

# Closing bodies in the capsular fruits of Ruschioideae (Aizoaceae)—a review

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**Keywords:** Aizoaceae, capsular fruits, closing bodies, hygrochasy, Mesembryanthema

## ABSTRACT

Capsular fruits of the Mesembryanthema<sup>\*</sup> are uniquely diverse and have been used to establish groupings within the tribe Ruschieae. The function, structure and development of the closing bodies of the Ruschioideae are reviewed from existing literature and are supplemented by personal observations, providing a framework for future research aimed at resolving critical issues regarding the structure and taxonomic implications of the closing bodies of the Ruschioideae. The number of species per taxon, distribution and presence or absence of covering membranes and closing bodies within the Mesembryanthema are tabulated.

## INTRODUCTION

In the past, the structure of the capsular fruits was considered critical in the systematics of the Mesembryanthema (Herre 1971; Hartmann 1988, 1991, 1993, 2001; Smith *et al.* 1998). In particular, it is the internal structure of the capsular fruits that yields most of the variable characters. However, with the publication of molecular data by Klak *et al.* (2003, 2007) it was found that the groupings proposed by Hartmann were not supported by molecular data.

In many Mesembryanthema the locules are covered by roof-like lids known as covering membranes, leaving only a narrow distal opening through which seeds can be dispersed. This entrance is frequently closed to some degree and the blockage has an immensely important role in the dissemination biology of the Mesembryanthema as it results in the complete or partial occlusion of the locule. Seeds are consequently locked in and cannot simply be washed out by raindrops as in other species that lack such blocking devices. This structure results in the seeds being forced out, jet-like, through the gaps between the covering membranes (Parolin 2006).

The distal closing devices are generally very diverse in their structure, but two main types are distinguished. By far the most striking are the closing bodies, which are prominent and often hemispherical structures formed on the fruit wall near the upper end of the placentas (Figure 1A). The second type of closing device (Figure 1B), in the form of bulges, ledges and rodlets (Hartmann 1991), occurs on the lower surface of the covering membrane near the distal end. In a number of species, none of these closing devices are present, but dense bundles of funi-

cles sometimes close the locule entrance to a certain extent (Figure 1C; *Lampranthus* Group, Hartmann 1988, 1991; some *Drosanthemum* species, Hartmann & Bruckmann 2000; *Hereroa*, Dehn 1992). In some Mesembryanthema, the free upper ends of the placentas contribute to the occlusion of the locules (Dehn 1992).

In this paper we are dealing only with the first type. Closing bodies are normally easily visible with the naked eye, particularly the larger ones, which can be up to 2 mm in diameter. In an open capsule they are very conspicuous as they are mostly pale and often have a shiny surface, thus contrasting with the dark brown remainder of the capsule. Owing to their prominent appearance, these bodies were already discovered in the early days of botanical exploration of the arid regions of southern Africa. The generic name of the genus *Disphyma* N.E.Br. is derived from the closing bodies (two-lobed in this case).

Much has been said about the function, structure and development of the closing bodies of the Ruschioideae (Berger 1908; Huber 1924; Lockyer 1932; Schwantes 1952, 1957; Volk 1960; Ihlenfeldt 1960, 1971; Haas 1976; Hartmann 1988, 1991, 1993; Hartmann & Gölling 1993; Kurzweil 2005). Comments on the closing bodies of individual species are also found in numerous floristic and taxonomic publications, but most of these are merely descriptions of their shape, size and colour. Detailed investigations and comparisons of these prominent capsule features are rare in literature (Poppendieck 1976; Hartmann 1988), and a number of problems exist, calling for further studies. While the overall appearance of the closing bodies was often used as a diagnostic feature of certain genera and species, there is as yet no clear and well-documented comparative survey of these bodies. Furthermore, information on fruit characters in general is scattered throughout the taxonomic literature and is often not easily accessible (language barrier, some journals not easily obtainable). The present paper aims to review the existing literature on the closing bodies of Mesembryanthema and is supplemented by personal observation. It is hoped that this review will provide the starting point for future research aimed at resolving critical issues regarding the structure and taxonomic implications of the closing bodies of the Ruschioideae.

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MS. received: 2007-04-20.

<sup>\*</sup> The subfamilies Mesembryanthemoideae and Ruschioideae together are termed Mesembryanthema (Hartmann 1991) and represent a group without taxonomic rank.



## THE CLOSING BODIES AND THEIR STRUCTURE

Closing bodies are mostly round and often hemispherical protrusions positioned on the fruit wall below the distal ends of the covering membranes at the upper end of the placentas (Figure 1A). Their size ranges from less than 1 mm to 2 mm in diameter. The closing bodies are

