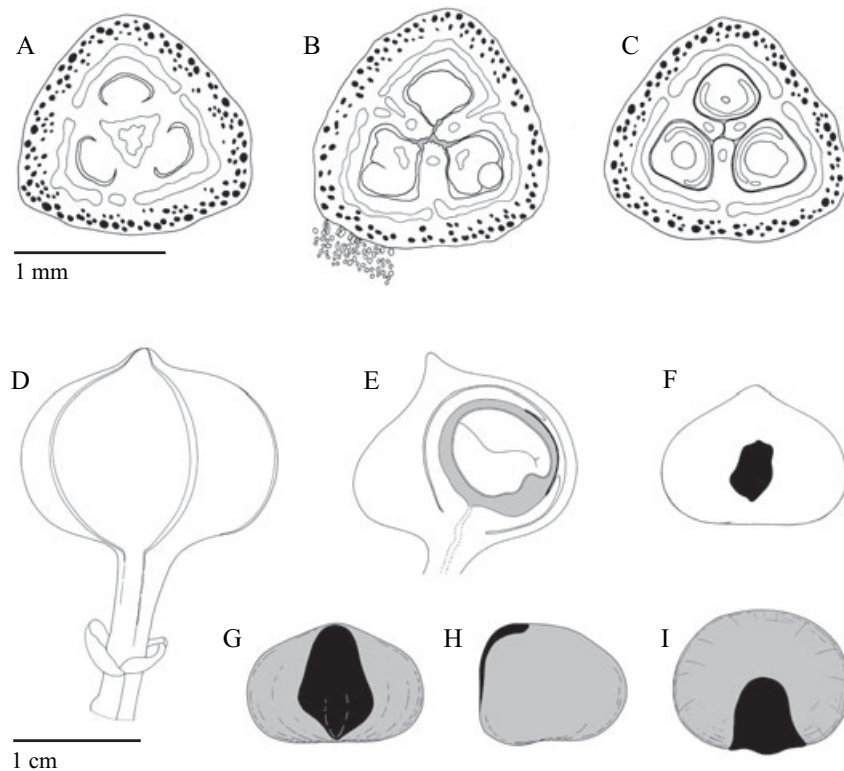
The mature fruit is 2–2.8 cm long, including the stipe and 1.7–2.2 cm wide (Fig. 49D). It is transversely ellipsoid with a slender stipe, half to two-thirds as long as the ovary. The mature pericarp is 1.5–2 mm thick, orange and covered with multicellular, lignified



**Figure 41.** *Paullinia obovata*. A–C, TS of anthetic gynoecium. Vascular bundles indicated with thin lines. Laticiferous cells indicated in black. Secretion of pollen tube transmitting tract (PTTT) shaded in grey. A, level of obturator, beginning of symplicate zone. B, transition from obturator to ovule, symplicate zone. C, symplicate zone; note the branching vascular bundles in the chalaza. D–I, mature fruit and seeds. Pseudo-hilum shaded in grey. Dry testa indicated in black. D, fruit. E, longitudinal section of seed and pericarp. F, seed with aril, abaxial view. G–I, seed with detached aril, abaxial view, side view, adaxial view.

**Figures 42–48.** *Paullinia pachycarpa*. Figs 42–44. Dissected female flower during anthesis. Fig. 42. Gynoecium from the side. Scale bar = 1 mm. Fig. 43. Stigmatic region, from above. Scale bar = 500  $\mu$ m. Fig. 44. Ovules (one per locule) from the side. Scale bar = 200  $\mu$ m. Figs 45–47. Seed development. Fig. 45. Abaxial view of postanthetic ovule. Scale bar = 100  $\mu$ m. Fig. 46. Abaxial view of immature seed. Scale bar = 500  $\mu$ m. Fig. 47. Same object, close-up of micropylar region. Scale bar = 200  $\mu$ m. Fig. 48. Inner and outer surface of immature capsule; its wall is labelled with asterisks. Scale bar = 2 mm. Abbreviations: a, aril; ii, inner integument; is, inner surface; mp, micropylar region; o, obturator; oi, outer integument; os, outer surface.





**Figure 49.** *Paullinia pachycarpa*. A–C, TS of anthetic gynoecium. Vascular bundles indicated with thin lines. Laticiferous cells indicated in black. Secretion of pollen tube transmitting tract shaded in grey. A, level of obturator, synascidiate zone. B, transition from obturator to ovule, beginning of symplicate zone. C, symplicate zone. D–I, mature fruit and seeds. Pseudo-hilum shaded in grey. Dry testa indicated in black. D, fruit. E, longitudinal section of seed and pericarp. F, seed with aril, abaxial view. G–I, seed with detached aril, abaxial view, side view, view from above.

hairs (Figs 12, 48, 49E). The exocarp is formed by a sclerenchyma layer four or five cells thick. After dehiscence the persistent capsule valves are bent downwards to the base of the fruit revealing the seed, which is almost completely enveloped by a white aril.

Usually one, rarely two seeds per fruit develop. Multicellular lignified hairs are produced on the inner epidermis of the locules (Figs 46, 48) and the space between the developing seed and the pericarp is filled with a pulpy secretion. Aril development begins with the differentiation of spherical cells in the basal parts of the chalaza and the outer integument. Approximately half of the cells are tanniferous, the other half contain starch granules. The young aril encloses the seed like a cap, leaving out an elliptic area abaxially (Figs 46, 47). In the mature seed the dry testa forms an ovate or elliptic area, which is partly overgrown by the aril (Figs 13, 49E–I). In the nearly mature seed, which is still enclosed in the indehiscent fruit, the testa is rather thick (Fig. 49E) but no sclerified cells could be detected. The dry testa is c. 520  $\mu\text{m}$  thick with columnar epidermal cells 80  $\mu\text{m}$  long. The dark colour is confined to the epidermal cells. The mature seeds

are depressed ovoid, 1–1.4 cm long and 1.5–2 cm wide including the aril (Fig. 49F).

#### *Germination and seedling*

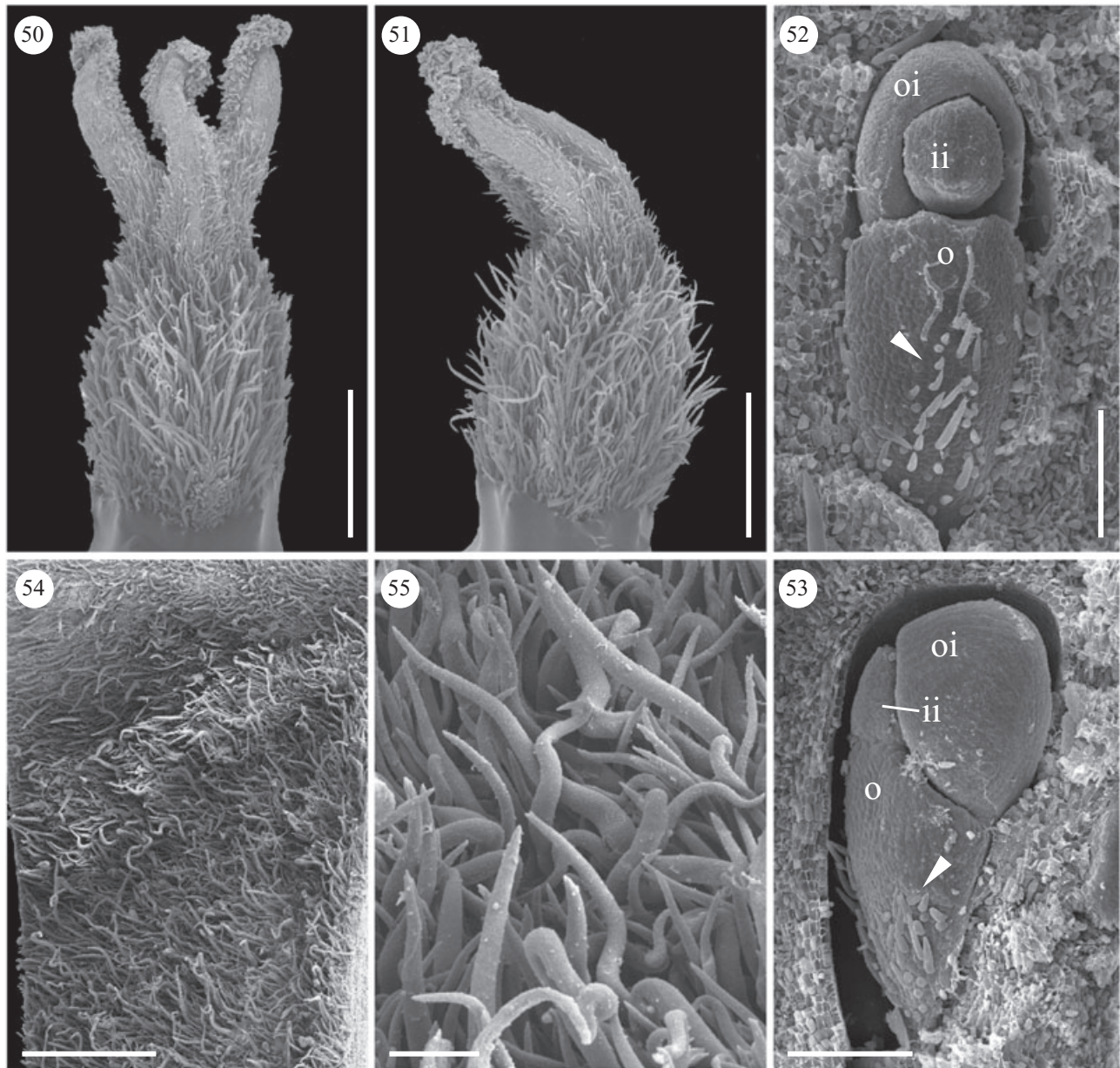
As in the other *Paullinia* species studied; the first opposite seedling leaves are trifoliolate with winged petioles.

