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SEM study of surface structures of the spathe in *Cryptocoryne* and *Lagenandra* (Araceae: Aroideae: Cryptocoryneae)

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SEM studies of the spathe structures in the two closely related genera *Cryptocoryne* and *Lagenandra* show differences between the inner and outer surfaces, as well as in cell structures in the various parts of the spathe. The cell structure reveals patterns that makes it possible to depict homologous structures of the spathe, even though the spathes of the two genera look different. The basal part of the kettle has a mucilage covering of the cells, interpreted as a hitherto unnoticed food source. The cells of the inner surface of the kettle and tube have downward pointing trichomes. On the second day of flowering these collapse and sink into the cell lumen, which is suggested to create a unique lattice-like structure that enables the insects to climb out of the kettle and tube. The cell structure of the flap shows that it is a prolongation and continuation of the spathe tube margin.

ADDITIONAL KEY WORDS:—cell structures – epidermis – pollination – trichomes.

CONTENTS

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INTRODUCTION

The genus *Cryptocoryne* Wydler (*c.* 50 species, e.g. Arends, Bastmeijer & Jacobsen, 1982; Hay *et al.*, 1995; Jacobsen, 1977, 1980, 1985; de Wit, 1990) consists of aquatic or amphibious herbs found throughout most of tropical Asia from India to New Guinea, while the genus *Lagenandra* Dalzell (15 species, e.g. de Wit, 1990) often has a more amphibious habitat and is only found in Sri Lanka and southwest to northeast India, as well as in Bangladesh (Sylhet).

Cryptocoryne and *Lagenandra* are generally accepted as being related (e.g. Mayo, Bogner & Boyce, 1997), and they have among the most specialized inflorescences within the family. *Cryptocoryne* may generally be considered the more specialized of the two in many characters (see e.g. Engler, 1920)

The leaves form a more or less distinct rosette on a usually short, vertical to horizontal rhizome. The form, size and colour of the leaves are characteristic for each species, but the variation within species is often wide, mostly due to environmental factors, and especially due to submersed and immersed habitat. It may therefore be difficult to identify the species unambiguously by their leaves. The genus *Cryptocoryne* is characterized by having leaves convolute (once-rolled) in vernation, female flowers united in one whorl, and an adaxial placentation with many ovules. *Lagenandra* is characterized by having leaves involute (double-rolled) in vernation, female flowers free and spirally arranged (two species with one or two whorls), and a basal placentation with few ovules (see e.g. Nicolson, 1987; Bogner & Jacobsen, 1987).

The spathe is on a short or long peduncle. The size, shape and colours of the spathe are the most important characters used for distinguishing the different species from one another.

Studies of the macromorphological structures of the spathes and spadices within the Araceae, including *Cryptocoryne* and *Lagenandra*, have been published (Griffith, 1851a, b; Goebel, 1897; Svedelius, 1910; Engler, 1920; Petch, 1928). Those of de Wit (1983, 1990) use the macromorphological characters mainly for taxonomic delimitation. Comparative studies of the fine structures, i.e. cell structures and their occurrence within or between related genera are, however, not available.

GENERAL MACROMORPHOLOGY

Cryptocoryne

The generalized *Cryptocoryne* spathe is shown in Figure 1. The lower part of the spathe is the kettle (Fig. 1A) which has no trace of spathe margin fusion. The inside surface of the kettle wall varies in macromorphology between the different species, e.g. rough, smooth or both in various degrees. Some species have so-called alveolae or 'windows' (Figs 4, 11, 12, 21) in the upper part of the kettle.

Above the kettle a tube is formed by fusion of the spathe margins (Fig. 1B). The fusion is clearly visible macroscopically as a more or less straight line running from

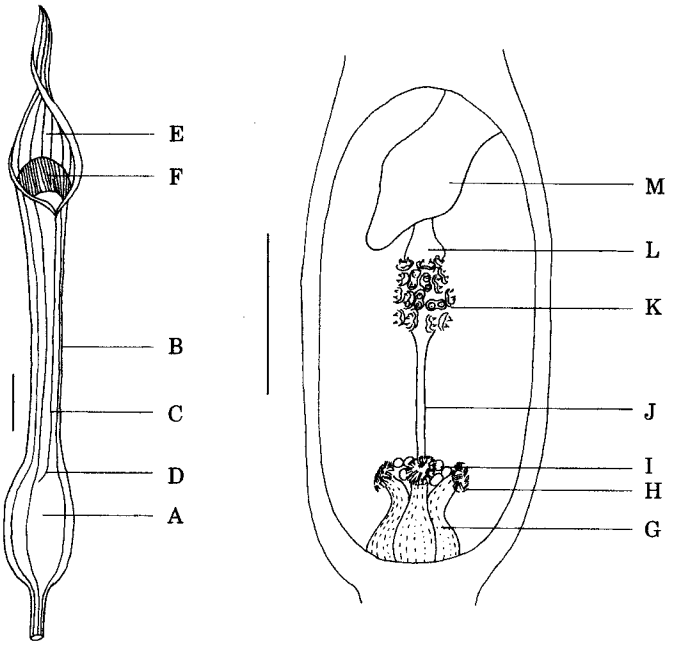


Figure 1. Generalized drawing of spathe and spadix of *Cryptocoryne*. A, kettle. B, tube. C, fusion line of the spathe margins. D, position of flap seen from the outside. E, limb of spathe. F, collar/collar zone. G, female flowers. H, stigmas. I, olfactory bodies. J, naked axis of spadix. K, male flowers. L, sterile appendix of the spadix. M, flap. Scale bar = 0.5 cm.

the kettle to the limb (Fig. 1C). At the transition between the kettle and the tube, the line curves, and this marks the position of the flap (Fig. 1D). The flap (Figs 1M, 21, 34) serves as a trap door for insects, as well as a protection shield for the male flowers against incoming insects at the beginning of anthesis when the stigmas of the female flowers are receptive. After about 12 hours the flap begins to move upwards, closing the entrance to the kettle. The flap stays closed for about 24 hours during which period the male flowers mature. On the third day the flap moves downwards again and opens the exit to the tube so the insects can leave with pollen attached.

The upper part of the tube continues into the limb of the spathe (Figs 1E, 14, 15, 33, 49, 50), which may have various shapes, sizes and colours. They constitute the main characters of the species. The limb generally has a pronounced, elevated collar around the opening into the tube (Figs 1F, 7, 33, 36, 51) or a broad, often less demarcated collar zone, and further a colour different from the outer part of the limb; the collar or the collar zone is lacking in some species.

The female flowers, usually 5–7, are unilocular, naked and situated in a single, connate whorl at the base of the spadix in the kettle (Figs 1G, 6). In a second whorl, just above the female flowers and between the stigmas, regular or irregular rounded structures which are olfactory bodies occur (Figs 1I, 6). These have traditionally been considered as neuter flowers of female origin due to their position adjacent to the female flowers. Buzgó (1997, 1998) has studied the odour differentiation of the flowers in *Cryptocoryne* and *Lagenandra* and suggests that the olfactory bodies are of male origin. The male flowers are found above the olfactory bodies on a usually

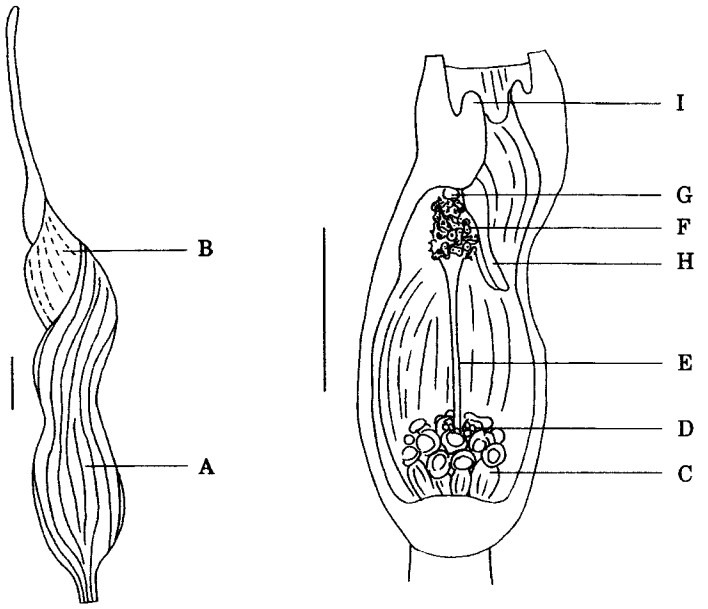


Figure 2. Generalized drawing of spathe and spadix of *Lagenandra*. A, kettle. B, limb of spathe. C, female flowers. D, olfactory bodies. E, naked axis of spadix. F, male flowers. G, sterile appendix of spadix. H, flap. I, collar. Scale bar = 0.5 cm.

long, thin, naked spadix axis (Fig. 1J). The naked male flowers each consist of a single stamen with two bilocular thecae (Figs 1K, 4, 5, 21, 22). The spadix ends in a dilated sterile appendix (Figs 1L, 4, 21).

Lagenandra

This genus resembles *Cryptocoryne* in many respects, but differs greatly in the overall proportions (Fig. 2). The kettle (Figs 2A, 60, 71) is comparable to that of *Cryptocoryne*, but a distinct tube is lacking. Just above the kettle, the limb of the spathe may be tube-like for 0.5–1(–2) cm, depending on the species and the degree to which the margins of the limb are fused. As in *Cryptocoryne* the fusion of the spathe margins forms a curved line above the kettle, indicating the location of the flap. However, in most species of *Lagenandra*, a thick, crescent-shaped, convex septum (Figs 2I, 63, 64), separating the kettle and the spathe limb is present (see e.g. Graaf & Arends, 1986). In this septum there is an oval opening which leads into the kettle. The flap is similar to that in *Cryptocoryne*. The elevation on the septum around the entrance to the kettle is interpreted as homologous to the collar structure (Fig. 1F) found in the transition between the tube and the limb in some species of *Cryptocoryne*.

In most species the surface of the limb has a more rough structure, often with horizontal ridges and protuberances (similar to those found in *C. spiralis*), but in a few species (e.g. *L. jacobsenii* de Wit, *L. thwaitesii* Engl., and *L. toxicaria* Dalzell) the surface has protuberances evenly spread on the limb.

The floral parts of *Lagenandra* differ from those of *Cryptocoryne* in that the female flowers (usually more than in *Cryptocoryne*) are arranged helically in whorls (Figs 2C,

TABLE 1. List of accessions of *Cryptocoryne* and *Lagenandra* and their origin

C. walkeri Schott, NJ 23–10, 23.3.1975, Halloluwa, Mahaweli Ganga, near Peradeniya Botanical Garden, Sri Lanka. $2n=28$.
C. albida RN Parker, NJ 77–81, 22.2.1977, Ban Wangyon, S of Ranong, Thailand. $2n=36$.
C. schulzei de Wit, Bogner 2123, 12.2.1992, *c.* 7 km N of Kota Tinggi, Johore, Malaysia. $2n=34$.
C. pontederiifolia Schott, NJ 85–29, 20.8.1985, Tapakis, N of Padang, Sumatra, Indonesia. $2n=30$.
C. ferruginea Engl., NJ 78–44, 19.9.1978, Stapok F.R., W of Kuching, Sarawak, Malaysia. $2n=34$.
C. alba de Wit, NJ 3172, 28.12.1980, cult. ex Sri Lanka. Leg. C. Christensen. $2n=36$.
C. spiralis (Retz.) Wydler, Cook 327/73, Ernakulam, Kerala State, India. $2n=66$.
Lagenandra lancifolia (Schott) Thwaites, NJ 3242, 5.3.1982, cult. ex Sri Lanka. Leg. H. Windeløv. $2n=36$.
L. nairii Ramam. & Rajan, M. Sivadasan s.n. 17.4.1985, Base of Athirapally Waterfalls, Trichur District, India. $2n=72$.

60) from the base of the spadix (except in *L. nairii* Ramam. & Rajan (Fig. 71) and *L. gomezii* (Schott) Bogner & N. Jacobsen in which the flowers are arranged in 1–2 whorls). The female flowers and ovaries are only basally attached to the spadix, the ovaries have one to a few seeds, and the ovules are basifixed. This is in contrast to *Cryptocoryne* which has many seeds with an adaxial placentation in upright, connate ovaries (syncarpium). Olfactory bodies are usually also present although often few in number and not easily recognized (Fig. 66). The male flowers (Figs 2F, 60, 68) are similar to those of *Cryptocoryne*.

