Floral anatomy of some neotropical Gentianaceae

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ABSTRACT

The floral anatomy of several Neotropical Gentianaceae, mostly belonging to the *Lisyantheae*, has been investigated.

INTRODUCTION

In addition to the morphological studies of the *Lisyantheae* (Gentianaceae) performed at the Institute of Systematical Botany, Utrecht by Maas and collaborators, the floral anatomy of some genera of this group was investigated.

The taxonomical position of several genera within the *Lisyantheae* has been subject of discussion. The tribe *Lisyantheae* was established by Grisebach (1838) as one of the seven tribes of the Gentianaceae. In the *Lisyantheae* he included the genera *Leianthus* Griseb. a.o. with section *Lisianthius* P. Br., *Lisyanthus* Aubl., a.o. with sections *Chelonanthus* and *Macrocarpaea, Leiothamnus* Griseb. (= *Symbolanthus*), *Irlbachia* Mart., and *Tachia* Aubl. One *Symbolanthus* species was placed in *Tachia*.

Bentham & Hooker (1876) made one large genus *Lisianthus* Aubl. and divided it into 8 sections, among them: *Symbolanthus* G. Don, *Megacarpaea* Griseb. (= *Macrocarpaea*), *Chelonanthus* Griseb. and *Irlbachia* Mart. while *Schultesia* Mart., *Coutoubea* Aubl. and *Leianthus* Griseb. (= *Lisianthius*) were considered as separate genera.

Gilg (1895) divided the Gentianaceae into several tribes among which the *Tachiinae* including *Lisianthus* L., and *Macrocarpaea* Gilg and the *Helieae* in-

cluding *Irlbachia, Schultesia, Coutoubea, Chelonanthus* Gilg, *Symbolanthus*, and *Lagenanthus* Gilg.

Maas et al. (1984) consider *Lisianthius* L., *Macrocarpaea, Irlbachia* (including *Chelonanthus* and *Macrocarpaea tepuiensis*), *Lagenanthus*, and *Symbolanthus* as belonging to the *Lisyantheae*.

The divisions made by the different authors are summarized in table 1.

The floral anatomy of Gentianaceae was studied by several authors in the past (Perrot, 1898; Woodson, 1936; Lindsey, 1940; Weaver, 1972), but the *Lisyantheae* were poorly represented. The aim of the present study is to investigate the general morphology of the flowers, especially the fusion of the placentas and the origin of the corona in *Symbolanthus*, and to indicate the taxonomic relevance of these features.

MATERIALS AND METHODS

As very few flowers of Gentianaceae preserved in alcohol were available, only a few specimens of one or two species per genus could be investigated. Moreover, sectioning specimens with a lot of sclereids or crystals proved problematical.

The following specimens, all from the Utrecht herbarium (U), were investigated (arranged according to morphological relationship as revealed by the studies by Maas et al., 1984):

Not-Lisyantheae
Schultesia aff. schomburgkiana Prog. Maas et al. 3661, Guyana
Schultesia aff. benthamiana Klotzsch Maas et al. 3692, Guyana
Schultesia brachyptera Cham. Maas et al. 3701, Guyana
Coutoubea spicata Aubl. Maas et al. 3667, Guyana
Coutoubea minor Kunth Maas et al. 5079, Venezuela