#### *PAULLINIA* AFF. *CALOPTERA* RADLK.

The species forms woody lianas occurring in tropical Central and South America. The mature stems contain a single stele. Leaves are five-foliolate, petiole and rachis unwinged. Inflorescences are elongate and axillary thyrses; they bear minute, triangular bracts.

#### *Gynoecium at anthesis*

The ovary is three-angled, c. 2 mm long and 1.4 mm wide. The surface is covered with unicellular hairs (Figs 50, 51). Few multicellular glandular hairs occur in the dorsal region of the carpels. The dorsal region is expanded into a longitudinal rib (Fig. 56A–C), more pronounced from the base towards the top. The ovary



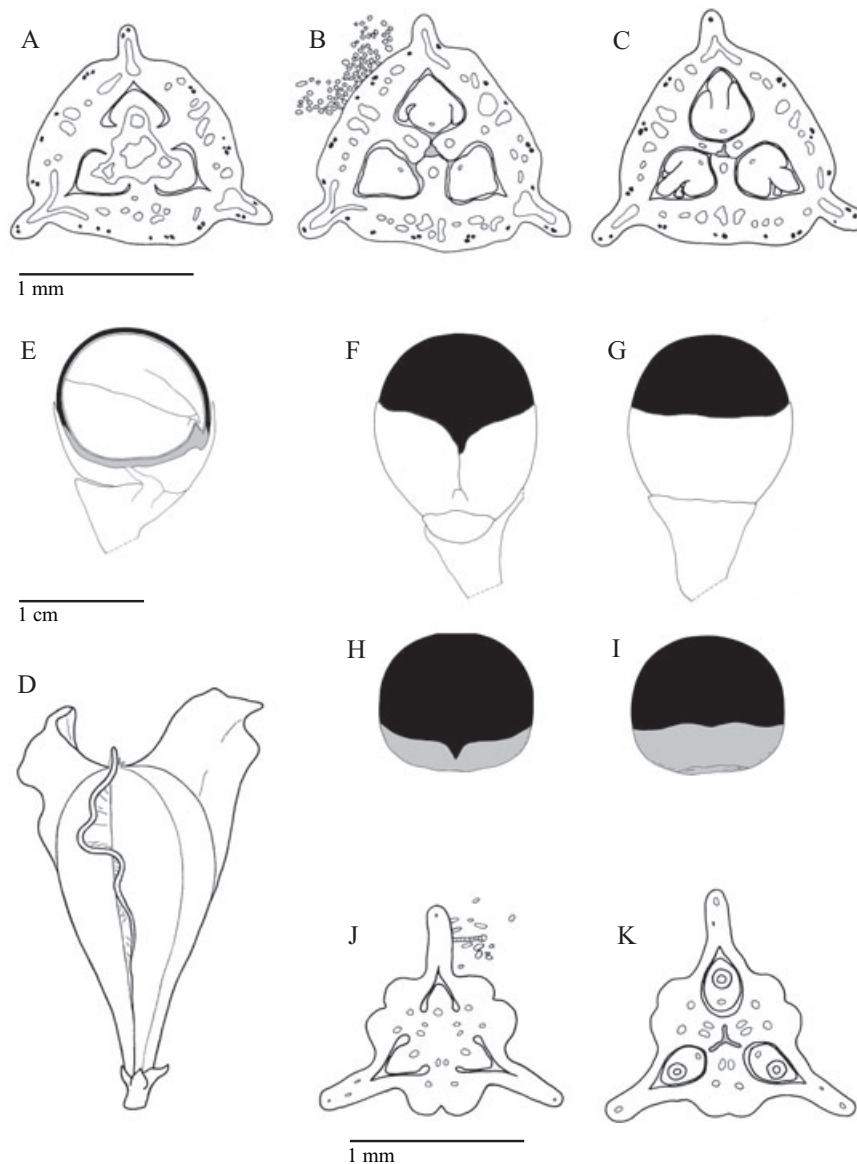
**Figures 50–55.** *Paullinia* aff. *caloptera*. Figs 50–53. Dissected female flower during anthesis. Figs 50–51. Gynoecium from two sides. Scale bars = 1 mm. Fig. 52. Abaxial view of ovule (one per locule); arrowhead points to hairs on obturator. Scale bar = 200 µm. Fig. 53. Ovule from the side. Scale bar = 200 µm. Fig. 54. Outer surface of immature capsule. Scale bar = 1 mm. Fig. 55. Same object, close-up of pluricellular hairs. Scale bar = 100 µm. Abbreviations: ii, inner integument; o, obturator; oi, outer integument.

is synascidiate for approximately half of its length (Fig. 56A). The PTTT is massive, i.e. it consists of elongate cells with mucilaginous cell walls. Beside the dorsal and synlateral vascular bundles secondary lateral bundles are present (Fig. 56A–C). Laticiferous cells and oxalate crystals (druses) are found in the ovary wall. The inner epidermis of the locules is glabrous and the hypodermis does not contain oxalate crystals. The ovules fit tightly into the locules (Fig. 56C); they

are 0.7 mm long including the obturator (Figs 52, 53). The inner integument is four or five cells thick, the outer five. The obturator is slightly longer than the ovule. It consists of large, mucilaginous cells and bears unicellular hairs on the surface (Fig. 52).

#### *Fruit and seed development*

The fruit has dorsal wings. They are wave-like and conspicuously pronounced towards the top of the fruit



**Figure 56.** *Paullinia* aff. *caloptera* and *Serjania altissima*. A–C, TS of anthetic gynoecium. Vascular bundles indicated with thin lines. Laticiferous cells indicated in black. Secretion of pollen tube transmitting tract shaded in grey. A–C, *Paullinia* aff. *caloptera*. A, level of obturator, synascidiate zone. B, beginning of symplicate zone. C, symplicate zone. D–I, mature fruits and seeds of *Paullinia* aff. *caloptera*. Pseudo-hilum shaded in grey. Dry testa indicated in black. D, fruit. E, longitudinal section of seed with aril. F, G, seed with aril, abaxial view, adaxial view. H, I, seed with detached aril, abaxial view, adaxial view. J, K, transverse sections of anthetic gynoecium of *Serjania altissima*. J, level of obturator, synascidiate zone. K, symplicate zone.

(Figs 19, 20). The fruit is up to 2.5 cm long, including the short stipe, and up to 1.7 cm in diameter without wings (Fig. 56D). The mature pericarp is 1 mm thick, covered with pluricellular, lignified hairs (Figs 54, 55). Sclerenchyma sheaths are differentiated around the vascular bundles, meso- and endocarp consists of spongy tissue with intercellular spaces.

Usually one seed per fruit develops (Fig. 21). The inner epidermis of the locules is glabrous. The

white aril develops around the base of the seed and covers approximately half of the seed (Fig. 56E–G). The spherical to slightly prolonged cells are tanniferous and contain starch granules. In the mature seed the testa consists of sclerified cells. The pseudo-hilum forms a strap around the base of the seed (Fig. 56H, I). The dry testa is 450–500  $\mu\text{m}$  thick with columnar epidermal cells c. 150  $\mu\text{m}$  long. The mature seeds are nearly spheri-



cal, c. 1.5 cm long including the aril and c. 1.3 cm wide (Fig. 56F, G).

*Germination and seedling*

No data.

*PAULLINIA DASYSTACHYA* RADLK.

The species forms woody lianas, occurring in tropical Central and South America. The mature stems contain a single stele. The whole plant is tomentose. Leaves are five-foliolate, petiole and rachis unwinged. Elongate inflorescences (thyrses) arise from leaf axils and bear minute, narrowly triangular bracts (Figs 22, 23).

*Gynoecium at anthesis*

The ovary is three-angled, c. 2.5 mm long and 1.7 mm wide. The surface is covered with unicellular hairs and multicellular glandular hairs (Figs 57, 58). The dorsal region of each carpel is expanded into a pronounced longitudinal rib (Fig. 65A–C). The ovary is synascidiate for approximately half its length (Fig. 65A). The PTTT is a canal filled with secretion. It is lined with two cell layers, the epidermis being papillate (Fig. 65B, C). Dorsal and synlateral as well as secondary lateral bundles are present. Only few laticiferous cells are found in the ovary wall (Fig. 65A–C). The inner epidermis of the locules is glabrous (Fig. 59) and the hypodermis does not contain oxalate crystals.

The ovules do not fill out the locules completely (Fig. 65C); they are 0.5 mm long including the obturator (Fig. 59). The inner integument is five or six cells thick, the outer seven or eight. The obturator is approximately one-third as long as the ovule, it is papillate and covered with secretion.

*Fruit and seed development*

The mature fruit has dorsal wings, which become more pronounced from the base towards the top (Fig. 65D). The fruit is 1.8–2.2 cm long, including the short stipe, and 0.9–1.3 cm in diameter (without the wings). The mature pericarp has a diameter of c. 1 mm (Fig. 65E). The surface is red and covered with unicellular, lignified hairs. Sclerenchyma sheaths are differentiated around the vascular bundles and the endocarp is formed by a layer of sclerified fibres. After dehiscence the shiny black seeds with a white aril at the base form a colour contrast with the persistent red capsule valves (Fig. 24).