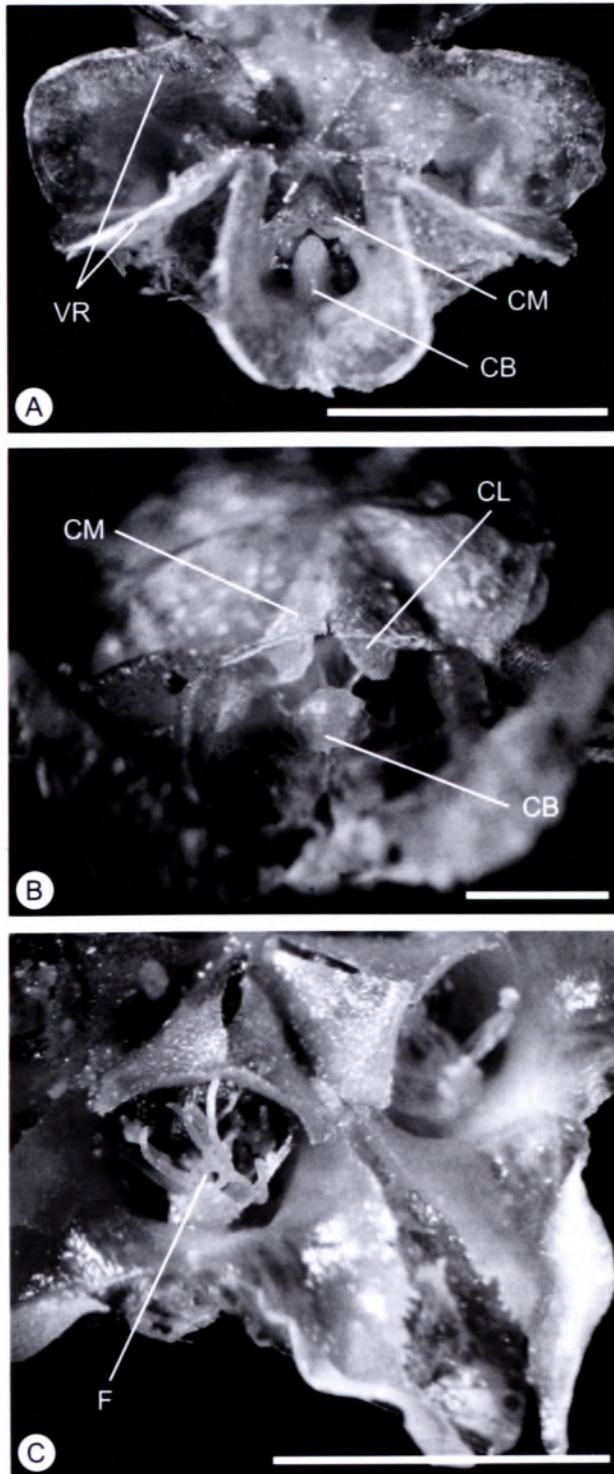


FIGURE 1.—A, *Ruschia lineolata*, Burgoyne 9848: closing bodies formed on fruit wall near upper end of placentas; B, *Ruschia* sp., Burgoyne 8102: closing ledges formed on lower surface of distal end of covering membranes; C, *Lampranthus watermeyeri*, Burgoyne 7562 or *Smicrostigma viride*, Steyn 384: dense bundles of funicles close locules. CB, closing bodies; CL, closing ledges; CM, covering membranes; F, funicles; VR, valve rims. Scale bars: A, 4 mm or 3 mm; B, C, 5 mm.

firmly united with the placentas, the upper ends of the latter often running in a pronounced groove. The larger closing bodies often touch the covering membranes and thus close the locule completely, and in many cases also reach partly under the latter. Small or tiny closing bodies are sometimes rather deeply positioned inside the locule (for example in some genera of the *Eberlanzia* Group). Prominent closing bodies have only been reported in subfamily Ruschioideae, and then only in genera that have complete or nearly complete covering membranes in their capsular fruit (although closing bodies do not occur in all of the genera with covering membranes).

The term 'closing bodies' was originally coined by Steinbrinck (1883). Later Huber (1924) considered these structures as formations of the placentas and consequently termed them 'Plazentarhöcker' (= placental tubercles). This term was subsequently adopted by many textbooks and taxonomic treatments. Ihlenfeldt (1960) on the other hand, interpreted these formations as a product of the endocarp and suggested reverting to the original term 'closing bodies'. After a detailed examination of the closing bodies of *Pleiospilos* N.E.Br., Hartmann & Liede (1986: 458) also rejected Huber's controversial term 'tubercle' as completely inadequate.

The shape of the closing bodies of the Ruschioideae is very diverse. Particularly elaborate closing bodies are found in Hartmann's (1993) *Leipoldtia* Group. They are normally rather large and consist of a 'head' borne on a distinct stalk. Anatomically, the central part is made up of large, spongy cells covered by several cell layers of sclerenchymatic tissue. Smaller rodlet-shaped closing bodies are found in the *Ruschia* type of fruit (Hartmann 1988) and have a similar anatomy. Comparatively small, hook-shaped closing bodies are found in the *Titanopsis* type of fruit, and they consist of sclerenchymatic cells only (Hartmann 1988: 327). The closing bodies of the *Mitrophyllum* type of fruit are not prominent hemispherical bodies, but appear as broad ridges or bosses where the placentas and expanding keels meet (Poppendieck 1976; Ihlenfeldt & Struck 1987). Their epidermis is only moderately thick-walled and an extensive spongy tissue is present. In some genera referred to this fruit type, broad, spongy closing bodies have the shape of ledges and have also been termed as such (Hartmann 1991); the closing ledge of *Dorotheanthus* Schwantes has been referred to as 'Verschlusswall' (= closing sill) (Ihlenfeldt & Struck 1987). Hartmann (1988) suggested that these aforementioned types of closing bodies are not all homologous.

According to their ontogenetic derivation, most of the closing bodies of the Ruschioideae are endocarpal structures. A few other species possess small placental closing bodies, which have a different texture and anatomy (Hartmann 1988). This emerged originally from a careful study of the closing bodies of *Pleiospilos* (Hartmann & Liede 1986) where the following were observed: 1, endocarpal closing bodies are often large, although small and insignificant endocarpal bodies have also been reported occasionally, e.g. *Tanquana* H.E.K.Hartmann & Liede (1986). Endocarpal closing bodies comprise an epidermis of sclerenchymatic cells over a body of isodiametric cells with equally thick walls, the central part of the closing body comprising



either parenchymatic or sclerenchymatic cells. Thus they differ markedly from the cells of the placentas which have unthickened walls throughout. The derivation of these prominent closing bodies from endocarpal tissue has also been found by Kurzweil (2005); 2, placental closing bodies are rare in the Mesembryanthema and contribute only a little to the occlusion of the locule. Examples include *Malephora* N.E.Br., *Pleiospilos nelii* Schwantes, *P. simulans* (Marloth) N.E.Br. and *P. bolusii* (Hook.f.) N.E.Br. (Hartmann & Liede 1986). They are made up of cells with only weakly thickened or unthickened walls, although the cell walls of the epidermis can be strongly thickened. In *Drosanthemum* Schwantes, the endocarp may form a little protrusion, lifting the closing body slightly (Hartmann & Bruckmann 2000: 81).