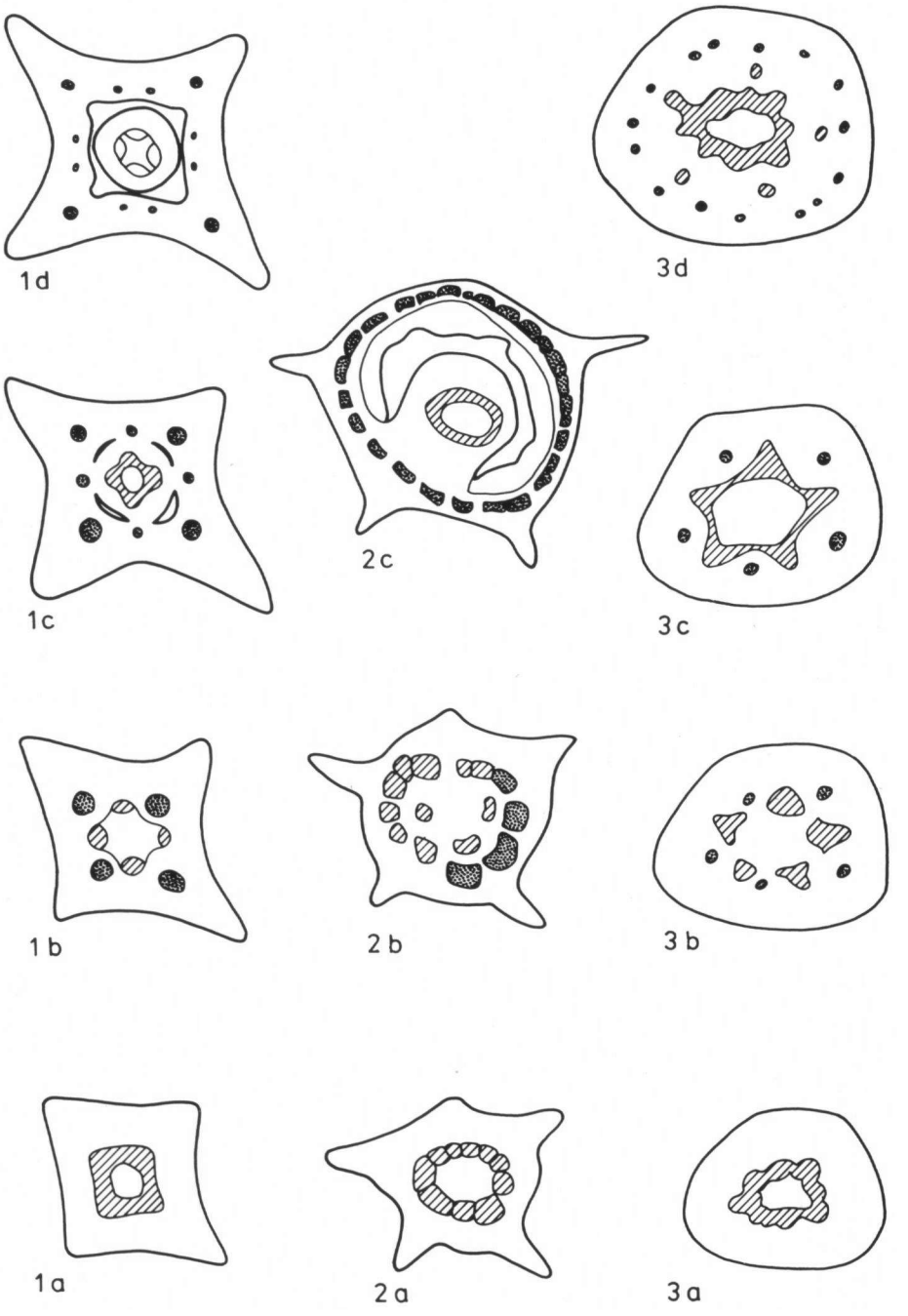
Lisyantheae
Lisianthius longifolius L. 80GR00040, Cult. Hort. Utrecht
Macrocarpaea sp. I Maas et al. 5300, Venezuela
Macrocarpaea sp. II Harling & Andersson 16984, Ecuador
Irlbachia caerulescens (Aubl.) Griseb Heijligers s.n., Suriname
Irlbachia nemorosa (Willd. ex R. & S.) Merrill Maas et al. 5370, Venezuela
Chelonanthus alatus (Aubl.) Pulle Maas et al. 5380, Venezuela*
Chelonanthus alatus (Aubl.) Pulle Leeuwenberg 11620, French Guiana*
Chelonanthus alatus (Aubl.) Pulle Maas et al. 5344, Venezuela*
Chelonanthus uliginosus (Griseb). Gilg Collector unknown 1687, Suriname*
Macrocarpaea tepuiensis (Gleason) Steyermark Maas et al. 5363, Venezuela*
Lagenanthus princeps (Lindl.) Gilg (flower + bud) Maas et al. 5242, Venezuela*
Symbolanthus calygonus (R. et P.) Griseb. Maas & Manara 5181, Venezuela
Symbolanthus calygonus (R. et P.) Griseb. Van Rooden & Akkermans 86, Venezuela

The flowers were preserved in alcohol 60%. Before sectioning the flowers were embedded in polyethylenglycol (PG 45-50). The material was sectioned at 15 μm and stained with saffranin and astrablue.

* Just before this manuscript will be published, several names will be changed by Maas (in press).

Table 1. Summary of the classifications by different authors of some tribes of the Gentianaceae, as far as regards the genera investigated in this study.

Grisebach (1838)	Bentham & Hooker (1876)	Gilg (1895)	Maas et al. (1984)
Chloreae:	Chironieae:	Helieae:	Not-Lisyantheae:
- Schultesia Mart.	- Schultesia Mart.	- Schultesia Mart.	- Schultesia Mart.
Hippieae:			
- Coutoubea Aubl.	- Coutoubea Aubl.	- Coutoubea Aubl.	- Coutoubea Aubl.
Lisyantheae:		Tachiinae:	Lisyantheae:
- Leianthus Griseb. *sect.* Lisianthius P. Br.	- Leianthus Griseb.	- Lisianthus L.	- Lisianthius L.
- Lisyanthus Aubl. *sect.* Macrocarpaea	- Lisianthus Aubl. *sect.* Megacarpaea Griseb.	- Macrocarpaea Gilg Helieae:	*sect.* Macrocarpaea Gilg
sect. Chelonanthus	*sect.* Chelonanthus Griseb.	- Chelonanthus Gilg	- Irlbachia Mart
- Irlbachia Mart.	*sect.* Irlbachia Mart.	- Irlbachia Mart.	- Irlbachia Mart.
- Leiothamnus Griseb.	*sect.* Symbolanthus G. Don	- Symbolanthus G. Don	- Symbolanthus G. Don
- Tachia Aubl. (= p.p. Symbolanthus)		- Lagenanthus Gilg	- Lagenanthus Gilg



Figs. 1–3: Vascularisation of the calyx (calyx veins dotted).

Except for the bud of *Lagenanthus*, and one flower of *Chelonanthus* which was sectioned just before opening, the flowers were at anthesis.

For describing the ovary the terminology of Leinfellner (1950) is followed.

Chelonanthus alatus (Maas 5380) = *Irlbachia alata ssp. angustifolia* (Kunth) Persoon & Maas
Chelonanthus alatus (Leeuwenberg 11620) = *Irlbachia alata ssp. longistyla* Persoon & Maas
Chelonanthus alatus (Maas 5344) = *Irlbachia alata* (Aubl.) Maas *ssp. alata*
Chelonanthus uliginosus = *Irlbachia purpurascens* (Aubl.) Maas
Macrocarpaea tepuiensis = *Irlbachia quelchii* (N.E. Brown) Maas
Lagenanthus princeps = *Lehmaniella princeps* (Lindley) Simonis

RESULTS

Receptacular stele

With regard to the vascular supply of the calyx 3 groups can be distinguished:

In *Schultesia* (fig. 1) the central stele first gives off the 4 calyx-midribs (fig. 1b), later followed separately by the secondary veins (fig. 1c).