Usually one, more rarely two, seeds per fruit develop. Multicellular lignified hairs are produced on the inner epidermis of the locules (Figs 59–63). The aril develops around the base of the seed (Fig. 64). The spherical cells are tanniferous and contain starch

granules. In the mature seed the testa consists of sclerified cells. The pseudo-hilum forms a narrow strap around the base of the seed (Fig. 65H–L). The dry testa is c. 400 µm thick with columnar epidermal cells 60 µm long. The mature seeds are ellipsoid, 1–1.4 cm long including the aril, and 0.8–1.2 cm wide (Fig. 65F, G).

*Germination and seedling*

Germination is similar to that in *Paullinia alata*; the whole seedling is tomentose; the first opposite seedling leaves are trifoliolate.

*CARDIOSPERMUM HALICACABUM* L.

The species forms herbaceous, annual vines, with pantropical distribution. The mature stems contain a single stele. Leaves are biternate. Umbel-like inflorescences (thyrses) usually associated with tendrils arise from leaf axils. They bear tiny, triangular bracts.

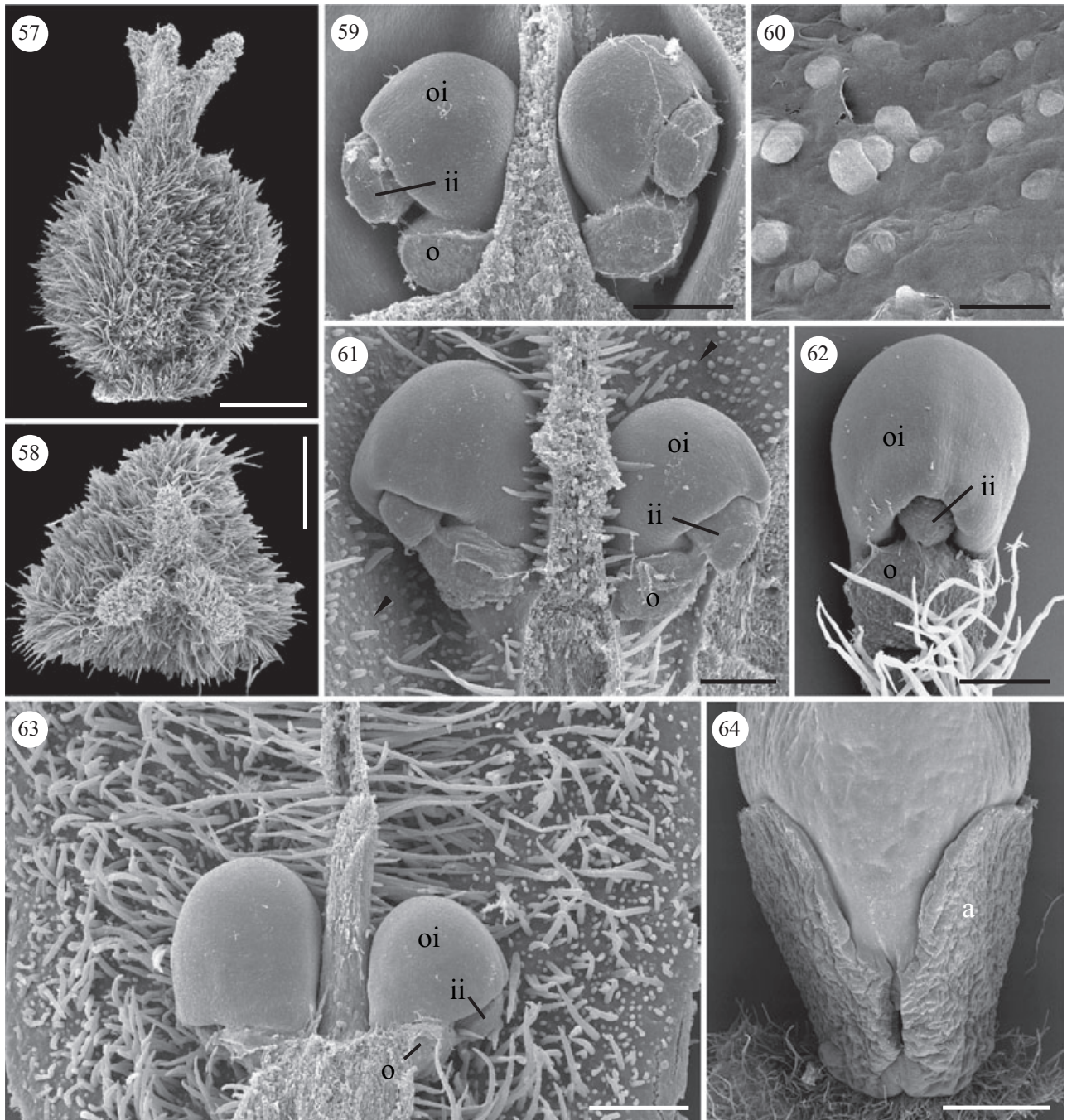
*Gynoecium at anthesis*

The ovary is three-angled, c. 1 mm long and 0.8–1 mm wide. Multicellular glandular hairs are scattered on the surface of the ovary (Figs 66–69). The dorsal region of each carpel is expanded into a pronounced longitudinal rib (Fig. 76A, B), covered with unicellular hairs. Style and stigmas are inclined (Fig. 66). The gynoecium is synascidiate for approximately half its length (Fig. 76A). The PTTT is a canal filled with secretion (Fig. 76B), formed by two cell layers with papillate epidermis. Dorsal and synlateral bundles are present. No laticiferous cells occur in the ovary wall. The inner epidermis of the locules is glabrous. In the tissue of the septa conspicuous intercellular spaces are found.

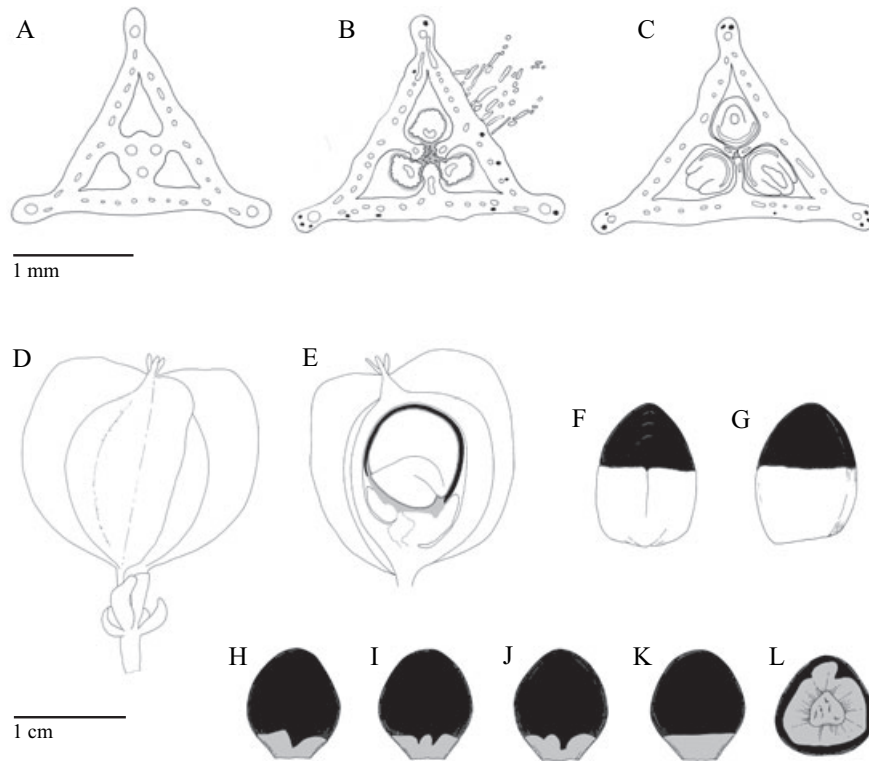
The ovules fit tightly into the locules (Fig. 76B); they contain tanniferous tissue and are c. 0.5 mm long including the obturator. The inner integument is six or seven cells thick, the outer eight or nine. The obturator is slightly shorter than the ovule, it is papillate and covered with secretion (Figs 70–72).

*Fruit and seed development*

The mature fruit is depressed obovoid with three inflated locules that are dorsally keeled (Figs 14, 76E); it is up to 1.5 cm long (including the short stipe) and up to 2 cm in diameter (including the wings). The mature pericarp is papery, reddish to pale brown, with scattered hairs. The mesocarp consists of spongy tissue, the endocarp of conspicuous elongate epidermal cells. Fruits are septifragal. The septa contain numerous oxalate crystals along the dehiscence line. In the mature dehisced fruit each septum may additionally divide up into two separated layers, consisting mainly of elongate epidermal cells.



**Figures 57–64.** *Paullinia dasystachya*. Figs 57–60. Dissected female flower shortly after anthesis. Fig. 57. Gynoecium from the side. Scale bar = 1 mm. Fig. 58. Gynoecium with stigmatic region, from above. Scale bar = 1 mm. Fig. 59. Ovules (one per locule) from the side. Scale bar = 200 µm. Fig. 60. Inner epidermis of locule with developing hairs. Scale bar = 20 µm. Figs 61–64. Seed development. Fig. 61. Immature seeds (postanthetic ovules) from the side; arrowheads point to developing hairs. Scale bar = 200 µm. Fig. 62. Abaxial view of immature seed. Scale bar = 200 µm. Fig. 63. Immature seeds of two locules from the side, surrounded by hairs of inner epidermis. Scale bar = 300 µm. Fig. 64. Abaxial view of further developed seed with aril. Scale bars = 1 mm. Abbreviations: a, aril; ii, inner integument; o, obturator; oi, outer integument.