The genera *Disphyma* and *Rhombophyllum* (Schwantes) Schwantes have two-lobed closing bodies. The situation in a few other genera is somewhat reminiscent of this condition as the closing bodies and their stalks have a more or less deep groove (although this is often largely obscured by the placentas). It is suggested that this partial or complete two-lobed condition is a reflection of the origin from two carpel margins (Kurzweil 2005).

While in most genera the closing bodies are constant in their size and can therefore be used as diagnostic characters, some intraspecific variation was found in *Mitrophyllum* Schwantes (Poppendieck 1976), *Dorotheanthus* subgen. *Dorotheanthus* (Ihlenfeldt & Struck 1987) and *Disphyma* (Chinnock 1996). The shape of the closing bodies of *Odontophorus marlothii* N.E.Br. varies even within the same capsule (Hartmann 1976).

#### DISTRIBUTION OF CLOSING BODIES IN THE RUSCHIOIDEAE

Only the subgroups of subfamily Ruschioideae are treated here, as closing bodies do not occur in subfamily Mesembryanthemoideae (Figure 2A). The following is a brief review of detailed investigations of the closing bodies of individual genera in the literature. Comparative descriptions and discussions of these structures can also be found in Hartmann (1983, 1988) and Dehn (1992). Overall descriptions of shape, size, colour and consistency of closing bodies are found throughout taxonomic and floristic literature and are not listed here.

The arrangement of the subfamilies and tribes follows the classification of Klak *et al.* (2003). The large subfamily Ruschioideae is divided in four groups (clades), two of these representing the tribes Apatesieae and Dorotheantheae (corresponding to the *Apatesia* and *Cleretum* Groups of Hartmann 1993). They form a monophyletic, well-supported group, supported by molecular data (Klak *et al.* 2003). The remaining two clades fall within the tribe Ruschieae in which few DNA sequence changes have been observed (Klak *et al.* 2003). Hartmann (1988) has proposed 10 groups for the species in the tribe Ruschieae. Table 1 gives a short summary of the number of species per taxon, distribution and presence or absence of covering membranes and closing bodies within the Mesembryanthema.

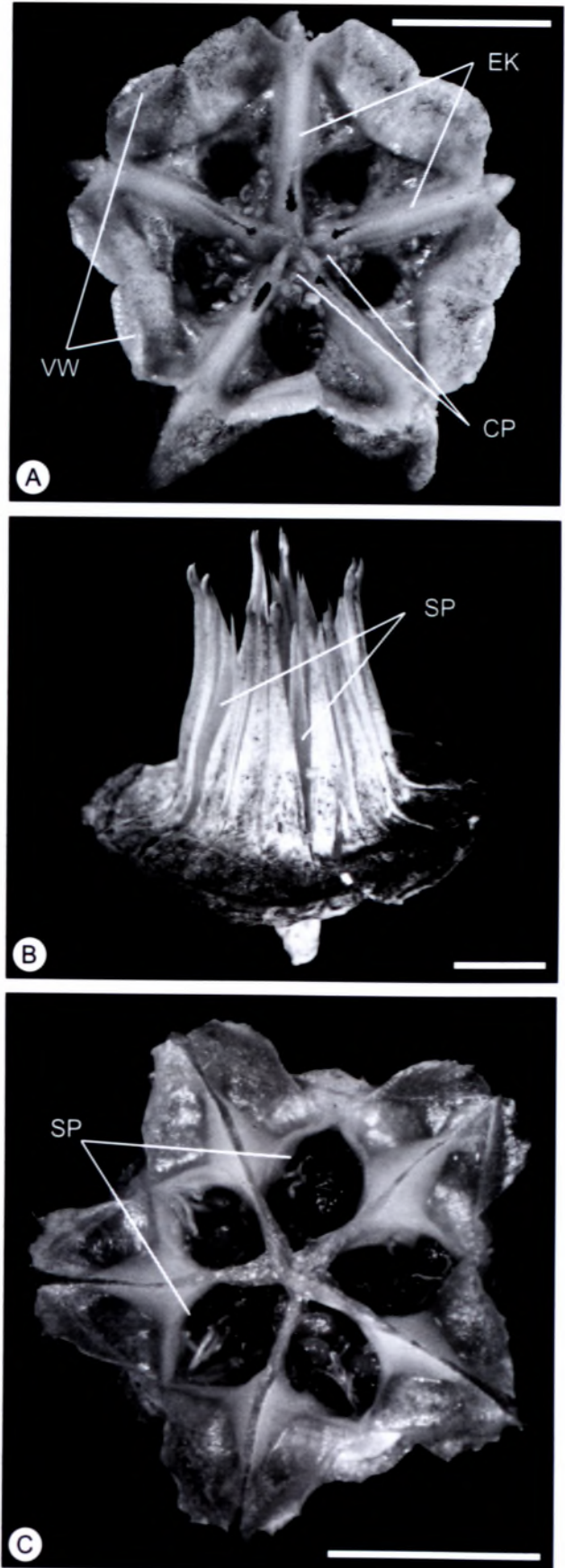


FIGURE 2.—Fruit types. Mesembryanthemoideae: A, *Mesembryanthemum hypertrophicum*, Burgoyne 10349. Tribe Apatesieae: B, *Conicosia pugioniformis* (L.) N.E.Br. subsp. *alborosea* (L.Bolus) Ihlenf. & Gerbault, Burgoyne 10378. Tribe Dorotheantheae: C, *Cleretum papulosum* (L.f.) L.Bolus subsp. *papulosum*, Burgoyne 9396(b), showing prominent seed pockets. CP, central placentation; EK, expanding keels (parallel); SP, seed pockets; VW, valve wings. Scale bars: A, 6 mm; B, 10 mm; C, 4 mm.