Svedelius (1910) made a thorough study of the spathe in *Lagenandra*, otherwise only treated for macromorphological characters in the works by de Wit (1978, 1983, 1990).

MATERIAL AND METHODS

The material consisted of fresh spathes and flowers from seven species of *Cryptocoryne* and two species of *Lagenandra*. The material used is listed in Table 1. The material was taken from the living collection held at the Royal Veterinary and Agricultural University, Copenhagen. Voucher specimens are placed at the Botanical Museum, Copenhagen (C). Spathes were taken at the first, second or third day of flowering.

Tissue for SEM study was fixed in 2.5% glutaraldehyde in 0.1 M phosphate-buffer, pH 7.2, dehydrated in a graded series of acetone, then dried in a critical point drier (Balzer CPD E 5400), and sputter-coated with gold (Polaron 020). For study of surface coating and non-dehydrated cells spathes were cryofixed, i.e. immediately after cutting the material was immersed in nitrogen slush and then transferred to the microscope (Jeol JSM-840A supplied with cryo-attachment Cryo-Trans CT 1000). After sublimation of ice from the surface and sputtering with gold the material was studied at a temperature of about -196°C.

The descriptive terminology is in accordance with Stearn (1992), and the author abbreviations in accordance with Brummit & Powell (1992).

RESULTS

In the following descriptions, *C. walkeri* has been used as a basic model; only structures in the following species different from those of *C. walkeri* are mentioned.

Cryptocoryne walkeri Schott
(Figs 3–12)

The kettle. The wall is differentiated into a basal and an upper part. The basal part is more or less smooth, covered with an almost continuous layer of mucilage (Fig. 9). The curvature of the outer walls of the inner epidermal cells changes gradually from the base of the kettle upwards, from slender, rounded tuberculate protrusions to aculeate trichomes.

In the upper 1/3–2/3 of the kettle wall numerous depressions, alveolae ('windows') are found except in the area just behind the flap (Figs 4, 11, 12). The outline of the alveolae is irregular rounded, 20–100 μm in diameter, the lower ones are smaller than the upper ones. The depth of the alveolae is 100–150 μm. The inner epidermal cells with the protrusions continue down the margins, but stop abruptly at the bottom of the alveolae. The cells forming the bottom are relatively large, hexagonal in outline and slightly convex without protrusions. The alveolae are empty and have no mucilage covering.

The tube. The inner surface is composed of cells which have downward pointing trichomes (Fig. 8) similar to those in the upper part of the kettle. There are no wall depressions or mucilage covering in the tube. The outer surface of the tube is composed of flat, elongated cells with almost straight, slightly raised junctions and longitudinal striations. Scattered stomata are present on the outer surface.

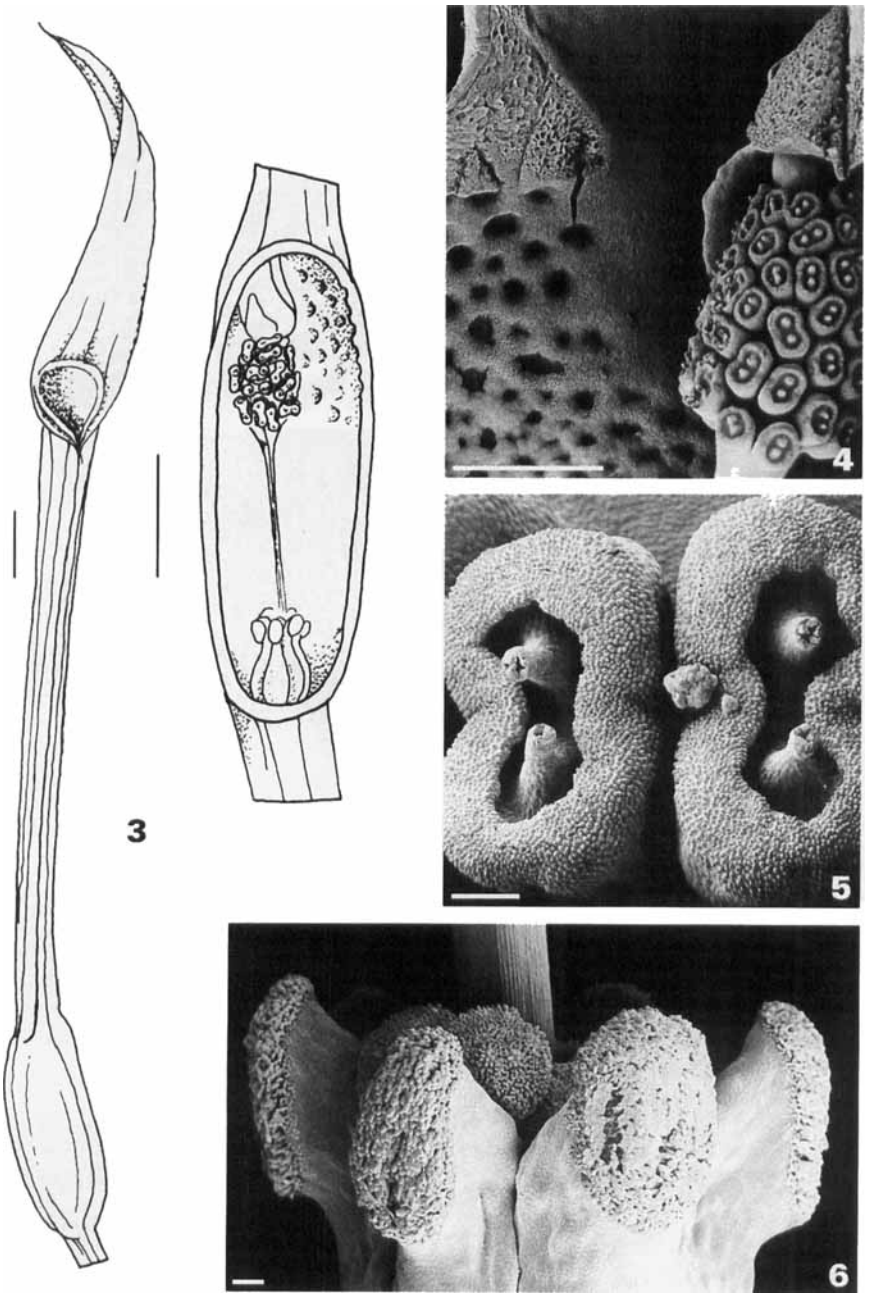
The flap (Fig. 4). The epidermal cells of the upper surface of the flap are more or less rectangular in outline, the outer walls slightly convex without tubercles (Fig. 10), thus quite different from the inner surface of the kettle. The lower surface of the flap has short trichomes. The flap structure continues into the tube as a tapering prolongation fusing with the tube margins.

The collar. The transition between tube and limb of the spathe is marked by a collar. Microscopically, this is marked as an abrupt transition from one epidermal cell type to another (Fig. 7), i.e. the inner epidermis of the tube wall is composed of cells with conspicuous downward pointing trichomes and the epidermis beyond the collar is composed of cells with slightly convex outer walls without tubercles.

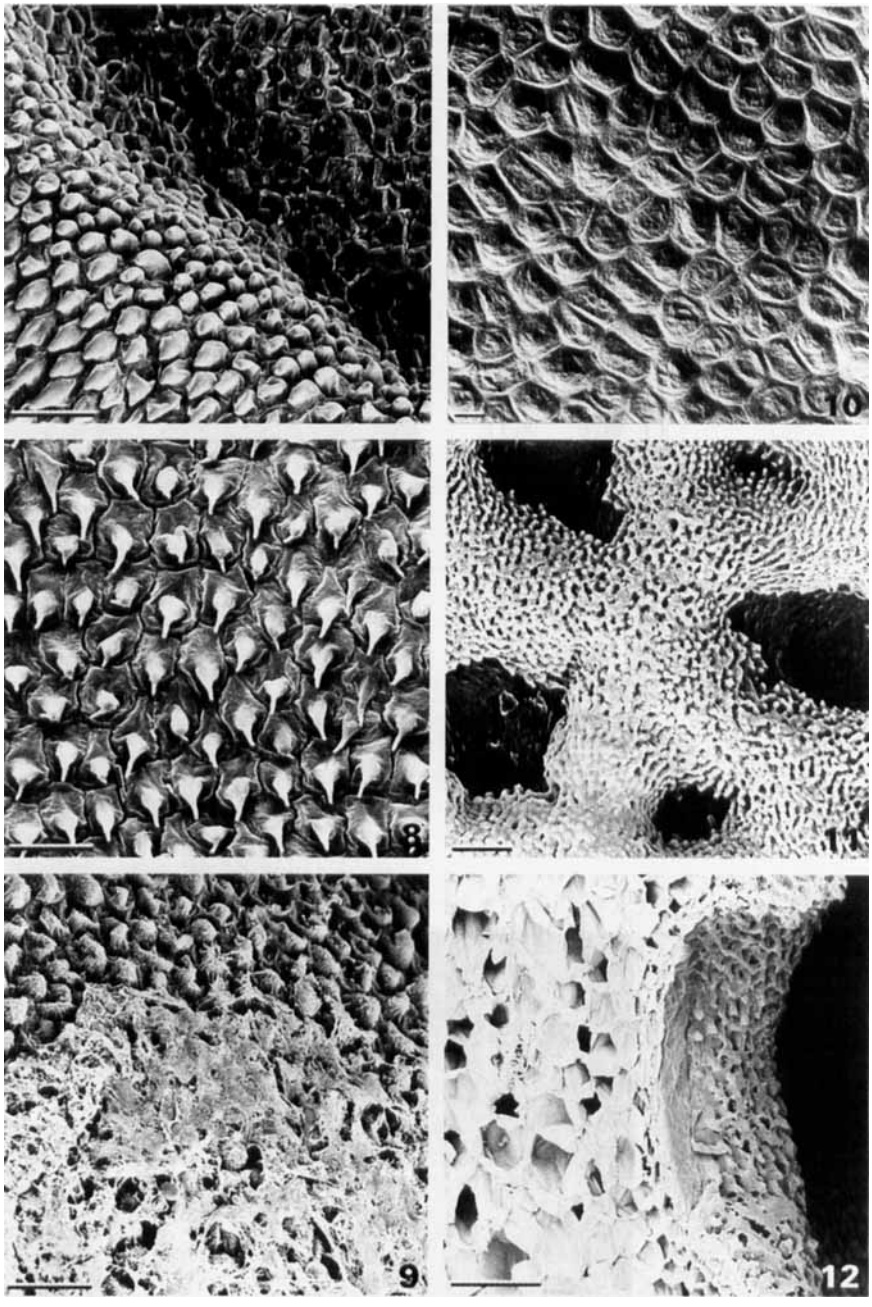
The limb. The cells of the inner surface of the limb are isodiametric in outline and the outer cell wall is slightly convex (Fig. 7).

The female flowers. Five to seven connate, female flowers without perianth are arranged around the spadix in the kettle bottom (Fig. 6). The style is about 0.2 × 0.5 mm, and the length about 3 mm. The epidermal cells of the style are irregular rectangular in outline and the surfaces of the outer walls are slightly convex. The stigma is capitate with a subglobose to flattened head (Fig. 6). The receptive surface is directed towards the wall of the kettle. The cells of the receptive part of the stigma are distributed uniformly over the head surface, they are unicellular, cylindrical, smooth papillae. Five to seven rounded olfactory bodies are inserted as an inner whorl between the stigmas and the spadix (Fig. 6). The surface cells of the olfactory bodies are quite similar to the receptive part of the stigma with unicellular, cylindrical smooth papillae.

