MESEMBS WITH NUT-LIKE SCHIZOCARPIC FRUIT AND *RUSCHIANTHEMUM* FRIEDRICH SUNK UNDER *STOEBERIA* DINTER & SCHWANTES

INTRODUCTION

Fruit of most Mesembryanthemaceae are hygrochastic: they open, disperse seed and close again in response to moisture. This moisture-mediated mode of seed dispersal is achieved through a sophisticated mechanism based on the hygroscopic properties of expanding keels that function to open and close the valves or lids of loculicidal capsules (Hartmann 1988; Croizat 1993). In the more complex hygrochastic fruit, the amount of seed dispersed and their trajectories, are controlled through various structures such as covering membranes and closing bodies (Parolin 2001). However, modes of dispersal in Mesembryanthemaceae vary widely depending on the construction of the fruit. The genus *Carpobrotus* N.E.Br., for example, has edible berry-like fleshy fruit (sour fig), with seeds embedded in thick, sticky mucilage. A few genera possess xerochastic fruit that dehisce when dry.

XEROCHASTIC FRUIT

Mesemb genera with fruit which open when dry are found mostly in the tribe Apatesieae emend. Chesselet, G.F.Sm. & A.E.van Wyk (Chesselet *et al.* 2001). Species of *Conicosia* N.E.Br., for example, have capsules which function as shakers, in a way similar to that of poppies. In addition to having seeds in their locules, the fruit of *Conicosia* and *Skiatophytum* L.Bolus have seed chambers or pockets, the 'Samentaschen' of Schwantes (1949, 1957), in which a few seeds are entombed in woody tissue. A few genera possess schizocarpic fruit which break up into mericarps when dry. The terms schizocarp and mericarp are not used in their strictest sense here, because the mericarps of mesembs are formed by two halves of neighbouring carpels (Leistner 1958). The genus *Hymenogyne* Haw. has schizocarpic fruit which break up into 8–12 one-seeded, flat, broadly winged, circular mericarps. Seeing that the fruit of certain species of *Conicosia* may disintegrate in a comparable way, Schwantes (1927) erected the genus *Herrea* which is no longer considered distinct. The retention of seeds in seed pockets outside the locules was mentioned above for *Conicosia* and *Skiatophytum*. Among the Apatesieae this syndrome has reached its highest degree of development in *Caryotophora skiatophytoides* Leistner (Figure 3G, H). Its fruit is a schizocarp which breaks up into 3 or 4 nut-like mericarps. Two genera outside the Apatesieae also encompass species with seed enclosed in hard, woody, nut-like mericarps: *Brownanthus* and *Ruschianthemum*.

EVOLUTION OF NUT-LIKE MERICARPS

The evolutionary development of nut-like fruit from hygrochastic capsules may be regarded as a convergent adaptive feature, since this has occurred more than once in the evolution of the Mesembryanthemaceae, with *Ruschianthemum gigas* (Dinter) Friedrich as an example from subfamily Ruschioideae (Figure 3A–D), and *Pseudobrownanthus nucifer* Ihlenf. & Bittrich from subfamily Mesembryanthemoideae (Figure 3E, F). We speculate that in these two species, the evolution of nuts may be a seed-protecting mechanism that has evolved under the extreme arid conditions that these species experience, both taxa being restricted to southern Namibia and the Richtersveld, South Africa. From a structural perspective, Hartmann (1988) ascribes the evolutionary derivation of nuts or nutlets in the mesembs to a process of increased sclerenchymatization of all tissues in the fruit. This phenomenon is supposedly associated with the evolutionary replacement of raindrops by wind as the prime dispersal agent in species exhibiting these characteristics (Hartmann 1988, 2001). However, diaspores are not accompanied by wings or plumes and the evolutionary change to nutlets may rather be an adaptation to larger seed size which may confer a competitive advantage to the seedlings, especially in areas with unpredictable follow-up rains. In *Caryotophora skiatophytoides* Leistner (Figure 3G, H) and in *Skiatophytum tripolium* (L.) L.Bolus (Figure 3I), the selective pressures are different from those acting in the arid parts of Namibia and South Africa. Both species occur in the fynbos vegetation of Western Cape, South Africa, with *C. skiatophytoides* from near Bredasdorp and *S. tripolium* from the Cape Peninsula and surrounding areas. Ecological factors that characterize this Mediterranean climate region include summer aridity, mineral-poor soils, wind and fire. *C. skiatophytoides* is only found in post-fire vegetation. This perennial plant is known to resprout from suckers following fire, whereas the annual *S. tripolium* reseeds after fire. In both cases seeds germinate with difficulty (Hickey & Van Jaarsveld 1995) and the nut-like fruit of

