

## Vivipary in the Cactaceae: Its taxonomic occurrence and biological significance

J. HUGO COTA-SÁNCHEZ

Department of Biology, University of Saskatchewan, Saskatoon, SK S7N 5E2 – Canada

Submitted: Sept 18, 2003 · Accepted: April 23, 2004

### Summary

Vivipary, a rare reproductive strategy in flowering plants, has been previously reported in only four species of the Cactaceae. In this paper, eight additional examples (*Cleistocactus smaragdiflorus*, *Disocactus martianus*, the hybrid *Epiphyllum X Fern la Borde*, *Harrisia martinii*, *Lepismium ianthothele*, *L. monacanthum*, *Rhipsalis micrantha* forma *micrantha*, and *R. baccifera* subsp. *horrida*) of vivipary in cultivated cacti from tribes Hylocereeae, Rhipsalideae, and Trichocereae are documented. The plants had fully-developed and mature fruits containing seeds at different stages of germination, including tiny embryos emerging from the seed coat to young, healthy seedlings with well-developed organs, such as cotyledons and radicles. Several features, though not unique, distinguish cactus fruits with viviparous seedlings. Foremost, the fruits are fleshy with abundant mucilage and a relatively thick, often transparent pericarp. The seeds are generally numerous and embedded in a transparent, white or red pulp. The occurrence of vivipary in taxa from four phylogenetically distinct tribes of the subfamily Cactoideae suggests an independent origin and indicates that this reproductive strategy may be more widespread in the family than originally thought. Vivipary in the Cactaceae is regarded as a form of cryptovivipary, a condition in which the zygote develops inside the fruit without penetrating the ovary wall for dispersal purposes, which in turn is considered a subcategory of true vivipary. Further, vivipary is interpreted as an adaptive reproductive strategy that enables seedlings to establish more rapidly.

Key words: Vivipary, Cactaceae, Cactoideae, epiphytic cacti, viviparous seeds, reproductive strategy

### Introduction

Vivipary is the process in which seeds germinate within the fruit with subsequent embryo development before the seeds are dispersed from the parent plant. The germination of viviparous seeds usually occurs prior to the complete desiccation of the fruit while they are still on the parent plant (precocious germination), a relatively unusual phenomenon in angiosperms (FARNSWORTH 2000). Vivipary has been reported in fewer than 100 flowering plant families (ELMQVIST & COX 1996), representing less than 0.1% of angiosperms.

Two main types of vivipary have been described in flowering plants: true vivipary and pseudovivipary, which are equally distributed (50/50) among plant families (ELMQVIST & COX 1996). In true vivipary, plants produce sexual offspring with subsequent dispersal via the rupture of the pericarp wall due to embryo growth. The best-known cases of true vivipary in angiosperms are documented in mangroves of the Rhizophoraceae (*Bruguiera* Lam., *Rhizophora* L.) and Avicenniaceae (*Avicennia* L.) (PANNIER & PANNIER 1975; RAO et al. 1986; TOMILDSON 1986). The second type, pseudovivipary, involves the production of asexual propagules.

---

\* **Corresponding author:** J. Hugo Cota-Sánchez, Department of Biology, University of Saskatchewan, Saskatoon, SK S7N 5E2 – Canada, e-mail: hugo.cota@usask.ca

This phenomenon is widespread in monocots, particularly in the Poaceae (BEETLE 1980; ELMQVIST & COX 1996), where numerous examples have been reported. For a comprehensive discussion of vivipary in plants, see ELMQVIST & COX (1996), FARNSWORTH (2000), and references therein.

Thus far, vivipary of Cactaceae has received little attention, and the limited number of case-studies on the reproductive biology and the dispersal of diaspores and propagules in the family accounts for the narrow understanding of its reproductive versatility. MADISON (1977) pointed out that vivipary is common in epiphytic taxa of the Araceae, Cactaceae and Gesneriaceae; however, available data indicate that this reproductive strategy is a rare event in the Cactaceae. At present, literature references have documented vivipary in only four species of the subfamily Cactoideae, namely *Epiphyllum phyllanthus* (CONDE 1975), *Coryphantha vivipara* [= *Escobaria vivipara* (Nutt.) Buxb.] (MITICH 1964; COTA 1993), and *Rhipsalis gibberula* and *R. pilocarpa* (LOMBARDI 1993). The goals of this paper are to document the occurrence of new examples of viviparous seeds in species from tribes Hylocereeae, Rhipsalideae and Trichocereae, and to address the adaptive significance of vivipary in the Cactaceae. While the great majority of previous reports of vivipary in flowering plants have been commonly associated with saline tropical habitats and dry alpine conditions, the examples discussed in this paper were grown under greenhouse conditions. In the wild they are found primarily distributed inland in tropical and subtropical areas, an apparently unusual environment for the existence of vivipary compared to the dry saline environments where most cases have been documented so far.

## Materials and methods

The accounts of vivipary discussed in this article were investigated in cultivated specimens at the Montréal Botanical Garden (MT) during a survey of 300+ species of cacti. A list of the taxa in which vivipary was observed is included in Table 1 along with general features regarding habitat, life form, and reproductive features. For convenience, taxonomic authorities for species reported here follow ANDERSON (2001), but do not necessarily reflect the author's taxonomic opinion.