The male flowers. The male part of the spadix has more than 50 flowers (Fig. 4), raised 3–10 mm above the female flowers by the thin, naked axis of the spadix. The



Figures 3–6. *Cryptocoryne walkeri*. Fig. 3. Generalized drawing of spathe and opened kettle. Scale bar = 0.5 cm. Fig. 4. Opened kettle showing the apical part of the spadix with male flowers partly covered by the flap. The spadix appendix partly shown. Alveolae are present in the upper part of the kettle wall. Scale bar = 1 mm. Fig. 5. Two male flowers showing the finely papillate outer surface, the two thecae with their dehiscence pores, and pollen grains embedded in pollenkitt. Scale bar = 100 μm. Fig. 6. The basal part of the spadix with the female flowers arranged in a whorl with the outwardfacing vertical stigmas, and the papillate olfactory bodies behind. Scale bar = 100 μm.



Figures 7–12. *Cryptocoryne walkeri.* Fig. 7. Limb of spathe showing the transition zone between the collar with trichomes pointing downwards, and the limb with isodiametric, flat cells. Scale bar = 50 µm (see also Fig. 10). Fig. 8. Inner surface of the tube showing the somewhat shrunken, downward pointing trichomes. Scale bar = 50 µm. Fig. 9. Inner surface of the kettle wall showing the transition zone between the upper part with trichomes, and the lower part with a mucilage coating. Scale bar = 50 µm. Fig. 10. Upper surface of the flap showing pentagonal, flat cells. Scale bar = 10 µm. Fig. 11. Surface of kettle wall showing alveolae. Scale bar = 100 µm. Fig. 12. Transection of the upper kettle wall showing alveolae. Scale bar = 100 µm.

flowers are naked, consisting of only one anther, about 0.7 mm long and 0.4 mm wide with two bilocular thecae (Fig. 5). The two thecae are united into a cushion-like structure where the tuberculate cells surround the whole structure. The loculi are flask shaped and dehisce by an apical pore. The pollen grains are slightly ellipsoidal, 15–20 μm in diameter, and are embedded by a sticky substance, the pollenkitt. At dehiscence the male flowers extrude a small droplet of imbedded pollen grains.

C. albida R.N. Parker
(Figs 13–22)

The kettle. The overall cellular arrangement of the inner epidermal cells are similar to *C. walkeri* except that there is a constriction of the kettle wall just below the male flowers (Fig. 21). The mucilage covering in the basal part is rather thick and placed on top of the tuberculate protrusions of the inner epidermal cells as an almost continuous coating. The mucilage gradually becomes thinner from the base of the kettle and upwards concurrently with the change in the surface sculpturing from rounded, tuberculate protrusions into aculeate trichomes curved downwards in the upper part. Here there are alveolae in the kettle wall (Fig. 21) with density less than in *C. walkeri.*

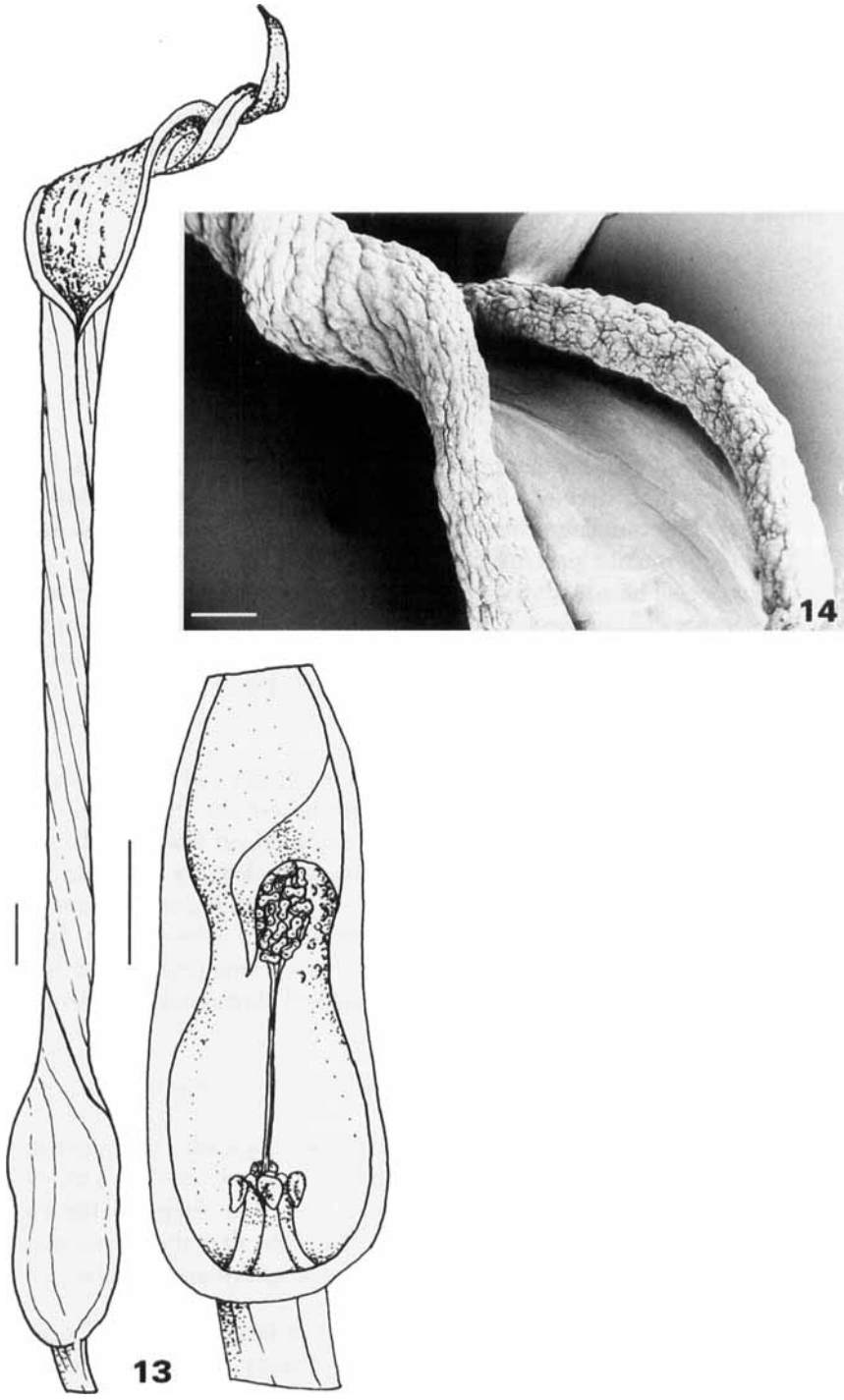
The tube. The shape and arrangement of the inner epidermal cells of the tube are similar to those in the upper part of the kettle throughout the length, i.e. unicellular, acute trichomes, curved downward in spathes sampled on first day. In spathes of second or third day the trichomes sink into the cell cavity leaving a minute depression in the wall corresponding to the inner surface of the trichome cell wall (Figs 18, 19). The same structure is found in *C. walkeri* but not shown in a figure. The epidermal cells of the outer surface of the tube are elongated with a fine striate cuticular surface (Fig. 16), and stomata are scattered throughout the length of the tube.

The flap. The lower surface of the flap has short trichomes (Fig. 20).

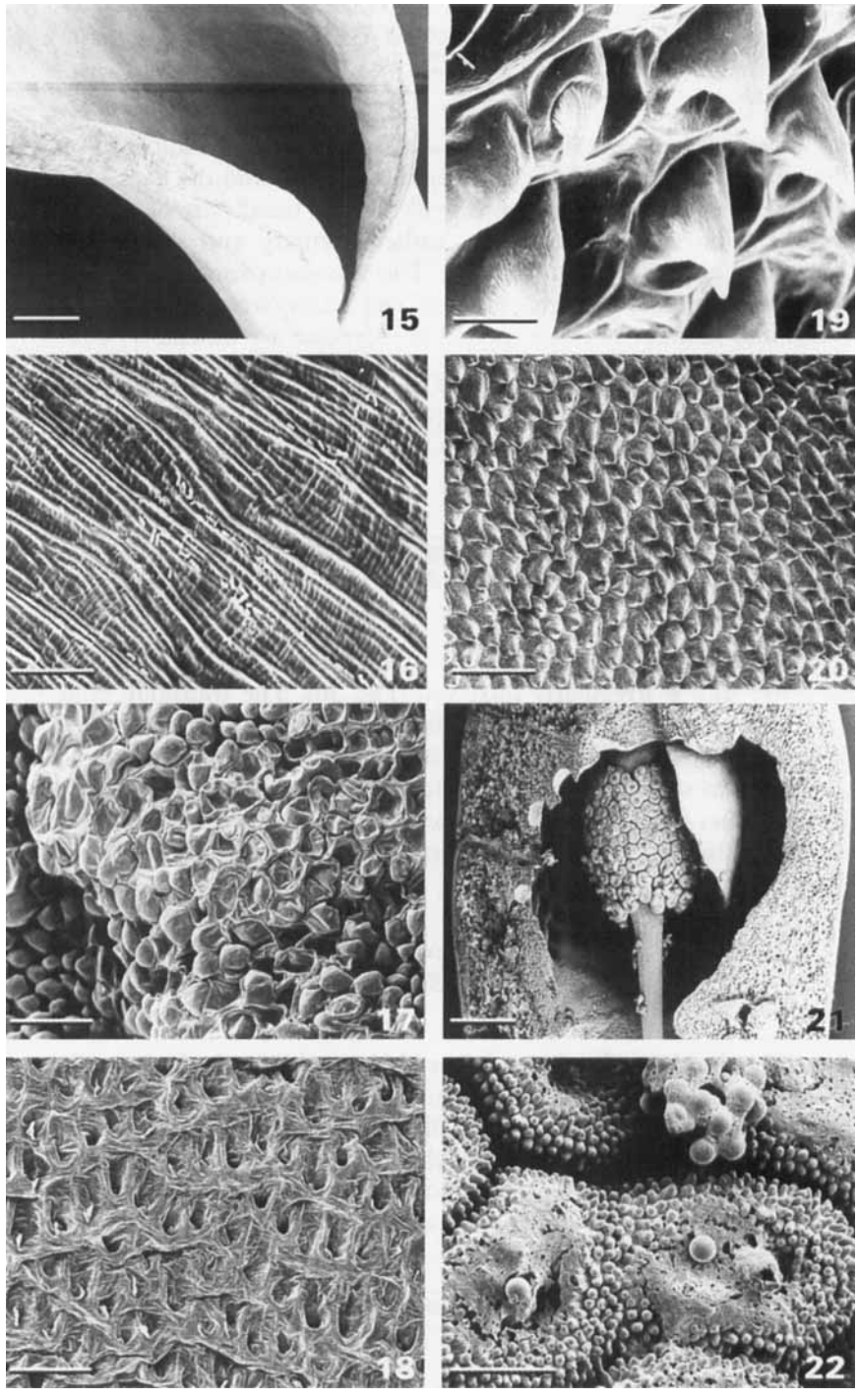
The limb. No collar or collar zone is revealed microscopically, there being no cell differentiation from the kettle and tube to the limb of the spathe. The surface of the limb is smooth to somewhat rough (Figs 14, 15). The shape of the epidermal cells of the limb are similar to those of the tube except that the protrusions of the outer walls are smaller and obtuse (Fig. 17). The pollen grains are globular, 25–30 μm.

The female flowers. The six to seven female flowers are larger than in *C. walkeri.* The receptive surface is subglobose and papillate. The seven to eight olfactory bodies are rounded, and the surface is also papillate.

The male flowers. The structure differs from those of *C. walkeri* in that the tuberculate cells that surround the two thecae are confluent centrically, circumventing the two thecae (Figs 21, 22). The outer walls of the cells have slender, rounded tuberculate papillae (Fig. 22).



Figures 13–14. *Cryptocoryne albida.* Fig. 13. Generalized drawing of spathe and opened kettle. Scale bar = 0.5 cm. Fig. 14. Distal part of the limb of the spathe showing the outer surface (see Fig. 20) with the recurved margins (see Fig. 17). Scale bar = 1 mm.