**Figure 65.** *Paullinia dasystachya*. A–C, TS of anthetic gynoecium. Vascular bundles indicated with thin lines. Laticiferous cells indicated in black. Secretion of pollen tube transmitting tract (PTTT) shaded in grey. A, synascidiate zone. B, level of obturator, beginning of symplicate zone. C, symplicate zone. D–L, mature fruit and seeds. Pseudo-hilum shaded in grey. Dry testa indicated in black. D, fruit. E, longitudinal section of seed and pericarp. F, G, seed with aril, abaxial view, side view. H–L, seed with detached aril, abaxial view (H–J), adaxial view, from below.

Usually three seeds per fruit develop (Fig. 15). The inner epidermis of the locules is glabrous. A thin reniform (cordiform) white aril develops around the base of the seed (Figs 73–75). In the mature seed it consists of spongy tissue containing numerous oxalate crystals (druses). It is separated from the testa by a white layer of columnar cells with thickened walls, containing rhomboidal crystals. In the mature seed the testa is rather thick, *c.* 500  $\mu\text{m}$ , but the cell walls are not sclerified; testa cell size increases towards the centre; the columnar epidermal cells are *c.* 60  $\mu\text{m}$  long. The mature seeds are spherical, *c.* 4 mm in diameter with a dull dark-blue or black surface.

#### *Germination and seedling*

Germination is epigeal. The first opposite seedling leaves are trifoliolate.

#### *SERJANIA ALTISSIMA* (POEPP.) RADLK.

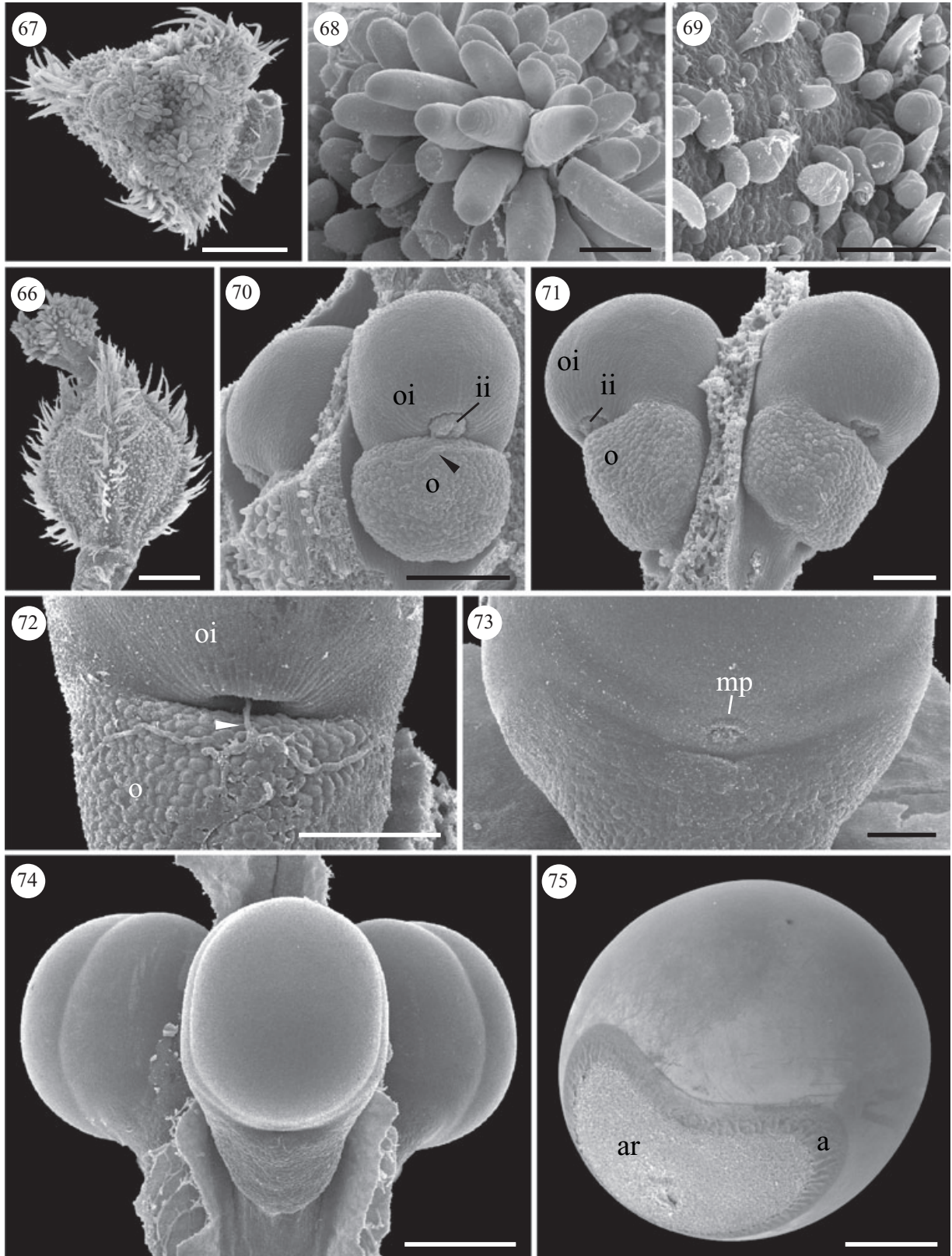
The species forms lianas, occurring in tropical South America. The conspicuously sulcate stems contain a single stele. The whole plant is tomentose with glandular hairs and rusty spreading trichomes. Leaves are

biterminate, petiole and rachis unwinged. Elongate inflorescences (thyrses), associated with tendrils, arise from leaf axils.

#### *Gynoecium at anthesis*

The ovary is three-angled, *c.* 1.6 mm long and 1.0 mm wide. Unicellular hairs and conspicuously prolonged multicellular glandular hairs are scattered on the surface (Figs 77–79). The dorsal region of each carpel is expanded into a pronounced longitudinal rib (Fig. 56J, K). The ovary is synascidiate for approximately half its length (Fig. 56J). The PTTT is a canal filled with secretion (Fig. 56K). It is lined with two cell layers, the epidermis being papillate. The epidermis of the locules is glabrous (Fig. 80). Beside the dorsal and lateral vascular bundles few secondary lateral bundles are present. Only very few laticiferous cells are found in the ovary wall.

The ovules fit tightly into the locules; they are *c.* 0.5 mm long including the obturator (Figs 80–82). The inner integument is five cells thick, the outer five or six. The obturator is approximately one-quarter as long as the ovule, its surface is slightly mucilaginous.

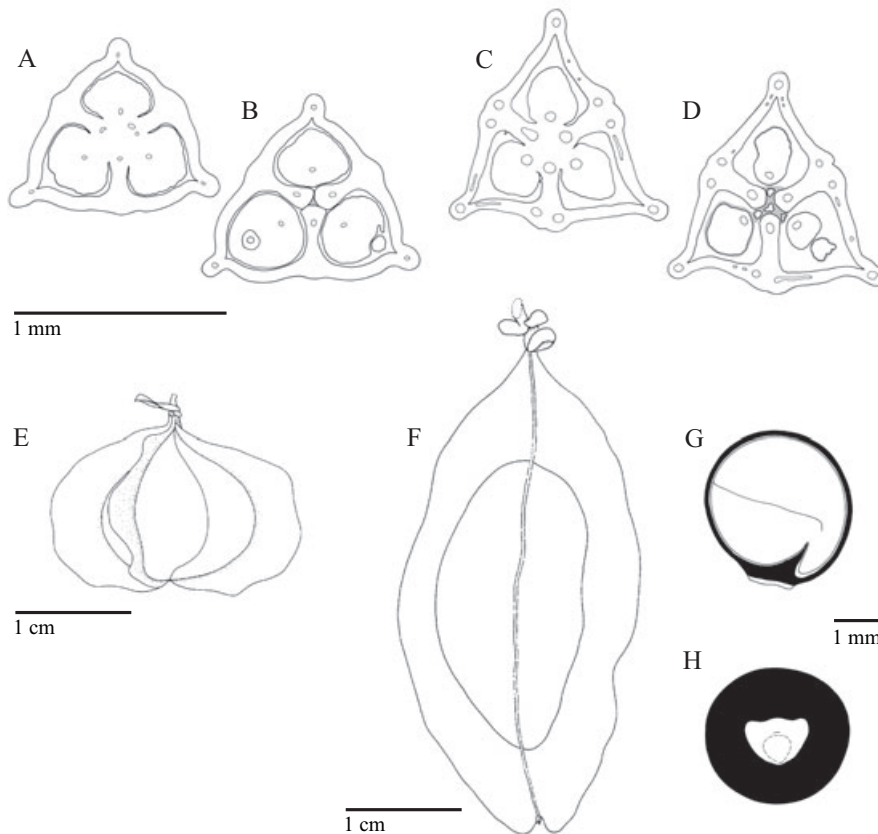


*Fruit and seed development*

The fruit is ovate to oblong, with distal locules and proximal wings (Fig. 16). It is up to 3 cm long and up to 2.5 cm wide (including the wings). The pericarp is papery, covered with unicellular hairs and prolonged multicellular glandular hairs. Conspicuous prolonged unicellular hairs occur on the outer locule wall, which are slightly crested. The outer epidermal cells of the locules have thickened periclinal walls. The mesocarp consists of parenchymatous tissue, the endocarp of