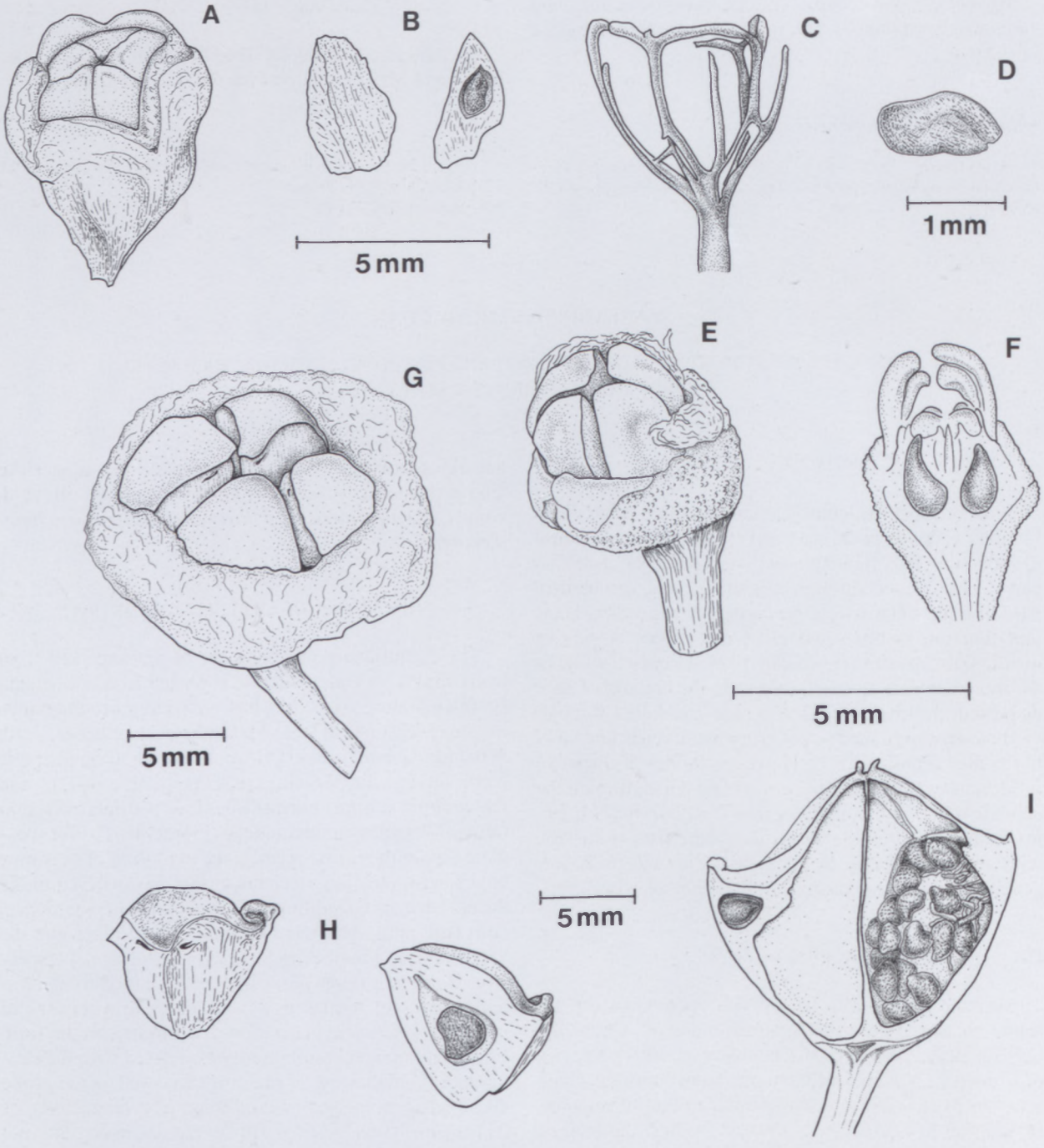

FIGURE 3.—Mesembs with nut-like schizocarpic fruit. A–D, *Stoeberia gigas*; E, F, *Brownanthus nucifer*; G, H, *Caryotophora skiatophytoides*; I, *Skiatophytum tripolium*. Scale bars: A–C, E–I, 5 mm; D, 1 mm. Artist: P. Chesselet.

C. skiatophytoides decay slowly in habitat. Hickey & Van Jaarsveld (1995) suggest that delayed seed germination is a survival strategy commonly found in fynbos plants.