Figures 15–22. *Crypotcoryne albida.* Fig. 15. Proximal part of the limb with the entrance to the tube. Scale bar = 1 mm. Fig. 16. Striate outer surface of the spathe of the limb. Scale bar = 10 μm. Fig. 17. Inner surface of the limb of the spathe. Scale bar = 50 μm. Fig. 18. Cells in the tube with sunken trichomes. Scale bar = 50 μm. Fig. 19. Inner surface of the tube with partly sunken trichomes. Scale bar = 10 μm. Fig. 20. Lower surface of the flap. Scale bar = 50 μm. Fig. 21. Upper part of the kettle showing the wall thickening, the alveolae, the male flowers, and the flap. Scale bar = 1 mm. Fig. 22. Male flowers strongly papillate and with pollen in pollenkitt. Scale bar = 100 μm.

C. schulzei de Wit
(Figs 23–26)

The kettle. The mucilage covering in the basal part is quite thick, completely sealing the tuberculate protrusions of the inner epidermal cells and the gaps between cells. The kettle wall is coated 2/3 up the kettle to the basal part of the male flower inflorescence. The coating disappears rather abruptly and is easily recognized macroscopically as a wavy line (Fig. 26). The transition zone between coated and non-coated superimpose the changing in cell shape from rounded, tuberculate protrusions into slender, aculeate trichomes. Alveolae are absent.

The flap. The cells of the upper surface of the flap (Fig. 24) are slightly convex, and the fusion with the surface of the kettle and tube wall with downward pointing trichomes is shown in Figures 24 and 25.

C. pontederiifolia Schott
(Figs 27–31)

The kettle. The inside surface of the kettle wall is similar to that of *C. walkeri* except that the lower 2/3 is irregularly furrowed (Fig. 30). The transition zone between the coated and non-coated surface is found about 3/4 up the inner surface of the kettle (Figs 30, 31) where it narrows concurrently with a change in surface structure from undulated to smooth, and in cell shape from round protrusions to downward pointing trichomes (Figs 29, 30). Alveolae are absent. Figure 28 shows the area of fusion between the flap and the inner kettle wall, similar to Figure 24.

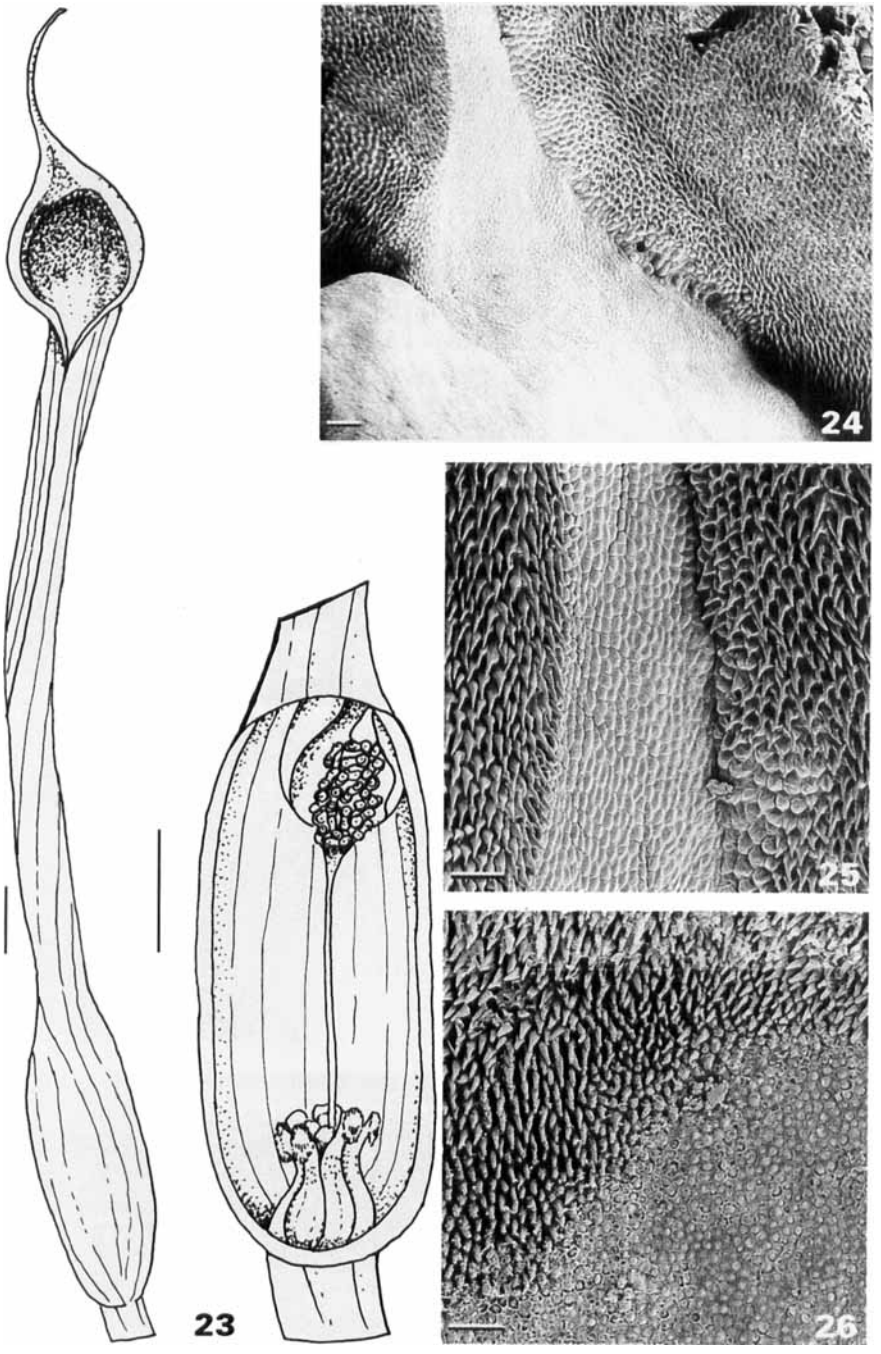
C. ferruginea Engl.
(Figs 32–40)

The kettle. The inside wall of the lower 3/4 of the kettle is very uneven and rough, and coated with a loosely, filamentous mucilage on top of the tuberculate protuberances of the inner epidermal cells. The mucilage coating disappears concurrently with the change in the kettle diameter, in wall structure from rough to smooth and in cell surface sculpturing from rounded, tuberculate protrusions (Fig. 40) into aculeate trichomes curved downwards. Similar trichomes are found in the short tube (Fig. 37). Alveolae are absent.

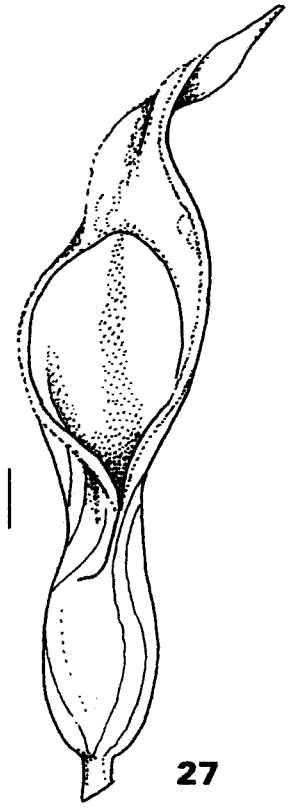
The flap. The upper surface of the flap is not completely smooth with some elevated veins (Fig. 34).

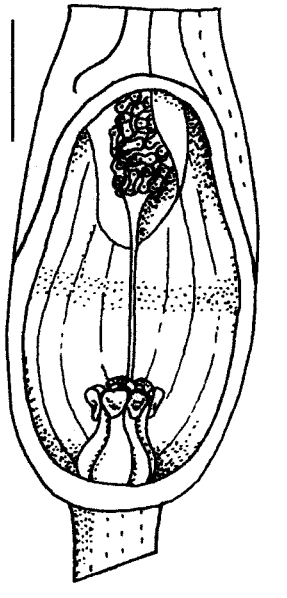
The collar. The transition between the tube and the spathe limb is quite distinct (Fig. 36) due to the pronounced collar and it is marked by an abrupt transition from downward pointing trichomes in the tube (Fig. 37) to flat, isodiametric cells on the spathe limb (Fig. 35).

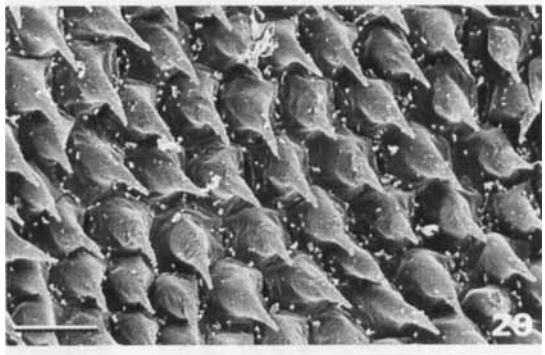
The limb. The surface of the limb is marked by multicellular, rounded protuberances (*c.* 0.5 mm long) (Figs 33, 38). On top of most of these protuberances a single stoma

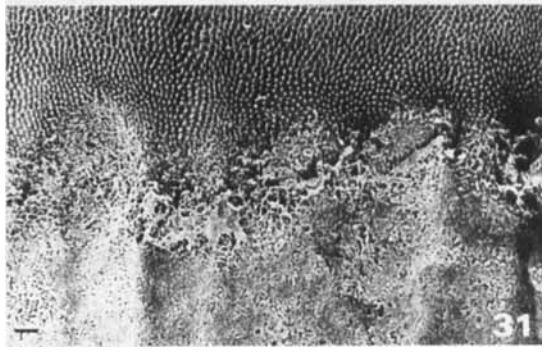


Figures 23–26. *Cryptocoryne schulzei.* Fig. 23. Generalized drawing of spathe and opened kettle. Scale bar = 0.5 cm. Fig. 24. Upper part of the flap and the fusion with the tube wall of the prolongation from the flap. Fig. 25. Fusion zone of upper part of the flap and the inner part of the tube. Fig. 26. Kettle wall showing transition zone between mucilage coated cells and downward pointed trichomes. Scale bars = 100 μm.