### Tribe **Apatesieae** *Ihlenf., Schwantes & Straka*

This tribe corresponds to the *Apatesia* Group of Hartmann (1993). Fruit capsules are characterized by the reduction of hygrochasy, absence of valve wings and frequent seed retention in seed pockets (Figure 2B, *Apatesia* type of fruit; Hartmann 1988). The capsules are sometimes schizocarps that break up into mericarps (especially prominent in the genus *Caryotophora* Leistner), which are then dispersed as a whole. Covering membranes as well as closing bodies are absent.

### Tribe **Dorotheanthae** (*Schwantes ex Ihlenf. & Struck*) *Chess., Gideon F.Sm. & A.E.van Wyk*

The species of this group (corresponding to the *Clertum* Group of Hartmann 1993) have capsules with or without covering membranes and prominent expanding sheets (Figure 2C). Sometimes they have comparatively insignificant closing bodies (Hartmann 1988, 1991), developed as swellings, spongy sills or ridges but not as large, hemispherical structures as in other Mesembryanthema genera. These closing bodies have a broad base, which is typical of the *Mitrophyllum* type of fruit to which the Dorotheanthae are referred (Hartmann 1988). Ihlenfeldt (1960) and Ihlenfeldt & Struck (1987) also described these ridge-like closing bodies (referred to as 'Verschlusswall' = closing sill), which are found in some species of the genus *Dorotheanthus*. They are best developed in *D. bellidiformis* (Burman) N.E.Br. subsp. *bellidiformis*. Generally, the ridge-like closing bodies of this group are interpreted as a product of the endocarp and not the placenta (Ihlenfeldt 1960: 49). In the genus *Dorotheanthus*, the occurrence of the seven different capsule

types defined on the basis of features of the covering membranes and closing bodies is geographically correlated, and species with capsules that have pronounced closing bodies are more frequent in the southern parts of the distribution area (Ihlenfeldt & Struck 1987).

### Tribe **Ruschiae** *Ihlenf., Schwantes & Straka*

This group comprises most of the Ruschioideae, currently including nearly 1 600 species. An enormous diversity in the capsular fruit structure is found in this group.

#### *Mitrophyllum* Group

The capsules have mostly been referred to the *Mitrophyllum* type of fruit (Figure 3A; Hartmann 1988). Covering membranes are mostly complete but are sometimes reduced, and the surface of expanding keels are extended to form flat expanding sheets. Closing bodies are sometimes present, and are mostly developed as spongy sills or ridges and have a broad base. They are rather variable in the extent of their formation but are rarely very large (*Glottiphyllum* (Haw.) N.E.Br.). Valve wings are mostly broad, though sometimes very narrow or absent.

In *Disphyma* the closing bodies are deeply two-lobed (Chinnock 1996). However, in *D. papillatum* Chinnock the closing bodies are variable in size and range from well developed to vestigial, and *D. australe* (Aiton) J.M.Black lacks closing bodies altogether. An abnormal population of this species with variously shaped finger-like outgrowths at the entrance of the locules was reported by Chinnock (1996). *Glottiphyllum* has large

TABLE 1.—Distribution of closing bodies in the Mesembryanthemaceae. Subfamilies and tribes after Klak *et al.* (2003), informal groups after Hartmann (1991, 1993, 1998a). Approximate numbers of species follow Hartmann (1993) and Klak *et al.* (2003, 2007)

Taxon	No. species	Distribution	Covering membranes	Closing bodies
Subfamily Mesembryanthemoideae	± 102	Widespread in South Africa and Namibia; <i>Mesembryanthemum</i> also in coastal areas worldwide	Absent	Absent
Subfamily Ruschioideae				
Tribe Apatesieae	11	Mainly western parts of South Africa, with <i>Conicosia</i> ranging into southern Namibia	Absent	Absent
Tribe Dorotheanthae	11	Western parts of South Africa	Present or absent	Present as a ledge or absent
Tribe Ruschiae				
<i>Mitrophyllum</i> Group	51	Widespread in South Africa, with <i>Disphyma</i> ranging into Australia and New Zealand	Present or absent	Present (broad-based) or absent
<i>Delosperma</i> Group	325	Widespread in southern Africa, with <i>Delosperma</i> ranging into eastern Africa and Yemen	Present or absent	Very rarely present
<i>Stomatium</i> Group	102	South Africa and southern Namibia	Present or absent	Mostly absent
<i>Titanopsis</i> Group	79	Widespread in South Africa and Namibia	Present or absent	Very rarely present
<i>Dracophilus</i> Group	122	Widespread in South Africa and southern Namibia	Mostly reduced	Absent
<i>Bergeranthus</i> Group	54	Widespread in South Africa and southern half of Namibia	Mostly complete	Mostly present, but often small
<i>Lampranthus</i> Group	248	Widespread in South Africa and southern Namibia, with <i>Carpobrotus</i> extending to coastal areas worldwide	Complete	Almost always absent
<i>Ruschia</i> Group	375	Widespread in South Africa and Namibia	Complete, often convex	Small to medium-sized, often hook-shaped
<i>Leipoldtia</i> Group	163	Widespread in South Africa and southern Namibia	Complete, often concave	Large and stalked, rarely small
<i>Eberlanzia</i> Group	17	Western parts of South Africa, southwestern Namibia	Complete	Large or small, sometimes deep in locule