In *Coutoubea minor* and *Lisianthius longifolius* the central stele gives off all veins towards the calyx at once (fig. 2).

In *Irlbachia, Macrocarpaea, Chelonanthus, Lagenanthus*, and *Symbolanthus*, the central stele gives off 5 calyx-veins which soon branch into one calyx-midrib and two secondary veins (fig. 3).

In *Schultesia, Coutoubea*, and *Lisianthius*, the size of the calyx veins is much larger than the remaining supply bundles to the corolla and the ovary. These 3 genera also have a relatively large calyx and a small-sized ovary. This is in contrast to all other genera investigated, where the size of the ovary and the corolla is relatively large and thus the supply more important. In these 5 genera the receptacular stele becomes more or less stellate after the calyx-veins have been given off (fig. 3c).

In all genera investigated the corolla veins are given off, soon followed by the veins to the stamens, before the corolla itself separates from the axis.

Squamellae

In *Chelonanthus, Lagenanthus, Symbolanthus*, and *Macrocarpaea sp.* I, squamellae are found at the inner side of the calyx, usually at the base, in

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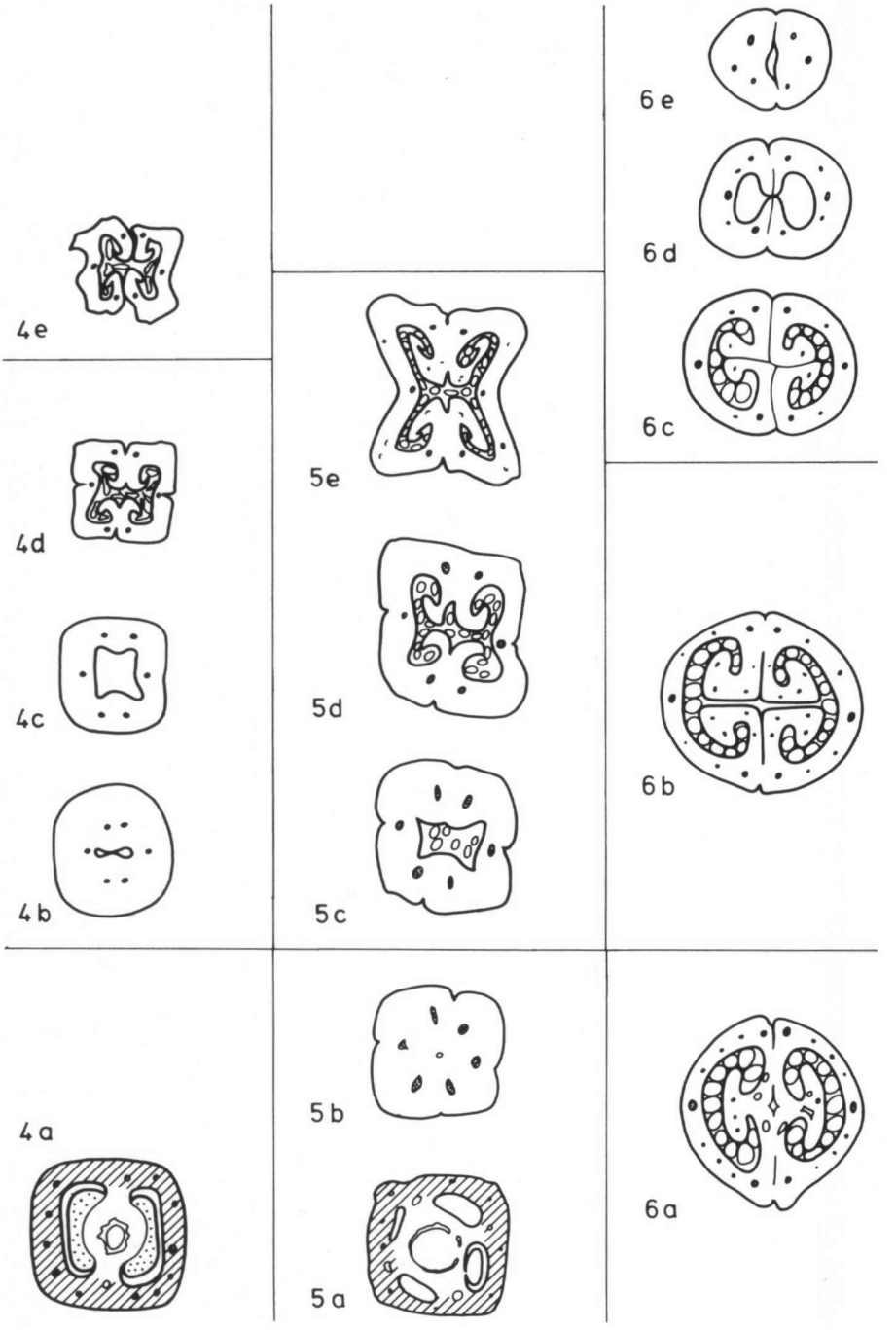
Fig. 1. *Schultesia aff. benthamiana:* Fig. 1a: central stele below the level where calyx midribs are split off; fig. 1b: the calyx midribs are given off; fig. 1c: the fused secondary veins of the calyx are given off while the calyx starts to separate from the receptaculum; fig. 1d: the calyx is free from the receptaculum, the commissurale calyx veins are split off. (Magnification 33×).