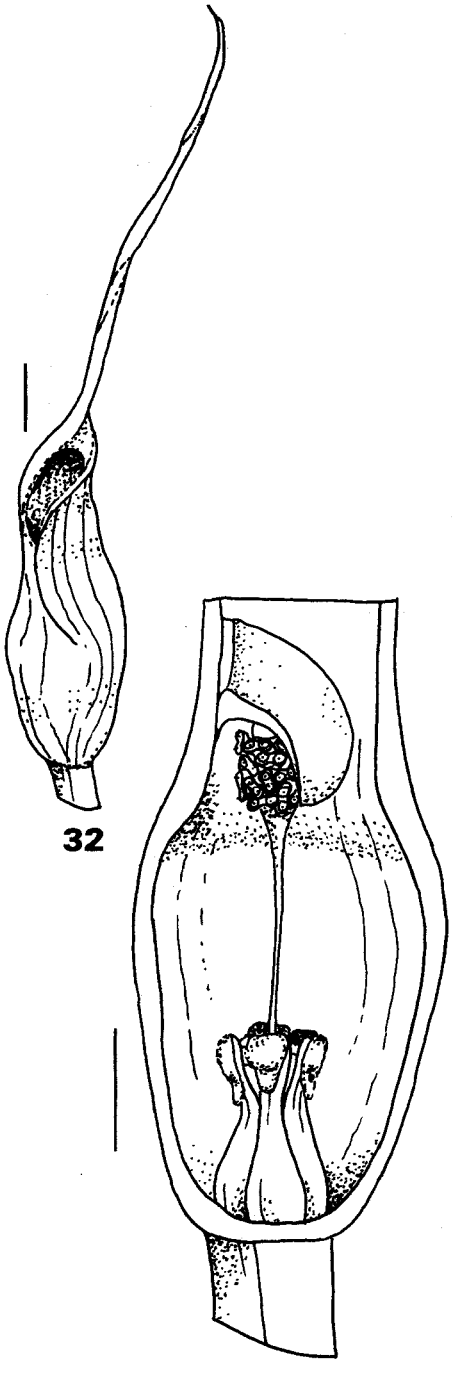


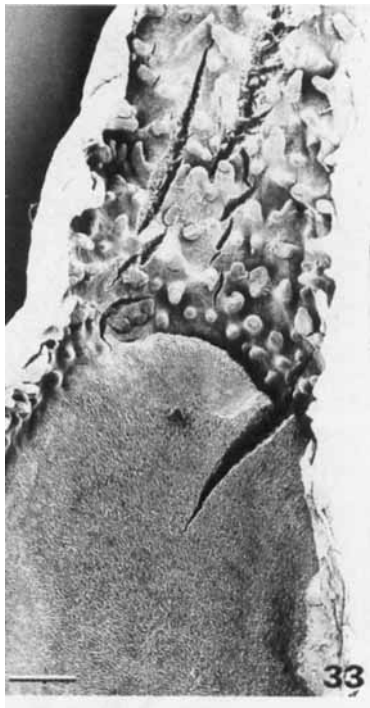


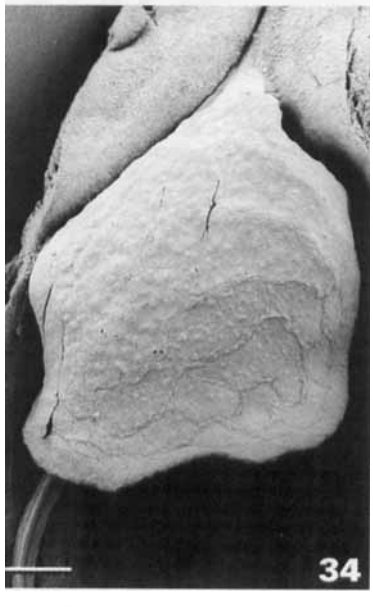




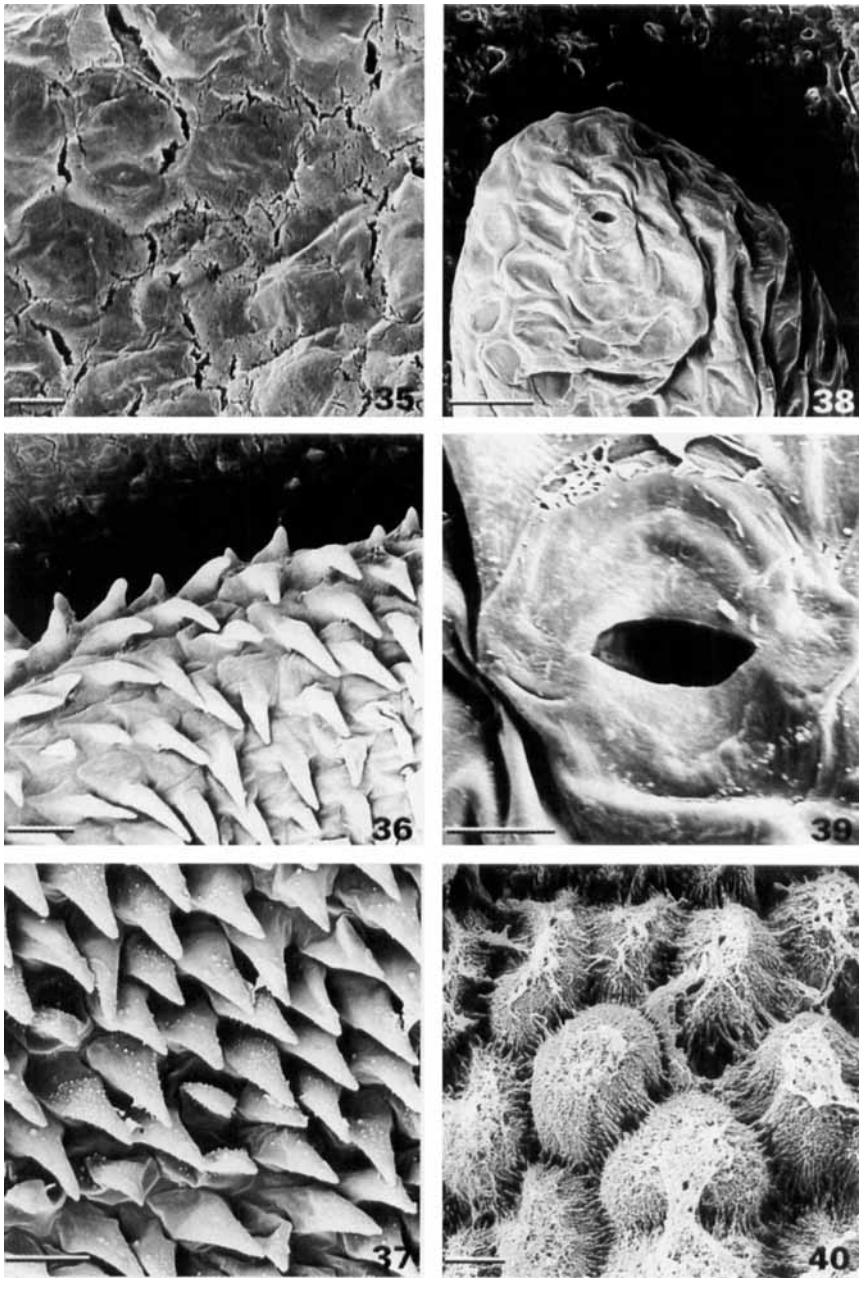
Figures 27–31. *Cryptocoryne pontederiifolia*. Fig. 27. Generalized drawing of spathe and opened kettle. Scale bar = 0.5 cm. Fig. 28. Upper part of the flap sinking into the kettle wall. Scale bar = 100 µm. Fig. 29. Trichomes in the upper part of the kettle. Scale bar = 50 µm. Fig. 30. (Scale bar = 1 mm) and Fig. 31. (Scale bar = 100 µm). Inner surface of the kettle wall showing the transition zone between the lower part with the mucilage coating, and the upper part with the trichomes.







Figures 32–34. *Cryptocoryne ferruginea*. Fig. 32. Generalized drawing of spathe and opened kettle. Scale bar = 0.5 cm. Fig. 33. Collar and limb of the spathe with protuberances. Scale bar = 1 mm. Fig. 34. The flap covering the male flowers. Scale bar = 1 mm.



Figures 35–40. *Cryptocoryne ferruginea*. Fig. 35. Inner surface of the limb of the spathe with flat, isodiametric cells. Scale bar = 10 µm. Fig. 36. Collar marking the cell transition zone. Scale bar = 50 µm. Fig. 37. Trichomes in the tube. Scale bar = 50 µm. Fig. 38. Protuberances on the limb of the spathe with apical stoma. Scale bar = 50 µm. Fig. 39. Stoma. Scale bar = 10 µm. Fig. 40. Inner surface of the basal part of the kettle wall showing the fibrillate mucilage coating. Scale bar = 10 µm.

of the anomocytic type is found (Figs 38, 39). The cells of the inner surface of the limb are isodiametric (hexagonal) with convex curvatures of the outer walls (Fig. 35).

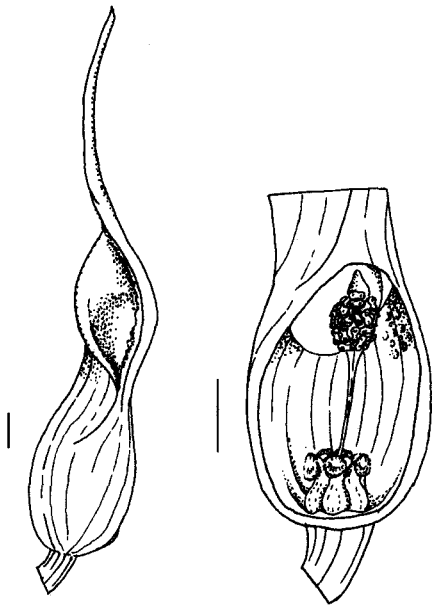


Figure 41. *Cryptocoryne alba.* Generalized drawing of spathe and opened kettle. Scale bar = 0.5 cm.

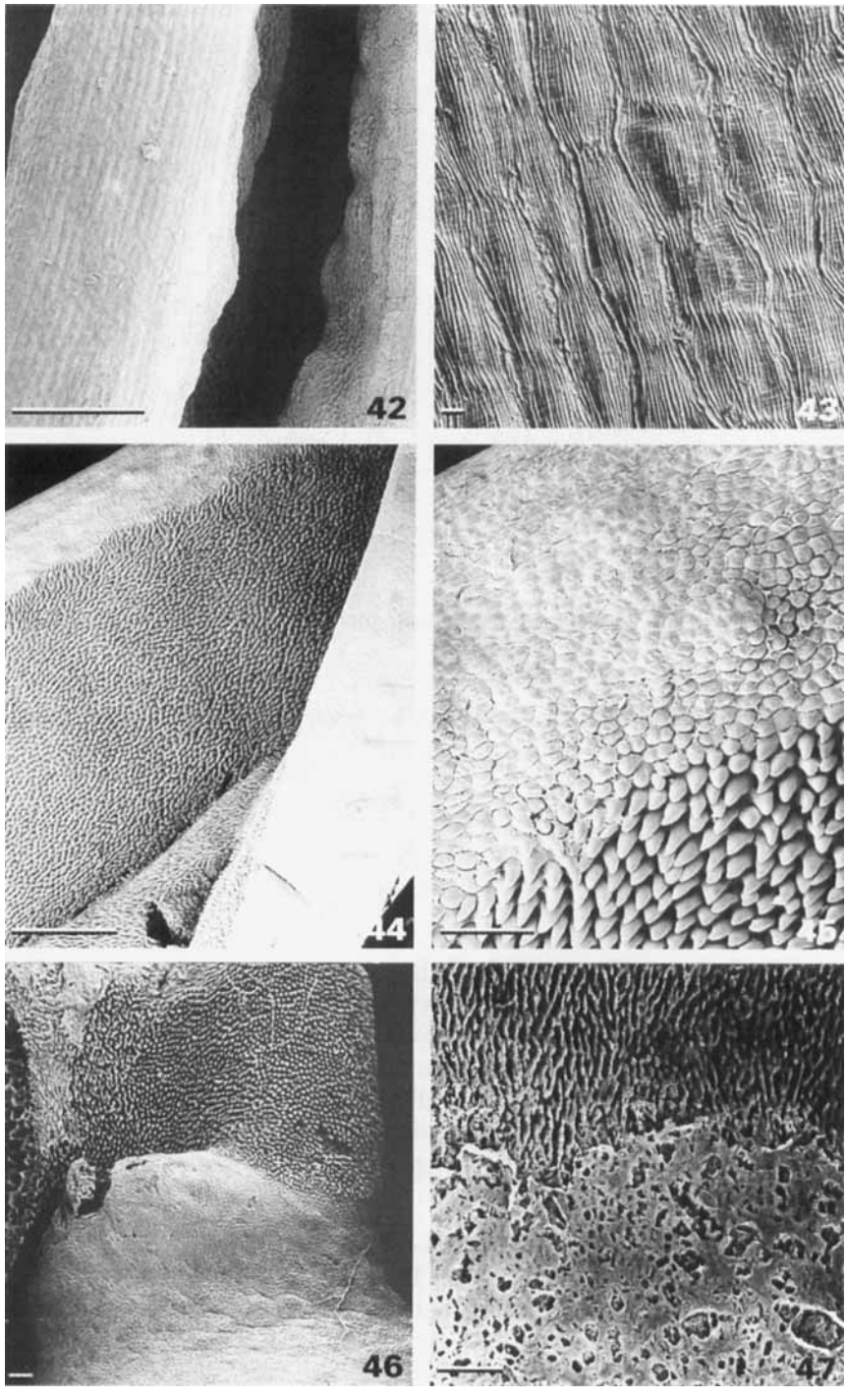
The olfactory bodies. The olfactory bodies differ from those of *C. walkeri*, being more irregular.

C. alba de Wit
(Figs 41–47)

The kettle. The inside surface of the kettle is smooth and even throughout. The basal half of the kettle is covered with a relatively thick layer of mucilage which seems to seal off the surface completely. About half way up the kettle wall the mucilage coating disappears abruptly (Fig. 47). The transition line is irregular and wavy, and above the transition the surface of the cells are similar to those found in the upper part of the kettle in *C. walkeri.* This cell structure is found throughout the upper half of the kettle wall and continues unchanged into the tube and limb. Alveolae are present in the upper part of the kettle.