BROWNANTHUS, *RUSCHIANTHEMUM* AND *STOEBERIA*

The unusual nut-like fruit of *Ruschianthemum gigas* and of *Pseudobrownanthus nucifer* were thought to be sufficient reason to establish the monotypic genera *Ruschianthemum* and *Pseudobrownanthus* (Friedrich 1960; Ihlenfeldt & Bittrich 1985). The widely accepted importance of fruit structure in the taxonomic subdivision of the family provided justification for these generic separations e.g. Dehn (1992), however, increasingly, fruit types are not regarded as superior characters for generic delimitation and all characters need to be considered (Klak 2001). In a recent study of *Brownanthus*, Pierce & Gerbaulet (1997) argued that *P. nucifer* is but a specialized member of *Brownanthus* which now contains 12 species, including the new combination *Brownanthus nucifer* (Ihlenf. & Bittrich) S.M.Pierce & Gerbaulet. This taxonomic decision is supported by molecular data, and *Pseudobrownanthus* is deeply embedded within *Brownanthus* (C. Klak, BOL, University of Cape Town, pers. comm.), suggesting that the nut-like fruit represents an autapomorphy for the species rather than a character providing resolution at genus level. The relative importance assigned to a character set, such as fruit structure,

and especially its relevance at a particular rank in the taxonomic hierarchy, needs to be carefully considered when establishing new genera based on autapomorphies. In an analysis of the genera of the Mesembryanthemaceae, Chesselet *et al.* (1995) showed a high number of monotypic genera in this family. Many taxonomists have misgivings about very large genera and genera with only one species, yet both are integral to classification schemes (Williams 1964). But, some monotypic genera are founded on peculiarities, and under such circumstances genus and species concepts may converge, as in the case of *Pseudobrownanthus*. In this paper, we use similar argumentation to resurrect *Stoeberia gigas* (Dinter) Dinter & Schwantes.

The type of *Ruschianthemum gigas* (Dinter) Friedrich was collected in the Klinghardt Mountains of southern Namibia in September 1922 by Moritz Kurt Dinter, a renowned botanist and botanical explorer of Namibia. Prior to the establishment of *Ruschianthemum*, *Mesembryanthemum gigas* Dinter (Dinter 1923) was placed in the genus *Stoeberia* Dinter & Schwantes emend. Friedrich, emend. Dehn (Schwantes 1927–1928; Friedrich 1960; Dehn 1992), together with *S. beetzii* (Dinter) Dinter & Schwantes and *S. rupis-arcuatae* (Dinter) Dinter & Schwantes, a species that is now classified in the genus *Amphibolia* L.Bolus. *Ruschianthemum* was established by Friedrich (1960) on account of its unusual fruit structure—the mature fruit of *R. gigas* is a five-locular schizocarp which breaks into nutlets consisting of parts of the septum enclosing one seed and the remains of valve wings and expanding keels adhering to each unit. Following the release of the nutlets, persistent dorsal and apical connecting vascular bundles present in the capsule remain on plants as a fibrous, basket-like skeleton (see Smith *et al.* 1998: 363; Burgoyne 2000: 8). Although used as a diagnostic feature of *Ruschianthemum* (Dehn 1992), similar basket-like fruit remains have now also been noted in *Stoeberia frutescens* (L.Bolus) Van Jaarsv. When not in fruit, *R. gigas* may be easily mistaken for a *Stoeberia* which it closely resembles (Van Jaarsveld 1994).

Ruschianthemum has been classified together with *Stoeberia*, *Amphibolia* and *Eberlanzia* Schwantes in the '*Eberlanzia* Group' by Hartmann (1998). This group shares the following characteristics: stems whitish; capsules with valve wings and closing bodies which are mostly small and often deep inside the locules so that they appear absent. In this group, *Ruschianthemum* is closest to *Stoeberia* (Hartmann 2001), sharing with it the nearly club-shaped leaves and the rich dichasial inflorescences. The flowers of *Ruschianthemum* closely resemble those in the genus *Stoeberia*—they are relatively small and numerous, with pink-tipped filamentous staminodes arranged in a cone; *S. carpii* Friedrich with its large white flowers, is unique in the genus but fruit and vegetative characters support its current placement in *Stoeberia*. Both genera have the lophomorphic holonectary characteristic of genera placed in Tribe Ruschieae Schwantes by Chesselet *et al.* (2001, in press).

In Schwantes' (Schwantes 1927–1928) key to mesemb genera, *Stoeberia* is distinguished from other genera by its capsule with rudimentary covering membranes that are developed as a narrow rim, with valve wings, and very large placental tubercles (closing bodies) and stigmas that are short, dark and feathered. In the present circumscription of *Stoeberia* the valves do not close again completely once they have opened, and hard (sclerified) valve wings and recurved valve rims characterize the fruit (Chesselet *et al.* 2000). If we amend these diagnostic characters to sclerification of fruit tissue in a broader sense, we can accommodate *R. gigas* in *Stoeberia* and reassign this species accordingly.

Stoeberia gigas *(Dinter) Dinter & Schwantes* in Zeitschrift für Sukkulentenkunde 3: 17 (1927).

Mesembryanthemum gigas Dinter in Feddes Repertorium 19: 153 (1923). *Ruschianthemum gigas* (Dinter) Friedrich in Mitteilungen der Botanischen Staatssammlung, München 3: 564 (1960). Type: Namibia, Klinghardt Mountains, September 1922, *Dinter 3791* (B!, holo.).

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