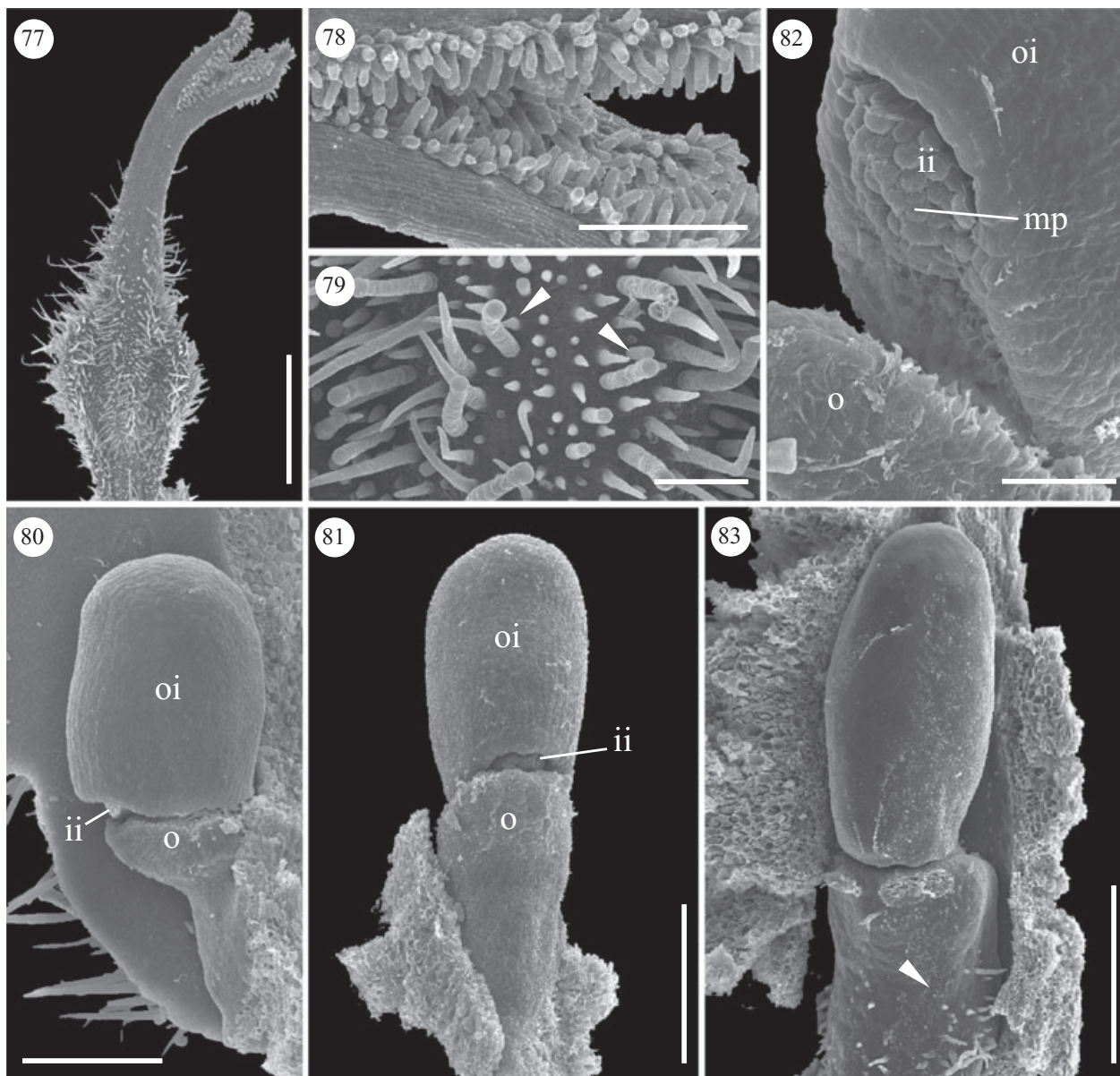
conspicuous prolonged, cross-layered sclerified fibres. Mesocarp and endocarp are separated by a cell layer containing numerous oxalate crystals. The wings consist of parenchymatous tissue with a network of vascular bundles. Finally, the three carpels separate along the speta into three winged (samaroid) mericarps leaving a common, thin carpophore.

Three seeds per fruit develop. The inner epidermis of the locules is glabrous. No aril develops around the base of the seed (Fig. 83).



**Figure 76.** *Cardiospermum halicacabum* and *Urvillea ulmacea*. A–D, TS of anthetic gynoecium. Vascular bundles indicated with thin lines. Secretion of pollen tube transmitting tract shaded in grey. A, B, *Cardiospermum halicacabum*. A, level of obturator, synascidiate zone. B, beginning of symplicate zone. C, D, *Urvillea ulmacea*. C, level of obturator, synascidiate zone. D, beginning of symplicate zone. E–H. Mature fruits and seeds. E, fruit of *Cardiospermum halicacabum*. F–H, *Urvillea ulmacea*. F, fruit. G, LS of seed. H, seed with dry testa (black) and aril (white), from below.

← **Figures 66–75.** *Cardiospermum halicacabum*. Figs 66–71. Dissected female flower during anthesis. Fig. 66. Gynoecium with curved style from the side. Scale bar = 400  $\mu$ m. Fig. 67. Gynoecium with stigmatic region, from above. Scale bar = 400  $\mu$ m. Fig. 68. Stigmatic papillae. Scale bar = 50  $\mu$ m. Fig. 69. Outer ovary epidermis with multicellular glandular hairs. Scale bar = 50  $\mu$ m. Fig. 70. Abaxial view of ovule; arrowhead points to pollen tube. Scale bar = 200  $\mu$ m. Fig. 71. Ovules (one per locule) from the side. Scale bar = 150  $\mu$ m. Fig. 72–75. Seed development. Fig. 72. Micropylar region of postanthetic ovule; arrowhead points to pollen tube. Scale bar = 200  $\mu$ m. Fig. 73. Micropylar region of further developed seed. Scale bar = 200  $\mu$ m. Fig. 74. Immature seeds after removal of septa. Scale bar = 500  $\mu$ m. Fig. 75. Mature seed with kidney-shaped abscission region and aril. Scale bar = 1 mm. Abbreviations: a, aril; ar, abscission region; ii, inner integument; mp, micropylar region; o, obturator; oi, outer integument.



**Figures 77–83.** *Serjania altissima*. Figs 77–80. Dissected female flower during anthesis. Fig. 77. Gynoecium from the side. Scale bar = 1 mm. Fig. 78. Stigmatic papillae. Scale bar = 150 µm. Fig. 79. Outer ovary epidermis with unicellular hairs and multicellular glandular hairs (arrowheads). Scale bar = 200 µm. Fig. 80. Ovule (one per locule) from the side. Scale bar = 200 µm. Fig. 81. Abaxial view of ovule. Scale bar = 200 µm. Fig. 82. Close-up of micropylar region. Scale bar = 50 µm. Fig. 83. Seed development; immature seed; arrowhead points to hairs within the locule. Scale bar = 250 µm. Abbreviations: ii, inner integument; mp, micropyle; o, obturator; oi, outer integument.

#### *Germination and seedling*

Germination is hypogeal. The whole seedling is tomentose; the first opposite seedling leaves are trifoliolate.

#### *URVILLEA ULMACEA KUNTH*

Herbaceous to woody vines, occurring in Central and South America. Stems with a single stele, usually

deeply trilobed. Leaves trifoliolate (less often biter-nate). Inflorescences are elongate thyrses; they are usually associated with a pair of coiled tendrils and arise from leaf axils (Figs 17, 18). They bear tiny, triangular bracts.

#### *Gynoecium at anthesis*

The ovary is three-angled, c. 1.3 mm long and 0.8 mm wide. Multicellular glandular hairs are scattered on

the surface (Figs 84–87). The dorsal region of each carpel is expanded into a pronounced longitudinal rib (Fig. 76C, D). The stigma extend almost the entire length of the style. The ovary is synascidiate for approximately half its length (Fig. 76C). The PTTT is a canal filled with secretion (Fig. 76D). It is lined with two cell layers, the epidermis being papillate. The epidermis of the locules is covered with multicellular glandular hairs (Fig. 88). Beside the dorsal and synlateral vascular bundles few secondary lateral bundles are present. Only very few laticiferous cells are found in the ovary wall. The tissue of the septa contains oxalate crystals (druses and rhomboids) and forms conspicuous intercellular spaces.

The ovules do not fill the locules tightly (Fig. 88); they are *c.* 0.5 mm long including the obturator. The inner integument is five or six cells thick, the outer six or seven. The obturator is one-third to half as long as the ovule, it is papillate and covered with secretion.

#### *Fruit and seed development*

Fruits are winged septifragal capsules. The mature fruit is ellipsoid in outline, with slightly inflated locules, each showing a dorsal wing (Figs 17, 18, 76F). It is up to 4 cm long (including the short stipe) and up to 2 cm in diameter (including the wings). The mature pericarp is papery, glabrous, reddish to brown. The mesocarp consists of spongy tissue, the endocarp of conspicuous prolonged, cross-layered cells. The septa contains numerous oxalate crystals.

Usually three seeds per fruit develop. Few multicellular glandular hairs remain on the inner epidermis of the locules. A small pale reniform aril develops around the base of the seed (Figs 89, 90). In the mature seed the testa is *c.* 120 µm thick, the columnar epidermal cells are *c.* 40 µm long. The mature seeds are spherical, *c.* 3 mm in diameter and shiny dark brown (Fig. 76G, H).

#### *Germination and seedling*

Germination is hypogeal. The whole seedling is tomentose; the first opposite seedling leaves are trifoliolate.