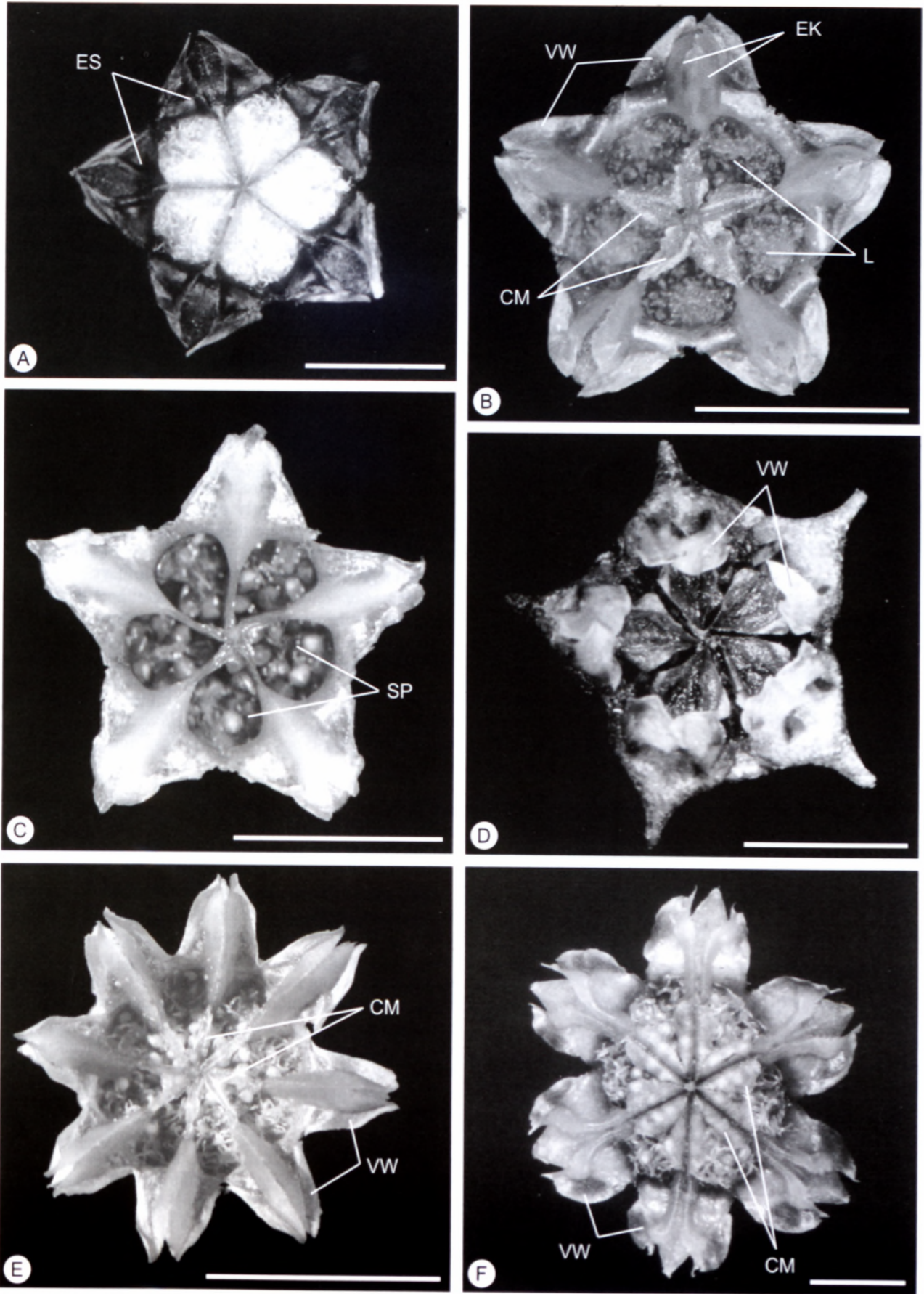


FIGURE 3.—Fruit types. *Mitrophyllum* type: A, *Monilaria chrysoleuca*, Burgoyne 9454B. *Delosperma* type: B, *Delosperma floribundum*, Muller 1776. *Stomatium* type: C, *Stomatium* sp., Burgoyne 8966. *Faucaria* type: D, *Faucaria* sp., Van Jaarsveld 11104, with prominent valve wings borne erect. *Dracophilus* type: E, *Juttadinteria deserticola* (Marloth) Schwantes, Burgoyne 8453B. *Titanopsis* type: F, *Titanopsis calcarea* (Marloth) Schwantes, Burgoyne 9619. CM, covering membranes (reduced); ES, expanding sheets; EK, expanding keels; L, locules; SP, seed pockets; VW, valve wings. Scale bars: A, B, 6 mm; C, 5 mm; D, 4 mm; E, 9 mm; F, 3 mm.



spongy closing bodies with a broad base; their endocarpal origin has been shown by Hartmann & Liede (1986). Hartmann's (1991) concept to include *Glottiphyllum* in the *Mitrophyllum* Group is also supported by features of the expanding tissue (Hartmann & Gölling 1993). Earlier, an alternative concept was proposed by Schwantes (1952) listing this genus under his *Glottiphyllum* type of fruit, together with the genera *Cheiridopsis* N.E.Br., *Pleiospilos* and *Argyroderma* N.E.Br. In *G. difforme* (L.) N.E.Br., *G. fergusoniae* L.Bolus, *G. nelii* N.E.Br. and *G. oligocarpum* L.Bolus, the closing bodies are over-arched by a tongue- or triangle-like tissue of the outer locule wall (Hartmann & Gölling 1993). The closing bodies of various species in the genus *Mitrophyllum* are variable in the extent of their formation even within the same population (Poppendieck 1976). They are generally apparent as swellings or swollen ridges in a position where the placentas and the expanding sheets meet. Anatomically, they are made up of isodiametric cells with strongly thickened walls. The epidermis in their proximal part consists of similar cells but the cells in the distal part are elongate (when seen in a longitudinal section) and have weakly thickened walls, thus resembling the cells of the adjacent expanding tissue.

#### *Delosperma* Group

The capsules of this group (Figure 3B) are rather diverse, and the different genera were referred to the *Delosperma* N.E.Br., *Drosanthemum* and *Lampranthus* N.E.Br. types of fruit (Hartmann 1988). Seed pockets occur occasionally. Expanding keels are usually distinct from the expanding sheets and the valves have mostly broad wings. Covering membranes are present or absent. Closing bodies are almost always absent, but the genus *Malephora* often has knobs on the distal end of the placentas which act as closing bodies (Hartmann 1988: 56); these placental closing bodies may also be bilobed. Small and often bilobed endocarpal closing bodies are found in some species of the genus *Drosanthemum*, and most species of this genus have placental closing bodies (Hartmann & Bruckmann 2000).