The accidental discovery of seeds germinating inside one fruit sparked this investigation. The fruits with viviparous offspring were discovered when fresh plant material was being collected to prepare herbarium vouchers. As the fruits were dissected, the viviparous seedlings were exposed, providing grounds for a detailed survey to examine plants bearing fruits. In general, the fruits were dissected to expose the different stages of germination. Information concerning the

general appearance and characteristics of fruits, seeds and seedlings was then documented and the material photographed. In addition to examining live plants at MT, herbarium specimens of the Missouri Botanical Garden (MO), which hosts one of the world's largest preserved cactus collections, were surveyed in search of evidence of the occurrence of vivipary in wild plants.

## Results

Vivipary, a rare reproductive strategy in flowering plants, has been previously reported in only four species of the Cactaceae. In this paper, I document the existence of eight additional examples of vivipary in cultivated cacti from tribes Hylocereeae (*Disocactus martianus* and the hybrid *Epiphyllum* X *Fern la Borde*), Rhipsalideae (*Lepismium ianthothele*, *L. monacanthum*, *Rhipsalis micrantha* forma *micrantha*, and *R. baccifera* subsp. *horrida*), and Trichocereae (*Cleistocactus smaragdiflorus* and *Harrisia martinii*) (Table 1). No additional records of vivipary were found in the survey of herbarium specimens in MO's cactus collection.

## General description of viviparous fruits in the Cactaceae

The plants in which vivipary was found had fully developed and mature fruits containing seeds at different stages of germination, including tiny embryos emerging from the seed coat to young, healthy seedlings with small cotyledons and radicles. Several features, though not unique, characterize cactus fruits with viviparous seedlings. Foremost, the fruits are fleshy with abundant mucilage and a relatively thick, often transparent, pericarp facilitating the screening of fruits with viviparous seeds. The seeds are generally numerous and embedded in a transparent, white or red pulp (Figs. 1–18; Table 1). As a rule, seed germination is *in-situ* with the seedlings remaining inside the fruit, i.e., the pericarp lacks openings produced by the seedling outgrowth. Propagule morphology was consistent within the same plant as long as they were at a similar developmental stage. However, the viviparous offspring were polymorphic among the different species surveyed. Following, I summarize the main features observed in each species documented in this paper. The order follows the tribal categories according to ANDERSON (2001). Taxa reported in previous literature are excluded from these descriptions, but they are included in Table 1 along with the new reports, as their viviparous features may be found in the original sources.