Fig. 2. *Lisianthius longifolius:* Fig. 2a: central stele below the level where the calyx bundles are split off; fig. 1b: most of the bundles of the central stele are destined to supply the calyx, a minority vascularizes the corolla and the ovary; fig. 2c: the calyx starts to separate from the receptaculum. (Magnification 27×).

Fig. 3. *Chelonanthus uliginosus*: Fig. 3a: central stele below the level where the calyx midribs are split off; fig. 3b: the calyx veins are given off, the receptacular stele becomes stellate (fig. 3c); fig. 3d: the calyx veins branch into a midrib and two secondary veins, while the corolla-veins have been given off. (Magnification 17×).



Figs. 4–12: Transsections through the ovaries with subdivision into "Synascidiate zone", "Symplicate zone", and "Asymplicate zone" (disc dotted, corolla shaded).

Lagenanthus nearer to the apices of the calyx. Possibly in *Irlbachia caerulescens* some squamellae are present, too.

Sclerenchymatous cells and crystals

Sclereids, single or in strands, are found in the calyx and the central stele of *Schultesia brachyptera, Irlbachia nemorosa,* one specimen of *Chelonanthus alatus, Lagenanthus princeps* (but not in the bud), *Macrocarpaea,* and *Symbolanthus.* Crystals are present in the receptaculum and the placentas of *Chelonanthus, Macrocarpaea, Lagenanthus,* and *Symbolanthus.*

Disc

In almost all specimens a glandular disc is present. Only in *Schultesia brachyptera,* in *Coutoubea minor,* and *Irlbachia nemorosa,* a disc or homologous organ was not observed. In *Lagenanthus* a disc was hardly visible, but the strong vascularisation towards the disc area such as in *Chelonanthus, Macrocarpaea tepuiensis,* and *Symbolanthus,* is present in *Lagenanthus,* too.

Ovary

The ovary consists of two united carpels, while the opposite placentas are free or fused to a various degree. Thus the ovaries may vary from completely unilocular to completely bilocular.

In the terms of Leinfellner (1950) syncarp ovaries usually consist of a "synascidiate zone", a "symplicate zone" and an "asymplicate zone" (zones indicated in figs. 4–12). In the "synascidiate zone" (basal part of the ovary) the carpels are completely bilocular and congenitally fused. In the "symplicate zone" the placentas are not or only postgenitally fused. In the "asymplicate zone" the carpels are free or only postgenitally fused.

"Synascidiate zone"

A "synascidiate zone" is completely lacking in *Schultesia brachyptera* (fig. 5) and *Coutoubea spicata.* In these specimens the ovary is completely unilocular. In *Schultesia aff. benthamiana* the most basal section through the locule of the ovary seems to be bilocular, but all other sections show an unilocular ovary (fig. 4). In *Coutoubea minor, Irlbachia, Chelonanthus, Macrocarpaea, Lagenanthus,* and *Symbolanthus,* a "synascidiate zone" is present (figs. 6–12).

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Fig. 4. *Schultesia aff. benthamiana:* Fig. 4a: The corolla is almost free from the ovary, the disc is well visible; fig. 4b: in the most basal section through the locule the ovary seems bilocular, in all other sections the ovary is unilocular (fig. 4c–e). (Magnification 33×).

Fig. 5. *Schultesia brachyptera:* Fig. 5a: the corolla separates from the ovary; fig. 5b–e: all sections show an unilocular ovary (sections through the "asymplicate zone" were not available). (Magnification 17×).

Fig. 6. *Irlbachia nemorosa:* The ovary is almost bilocular. Fig. 6a: Placentas congenitally fused; in some sections (fig. 6b) the placentas do not touch each other; fig. 6c–e: placentas and carpels postgenitally fused. (Magnification 27×).