#### *Stomatium* Group

The capsules can mostly be referred to the *Delosperma* and *Drosanthemum* types of fruit of Hartmann (1988). Covering membranes are present or absent, and valve wings are broad to reduced or absent. Seed pockets derived from basal false septa are found in *Stomatium* Schwantes (Figure 3C). Closing bodies are normally absent in the group but small, obscure ones are found in *Orthopterum* L.Bolus.

Herre (1971) stated that distinct bifid closing bodies were also found in *Chasmatophyllum maninum* L.Bolus, whereas they were absent in the rest of this genus. We examined the notes accompanying the protologue made by Bolus (1927), where she stated that capsules of *C. maninum* were not yet available and a drawing of the portion of a capsule of *C. musculinum* (Haw.) Dinter & Schwantes was given, showing bifid closing bodies. Both Bolus and Herre made an error in citing bifid closing bodies for *Chasmatophyllum maninum*. Examination by the authors of many recently collected specimens of *C. musculinum* has shown no bifid closing bodies.

Hartmann (1988) placed *Faucaria* Schwantes and *Orthopterum* in this group, but for an alternative view, which is followed below, see Groen & Van der Maesen (1999).

#### *Faucaria* Group

This group corresponds to the section established by Schwantes (1952) and reinstated by Groen & Van der Maesen (1999) and comprises only two genera (*Faucaria* and *Orthopterum*) as their capsules are unique (Figure 3D). When the capsules are viewed after wetting, one gets the impression that they are empty, as locules are hidden by lamellae curving over the top of the locules. The capsules are 5(6)-locular and are deep, the valves with fissures between them. Conventional covering membranes and closing bodies are absent and expanding keels end in an awn. The deep locules combined with curved lamellae are highly effective in retaining seeds during periods of low rainfall. Capsules can become detached after ripening by being pushed out by the enlarging leaf pair produced the following season and may roll away, but are never found more than a few centimetres from the parent plants (Groen & Van der Maesen 1999). Particularly prominent valve wings are found in *Faucaria* where they are borne erect when the capsule is open. When dry, these valve wings fold back into thin grooves. *Orthopterum* has similar fruits with their septa separated into two parts, the upper part arching on top of the capsule.

#### *Titanopsis* Group

The capsules of this group (Figure 3F), mostly referred to Hartmann's (1988) *Titanopsis* Schwantes and *Delosperma* types, have well-developed or reduced covering membranes and broad valve wings which taper distally. Closing bodies are mostly absent, although they are developed as tiny (rarely prominent) structures in some species of *Aloinopsis* Schwantes, *Tanquana* and *Ihlenfeldtia* H.E.K.Hartmann.

The genus *Ihlenfeldtia* was established to include two species previously included in *Cheiridopsis* (Hartmann 1992). This genus is characterized by its distinct fruit morphology, with mostly 10 locules, thin, straight, complete covering membranes, and valve wings that are broad at the base. Endocarpal closing bodies are present and are illustrated by line drawings in Hartmann's publication. Anatomically, they comprise a translucent layer of vertical cells on top of a sclerenchymatic body. The small genus *Tanquana* was separated from *Pleiospilos* as it differs in several characters including its fruit structure (Hartmann & Liede 1986). Capsules were shown to be generally less robust than those of *Pleiospilos*, having thinner valves and covering membranes. Important distinguishing features were found in the structure of the closing bodies, which are small and of endocarpal origin.

#### *Dracophilus* Group

Fruits of this group (Figure 3E) mostly belong to the *Delosperma* type of capsule (Hartmann 1988). Covering membranes are mostly reduced to form a narrow rim, and valve wings are usually prominent. Closing bodies are generally absent.



*Bergeranthus* Group

This group has fruits that are close to the *Mitrophylum* type of Hartmann (1988) but generally have stout and firm covering membranes (Figure 4A). The valve wings are mostly reduced to narrow organs and are often awn-like; occasionally they are absent altogether. Closing bodies are present or absent.

The spongy closing bodies of *Bergeranthus* Schwantes are rather large plates (Schwantes 1952: 16; Hartmann 1993: 61). In *Cerochlamys* N.E.Br., the small closing bodies are of placental origin and they are frequently over-arched by a translucent layer of tissue that is derived from the expanding sheets (Hartmann 1998b: 52). The placental closing bodies of *Hereroa* (Schwantes) Dinter & Schwantes are tiny (Hartmann 1993: 61). In this genus the locule entrance is often closed by long funicles (Dehn 1992: 135). Small and frequently deeply set closing bodies are found in *Machairophyllum* Schwantes where they may be irregular in shape (Kurzweil & Chesselet 2003). *Rhombophyllum* species have large, flat or rounded and bipartite closing bodies (Schwantes 1952: 15–17; Hartmann 1993: 61).

*Lampranthus* Group

Most genera of this group have capsules of the *Lampranthus* type (Figure 4B; Hartmann 1988). While hygrochastic capsules are the norm, *Carpobrotus* N.E.Br. species differ by being the only genus within the tribe Ruschieae to have indehiscent fleshy berries (Figure 5A). Locules have rigid covering membranes with additional closing devices at the distal end. Together with sterile funicles, these closing devices on the underside of the covering membranes are largely responsible for closing the entrance to the locule. Valve wings are present or absent. Prominent closing bodies have only been reported in the genus *Enarganthe* N.E.Br. (Herre 1971) but are absent in all other genera.