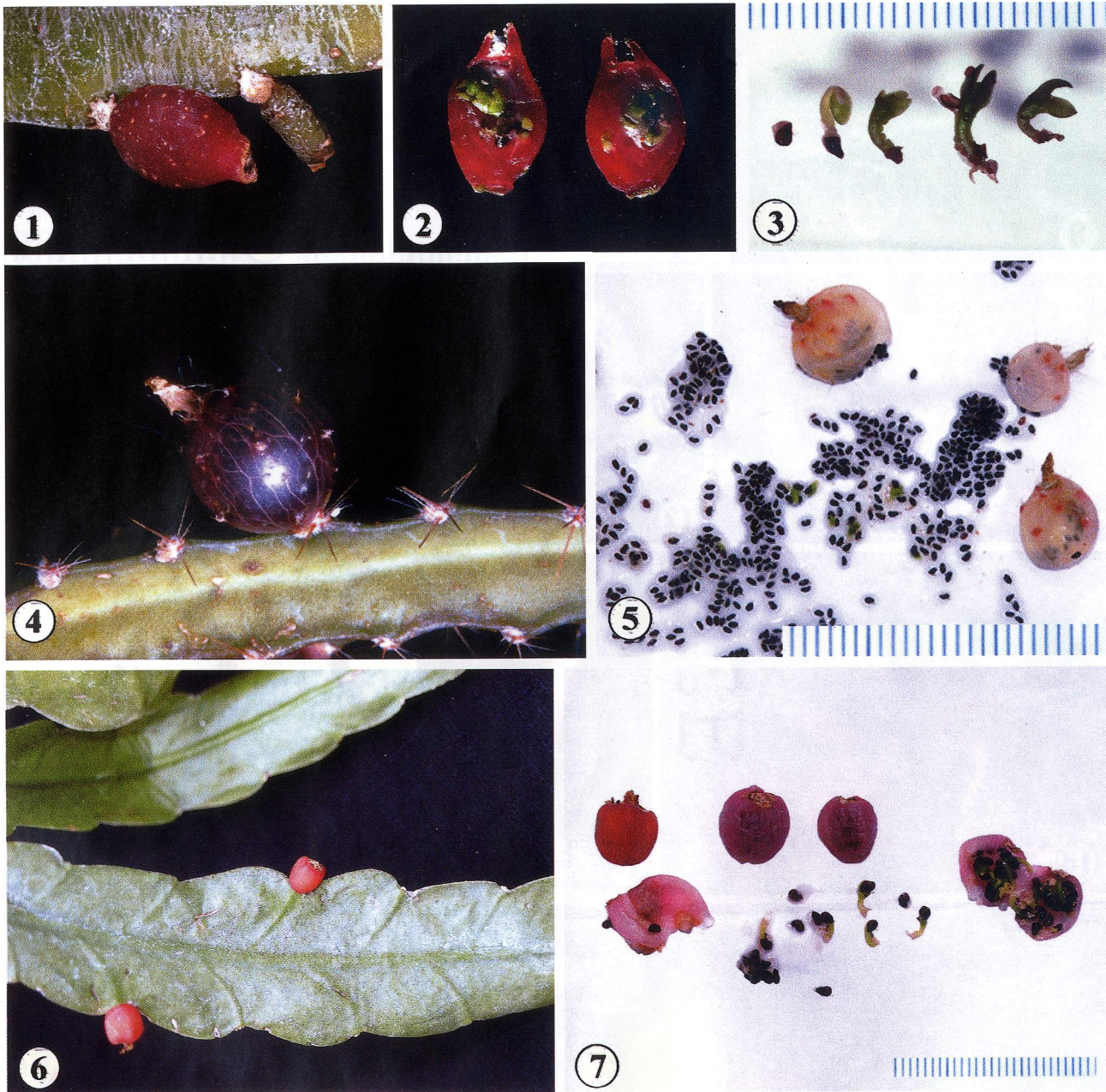


Plate 1.

Fig. 1: Entire fruit of the hybrid *Epiphyllum X Fern la Borde*; Fig. 2: Longitudinal section of *E. X Fern la Borde* fruit showing viviparous offspring; Fig. 3: Different stages of the viviparous offspring of *E. X Fern la Borde*. Scale bar in mm; Fig. 4: Stem and fruit of *Lepismium ianthothele*; Fig. 5: Fruits of *L. ianthothele* with seeds and viviparous offspring. Scale bar in mm; Fig. 6: Phylloclade and mature fruits of *L. monacanthum*; Fig. 7: Dissected fruits of *L. monacanthum* with viviparous seedlings. Scale bar in mm.

### Tribe Hylocereeae

Two examples of vivipary were observed in this tribe, namely in *Epiphyllum X Fern la Borde* and *Disocactus martianus*. This tribe includes climbing and epiphytic

cacti with flattened or few-ribbed stems bearing adventitious roots, and is distributed mostly in tropical forests of Central America (ANDERSON 2001), including southern Mexico and the Caribbean. Some species also extend their range into South America.

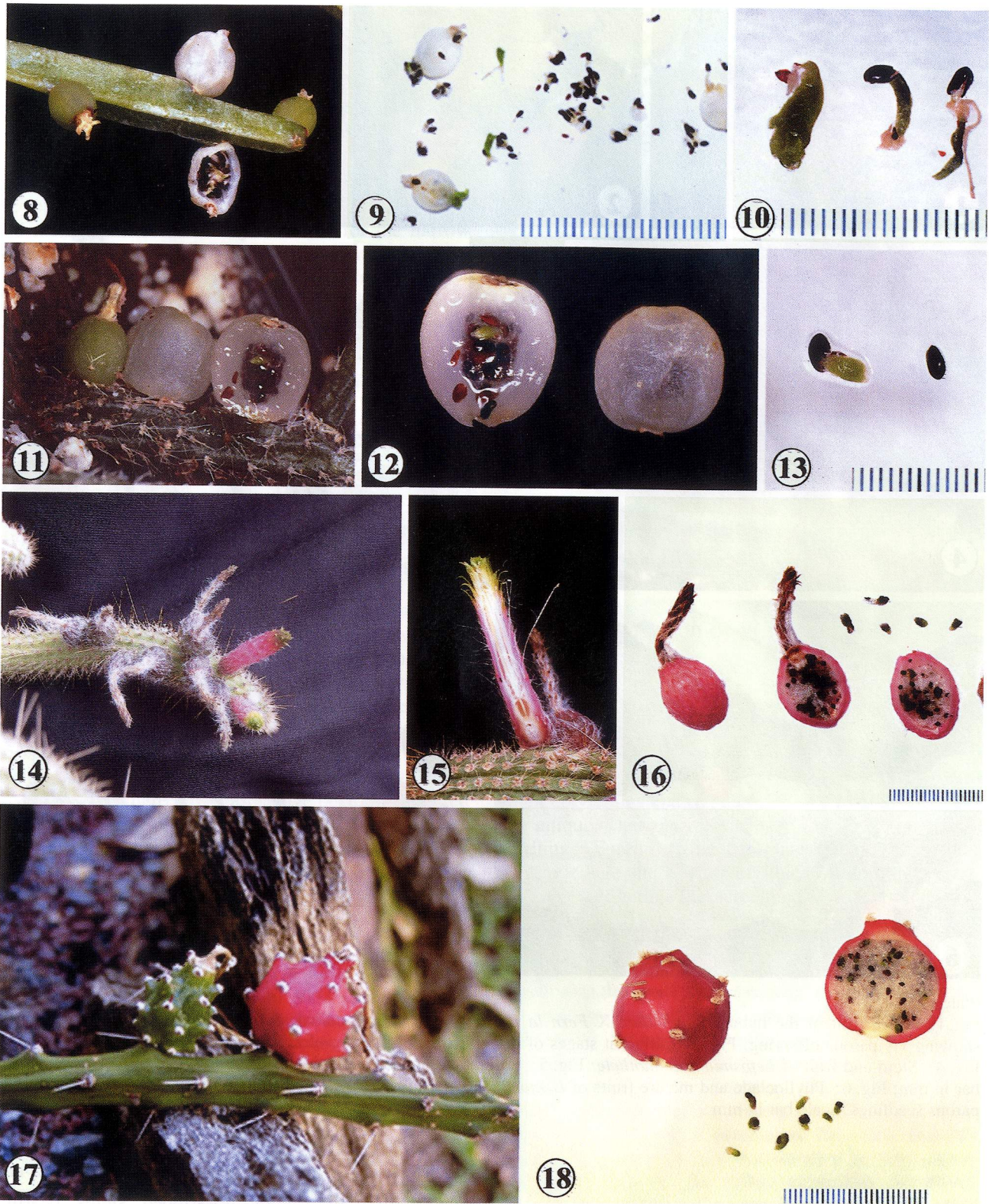


Plate 2.