## DISCUSSION

Fruit characters are important for the distinction of genera and species within Paullinieae, because vegetative and floral characters usually do not allow a clear identification of taxa. For example, Radlkofer's classifications of Paullinieae (Radlkofer, 1933), *Paullinia* (Radlkofer, 1895a) and *Serjania* (Radlkofer, 1875), as well as Acevedo-Rodríguez's (1993a) more recent treatment of a section of *Serjania* are based on the structure of the pericarp. The present paper adds

a detailed description of gynoecium and fruit characters of nine members of Paullinieae. In the following paragraphs the gynoecium and fruit characters of the investigated taxa are discussed and compared with other sapindalean taxa in order to test their systematic value. Emphasis is given to the structural base of different dispersal mechanisms within Paullinieae.

#### GYNOECIUM AT ANTHESIS

In Paullinieae three carpels are always present. It is usually three in Sapindaceae, more rarely two up to eight. This character is generally stable at the generic or tribal level (Radlkofer, 1933, 1934). In other sapindalean families carpel number varies from one to many (up to 20 in Meliaceae; Pennington & Styles 1975) but five carpels seem to be the plesiomorphic state for Sapindales (Wannan & Quinn, 1991; Stevens, 2001; Judd *et al.*, 2002).

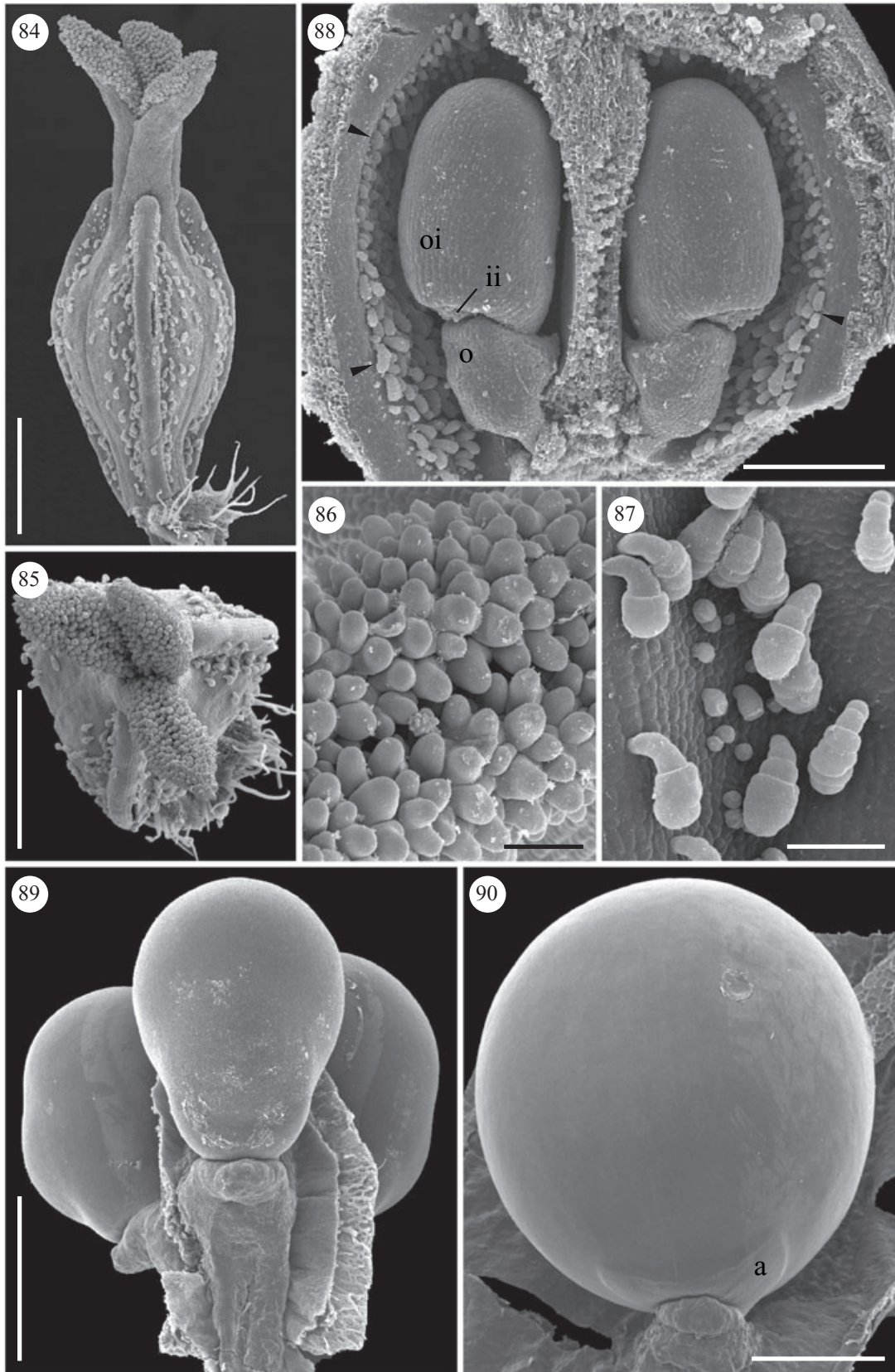
Within the taxa studied the carpels are free in the upper portion of the style, which is recurved to different degrees, presenting the stigma on the ventral side. The stigma extends along half to almost the entire length of the style (*Urvillea ulmacea*). The stigma has unicellular papillae. The ovaries are synascidiate for approximately half their length and are symplicate up to the stigmas.

In Sapindaceae ovary and style are symplicate to different degrees, and also capitate stigmas occur (Radlkofer, 1933, 1934). In the related families Anacardiaceae, Burseraceae, Rutaceae and Simaroubaceae the ovary structure is highly diverse, whereas in Meliaceae style and style-head vary considerably (Gut, 1966; Pennington & Styles, 1975; Ramp, 1988; Wannan & Quinn, 1991).

#### SHAPE AND ANATOMY OF THE OVARY WALL

The ovaries of all taxa studied are spherical to triangular, with pronounced dorsal longitudinal ribs in *P.* aff. *caloptera*, *P. dasystachya*, *C. halicacabum*, *S. altissima* and *U. ulmacea*. The ribs develop into wing-like structures during fruit maturation.

The vascular patterns of the ovary wall differ between the species. In most taxa studied, dorsal and synlateral bundles are present. In *S. altissima* separate lateral bundles occur, most probably related to the later development of the schizocarpic fruits, separating into samaroid mericarps. In most species studied a network of secondary lateral vascular bundles is found (*Paullinia alata*, *P. clavigera*, *P.* aff. *caloptera*, *P. dasystachya*, *P. obovata*, *P. pachycarpa*; to a lesser degree also in *Serjania altissima* and *Urvillea ulmacea*). In *P. pachycarpa* they form almost a continuous band with the dorsal bundles. Outside the secondary lateral vascular bundles numerous inconspicuous





**Figures 84–90.** *Urvillea ulmacea*. Figs 84–88. Dissected female flower during anthesis. Fig. 84. Gynoecium from the side. Scale bar = 500 µm. Fig. 85. Gynoecium with stigmatic region, from above. Scale bar = 500 µm. Fig. 86. Stigmatic papillae. Scale bar = 50 µm. Fig. 87. Outer ovary epidermis surface with club-shaped multicellular glandular hairs. Scale bar = 50 µm. Fig. 88. Ovules (one per locule) from the side; arrowheads point to multicellular glandular hairs inside the locule. Scale bar = 200 µm. Figs 89–90. Seed development. Fig. 89. Immature seeds. Scale bar = 100 µm. Fig. 90. Nearly mature seed with aril. Scale bar = 1 mm. Abbreviations: a, aril; ii, inner integument; o, obturator; oi, outer integument.

bundles and/or laticiferous cells may be present (*P. alata*, *P. clavigera*, *P. obovata*, *P. pachycarpa* and *P. dasystachya*). Dense vascularization of the ovary walls is also known from Rutaceae (Gut, 1966; Ramp, 1988).

#### HAIRS INSIDE AND OUTSIDE OVARY AND FRUIT

The indumentum of the anthetic ovary is highly variable at species level. The outer surface of the ovary wall is glabrous in *Paullinia alata*, but covered with unicellular hairs in *P. clavigera*, and with unicellular hairs as well as multicellular glandular hairs in *P. aff. caloptera*, *P. dasystachya*, *P. obovata* and *P. pachycarpa*. Long multicellular glandular hairs occur in *Serjania altissima*. In *Cardiospermum halicacabum* the unicellular hairs are confined to the dorsal ribs of the carpels, whereas between the ribs scattered multicellular glandular hairs are found. In *Urvillea ulmacea* only multicellular glandular hairs are present. Hairs on the outer ovary surface are common in Sapindaceae and other Sapindales. They seem to have a protective function especially in the young fruit (Roth, 1977).

The inner epidermis of the carpels (locules) is glabrous (*P. alata*, *P. aff. caloptera*, *P. dasystachya*, *P. obovata*, *P. pachycarpa*, *C. halicacabum* and *S. altissima*). It is covered with unicellular hairs (*P. clavigera*) or with multicellular glandular hairs (*U. ulmacea*). Locular hairs are also known from other sapindaceous taxa and are considered to supply moisture to the locules (Kaniewski & Wazynska, 1970).

During fruit development the indumentum may undergo strong alteration. The inner surface remains or becomes nearly glabrous (*P. alata*, *P. aff. caloptera*, *P. clavigera*, *P. obovata*, *C. halicacabum* and *S. altissima*), shows scattered multicellular glandular hairs (*U. ulmacea*) or becomes covered with multicellular lignified hairs (*P. dasystachya*, *P. pachycarpa*). The outer surface remains or becomes glabrous (*P. alata*, *P. clavigera* and *P. obovata*), is covered with unicellular hairs (*P. dasystachya*), with few scattered glandular hairs (*C. halicacabum*, *U. ulmacea*), with unicellular hairs as well as prolonged multicellular glandular hairs (*S. altissima*) or with multicellular lignified hairs (*P. aff. caloptera*, *P. pachycarpa*).