The 'collar'. A distinct collar has not been observed in the material investigated (see Discussion: The collar or collar zone). The trichomatous cell type found in the upper part of the kettle and throughout the tube continues into the limb (Figs 44–46). Only on the inner surface of the caudal part of the limb are cells which could be of the type found on the limb of e.g. *C. walkeri*, but they are difficult to interpret because of the reduction into a thin caudate limb (Fig. 42).

The tube and the limb. The cell surface structure of the inner side of the tube and limb is similar to that found in the upper part of the kettle wall. Stomata have not been observed. The outline of cells of the outer surface of the limb of the spathe are flat and elongated with straight, raised lateral, cell boundaries (Fig. 43). The surface of



Figures 42–47. *Cryptocoryne alba*. Fig. 42. Distal part of the limb of the spathe showing the outer and inner surface. Scale bar = 0.5 mm. Fig. 43. Striate outer surface of the limb of the spathe. Scale bar = 10 µm. Fig. 44. Proximal part of the inner surface of the limb with trichomes. Scale bar = 0.5 mm. Fig. 45. Margin of the limb showing the transition between cells of the trichomatous type and cells of the slightly convex, isodiametric type. Scale bar = 100 µm. Fig. 46. Lower part of the tube with the flap. Scale bar = 100 µm. Fig. 47. Inner surface of the kettle showing the transition zone with trichomes in the upper part and mucilage coating in the basal part. Scale bar = 100 µm.

the outer cell wall (the cuticle) is finely striated (Fig. 43). Figure 46 shows the transition between the upper surface of the flap and the fusion to the tube wall.

C. spiralis (Retz.) Wydler
(Figs 48–58)

The kettle. The lower part of the wall is covered with fibrous mucilage (Fig. 55). The outer cell walls are convex in the lower part, but are gradually changed (Fig. 55) into unicellular downward pointing trichomes in the upper part of the kettle (Figs 56–58). In Figures 57 and 58 the inside surface is shown with some collapsed trichomes sunken into the cell cavity, thereby forming a lattice-like structure.

In the upper 1/3 of the kettle, in the area just opposite the male flowers, some alveolae, *c.* 0.3 mm in diameter and depth, are present. The cells forming the bottom of the alveolae are hexagonal in outline and the outer walls are flat. The outer cell walls forming the sides of the alveolae are convex or trichomatous depending on the position of the alveolae in the kettle wall.

The tube. A tube is lacking.

The flap. The cells of the lower surface of the flap are of the trichomatous type (Fig. 53), whereas the cells of upper surface of the flap are hexagonal in outline (Fig. 54) and the outer walls are slightly convex.

The collar. Above the flap is a collar which is remarkably thick and forms a broad septum covering the opening to the kettle, leaving just a small, oval opening (Fig. 51).

The limb. The limb is characterized by numerous transverse, shelf-like ridges with fringed edges (Figs 49, 50). The outline of the cells are elongated and fusiform with a flat or slightly convex surface (Fig. 52).

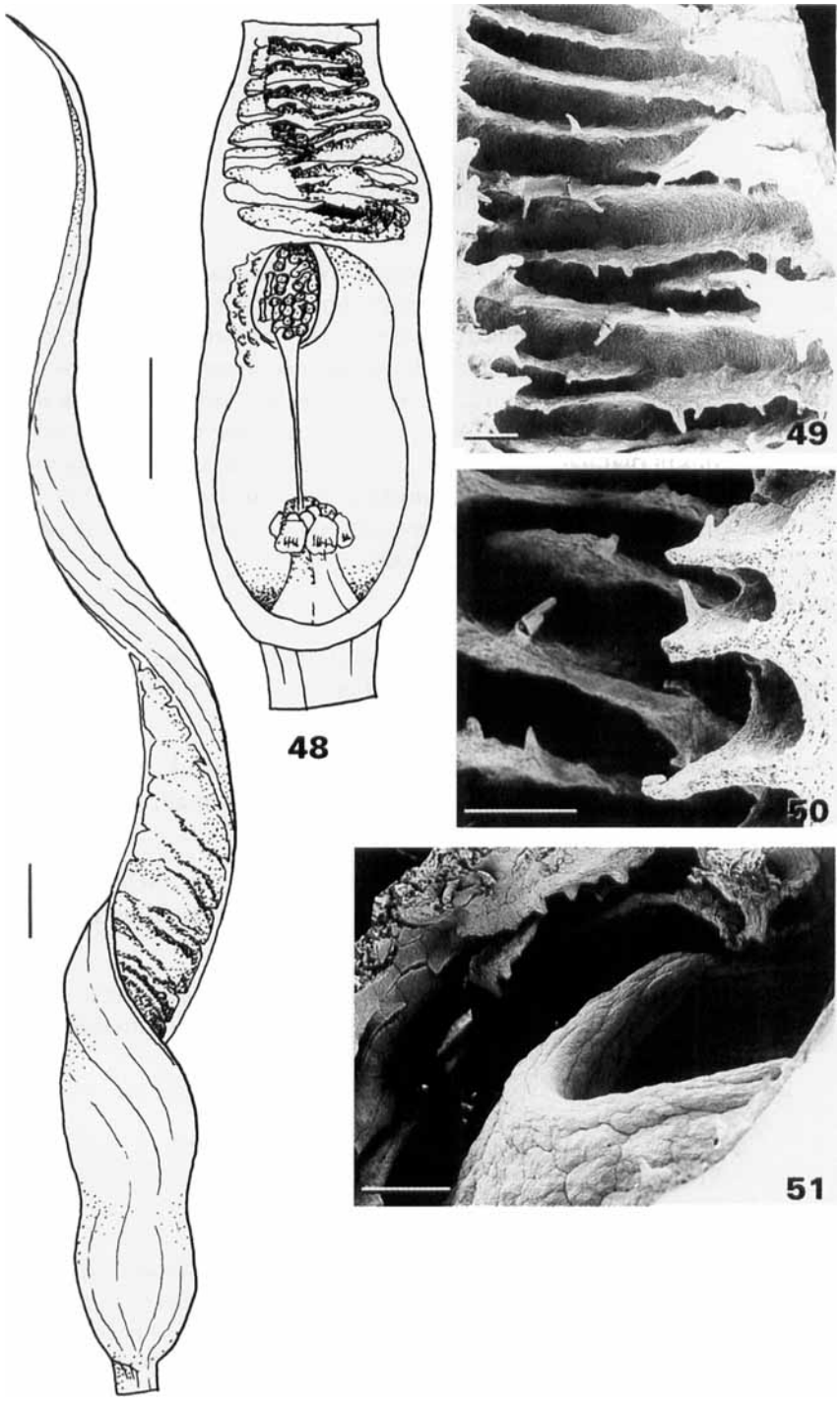
C. affinis Hook.f., *C. minima* Ridl. and *C. pygmaea* Merr. have also been studied, and their cell structure coincide with those found in the other species investigated in this study.

Lagenandra lancifolia (Schott) Thwaites
(Figs 59–69)

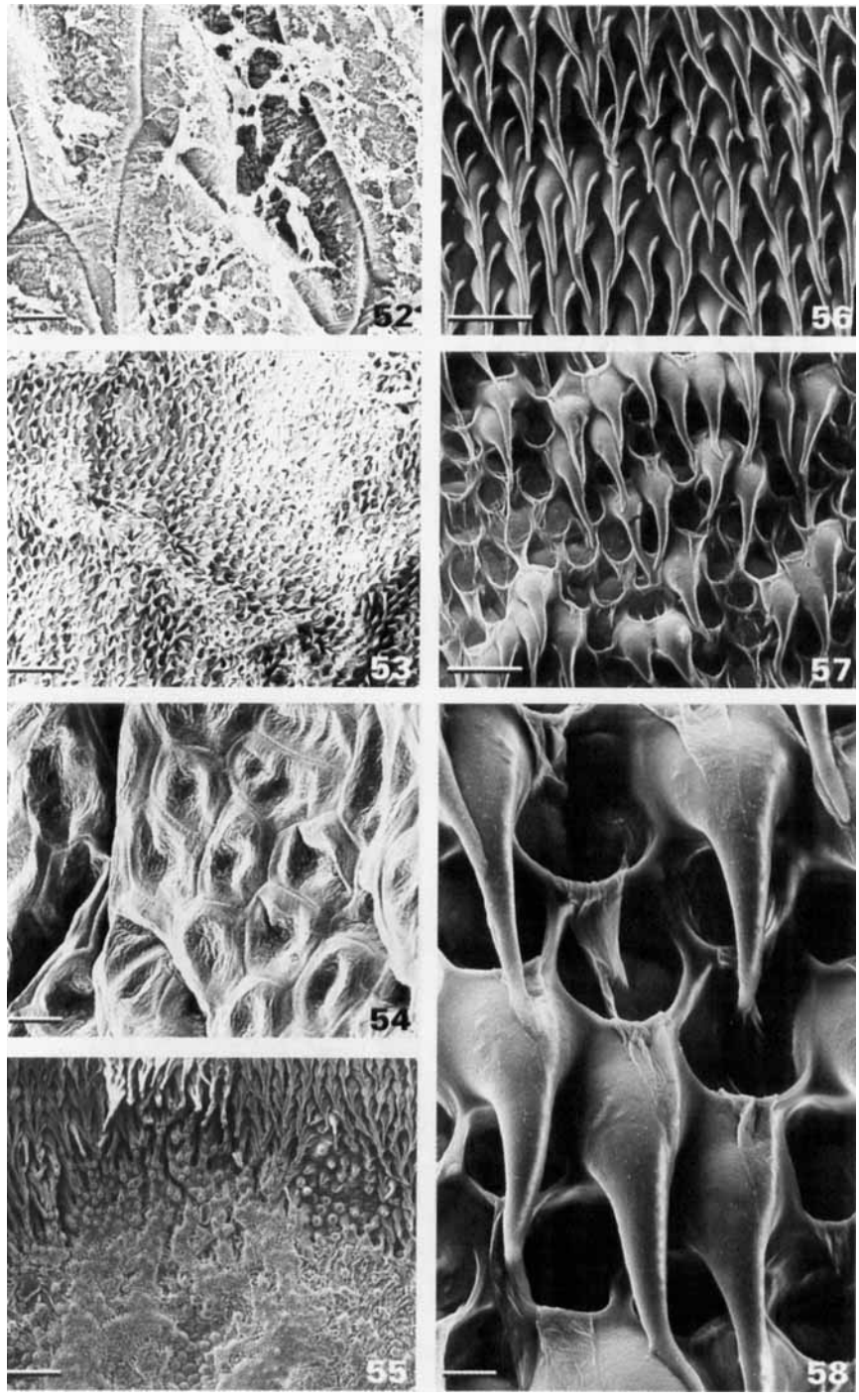
The kettle. The basal 2/3 of the wall is rough and longitudinally furrowed. The outline of the cells in this part is isodiametric with a convex outer curvature. Scarce patches of a thin mucilage covering occur (Fig. 69). The kettle compartment is constricted about 2/3 up (Fig. 60) and the surface of the wall becomes smooth and the outer curvature of the cells is gradually changed into downward pointing trichomes (Fig. 65). No alveolae are present.