Table 1. Taxonomic distribution of viviparous species in the Cactaceae, subfamily Cactoideae. New reports of vivipary are indicated with a plus (+) symbol. Binomials for previously published viviparous taxa (indicated with an asterisk) are kept according to the original literature sources. The binomials for new reports of vivipary follow ANDERSON (2001).

Taxon	Life form and habitat	Fruit characteristics	Pollination syndrome
<b>Tribe Cacteeae</b>			
<i>Coryphantha vivipara</i> * (Nutt.) Britton & Rose	Terrestrial, arid-dry	Ovoid, fleshy, pericarp naked, red, ca. 50–100 seeds.	Insect
<b>Tribe Hylocereeae</b>			
<i>Disocactus martianus</i> + (Zucc.) Barthlott	Epiphytic, lithophytic, tropical	Round, fleshy, whitish to semi-transparent, pericarp semi-naked, pulp reddish, >100 seeds.	Bird
<i>Epiphyllum X Fern la Borde</i> + <i>E. phyllanthus</i> * (L.) Haw.	Epiphytic, cultivated Epiphytic, tropical	Ovoid, fleshy, pericarp naked, red, pulp red, sweet, >100 seeds. Ovoid, fleshy, pericarp naked, red, pulp red, >100 seeds.	Bird Bird
<b>Tribe Rhipsalideae</b>			
<i>Lepismium ianthothele</i> + (Monv.) Barthlott	Epiphytic, tropical	Round, fleshy, reddish to whitish, semi-transparent, pericarp spiny, pulp reddish, slightly sweet, >100 seeds.	Insect
<i>L. monacanthum</i> + (Griseb.) Barthlott	Epiphytic, tropical	Round, fleshy, red, pericarp naked, pulp reddish, >100 seeds.	Insect
<i>Rhipsalis baccifera</i> (J. S. Mueller) Stearn. subsp. <i>horrida</i> + (Baker) Barthlott	Epiphytic, epilithic, dry	Round, fleshy, white, pericarp naked, pulp transparent, ca. 50 seeds.	Insect
<i>R. gibberula</i> * F. A. C. Weber	Epiphytic, tropical	Round, fleshy, reddish, pericarp naked, ca. 20 seeds.	Insect
<i>R. micrantha</i> (Kunth) DC forma <i>micrantha</i> + <i>R. pilocarpa</i> * Löefgren	Epiphytic, tropical Epiphytic, tropical	Round, fleshy, white, transparent, naked, pulp white, ca. 15–30 seeds. Round, fleshy, red, pericarp spiny, pulp translucent, ca. 25 seeds.	Insect Insect
<b>Tribe Trichocereae</b>			
<i>Cleistocactus smaragdiflorus</i> + (F. A. C. Weber) Britton & Rose <i>Harrisia martinii</i> + (Labour.) Britton	Terrestrial, arid-dry Terrestrial, arid-dry	Round, red, fleshy, pericarp spiny, pulp red, >100 seeds. Round, fleshy, pericarp naked, red, pulp white, >100 seeds.	Bird, cleistogamy Insect

### *Epiphyllum X Fern la Borde*

This epiphytic hybrid has flat stems with pink to lavender flowers, which after fertilization produces red, fleshy, smooth fruits, ca. 1 cm in diameter (Fig. 1) with many shiny seeds and seedlings inside the fruit (Fig. 2). The viviparous offspring inside the fruits of this plant exhibited an impressive degree of development, from

small embryos emerging from the seed coat to well-developed young seedlings (larger than most examples discussed here) bearing radicles and cotyledons (Fig. 3). While CONDE (1975), who documented vivipary in *E. phyllanthus*, observed apertures in fruits with viviparous seedlings, the fruits of *Epiphyllum X Fern la Borde* are indehiscent and lack natural openings or breakdown of the ovary wall caused by seedling growth (Figs. 1, 2).

#### Plate 2.

Fig. 8: Stem portion of *Rhipsalis micrantha* forma *micrantha* with whole and dissected fruits; Fig. 9: Dissected fruits of *R. micrantha* forma *micrantha* with viviparous seedlings. Scale bar in mm; Fig. 10: Different stages of *R. micrantha* forma *micrantha* viviparous offspring. Scale bar in mm; Fig. 11: Mature and immature fruits of *R. baccifera* subsp. *horrida*; Fig. 12: Dissected fruit of *R. baccifera* subsp. *horrida*; Fig. 13: Seeds and viviparous offspring of *R. baccifera* subsp. *horrida*. Scale bar in mm; Fig. 14: Stem of *Cleistocactus smaragdiflorus* with flowers and fruits; Fig. 15: Tubular flower of *C. smaragdiflorus* in longitudinal section. Scale bar in mm; Fig. 16: Fruits of *C. smaragdiflorus*. Note dissected middle fruit with viviparous offspring. Scale bar in mm; Fig. 17: Stem portion and fruit of *Harrisia martinii*; Fig. 18: Longitudinal section of the fruit of *H. martinii* showing viviparous seedlings. Scale bar in mm.