*Ruschia* Group

This is a large group with fruits mostly of the *Ruschia* type (Figure 4C; Hartmann 1988). Fruits normally remain on the plants (occasionally up to several years) and release the seeds after dehiscence, but tumble fruits are found in *Khadia* N.E.Br. and rarely also in *Ruschia* Schwantes. The frequently deep locules have firm, complete covering membranes with additional closing devices at the distal end. Expanding keels are often widely diverging and valve wings are mostly absent or reduced. Closing bodies are small or medium-sized and hook- or rodlet-shaped. They are comparatively large in *Acrodon* N.E.Br. (Burgoyne 1998), a genus with a capsule structure that is somewhat reminiscent of the *Leipoldtia* type of fruit according to Hartmann (1988).

An endocarpal closing body that is largely covered by the placenta was reported in *Ebracteola montis-moltkei* (Dinter) Dinter & Schwantes (Hartmann 1996: 39). Closing bodies of *Khadia* are of complex composition (Chesselet & Hartmann 1995; Chesselet *et al.* 1998), and the various types can be used to identify the different species of the genus: the 'closing bodies' are either prominent placental formations or endocarpal protrusions and



FIGURE 4.—Fruit types. *Bergeranthus* type: A, *Bergeranthus multi-ceps* (Salm-Dyck) Schwantes, Burgoyne 8918. *Lampranthus* type: B, *Lampranthus watermeyerii*, Burgoyne 7562. *Ruschia* type: C, *Ruschia maxima* (Haw.) L.Bolus, Burgoyne 8767. CB, closing bodies; CM, covering membranes; EK, expanding keels; F, funicles; VW, valve wings. Scale bars: A, 4 mm; B, 7 mm; C, 5 mm.



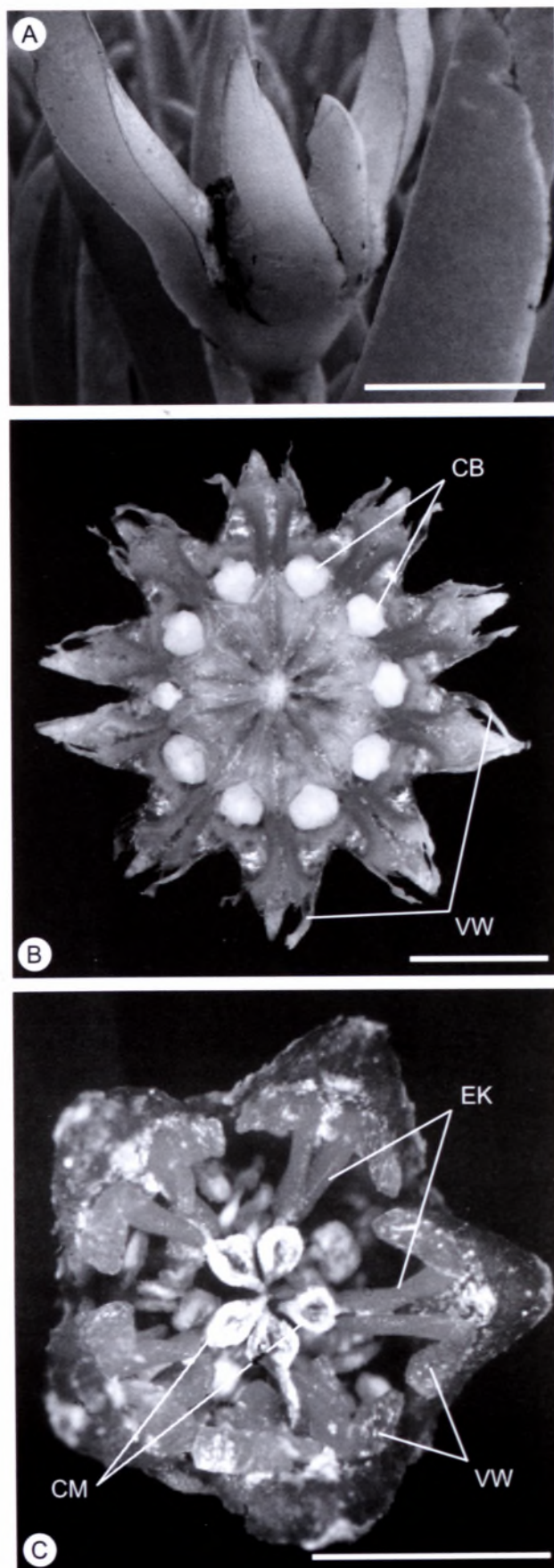


FIGURE 5.—Fruit types. Fleshy in A, *Carpobrotus edulis* (L.) L.Bolus subsp. *edulis*, Burgoyne 6317. *Leipoldtia* type: B, *Cheiridopsis namaquensis* (Sond.) H.E.K.Hartmann, Burgoyne 9487. *Eberlanzia* type: C, *Stoeberia frutescens* (L.Bolus) Van Jaarsv., Burgoyne 10323. CB, closing bodies; CM, covering membranes; EK, expanding keels; VW, valve wings. Scale bars: A, 25 mm; B, 5 mm; C, 4 mm.

are partly covered by some outgrowth of the expanding sheets. Dehn (1992) showed that the endocarpal closing bodies of *Ruschia* are comprised mainly of irregular, thin-walled cells, and are covered by 3–6 layers of prosenchymatic and moderately thick-walled cells plus a one-layered sclerenchymatic epidermis, which corresponds well with the observations of Hartmann & Liede (1986). Based on structure, six types of closing bodies were distinguished by Hartmann & Liede (1986) in the study of *Ruschia* and related genera.

#### *Leipoldtia* Group

Most genera of this group were referred to the *Leipoldtia* type of fruit (Figure 5B; Hartmann 1988), characterized by: 1, persistent,  $\pm$  concave, complete covering membranes that frequently have additional closing devices in the form of bosses or ledges; 2, mostly large and distinctly stalked closing bodies; 3, broad (rarely reduced) valve wings.