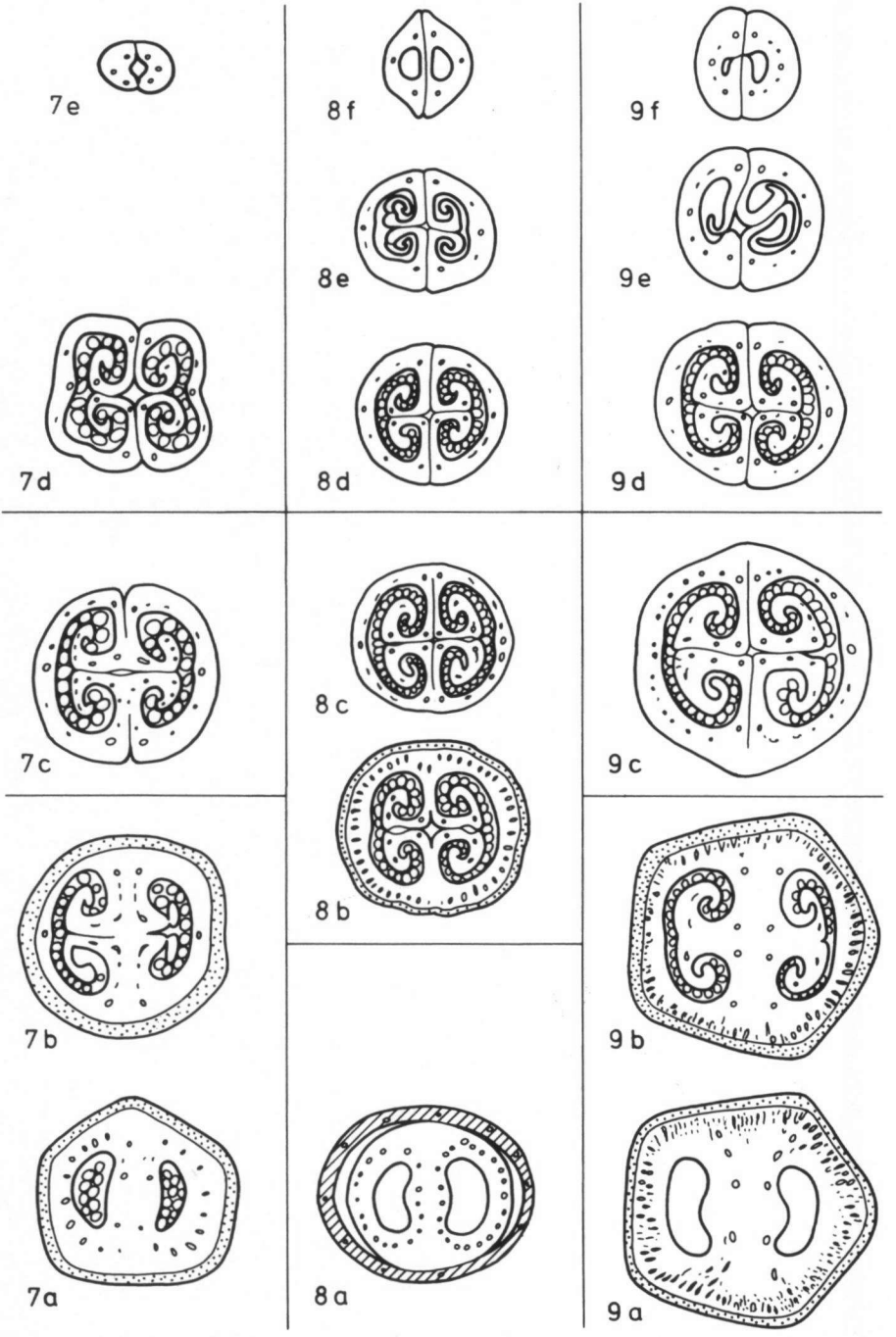

Fig. 7. *Chelonanthus alatus* (Maas 5380): Fig. 7a shows a bilocular ovary. Fig. 7b: the placentas start to separate from each other, from the periphery towards the centre; fig. 7c. placentas of the same carpel postgenitally fused; fig. 7d: carpels postgenitally fused; fig. 7e: the style. (Magnification 17×).

Fig. 8. *Chelonanthus uliginosus:* Fig. 8a: The ovary is bilocular. Fig. 8b–d: placentas postgenitally

"Symplicate zone"

In *Schultesia* and *Coutoubea spicata* the placenta pairs (belonging to two carpels) do not reach each other, leaving the ovary unilocular (figs. 4 and 5).

In *Coutoubea minor* and all other genera the opposite placentas reach each other and are usually fused (postgenitally), making the ovary bilocular. In *Lagenanthus*, one specimen of *Chelonanthus alatus*, and *Symbolanthus*, the placentas are not fused in the "symplicate zone".

The transition from "synascidiate zone" to "symplicate zone" may start in the centre, as shown in *Irlbachia* (fig. 6a) and in *Symbolanthus* (figs. 11b and 12a), or at the periphery of fused placentas, as shown in one specimen of *Chelonanthus alatus* (fig. 7b) and *Macrocarpaea tepuiensis* (fig. 9b).

"Asymplicate zone"

In *Schultesia brachyptera* and *Coutoubea spicata* no sections of the "asymplicate zone" are found. Although apical sections through the ovary were not available, the carpels seem congenitally fused to a considerable height. In all other investigated specimens the "symplicate zone" seems quite short and the carpels are postgenitally fused in the upper part of the ovary.

The transition from the "symplicate zone" to the "asymplicate zone" in most cases starts at the centre of the ovary.

Many sections through the ovaries seem to indicate an ontogenetical process of separation of carpels and placentas. Often a gap is found in the centre of the ovary, the cells around it not being epidermis cells. In fruit the carpels are more or less free.

Prolonged sterile placentas

In some specimens the placentas are prolonged and narrower near the apex and often divided in two parts. This fact is observed in *Macrocarpaea tepuiensis, Chelonanthus uliginosus* (fig. 8e), one specimen of *Chelonanthus alatus*, and one specimen of *Symbolanthus*.

Apical septum

An "apical septum" (fig. 13a at level 11f) is found in *Macrocarpaea tepuiensis, Chelonanthus uliginosus* (fig. 8f), *C. alatus*, *Lagenanthus princeps* (fig. 10e), and one specimen of *Symbolanthus calygonus* (fig. 11f).

Corona

In *Symbolanthus* a corona is present at the base of the filaments. Anatomical study of the corolla revealed that before the filaments separate from the cor-

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fused. Near the apex the placentas are prolonged and lobed (fig. 8e). Fig. 8f indicates an apical septum. (Magnification 12×).

Fig. 9. *Macrocarpaea tepuiensis:* Fig. 9a shows a strong vascularisation near the disc. The process of separating of the placentas starts at the periphery (fig. 9b). Fig. 9c–d: placentas postgenitally fused. Near the apex the placentas are prolonged (fig. 9f). An apical septum is present (fig. 9g). (Magnification 8×).