## *Disocactus martianus*

This Mexican endemic cactus has a creeping to pendent growth habit, and the flowers are pink to red, funnel-form to almost tubular. The cultivated plant showed the ability to produce viviparous offspring contained within globose fruits ca. 1 cm in diameter with a rather thin pericarp turning yellowish/whitish as the fruit ripens. The thin nature of the pericarp assists in the identification of viviparous fruits, as the germinating seedlings are visible through it with the naked eye. Unlike *Epiphyllum X Fern la Borde*, its tribal relative, *D. martianus* produced significantly fewer and smaller viviparous seedlings, though seed production was also high.

### Tribe Rhipsalideae

The Rhipsalideae is a mainly South American lineage with numerous epiphytic species with round, angled, flattened to segmented stems (ANDERSON 2001). Although some taxa distribute northwards in Central and North America, *Rhipsalis baccifera* is found in areas of the Old World. Within this tribe, vivipary was observed in two genera: *Lepismium* Pfeiff. and *Rhipsalis* Gaertn., each with two species, which are discussed separately below.

## *Lepismium ianthothele*

This epiphytic species has tetragonal stems, white to yellowish flowers, and spherical to globose fleshy fruits ca. 1 cm in diameter (Fig. 4). The pulp is sweet and transparent, containing abundant black seeds (Fig. 5). The fruits are at first red to pinkish, but the pericarp then turns whitish and semi-transparent as the fruit matures. In this species the viviparous offspring appear to be particularly more abundant in older fruits. The cotyledons and radicular organs were easily identifiable in the characteristically small seedlings, which were also conspicuous through the thin pericarp prior to fruit dissection.

## *L. monacanthum*

This is a strict epiphytic cactus with dimorphic (triangular to flat) stems that produce lateral orange flowers. The fruit is fleshy, red to pinkish, and less than 1 cm in diameter (Fig. 6) with small black seeds germinating inside (Fig. 7). The small viviparous seedlings inside the fruit were visible through the pericarp only in well-ripened fruits in which this structure had turned semi-transparent.

## *Rhipsalis micrantha* forma *micrantha*

This is the most common form of this robust epiphytic plant with apparent dimorphic stems varying from flat to triangular (Fig. 8). The flowers are small and white and produce fleshy, circular-ovoid fruits ca. 0.5 to 0.9 cm in diameter (Fig. 8). The pulp is scanty, semi-sweet and contains 15–30 minute, black, shiny seeds (Fig. 9) in several stages of germination, including young seedlings with well-developed radicles and cotyledons (Fig. 10). The size of some offspring found in this species is unusually large (Fig. 10) compared with the viviparous seedlings of the other species, but matches those observed in *Epiphyllum X Fern la Borde*.

## *R. baccifera* subsp. *horrida*

This epiphytic plant is found in Madagascar, where tetra- and octaploid populations have been reported (BARTHOLOTT 1983). It bears more robust stems than its American relative *R. baccifera* subsp. *baccifera*. In addition, the production of more and larger fruits (Fig. 11) has been associated with polyploidy (BARTHOLOTT 1983). The fruits are fleshy and have a thick white ovary wall with seedlings inside (Fig. 12), which are by far the smallest (Fig. 13) observed among the viviparous examples discussed here.

### Tribe Trichocereae

The last two instances of vivipary were observed in members of the Trichocereae, a South American tribe consisting of globose and columnar plants with ribbed to tuberculate stems (ANDERSON 2001). Unlike the previous examples of tribes Hylocereae and Rhipsalideae, vivipary in the Trichocereae occurs in species that are mainly terrestrial, namely *Cleistocactus smaragdiflorus* and *Harrisia martinii*.

## *Cleistocactus smaragdiflorus*

*C. smaragdiflorus* is a strictly terrestrial species with prostrate to trailing growth habit and long tubular flowers apparently adapted to bird pollination (Figs. 14, 15). Unlike the other taxa, cleistogamy is characteristic of this species. The plant produces red, fleshy fruits with long trichomes and numerous seeds, some of which produce viviparous seedlings (Fig. 16). The pericarp is somewhat thick, and the fruit's pulp is white and firm, semi-sweet, with embedded seeds and seedlings inside.

## *Harrisia martinii*

This many-branched clambering plant has large (ca. 2–3 cm in diameter) red, fleshy fruits (Fig. 17) with numerous seeds. As in the previous case, viviparous offspring were found enclosed in white, firm pulp (Fig. 18). In spite of the large fruit size, the seedlings inside were small, no larger than 2 mm in length. This fact, however, may have been due to the predominance of early developmental stages when the fruits were dissected.