The flap. The flap is similar to that of *Cryptocoryne.*

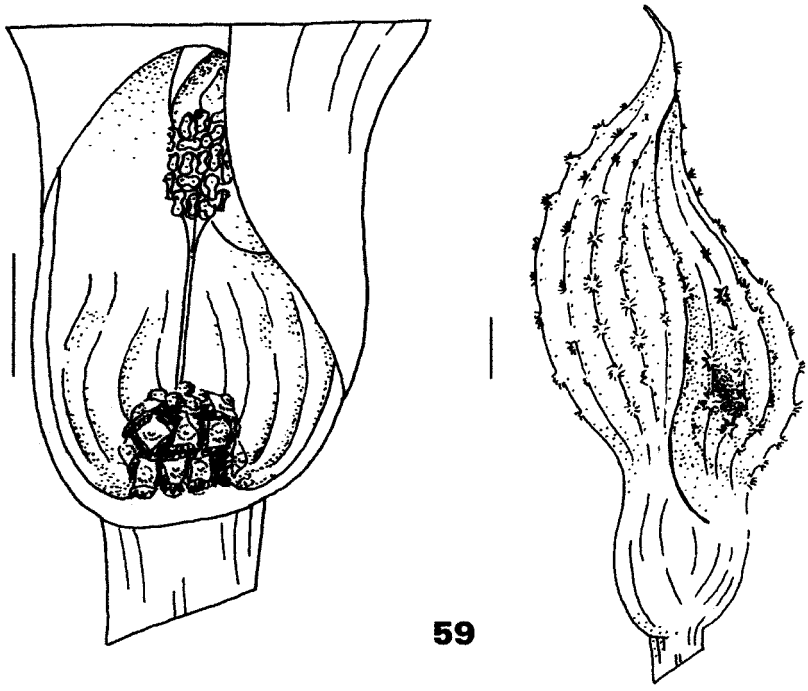
The collar. The kettle and the limb are separated by a crescent-shaped, slightly convex horizontal septum which leaves an oval opening (Fig. 63). The cells constituting the

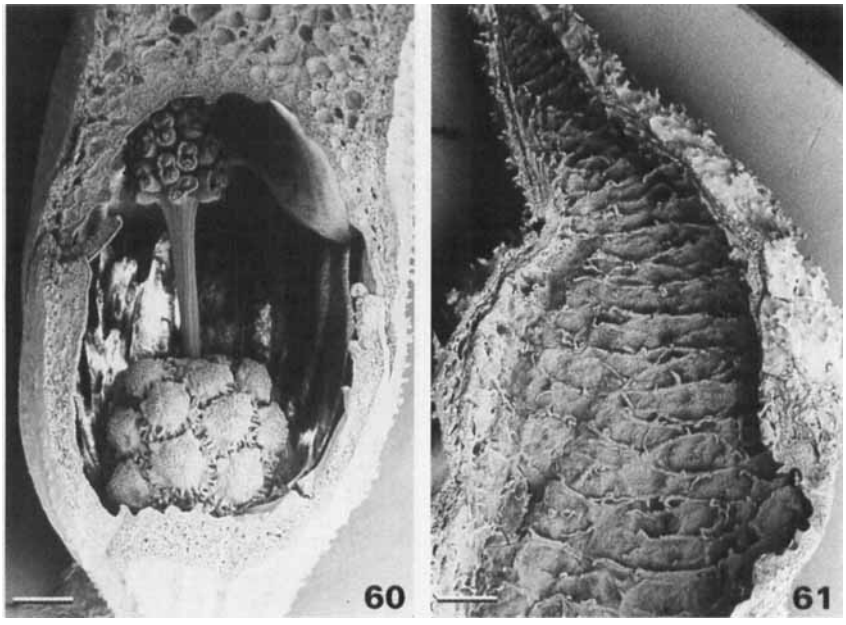


Figures 48–51. *Cryptocoryne spiralis*. Fig. 48. Generalized drawing of spathe and opened kettle. Scale bar = 0.5 cm. Fig. 49. and Fig. 50. Limb of the spathe with horizontal ridges. Scale bar = 1 mm. Fig. 51. Collar forming the septum. Scale bar = 1 mm.

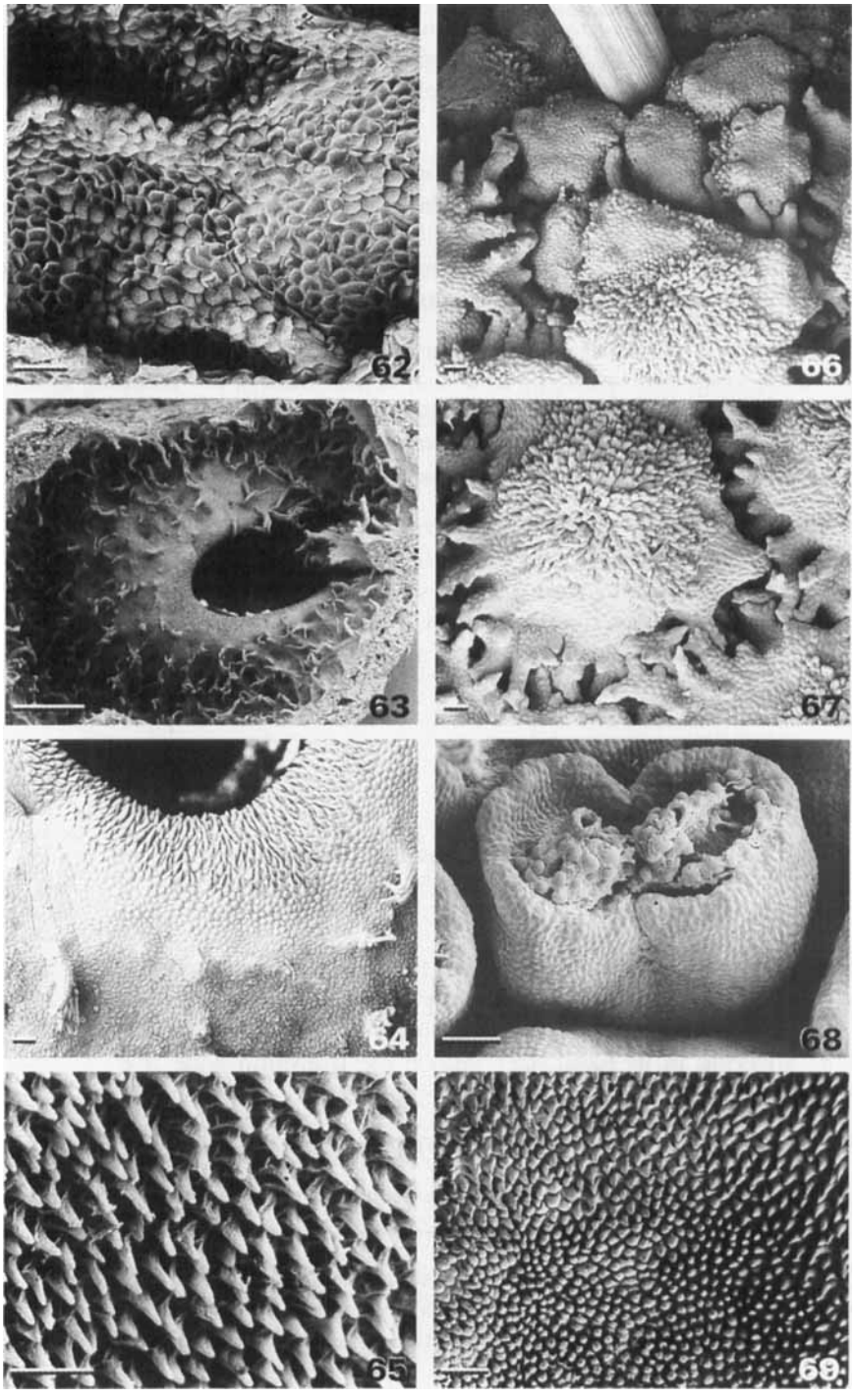


Figures 52–58. *Cryptocoryne spiralis*. Fig. 52. Flat fusiform cells of the inner surface of the limb in between the ridges. Scale bar = 10 μm. Fig. 53. Lower surface of the flap with trichomes. Scale bar = 100 μm. Fig. 54. Upper surface of the flap with slightly convex, isodiametric cells. Scale bar = 10 μm. Fig. 55. Inner surface of the kettle showing the transition zone. Scale bar = 100 μm. Fig. 56. Trichomes in the upper part of the kettle. Scale bar = 50 μm. Fig. 57. (scale bar = 50 μm) and Fig. 58. (scale bar = 10 μm). Upper part of the kettle wall with dense, downward pointing trichomes, some sunken into the cell cavity.





Figures 59–61. *Lagenandra lancifolia*. Generalized drawing of spathe and opened kettle. Scale bar = 0.5 cm. Fig. 60. Opened kettle showing spadix with female flowers situated basally and male flowers apically. Scale bar = 1 mm. Fig. 61. Limb of the spathe with horizontal ridges and protuberances. Scale bar = 1 mm.



Figures 62–69. *Lagenandra lancifolia*. Fig. 62. Limb of the spathe with horizontal ridges and protuberances. Scale bar = 100 μm. Fig. 63 (scale bar = 1 mm) and Fig. 64 (scale bar = 100 μm). Septum and collar. Fig. 65. Wall of the upper part of the kettle with trichomes. Scale bar = 50 μm. Fig. 66. Female flowers arranged in helical whorls and olfactory bodies towards the thin spadix axis. Scale bar = 100 μm. Fig. 67. Stigmas with protuberances. Scale bar = 100 μm. Fig. 68. Male flower showing the two thecae with their dehiscence pores, and pollen grains embedded in pollenkitt. Scale bar = 100 μm. Fig. 69. Wall of the lower part of the kettle showing the transition zone and the lower part with sparse mucilage coating. Scale bar = 100 μm.

edge of the opening are of the trichomatous type similar to those constituting the upper kettle wall (Fig. 64). They are gradually transformed into isodiametric cells with a convex surface. The upper surface of the septum is characterized by numerous multicellular fringes (Fig. 63).

The limb. The inside surface of the limb is rough with irregular, horizontal ridges, with numerous multicellular fringes from the ridges (Fig. 61). The cells are isodiametric in outline with a convex surface (Fig. 62). The outer surface of the spathe has multicellular fringes as well, but they occur scattered and more scarce than on the inside. The cells are isodiametric in outline, flat and with cuticular striation.

The female flowers. The female inflorescence comprises 20–30 flowers, situated at the bottom of the kettle and arranged in dense, helical whorls, not connate, around the central axis of the spadix (Figs 60, 66). Below the stigmas the flowers have many branched protuberances (Fig. 67). The stigma is papillose and globose (Fig. 67). Irregular olfactory bodies are located upwards towards the spadix axis (Fig. 66).

The male flowers. A spadix comprising more than 50 male flowers is raised 3–10 mm above the female flowers (Fig. 60). The flowers are naked, consisting of only one anther, about 0.5 mm long and 0.3 mm wide with two bilocular thecae (Fig. 68). The two thecae are united into a cushion-like structure where tuberculate cells surround the whole structure. The loculi are flask shaped and dehisce by an apical pore. The pollen grains are globular, *c.* 25 µm in diameter, and are imbedded in pollenkitt. At dehiscence the male flowers extrude a small droplet with imbedded pollen grains.

L. nairii Ramam. & Rajan
(Figs 70–73)

The kettle. About halfway up the kettle, the kettle is constricted by an increased thickness (Fig. 71). The wall is relatively smooth and even, without longitudinal furrows. The cell structure of the kettle wall is similar to that of *L. ovata* with a mucilage covering in its basal part. Above the transition zone (Fig. 73) there are cells with downwards pointing trichomes (Fig. 72).

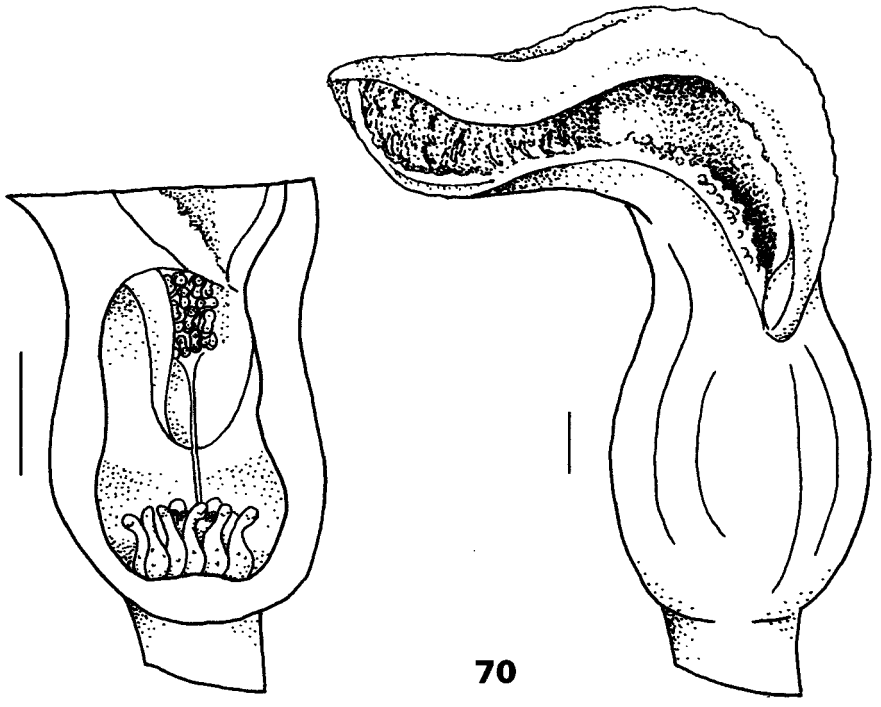
The flap. The flap is relatively large, covering the male inflorescence (Fig. 71).