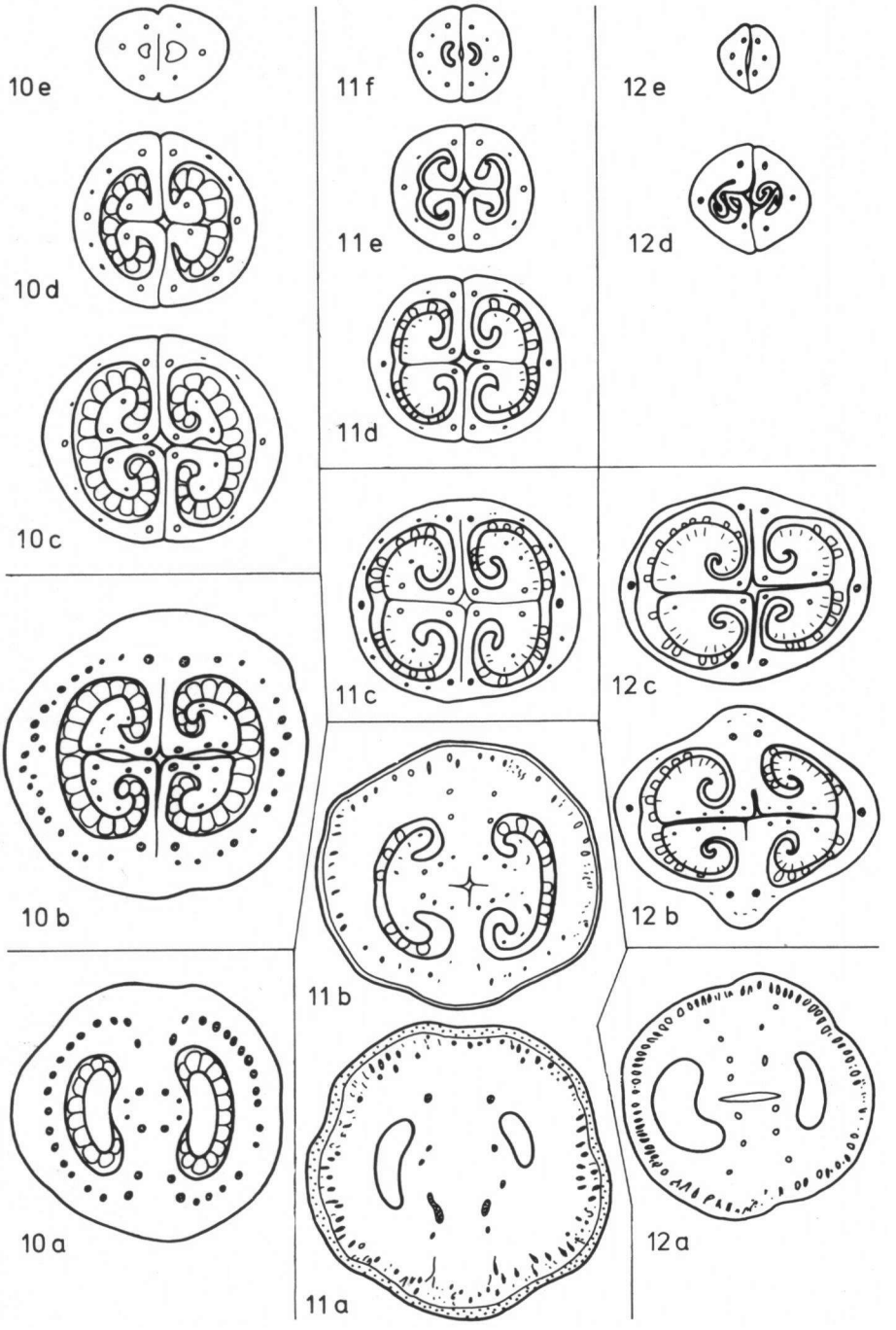

Fig. 10. *Lagenanthus princeps:* The ovary is bilocular (fig. 10a). The placentas separate (fig. 10b); fig. 10c–d: carpels postgenitally fused. An apical septum is present (fig. 10e). (Magnification 12×).
Fig. 11. *Symbolanthus calygonus* (Maas 5181): Fig. 11a showing the two locules. Fig. 11b: the process of separation of the placentas starts at the centre. Fig. 11c: placentas postgenitally fused; figs.

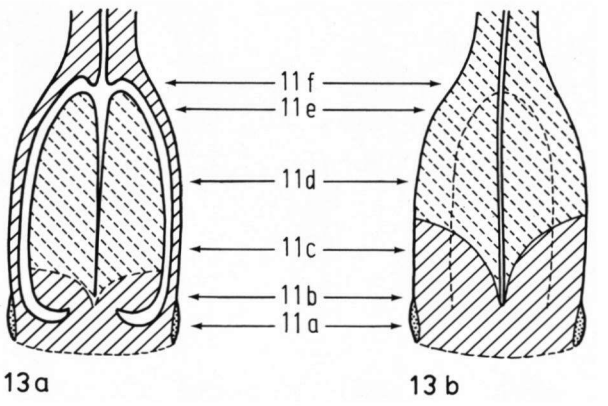

Fig. 13. Diagrams of longitudinal sections through the ovary of *Symbolanthus calygonus*. Fig. 13a: through the medium plane of the carpels: placentas basally congenitally fused, upper part postgenitally fused; fig. 13b through the transversal plane: carpels basally congenitally fused, upper part postgenitally fused. (Sectioned parts shaded; postgenitally fused parts shaded with broken lines. The numbers 11a–f indicate the levels of transverse sections.

olla, gaps appear between the stamen veins and the corolla, which enlarge until the inner (= corona) and outer (= corolla) layer are completely free. Meanwhile the filaments separate from the corona (fig. 16). *Lagenanthus, Macrocarpaea tepuiensis, Chelonanthus uliginosus*, and one specimen of *Chelonanthus alatus* show gaps behind the stamen veins too, but here no inner layer separates from the corolla (fig. 15).