## Discussion

In the Cactaceae, particularly in *Coryphantha vivipara*, vivipary is considered a type of pseudovivipary (ELMQVIST & COX 1996), which involves the formation of asexual offspring. However, based on personal observations and the evidence presented here, I believe that in the cactus family one should not rule out cryptovivipary, a condition in which the zygote develops inside the fruit without penetrating the ovary wall for dispersal purposes (TOMILDSON 1986) and is considered a subcategory of true vivipary (ELMQVIST & COX 1996). Wild plants of *C. vivipara* produce minute seedlings (COTA-SÁNCHEZ, pers. obs.). Presumably, these viviparous offspring are shed when the ovary wall ripens and dries. Whether the offspring are sexually or asexually produced is unknown, but the seeds fully develop after fertilization with subsequent germination and embryonic growth without protrusion through the ovary wall. Similarly, in all of the cases discussed here, the fruits had seedlings in different developmental stages, which did not penetrate the ovary wall. The integrity of the pericarp throughout the different seedling developmental stages may denote an adaptive strategy in cacti, in which the fruit thermoregulates the internal conditions of the offspring and protects seedlings from desiccation and adverse environmental conditions. Since the developing seedlings do not protrude through the pericarp at any developmental stage (unless the pericarp decays naturally), I am inclined to regard this pattern as cryptovivipary rather than pseudovivipary, which is, in turn, mostly associated with monocots (BEETLE 1980). In addition, numerous small flies have been observed around these cultivated specimens, quite possibly acting as pollinators of the small to medium size flowers of epiphytic cacti, hence promoting sexual reproduction. However, even if there is no evidence indicating whether the seeds have been produced via agamospermy, the possibility of the existence of apomictic seeds should not be ruled out until further studies of reproductive systems and dispersal mechanisms of the Cactaceae are conducted.

Although cacti with viviparous fruits have flowers adapted to various pollinators (Table 1), seed production may occur via autogamous and outcrossing reproductive mechanisms. For instance, the majority of cacti with viviparous seedlings promote outcrossing by having insect pollinated flowers varying in size, color and number of perianth parts, whereas large, bright red to scarlet, tubular flowers prevail in ornithophilous flowers (Table 1). Among these, one example is worth mentioning: the large red, tubular flowers of *Cleistocactus smaragdiflorus* (Figs. 14, 15), which are clearly adapted to hummingbird pollination and have most likely evolved to promote cross-pollination. In spite of this bird pollination syndrome, its flowers are seemingly autogamous obligated by cleistogamy (the term for which the generic name originated) because plants cultivated in greenhouse conditions produce mature fruits with seeds and viviparous seedlings without the assistance of a pollinating agent (COTA-SÁNCHEZ, pers. obs.). The production of fruits without visitation by pollinators has also been observed in the epiphytic cactus *Epiphyllum phyllanthus*, but in this case selfing has been associated with ants (MADISON 1979). The disadvantage of these two latter examples of endogamy (cleistogamy and selfing) is the lack of new genetic information in the offspring as opposed to purportedly enhanced fitness and genetic diversity in outcrossing species.

It has been suggested that the development of vivipary in flowering plants has had independent evolutionary origins because of its prevalence in a wide range of families (ELMQVIST & COX 1996). Within the Caryophyllid clade this reproductive strategy has been identified in the Caryophyllaceae and Nyctaginaceae (FARNSWORTH 2000), two families placed at the core of the Caryophyllales, and in the Plumbaginaceae and Polygonaceae (ELMQVIST & COX 1996), two families within the Polygonales. In the Cactaceae, the tribes Cacteae, Hylocereeae, Rhipsalideae, and Trichocereae form phylogenetically distinct lineages (NYFFELER 2002) of the subfamily Cactoideae. Based on phylogenetic evidence, FARNSWORTH (2000) suggests that features related to vivipary have evolved repeatedly in descendants of xerophytic taxa. Similarly, the existence of vivipary in different life-forms (terrestrial, facultative, and strict epiphytic cacti) converging in a similar degree of specialization, i.e., desiccation intolerance, exemplifies a new case of parallelism of character-state evolution in phylogenetically distant terminal lineages in the Cactaceae. The incidence of vivipary in unrelated tribes of the Cactoideae (Table 1) confirms its multiple origins in the cactus family.

Although the apparently low frequency of vivipary in plants suggests that this reproductive strategy in response to environmental stress has not been very

successful in nature (LEE & HARMER 1980), its scarcity also indicates the need for more field studies to document its taxonomic and ecological distribution. Indeed, vivipary has not been investigated enough to conclusively address its ecological and evolutionary significance. FARNSWORTH (2000) indicates that in order to understand the evolutionary significance of vivipary, it is desirable to assess whether the characteristics associated with seed intolerance to desiccation and habitat are of recent or ancient origin. This issue is even more complex if we consider that in the Cactaceae there are relatively few discrete morphological characters available to use in cladistic analyses, making it difficult to explain the evolution of vivipary as well as its adaptive costs, consequences and benefits in the family. Personally, I interpret its occurrence in unrelated taxa as a convergent adaptive strategy that enables seedlings to establish more rapidly.