Capsules normally remain on the plant but tumble fruits are known in *Fenestraria* N.E.Br. and *Cephalophyllum* N.E.Br. This is the only group of Mesembryanthema in which the closing bodies are consistently present as prominent structures. They are also large in most genera—comparatively small closing bodies are found only in *Fenestraria* (Hartmann 1982), *Jordaaniella* H.E.K. Hartmann (Hartmann 1984) and *Cylindrophyllum* Schwantes (Herre 1971). Their surface is often rugose (Hartmann 1991: 124). The texture of the closing bodies of this group is corky, with sclerenchymatic outer layers. Most genera of this group have been taxonomically revised by H.E.K. Hartmann (several papers, see below; sometimes with co-workers), with detailed comments on many plant features including the closing bodies.

As part of a detailed study of the genus *Antimima* N.E.Br. emend Dehn, Dehn (1988) described the closing bodies and illustrated them by means of line drawings and SEM micrographs. The large closing bodies are short-stalked and of endocarpal origin. Hartmann (1977) revised the genus *Argyroderma* and examined the late development of the closing bodies of *A. congregatum* L.Bolus. It was shown that the cells of the closing bodies still have unthickened walls at the time of anthesis and become thickened only later. The structure and position of the closing bodies of the genus *Cephalophyllum* was described by Hartmann (1978). According to Hartmann & Dehn (1987), species of *Cheiridopsis* have large closing bodies in the mature fruits, which often partly reach under the distal parts of the covering membranes and close their entrance entirely. No taxonomic correlation of the different types of closing bodies was found. An informative SEM micrograph of the stalked closing body of *Leipoldtia schultzei* (Schlechter & Diels) Friedrich was shown by Hartmann & Rust (1994). The shape and surface of the closing bodies of *Odontophorus marlothii* was found to be variable within one population and even within the same capsule, and can therefore not be used as a diagnostic feature (Hartmann 1976). The genus *Pleiospilos* was examined in detail by Hartmann & Liede (1986). It was shown that the five species of *P.* subgenus *Punctillaria* have large endocarpal closing bodies that close the locule entrance almost completely and are entirely made up of sclerenchymatic cells. The epidermis cells are elongate (vertically arranged), whereas the cells of subja-



cent layers are isodiametric. The three species of *P.* subgenus *Pleiospilos* have small placental closing bodies comprising isodiametric cells with unthickened walls although their epidermis cells can have slightly thickened walls.

In our opinion, *Antimima* and *Cylindrophyllum* do not belong in the *Leipoldtia* Group. *Antimima* is better placed within the *Ruschia* Group and *Cylindrophyllum* belongs in the *Bergeranthus* Group.

#### *Eberlanzia* Group

This small informal group was established by Hartmann (1998a). In *Eberlanzia* Schwantes (Figure 5C) and *Amphibolia* L.Bolus, the fruit structure is similar to that of *Ruschia* except for the broad valve wings. Closing bodies in the group are small or large, sometimes deeply set in the locule. Fruits breaking up into nutlets are found in *Stoeberia* Dinter & Schwantes where the anemochoric seeds are also unusual. SEM illustrations of closing bodies of *Amphibolia laevis* (Aiton) H.E.K.Hartmann were shown by Hartmann & Dehn (1989).

#### FUNCTIONAL ASPECTS

Seed dispersal in the Mesembryanthemaceae is defined as ombrohydrochorous, i.e. triggered by rain drops. The covering membranes, which prevent the simple washing-out of the seeds, always comprise two parts that are arranged roof-like but are never fused on top. It has been shown that the association of flexible covering membranes and prominent closing bodies results in an increased water pressure in the locule after a direct hit by a rain drop (Parolin 2006), and consequently the seeds are expelled jet-like, following a bending of the covering membranes (Berger 1908; Lockyer 1932; Schwantes 1952). Lockyer (1932) showed that this complete occlusion of the locule actually promoted dissemination in space, as jet-like expelled seeds fell further from the parent plant than merely washed-out seeds would. The same mechanism also protracts dispersal in time, i.e. results in slow or delayed release of the seeds (Ihlenfeldt 1971), and this is obviously ecologically advantageous in the arid habitat of the Mesembryanthemaceae. The role of the small closing bodies of some species that close the distal entrance of the covering membranes only partly is not fully understood as yet, e.g. *Tanquana* (Hartmann 1983: 37; Hartmann & Liede 1986: 461). Those species that lack prominent closing bodies altogether often have other devices to achieve the occlusion of the locules, such as protrusions from the covering membranes in the form of ledges, sills, bulges or rodlets, by sterile funicles or by free ends of placentas. This seems to suggest that the occlusion of the locules is favoured by natural selection but is achieved by different means. Capsule types that have only very incomplete or no covering membranes are clearly less efficient with regard to their seed dispersal (e.g. Ihlenfeldt & Struck 1987). These species also tend to be found in areas of higher rainfall (e.g. *Delosperma*), where it is not critical if seed is disseminated in one rainfall event if this is closely followed by more rain.

From an evolutionary point of view, certain adaptive pressures on dispersal mechanisms can influence the

size and shape of the closing bodies, as they are obviously correlated with the dispersal syndrome. This was illustrated by Hartmann (1988: 329) in the example of *Fenestraria*—this species is dispersed as tumble fruits, and therefore only small closing bodies have evolved in its capsules.

#### TAXONOMIC SIGNIFICANCE

In view of our incomplete knowledge of the closing bodies of the Mesembryanthemaceae, it is premature to make firm proposals regarding the taxonomic significance of their structure. Owing to the variation observed in some genera and the only sporadic occurrence of these bodies, it is unlikely that extensive studies will eventually yield taxonomically significant features. While the structure of the closing bodies does not permit a new classification, some correlations to fruit types can be observed (Hartmann 1988: 327). Nevertheless, the structure and size of the closing bodies can mostly be used as diagnostic features of individual species and genera, and partly also of larger informal groups (Hartmann 1991, 1993).

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