In *Schultesia, Lisianthius, Irlbachia*, and most specimens of *Chelonanthus alatus* the filaments simply separate from the corolla (fig. 14).

All features are summarized in table 2.

DISCUSSION

Compared with *Schultesia* and *Coutoubea*, the *Lisyantheae* are characterized by a more specialized vascularisation (ovary and corolla dominant, receptacular stele becoming stellate) and a more complete postgenital fusion of the placentas. Within the *Lisyantheae* the receptacular stele is simple in *Irlbachia caerulescens* and in *Lisianthius*, it starts to differentiate in *Irlbachia nemorosa*, and it is stellate in the remaining genera.

Outside the *Lisyantheae* the ovary is often unilocular, but bilocular ovaries also occur, for instance in *Coutoubea minor*. Weaver (1972) found in *Lisianthius* both bilocular and unilocular ovaries. In the other *Lisyantheae* the ovaries are bilocular, although in some specimens this is not complete. In the here

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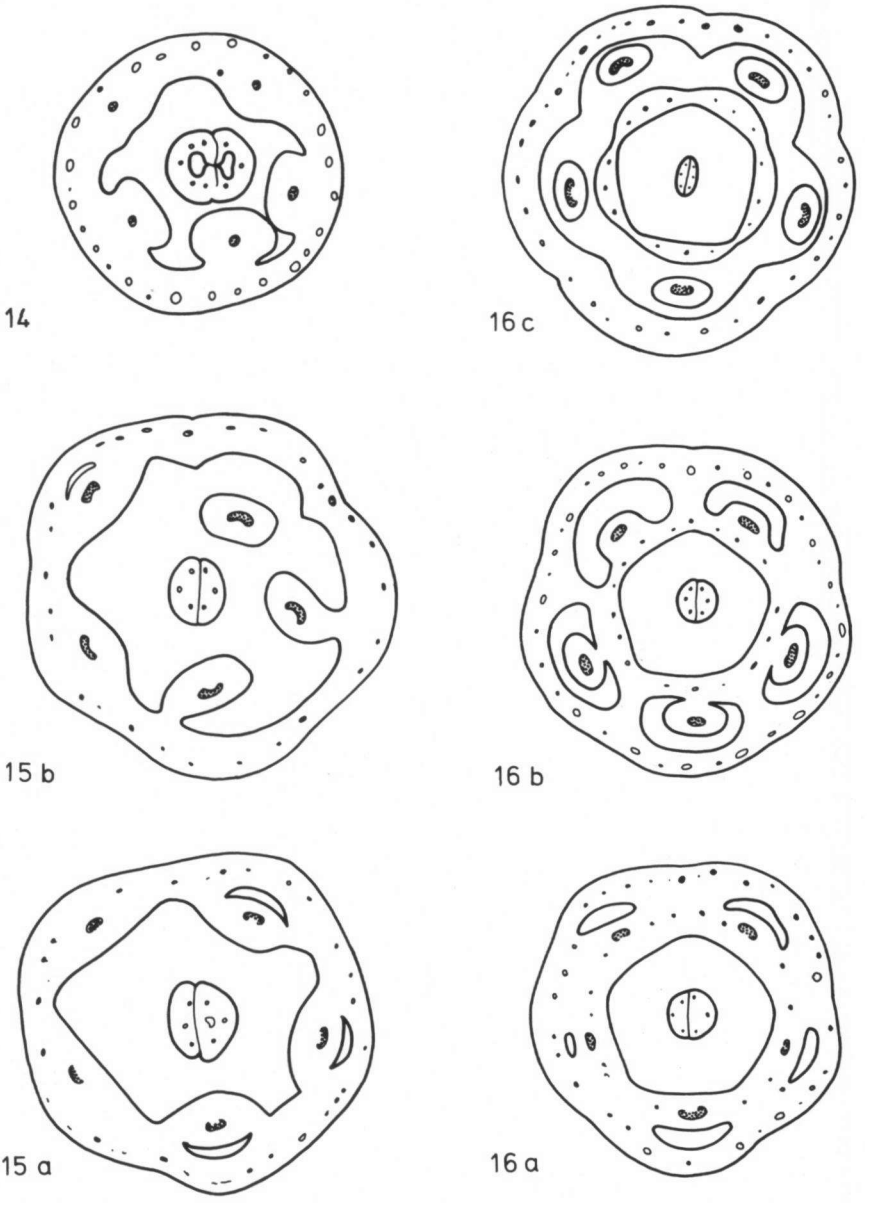
11d–e: carpels postgenitally fused. An apical septum is present (fig. 11f). (Magnification 6×).
Fig. 12. *Symbolanthus calygonus* (Van Rooden & Akkermans 86): fig. 12a: shows the two locules, while the process of separation of the carpels has been started already; fig. 12b shows free placentas. Fig. 12c: the carpels start to separate. Near the apex the placentas are prolonged (fig. 12d). (Magnification 4×).



Figs. 14–16: Sections through the corolla showing the 3 different ways in which the filaments of the stamens separate from the corolla.

Fig. 14. *Irlbachia nemorosa:* The filaments simply separate from the corolla. The corolla tube narrowly encloses the ovary. (Magnification 17×).

Fig. 15. *Macrocarpaea tepuiensis:* Before the filaments actually separate, there appears a gap between each filament and the corolla (fig. 15a), then the filaments separate from the corolla (fig. 15b). (Magnification 6×).

Fig. 16. *Symbolanthus calygonus* (Maas 5181): Gaps appear between the filaments and the corolla (fig. 16a), but these enlarge (fig. 16b) until the corona has been separated from the corolla and the filaments (fig. 16c). (Magnification 4×).