Conceivably, vivipary has evolved in response to similar selective pressures as a mechanism to overcome the adverse conditions characteristic of the dry deserts and canopy environments in which cacti develop. The disparity in habitats (alpine dry to tropical humid) of taxa in Table 1 suggests that the same selective forces have influenced the occurrence of this reproductive alternative. I hypothesize that vivipary enhances the chances of survival of newly produced offspring whenever the seedlings reach ideal conditions for establishment. It follows that this may be the case more so in alpine habitats where the seasonal growing conditions are short and the production of viviparous seedlings would be selectively advantageous, e.g., *Coryphantha vivipara*. In fact, it has been proposed that vivipary is a favorable mechanism in areas of high latitude subject to relatively fast photoperiodic changes (shortening of day length and extreme variations in environmental conditions) by providing shelter for young seedlings and protection from desiccation and low temperatures (COTA-SÁNCHEZ 2002). Conversely, the seasonal fluctuations in tropical forests and subtropical deserts are less dramatic than alpine and high latitude habitats; nonetheless, different life-forms in tree canopies are subject to extreme changes, and adaptation to drought resistance is a key factor (MADISON 1977; BENZING 1990). In the same way, seed dormancy may be a strategically necessary process for cacti inhabiting regions with seasonal climatic changes and arid environments, while the opposite may be the case in tropical and subtropical regions.

Seed dormancy, a condition of physiological inactivity, may be innate, enforced or induced (ROBERTS 1972), and has significant survival value under adverse conditions for germination (ROJAS-ARÉCHIGA & VÁZQUEZ-YANES 2000). In the Cactaceae, dormancy has been corroborated in seeds of various taxa, e.g., *Opuntia*

Mill. (BREGMAN & BOUMAN 1983) and *Stenocereus gummosus* (Engelm. Ex. Brandege) Gibson & Horak (LEÓN DE LA LUZ & DOMÍNGUEZ-CADENA 1991), among others, and the maintenance of the dormant state in cactus seeds has been associated with the presence of inhibitory substances in the testa (ROJAS-ARÉCHIGA & VÁZQUEZ-YANES 2000). Whether the dormant condition is characteristic in the species discussed here is unknown, but it is possible that the seeds have no dormancy period because they lack the compounds that prevent seeds from germinating. Similarly, as the fruit may not be dispersed in a timely fashion, seed germination would occur while they are still attached to the fruit.

How then can vivipary be advantageous in tropical and subtropical environments? LEE & HARMER (1980: 263) pointed out that “vivipary can be looked upon not simply as a substitute for sexual reproduction, but also as an additional method of vegetative propagation.” In the Cactaceae, I regard vivipary as a reproductive strategy to perpetuate species with characteristically low germination rates in tree canopies. The cactus ovary and fruit are extremely exceptional in being surrounded by vegetative tissues, which in most species consist of many nodes, internodes, axillary buds, and even rather ordinary leaves. The combination of fruit characters (fleshy, mucilaginous, often with thin transparent pericarp) provides a suitably moist environment that promotes germination and incubation while embedding the seeds and young seedlings in an insulating barrier that protects them from extreme environmental conditions, e.g., drastic temperatures, desiccation, and exposure to direct sunlight, wind and rain. As a result, the internal conditions prevalent in the fruit may be important in the establishment and success of viviparous seedlings. However, once they are shed from the fruit and become independent, young seedlings face the effects of environmental factors. It is feasible that the unusually large viviparous seedlings observed in *Epiphyllum X Fern la Borde* (Fig. 3) and *Rhipsalis micrantha* forma *micrantha* (Fig. 10) represent an adaptive advantage for survival. SALISBURY (1942) has shown that increase in seed and propagule size in *Atriplex* L. is beneficial under conditions of competition and unfavorable circumstances and that larger, more vigorous seedlings produced from larger seeds were able to survive in adverse conditions as opposed to smaller seedlings produced from smaller seeds.

Finally, although there is uncertainty about the survival rates of viviparous propagules and whether they are shed from the parent fruit, the marked capacity for vegetative reproduction in cacti coupled with vivipary may provide fitness advantages by disseminating offspring in time and space in new areas of the phorophyte or on the ground. In fact, it has been postulated



that the lack of dormancy in seeds with subsequent early, precocious germination confers adaptive advantages associated with dispersal and degree of habitat specialization (FARNSWORTH 2000). While the above discussion centers on the adaptive nature of vivipary in the Cactaceae, there are also equally plausible non-adaptive explanations. For example, vivipary may be a by-product of the lack of seed dormancy. Without seed dormancy, some seeds may require less exposure to moisture before germinating. The key requirement for this trait to be adaptive is that the individuals carrying this trait have higher relative fitness than those not carrying it. The only evidence suggesting that viviparous seedlings are able to survive in artificial conditions are those obtained from ongoing experimental tests being conducted in the author's institution greenhouses with viviparous offspring from *Cleistocactus smaragdiflorus*, *Disocactus martianus*, *Rhipsalis bacifera*, and *R. micrantha*. Six months after being transplanted to potting soil, the viviparous seedlings were able not only to establish, but also to continue development under appropriate substrate and moisture conditions.