#### POLLEN TUBE TRANSMITTING TRACT

In all species examined the PTTT forms a central canal or column in the style and upper part of the ovary, which seems to serve as a compitum. The PTTT extends into the locules at the level of the transition from the synascidiate to the symplicate region (at the ventral side of the obturator). From there the pollen tubes continue their growth towards the micropyle on the secretory surface of the obturator (observed for *Paullinia pachycarpa* and *Cardiospermum halicacabum*). The following differences are found at species level. In *Paullinia alata* and *P. obovata* the canal is filled with secretion and lined with one cell layer, which produces hair-like cells protruding into the centre of the canal. In *P. aff. caloptera* and *P. clavigera* the PTTT forms a column of a compact tissue with extremely swollen cell walls. In *P. pachycarpa* the PTTT is narrow and comprises only one cell layer (the epidermis). In *P. dasystachya*, *Cardiospermum halicacabum*, *Serjania altissima* and *Urvillea ulmacea* the PTTT is formed by two cell layers, the epidermis being more or less papillate.

#### OVULES

Little is known about ovule structures in Sapindaceae (Mauritzon, 1936; Kadry, 1946; Baehni & Bonner, 1953; van der Pijl, 1957; Corner, 1976; Batygina, 1985; Ronse Decraene, Smets & Clinckemillie, 2000). Corner (1976) described the ovules of Sapindaceae in general as anatropous or campylotropous (at least after fertilization), bitegmic, crassinucellate and usually erect. In Paullinieae there is regularly one median ovule per carpel. The ovules are campylotropous, erect, with the micropyle directed downwards. In all taxa studied, the inner integument forms the micropyle. The outer integument of the ovules is thicker than or equal to the inner integument (five to nine cells vs. four to seven cells).

No clear distinction between placenta and funicle is possible. It is a matter of discretion at which point a placental protuberance may be called a short funicle (cf. van der Pijl, 1957; the criticism of Kadry, 1960). Corner (1976) described in Sapindaceae similar ovules as shortly and thick funiculate (e.g. ovules of *Cupania*; *ibid.*: 434). However, he was inconsistent in this topic, describing the ovules of *Dodonaea viscosa* once as

short funiculate (*ibid.*: 243) and once as sessile on a placental projection (*ibid.*: 436). The ovule-bearing structure in Sapindaceae could also be interpreted as a placental protuberance with a very short funicle at the top. In order to avoid artificial distinctions we follow the terminology of Kadry (1960) and Corner (1976), and label the whole insertion area of the ovule as short funicle.

#### OBTURATOR

An obturator is formed mainly on the micropylar side of the ovule, guiding the pollen tube to the micropyle (see 'Pollen tube transmitting tract' above). According to Corner (1976) an obturator stretches around the entire base of the ovular body in many Sapindaceae. Following Shamrov's (1998) classification it may be termed a funicular obturator. The obturator of the taxa studied has a secretory surface. It is usually papillate, but smooth in *Paullinia clavigera*, *P. obovata* and *Serjania altissima*. In *P. alata*, *P. aff. caloptera*, *P. obovata* and *Cardiospermum halicacabum* the obturators have approximately the same length as the ovules, whereas in the other species they are 1/4–1/2 as long as the ovules. The length of ovule and obturator together is 0.5–0.6 (–0.7) mm in all taxa studied. Obturators also occur in Rutaceae (Ramp, 1988), but are not reported for other sapindalean families (Corner, 1976; Batygina, 1985).

#### FRUIT DEVELOPMENT

In many Sapindaceae the pericarp grows earlier than the seeds, and thus in fruits with nearly mature size the seeds may still be rather small and immature (van Welzen, 1998). A similar type of development is found in Anacardiaceae (Copeland & Doyle, 1940; Grundwag, 1976). Similar to the ovary wall, the pericarp provides useful anatomical characters for generic and infrageneric grouping in Sapindaceae. Sclerenchyma sheaths are present around the numerous inconspicuous vascular bundles (*Paullinia alata*, *P. clavigera* and *P. obovata*), or around the secondary lateral bundles (*P. aff. caloptera*, *P. dasystachya*). The exocarp consists of sclerified cell layers (*P. pachycarpa*), the endocarp of sclerified fibres (*P. dasystachya* and *Serjania altissima*). These anatomical characters are known also from other sapindaceous genera and play an important role in the classification of Sapindaceae by Radlkofer (1895b; see last paragraph of Discussion).

The pericarp of *Cardiospermum halicacabum* and *Urvillea ulmacea* is papery and the locules are inflated. The exocarp consists of regular epidermal cells with wavy anticlinal walls, the mesocarp of few layers of spongy tissue and the endocarp of conspicu-

ously elongate cells. A similar pericarp structure with an exocarp consisting of conspicuously elongate epidermal cells has been found in *Serjania inflata* (C. S. Weckerle, unpubl. data). In *S. altissima* the exocarp consists of regular epidermal cells with thickened periclinal walls, the mesocarp of parenchymatous tissue and the endocarp of cross-layered sclerified fibres. It is separated from the mesocarp by a layer containing numerous oxalate crystals. This pericarp structure seems to be common in *Serjania* (Acevedo-Rodríguez, 1993a).

#### ARIL DEVELOPMENT

All Paullinieae studied (except for *Serjania*) have seeds with an aril, i.e. a collar-like or lobed white structure, which is conspicuous and fleshy (*Paullinia*) or inconspicuous and dry (*Cardiospermum*, *Urvillea*). In these three genera the aril is initiated after fertilization. The basal parts of the chalaza as well as the outer integument contribute to the development of the aril, but the secretory obturator tissue does not. The young aril of the *Paullinia* species studied forms two lobes on both sides of the micropyle, except in *Paullinia pachycarpa* where the young aril encloses the seed like a cap. The shape of the mature aril is a valuable character at the infrageneric level in *Paullinia*. In *P. alata* and *P. obovata* the aril forms two lobes which envelope two-thirds or three-quarters of the seed. In *P. clavigera* the seed is almost completely enveloped by the two lobes. In *P. pachycarpa* only a small elliptic area on the abaxial side of the seed is left uncovered. In *P. aff. caloptera* and *P. dasystachya* only the basal half of the seed is enveloped.

In *C. halicacabum* and *U. ulmacea* the young aril at the base of the seed has a reniform outline. It remains very thin, and does not overgrow the dry testa region. In *C. halicacabum* the aril is made up of spongy tissue, containing numerous oxalate crystals, which were not mentioned by Nair & Joseph (1960). As the development is basically the same as in the other taxa, i.e. the aril is built by basal parts of the chalaza, we disagree with Corner (1976: 242) who describes the aril of *C. halicacabum* as a funicular aril. We also disagree with Kapil *et al.* (1980: fig. 1C) who describe and illustrate in *C. halicacabum* as 'funicular aril' what we label as obturator in our Figures 70–72. Kapil *et al.* present in their figure 1C a dissected ovary with two ovules (about the same developmental stage as shown in Figs 70–72). The white reniform aril of mature *Cardiospermum* seeds (Fig. 75) grows out later and is not identical to what is erroneously called 'funicular aril' by Kapil *et al.* (1980, fig. 1C).

In *Serjania* usually no aril occurs. However, in *S. inflata* a reniform structure has been detected at

the base of the seed, similar to that in *U. ulmacea* (C. S. Weckerle, unpubl. data).

In part of Sapindaceae one or more layers of radially elongate cells are formed at the periphery of the aril (Corner, 1976). However, they are absent in Paullinieae. In all taxa studied the aril tissue is tanniferous. In *Paullinia alata* and *P. dasystachya* the tissue appears speckled from tanniferous and non-tanniferous cells. Starch is present in *P. alata*, *P. aff. caloptera*, *P. dasystachya* and *P. pachycarpa*, mainly in the tannin-free cells. In *P. obovata* and especially in *P. clavigera* all cells of the mature aril are conspicuously elongate. According to Radlkofer (1890) the arils of *Paullinia* are mainly starch-containing, those of the related Cupanieae mainly oily.

#### SEED COAT AND PSEUDO-HILUM

In the species examined the outer integument mainly contributes to the seed coat, the inner does not develop any further and remains unspecialized, as shown for *Cardiospermum* by Nair & Joseph (1960). The surface of the dry testa is smooth in all taxa studied. No data exist for *Serjania altissima*, but the genus is reported to contain seeds with a subrugulate to strongly rugulate surface (Acevedo-Rodríguez, 1993a). The different shapes of the pseudo-hilum (i.e. testa region to which the aril is attached) are useful characters for the distinction of *Paullinia* species. The pseudo-hilum might form two lobes of different shape and size, united to different degrees on the adaxial side (*Paullinia alata*, *P. clavigera* and *P. obovata*), or a narrow strap around the base of the seed (*P. aff. caloptera* and *P. dasystachya*), or envelop the seed like a cap (*P. pachycarpa*). Thickness of the testa varies between 150 and 520 µm in the taxa studied, that of the epidermis (columnar cells with conspicuously thickened anticlinal walls) between 25 and 150 µm. A thin dry testa is found in *P. alata* (testa 150 µm and epidermis 25–30 µm). In some Sapindaceae the testa is up to 900 µm (Corner, 1976). The pseudo-hilum usually contains several sclerified cell layers below the aril. In the material of *P. pachycarpa* studied, this layer was absent, but the testa was rather thick (520 µm). However, the fruits analysed were not yet dehisced and therefore a sclerenchyma layer might still be produced. In *C. halicacabum* one cell layer with white, columnar cells with thickened cell walls and single rhomboidal crystals is present below the aril (Guérin, 1901).