Table 2

	Schultesia aff. schomburgkiana	Schultesia aff. benthamiana	Schultesia brachyptera	Coutoubea spicata	Coutoubea minor	Lisianthius longifolius	Macrocarpaea sp. I	Macrocarpaea sp. II	Irlbachia caerulescens	Irlbachia nemorosa	Chelonanthus alatus (Maas 5380)	Chelonanthus alatus (L. 11620)	Chelonanthus alatus (Maas 5344)	Chelonanthus uliginosus	Macrocarpaea tepuiensis	Lagenanthus princeps	Symbolanthus calygonus (Maas 5181)	Symbolanthus calygonus (v. R. & A. 86)
vascularisation of calyx in one or two steps	?	2	2	?	1	1	1	1	?	1	1	1	1	1	1	1	1	1
receptacular stele stellate	−	−	−	−	−	−	−	+	+	−	±	±	+	+	+	+	+	+
sclereids	−	−	+	−	−	−	+	+	−	+	+	−	−	−	+	+	+	−
squamellae	−	−	−	?	−	−	+	−	(+)	−?	+	+	+	−?	+	+	+	+
disc	+	+	−	+	−	+	+	+	+	−	+	+	+	+	+	+	+	+
vascularisation of disc	−	−	−	−	−	−	−	−	−	−	+	−	−	+	+	+	+	+
crystals	−	−	−	−	−	−	+	+	−	−	+	+	+	+	+	+	+	+
number of locules	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2
synascidiate zone	?	(+)	−	−	+	(−)	+	+	+	+	+	+	+	+	+	+	+	+
prolonged placentas	?	?	?	?	?	?	−	−	−	−	−	−	+	+	+	−	−	+
apical septum	?	?	?	?	?	?	−	−	?	−	−	+	+	+	+	+	+	−
gaps	?	−	−	?	?	−	−	−	?	−	+	−	−	+	+	+	+	?
corona	?	−	−	?	?	−	−	−	?	−	−	−	−	−	−	−	+	−

Legend: + = present, − = absent, ? = data not available.

reported *Lisyantheae* a synascidiate part is always present, and the placentas are enlarged and reaching each other, so postgenital fusion can easily take place.

Other features which are found in most *Lisyantheae*, but not in the investigated specimens of *Schultesia* and *Coutoubea*, are the presence of squamellae at the inner side of the calyx, and the presence of crystals and sclereids. These features are not or infrequently found in *Lisianthius* and *Irlbachia*, but often occur in the other genera. However, Lindsey (1940) found squamellae in *Schultesia*, too. In *Coutoubea* he found heavy fiber-bundles in the floral organs.

Some genera or species of the *Lisyantheae* have developed some special features, like the apical septum or the lobed placentas near the apex of the ovary, or a corona. These specialised features are most common in *Chelonanthus uliginosus*, sometimes in *Chelonanthus alatus, Lagenanthus princeps, Macrocarpaea tepuiensis,* and *Symbolanthus*. These genera seem to be the most specialised genera of the *Lisyantheae*, while *Irlbachia* and especially *Lisianthius* are the least specialized. *Chelonanthus alatus* seems to have a midway position.

When this study started, the taxonomical position of several species of the *Lisyantheae* was in discussion. These species are discussed here, but it is not possible, to draw definite conclusions because of the few specimens investigated.

- *Irlbachia*: although *I. caerulescens* and *I. nemorosa* differ in some features, there is no reason to split them up in 2 genera.
- *Chelonanthus: Chelonanthus* is included by Maas et. al (1984) in *Irlbachia. Chelonanthus alatus*, morphologically a very variable species, also anatomically shows a lot of variation (see table 2), and seems close to *Irlbachia*, although more specialized. *C. uliginosus* resembles both *Lagenanthus*, and *Macrocarpaea tepuiensis*, rather than *Irlbachia*.
- *Macrocarpaea: M. tepuiensis* does not seem to be related to the other two species of *Macrocarpaea*, which is confirmed by general morphology (Maas et al., 1984). Maas et al. include *M. tepuiensis in Irlbachia*, but in floral anatomy *M. tepuiensis* seems closest to *Lagenanthus* and *Chelonanthus uliginosus. Macrocarpaea* s.s. most resembles *Irlbachia* and *Chelonanthus alatus.*
- *Lagenanthus:* this genus most resembles *Macrocarpaea tepuiensis* and *Symbolanthus.*
- *Symbolanthus*: most *Symbolanthus*-specimens belong to one large species (van Heusden, in prep.), although remarkable differences were observed. For instance, the investigated specimen v. Rooden & Akkermans 96 is green-flowered and campanulate-shaped, while the specimen Maas & Manara 5181 is red-flowered and salver-shaped. As can be seen in table 2, they show several differences in their flower-anatomy, too.

Summarizing the above, no clear demarcation line could be found between the *Lisyantheae* and the not-*Lisyantheae*. Lindsey (1940) found more or less the same for the *Tachiinae* and the *Helieae*, the *Helieae* being more specialised. A higher specialisation seems to correlate with a bigger size of the flowers. The

scarce material investigated showed a lot of variation, suggesting that these genera are quite variable and highly plastic in their anatomy. No strong differences between the genera of the *Lisyantheae* could be found. The taxonomical position of *Lisianthius* is unclear. The true *Macrocarpaea* species rather than *M. tepuiensis* resemble *Irlbachia* in flower-anatomy, this is in contrast with the conclusions of Maas et al. (1984).

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