### Concluding remarks

The occurrence of vivipary in taxa from four taxonomic tribes (Table 1) indicates that this trait may be more widespread in the family than originally thought and more attention should be given to the different stages of fruit development in wild and cultivated specimens. Thus far, limited field-based observations hinder the understanding of the reproductive biology of the Cactaceae, especially since this paper deals with examples from specimens under cultivation. At present, there is no evidence of the occurrence of vivipary in tropical and subtropical cacti in nature, and it is unknown whether viviparous offspring are, in effect, able to survive and succeed in natural habitats. Although the examination of herbarium specimens at MO failed to provide an indication of vivipary in specimens collected in the wild, future work should contemplate a thorough inspection of herbarium material from wild plants seeking evidence of its occurrence in nature. Whether the fruits from the species discussed here behave differently in the wild is unknown. Perhaps the artificial conditions under which they are being kept in cultivation promote vivipary. Future research involving *in-situ* and *ex-situ* experimental tests to evaluate the production, establishment, developmental frequencies, and the relative fitness of viviparous seedlings should provide a better understanding of vivipary to determine whether this trait is adaptive in the Cactaceae. However, until more field-

work and detailed studies of reproductive biology are undertaken, vivipary should be regarded as a mechanism that provides new avenues and conditions for cactus diversification while contributing to its reproductive versatility.

### Acknowledgements

I thank Dewey Litwiller, Jim Mauseth, and Scott Zona for valuable comments that have improved this manuscript. To Marcia Bomfim-Patricio, Shannon Crutch, and Dennis Dyck for their technical assistance. To two anonymous reviewers for providing helpful comments. The kind assistance of the Montréal Botanical Garden personnel is greatly appreciated for facilitating access to the living collection to study plant material. To the Missouri Botanical Garden for facilitating the examination of fruit material in herbarium specimens. This research was funded by grants from the National Geographic Society (7382-02), the Cactus and Succulent Society of America, and the Deutsche Kakteen-Gesellschaft e.V.

### References

- ANDERSON, E. F. (2001): *The Cactus Family*. – Timber Press, Portland.
- BARTHOLOTT, W. (1983): Biogeography and evolution in Neo- and Paleotropical Rhipsalinae (Cactaceae). In: KUBITZKI, K. (ed.): Proc. Int. Symp. Dispersal and Distribution, **7**: 241–248. – Sonderbd. naturwiss. Ver. Hamburg.
- BEETLE, A. A. (1980): Vivipary, proliferation, and phyllody in grasses. – *J. Range Manage.* **33**: 256–261.
- BENZING, D. H. (1990): *Vascular Epiphytes*. – Cambridge University Press, Cambridge.
- BREGMAN, R. & BOUMAN, F. (1983): Seed germination in the Cactaceae. – *Bot. J. Linn. Soc.* **86**: 357–374.
- CONDE, F. L. (1975): Vivipary in *Epiphyllum*. – *Cactus Succ. J.* **47**: 38–39.
- COTA, J. H. (1993): Pollination syndromes in the genus *Echinocereus*. – *Cactus Succ. J.* **65**: 19–26.
- COTA-SÁNCHEZ, J. H. (2002): Taxonomy, distribution, rarity status and uses of Canadian cacti. – *Haseltonia* **9**: 17–25.
- ELMQVIST, T. & COX, P. A. (1996): The evolution of vivipary in flowering plants. – *Oikos* **77**: 3–9.
- FARNSWORTH, E. (2000): The ecology and physiology of viviparous and recalcitrant seeds. – *Annu. Rev. Ecol. Syst.* **31**: 107–138.
- LEE, J. A. & HARMER, R. (1980): Vivipary, a reproductive strategy in response to environmental stress. – *Oikos* **35**: 254–265.
- LEÓN DE LA LUZ, J. L. & DOMÍNGUEZ-CADENA, R. (1991): Evaluación de la reproducción de semilla de pitaya agria (*Stenocereus gummosus*) en Baja California Sur, Mexico. – *Acta Bot. Mex.* **14**: 75–87.
- LOMBARDI, J. A. (1993): Viviparity in *Rhipsalis pilocarpa* Löefgren (Cactaceae). – *Ciênc. Cult.* **45**: 407.

- MADISON, M. (1977): Vascular epiphytes: Their systematic occurrence and salient features. – *Selbyana* **2**: 1–13.
- MADISON, M. (1979): Additional observations on ant-gardens in Amazonas. – *Selbyana* **5**: 107–115.
- MITICH, L. W. (1964): North Dakota native cacti. – *Cactus Succ. J.* **36**: 42–44.
- NYFFELER, R. (2002): Phylogenetic relationships in the cactus family (Cactaceae) based on evidence from *trnK/matK* and *trnL/trnF* sequences. – *Amer. J. Bot.* **89**: 312–326.
- PANNIER, F. & PANNIER, R. F. (1975): Physiology of vivipary in *Rhizophora mangle* L. – *Proc. Int. Symp. Biol. Mgt. Mangroves* **2**: 632–639.
- RAO, T. A.; SURESH, P. V. & SHERIEF, A. N. (1986): Multiple viviparity in a few taxa of mangroves. – *Curr. Sci.* **55**: 259–261.
- ROBERTS, E. H. (1972): Dormancy: A factor affecting seed survival in the soil. In: ROBERTS, E. H. (ed.): *Viability of Seeds*, 321–359. – Chapman & Hall, London.
- ROJAS-ARÉCHIGA, M. & VÁZQUEZ-YANES, C. (2000): Cactus seed germination: A review. – *J. Arid Environ.* **44**: 85–104.
- SALISBURY, E. J. (1942): *The Reproductive Capacity of Plants*. – G. Bell & Sons, London.
- TOMILDSON, P. B. (1986): *The Botany of Mangroves*. – Cambridge University Press, Cambridge.