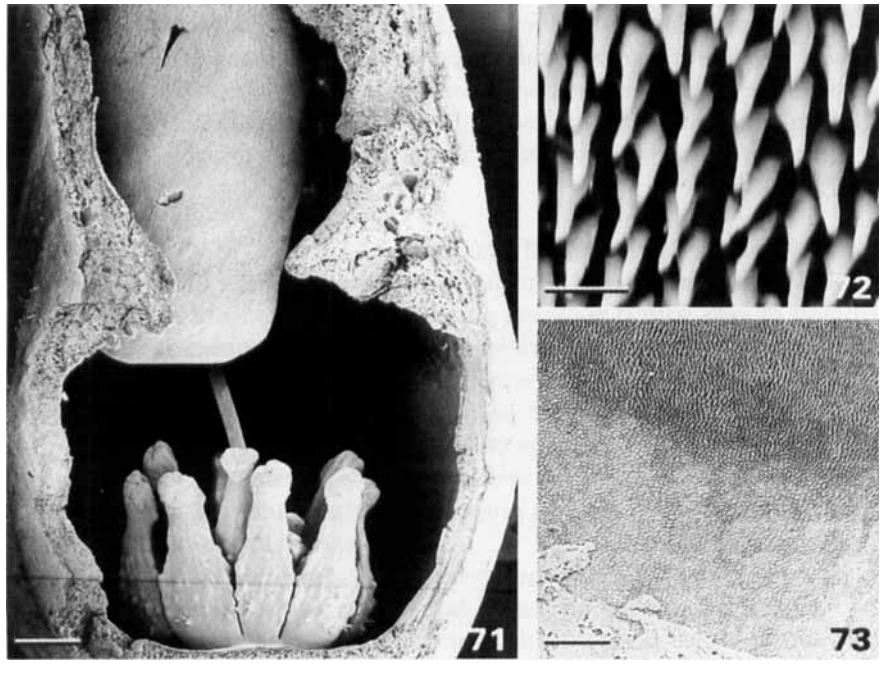
The collar. There is no septum as in *L. lancifolia*, but a collar on the limb (indicated on Fig. 70), similar to that found in e.g *C. walkeri.*

The female flowers. The female inflorescence is composed of about 10–15 flowers arranged in two whorls around the central axis of the spadix. The olfactory bodies are smaller, rounded and situated inside the whorls of female flowers (Fig. 71).

DISCUSSION

The overall macroscopical appearance and structure of the spathe in *Lagenandra* is much sturdier and firmer than in that of *Cryptocoryne.* The outer surface of the





Figures 70–73. *Lagenandra nairii*. Fig. 70. Generalized drawing of spathe and opened kettle. Scale bar = 0.5 cm. Fig. 71. Opened kettle with the flap in the upper part and free, female flowers in two whorls in the basal part. Scale bar = 1 mm. Fig. 72. Upper part of the kettle wall with trichomes. Scale bar = 50 μm. Fig. 73. Kettle wall showing the transition zone. Scale bar = 0.5 mm.

spathe in *Lagenandra* is also coarser and rougher. These features may be linked to the non-aquatic habitat of *Lagenandra*.

The SEM investigations of the cell structures of the spathes of *Cryptocoryne* and *Lagenandra* reveal that it is possible to ascertain homologous structures, even though their overall proportions and structures may differ markedly.

The kettle. The differentiation of the inner kettle wall into a basal and an upper part, often visible macroscopically, becomes very distinctive using SEM. There is often a clear cut, although uneven border, drawn by the mucilage covering in the basal part. The composition of the hitherto unobserved mucilage is unknown, but it is interpreted as a food source which attracts and feeds insects trapped in the kettle.

The curvature of the outer walls of the inner epidermal cells changes from the kettle base and upwards from long, slender, rounded tuberculate protrusions in the basal part to aculeate, downward pointing trichomes in the upper part. Vertical ridges on the kettle wall are also seen macroscopically in *Lagenandra*, a feature which is seldom seen in *Cryptocoryne* (e.g. *C. pontederiifolia*), but there is no microscopically differentiation of these ridges.

In the upper 1/3–2/3 of the kettle, alveolae are found in some species of *Cryptocoryne* (*C. albida* (Fig. 21), *C. alba*, *C. beckettii* Trimen, *C. cognata* Schott, *C. consobrina* Schott, *C. crispatula* Engl. *s.l.*, *C. cruddasiana* Prain, *C. parva* de Wit, *C. nevillii* Hook.f., *C. retrospiralis* (Roxb.) Kunth, *C. spiralis*, *C. thwaitesii* Schott, *C. undulata* A. Wendt, *C. walkeri* (Fig. 4), and *C. wendtii* de Wit). They seem to be reductions in the layer of cells constituting the kettle wall (Figs 11, 12). Cells forming the bottom of the alveolae are slightly convex without protrusions. McCann (1943) suggested that the alveolae are 'light-windows', which encourage or trick the insects to crawl up the kettle wall, in their attempt to escape from the kettle. However, it is characteristic that in most species the kettle is usually situated below the ground, so light normally does not reach the kettle.

The tube. Although the length of the tube is variable in *Cryptocoryne*, the micromorphology is quite similar. Throughout the length of the tube the inner surface is composed of cells with downward pointing trichomes identical with those in the upper part of the kettle, i.e. the cell type in the kettle continues into the tube. The downward pointing trichomes are very pronounced for the first 24 hours of anthesis. Thereafter, the cells collapse, the trichomes flatten and sink into the cell cavity creating lattice-like steps for the insects to use when leaving the spathe (Figs 18, 57, 58). This 'sinking in' of the trichomes occurs in all structures in which trichomes occur. In *Lagenandra* no real tube is present, the area around the flap up to the collar being equivalent to the tube.

The outer surface of the tube in *Cryptocoryne* is composed of flat, elongated cells with almost straight and slightly raised boundaries and longitudinal striations (Figs 16, 43). Stomata have been identified on both the outer and inner surface of the limb. The basic cell structure on the outer surface of the spathe in *Lagenandra* differs as the cells are isodiametric in outline and protuberances are more or less pronounced depending on the species (de Wit, 1978, 1990).

The flap. This structure forms a barrier separating the entrance of the kettle from the tube (Figs 21, 34, 71). The epidermal cells of the upper surface of the flap (Figs 10, 54) are isodiametrically rectangular in outline, the outer walls slightly convex

without tubercles. The upper epidermal surface of the flap is thus quite different from the inner surface of the kettle (Figs 9, 26, 29, 40).

Cells of the lower surface of the flap are comparable to those of the inner surface of the upper part of the kettle and the tube, e.g. trichome-like (Figs 20, 53). The flap structure extends into the tube as a tapering prolongation confluent with the tube margins (Figs 24, 25, 28). These findings of homologous cell structures indicate that the flap has evolved as a prolongation from the margin of the spathe.

The SEM studies have not revealed clearly identifiable stoma on either epidermal surfaces of the flap.

The collar or collar zone. Macroscopically the collar or collar zone, present in some species of *Cryptocoryne* (and a few species of *Lagenandra*), is the upper limitation of the tube demarcating the transition to the limb, often also visualized as a conspicuous difference in colour. The SEM survey reveals that microscopical changes in cell types are responsible for this visible zonation. The curvature of the outer walls of cells change rather abruptly from the trichomatous type to flat cells (Figs 7, 36).

In *Cryptocoryne* and *L. mairii* the collar or collar zone coincides with the transition of trichomes to cells with slightly convex outer walls. In *Lagenandra* the same transition (Fig. 64) is found on the crescent-shaped, slightly convex horizontal septum enclosing the kettle (also found in *C. spiralis*, Fig. 51). This indicates that the two structures are homologous, and that the shorter or longer tube found in *Cryptocoryne* is an elongation of the upper kettle wall from the area around and above the flap to the collar as in *Lagenandra.*

The structures of the spathe in *Lagenandra* and *C. spiralis* resemble each other very much, the differences being that the whole structure of the *Lagenandra* spathe is more massive and thicker. Alveolae are not found in *Lagenandra* but are in *C. spiralis.* A mucilage coating is not pronounced in *Lagenandra* and the surface of the kettle is often with vertical ridges. *Lagenandra* has free female flowers with horizontal apical stigmas, whereas *Cryptocoryne* has connate flowers and the receptive area of the stigmas is vertically bent.

In *C. albida* the collar is not present on the limb of the spathe, as the whole surface is covered with trichomes, save perhaps for the terminal upper surface of the distal part, where it was not possible to distinguish the cell type. Other species of *Cryptocoryne* which probably lack a collar structure on the limb are *C. crispatula* Engl. and *C. retrospiralis* (Roxb.) Kunth, both related to *C. albida* (Jacobsen, 1980), *C. thwaitesii* Schott related to *C. alba*, and perhaps also *C. lingua* Engl., *C. striolata* Engl., *C. keei* N. Jacobsen, *C. hudoroi* Bogner & N. Jacobsen, and *C. dewitii* N. Jacobsen. Bastmeijer & Kettner (1993) presented a collection of *C. alba* in which there is a collar structure just above the tube opening. Light microscopical investigations of the cell structure of this material show that it is a collar. Our material of *C. alba* did not show such a collar structure on the limb, although in the caudate part of the limb, cell structures could indicate the presence of a dislocation of a collar. It seems that there is a plasticity in *C. alba* regarding the position of the collar on the surface of the limb, either present as a normal collar or it may be 'present' in the caudate part where it is not recognizable.

The limb. The most prominent feature of the inner surface of the limb in *Cryptocoryne* is the irregular, often warty appearance. The SEM studies show an uneven surface composed of slightly convex cells. Stomata are rather common in this part of the spathe. Frequently they are found at the top of the protuberances (Figs 38, 39).

Horizontal ridges with protuberances are found only in *C. spiralis*. The margins of the limb are delimitated by a gradual transition from trichomes to slightly convex isodiametric cells (Fig. 45).

In *Lagenandra* the surface of the limb is completely covered by protuberances and often with ridges depending on the species (de Wit 1978, 1983, 1990).

CONCLUSIONS

It is shown that the kettle, the tube and the collar possess cell structures with unique, downward pointed trichomes. It is suggested that the downward pointed trichomes prevent insects from climbing out before they have collected pollen from the protogynous inflorescence. At the time of maturation of the male flowers, the trichomes collapse and the cell walls sink into the cell cavity, and this is suggested to create lattice-like steps for the insects to use when leaving the inflorescence. This trap-escape mechanism can be compared to the inflorescence of *Arum* L. (Araceae), which also has downward pointed papillae on the surface of the spathe, as well as flat surface cells and oil drops; here the insects climb the spadix to escape when the cells have lost their turgidity (Knoll, 1926). In the flower of *Aristolochia* L. (Aristolochiaceae) multicellular hairs protruding from the inner surface of the perianth tube prevent trapped flies, feeding on the mucilage in the 'kettle', to escape. At the time of ripening of the stamens the hairs in the perianth tube of *Aristolochia* collapse like in *Cryptocoryne* but do so by curling up (e.g. Meeuse, 1961).

The observed mucilage covering in the lower part of the kettle wall is not visible in a stereo microscope, and therefore no food attractant was known in *Cryptocoryne* and *Lagenandra*. It has been assumed that the flies were tricked into visiting the flowers lured by the carrion smell emitted from the spathe (sapromyophily). Buzgó (1997, 1998) suggested that insects are attracted over long distances by the carrion smell emitted by the spathe, and upon entering the spathe they are attracted by a more sweet odour emitted by the male flowers and olfactory bodies in search for food. The discovering of the mucilage in *Cryptocoryne* and *Lagenandra* may indicate that other, apparently sapromyophilous flowers have unobserved food attractants which are excreted from the cells as a thin residue on the floral parts.

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