#### SEED SHAPE AND SIZE

Shape and size of the seeds in Paullinieae are important characters at species level. In the taxa studied, they are 0.3–2.5 cm long and 0.3–2 cm wide (including

the aril), and spherical, ellipsoid, ovoid or depressed ovoid, as usually found in Sapindaceae. The embryo is straight or incurved to various degrees in Paullinieae (Acevedo-Rodríguez, 1993a). The usually thick cotyledons are straight (e.g. *Serjania*) or curved (e.g. *Cardiospermum*). The cotyledons are thin and spirally inrolled in other tribes of Sapindaceae (Radlkofer, 1933, 1934). The short radicle lies in a radicle pocket, a character typically found in Sapindaceae.

#### GERMINATION AND SEEDLING STRUCTURE

Germination ability is lost as soon as the seeds dry up. Usually they germinate after a few days, but at most after 3 weeks. Except for *Cardiospermum* germination is hypogeal. Whether epigeal germination (as observed for *C. halicacabum* and *C. grandiflorum*) is generally found in *Cardiospermum* is unknown to us. Epigeal and hypogeal germination seems to be equally distributed within Sapindaceae (de Vogel, 1980). The first and opposite seedling leaves are simple in *P. alata* and *P. clavigera*, simple or trifoliolate in *P. obovata* and trifoliolate in the remaining species studied. In Sapindaceae seedling leaves generally vary from simple to trifoliolate and variously pinnate. They start with decussate or spiral phyllotaxis (de Vogel, 1980).

#### FRUIT DEHISCENCE AND DISPERSAL MECHANISMS

Within Paullinieae fruits are either schizocarpic fruits separating into samaroid mericarps or septifragal capsules exposing the seeds. *Serjania*, *Lophostigma* and *Houssayanthus* share the presence of schizocarpic fruits with a carpophore (Acevedo-Rodríguez, 1993a,b). In *Serjania* and *Lophostigma* the mericarps have a distal locule and a proximal wing. In *Houssayanthus* a central locule surrounded by a marginal wing is present. *Paullinia*, *Cardiospermum* and *Urvillea* have septifragal fruits (Radlkofer, 1895a, 1933; Croat, 1976; Ferrucci, 1991; Acevedo-Rodríguez, 1993a). Septifragal and schizocarpic fruits in Paullinieae are structurally similar. In *Cardiospermum* the fruits are septifragal with septa containing numerous oxalate crystals along the dehiscence line. However, in the mature fruit of *C. halicacabum* each septum divides up into two separated layers, remaining fixed at the central axis. In *C. grandiflorum* these layers may separate from each other (C. S. Weckerle, unpubl. data). Thus, *Cardiospermum* with septifragal capsules may show septicidal dehiscence in addition. In *Urvillea ulmacea* no dehiscence line is formed by oxalate crystals, and the fruits are easily separated into winged mericarps by hand. However, the fruits seem to be exclusively septifragal and Croat's (1976)

description of schizocarpic fruits is erroneous (*P. Acevedo-Rodríguez*, pers. comm.).

Anemochory is found in all schizocarpic taxa of Paullinieae. In *Cardiospermum* the inflated capsules are also reported to be anemochorous (Radlkofer, 1895b) or dispersed by sea currents (Ridley, 1930: 73). However, the capsules are septifragal, and after dehiscence the seeds remain fixed to the septa. Because the seeds are relatively heavy compared with the septa, anemochory or hydrochory is unlikely at this state, but until now no other dispersal mechanism of the dehisced fruits has been suggested for *Cardiospermum*.

Fruit types are most diverse in *Paullinia*. The major dispersal mode in the large genus is zoochory. Three main capsule types are found: (1) the majority of species (*c.* two-thirds) have globose, subglobose, fusiform, obovate or clavate capsules; (2) several species (*c.* one-third) have capsules with dorsal wings; (3) five species have echinate fruits (Radlkofer, 1933). The mature capsules of *Paullinia* are often reddish, more rarely yellowish, greenish and/or completely covered with golden hairs. The seeds have a black or brown exotesta and they are partly or completely enclosed by a white aril. In *Paullinia alata*, *P. pachycarpa* and *P. dasystachya* the red valves of the capsules remain attached after dehiscence, but they fall off in *P. clavigera* and *P. obovata*. In all species a conspicuous colour contrast of testa, aril and pericarp is displayed either with the remaining valves of the capsule or neighbouring undehisced fruits. The contrasting colours of the dehisced fruits (white, black and red) match a bird dispersal syndrome (Ridley, 1930; van der Pijl, 1982; Howe, 1986). However, dispersal by monkeys may also be expected (van Welzen, 1998). Tucans are reported to gulp the seeds and arils of the cultivated *P. cupana* (guaraná plant). They regurgitate the caffeine-rich seeds after having digested the aril, avoiding intoxication (Baumann, Schulthess & Hänni, 1995). Only two additional species of *Paullinia*, *P. yoco* and *P. pachycarpa*, are known to contain purine alkaloids, at least in plant parts other than the fruits. The fruits of *P. pachycarpa* are practically free of these alkaloids (Weckerle, Stutz & Baumann, 2003). Thus, other protective substances in the seeds might be expected. The mature fruits of *P. yoco* are unknown to us.

The role of the dorsal wings present in many *Paullinia* species remains obscure. *Paullinia alata* is cauliflorous and the fruits are presented from near the ground up to 2 or 3 m. Therefore in addition to birds, terrestrial mammals could play a role as dispersal agents. Dispersal by rodents is also found in *P. sphaerocarpa*, in which the pericarp remains greyish green and the whole fruit with slightly dehisced valves falls off (J. Aristides, pers. comm.; C. S. Weckerle, pers. observ.). In *P. clathrata*, which mainly occurs along river edges, a single seed with a white

sarcotesta develops and the mature pericarp is yellow. After dehiscence the membranaceous septa remain fixed to the seed and enclose half of the sarcotesta. The septa are water-repellent and allow the seed to float (C. S. Weckerle, pers. observ.); the seeds seem to be dispersed by water and/or fishes. Similar observations have been made for *P. hystrix*, which has yellow and echinate fruits. In this species an aril is developed which envelops almost the whole seed. The septa, consisting of spongy tissue, are slightly thickened, allowing the seed to float on the water surface. Whether the spines of the pericarp play any role for dispersal is unknown.

#### SYSTEMATIC VALUE OF THE GYNOCIDIUM, FRUIT AND SEED CHARACTERS IN PAULLINIEAE

According to Radlkofer (1895a) the sections of *Paullinia* are mainly based on characters of the fruit morphology, including pericarp. *Paullinia alata*, *P. clavigera* and *P. obovata* belong to section *Neurotaechus*, now correctly known as sect. *Paullinia* (I). They are characterized by capsular fruits with short stipes and a thick mesocarp with a dense system of mainly parallel bundles, visible on the outer surface of dry fruits. *Paullinia pachycarpa* belongs to section *Pachytoechus* (IV), specified by fruits with a relatively long stipe and few bundles in the mesocarp. *Paullinia* aff. *caloptera* and *P. dasystachya*, belonging to section *Caloptilon* (XII), are characterized by winged fruits and a sclerified endocarp. Whereas the above-mentioned anatomical characters of the ovary wall and pericarp coincide with Radlkofer's sections, other characters of the *Paullinia* species studied, e.g. PTTT, surface and length of the obturator, and anatomy of the aril, might suggest a different infrageneric grouping.

Detailed morphological analyses of additional species of the two large genera *Paullinia* and *Serjania* as well as the smaller Paullinieae genera are needed to find accurate circumscriptions of the generic sections and to test Acevedo-Rodríguez's (1993a) preliminary results, grouping Paullinieae in two monophyletic subclades (see 'Introduction'). This has to be done in combination with molecular analyses, which are still lacking in Paullinieae.

#### CONCLUSIONS

1. New characters of potential systematic value at the genus and species level are described in Paullinieae. These characters refer to the ovules (shape and surface of the obturator), the ovary (type of PTTT, indument of inner and outer surface of the carpels, anatomy of the ovary wall), the seeds (anatomy of the aril and form of the pseudo-hilum)

and the seedling (seedling leaves). Seed surface and germination type are important characters at genus level.

2. Although some of these characters (e.g. anatomy of the ovary wall and pericarp, seedling leaves) support Radlkofer's (1895a) *Paullinia* sections, other characters such as PTTT, surface and length of the obturator and aril anatomy are in conflict. However, molecular phylogenetic analyses combined with structural data from additional taxa are needed to highlight the phylogenetic relationships among *Paullinia* species.
3. The structure of the fruit is usually anticipated by the structure of the gynoecium during anthesis. Pronounced longitudinal ribs in the gynoecium relate to winged fruits, a dense net of secondary lateral bundles and laticiferous cells give rise to a leathery pericarp whereas few secondary vascular bundles are found in an ovary wall ending up as a dry pericarp.
4. Schizocarpic fruits (separating along septae into winged mericarps) and septifragal fruits (capsules) within Paullinieae are structurally similar. *Cardiospermum* with septifragal capsules also show longitudinal splitting of the septa (septicidal dehiscence), similar to the fragmentation of the schizocarpic fruits along the septa in, for example, *Serjania* and *Lophostigma*. In *Paullinia* with septifragal fruits, minor structural changes have caused switches from bird dispersal to rodent dispersal in *Paullinia sphaerocarpa* and to water in *P. clathrata* and *P. hystrix*.

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