

INVITED REVIEW

Structure–Function Relationships in Highly Modified Shoots of Cactaceae

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• *Background and Aims* Cacti are extremely diverse structurally and ecologically, and so modified as to be intimidating to many biologists. Yet all have the same organization as most dicots, none differs fundamentally from *Arabidopsis* or other model plants. This review explains cactus shoot structure, discusses relationships between structure, ecology, development and evolution, and indicates areas where research on cacti is necessary to test general theories of morphogenesis.

• *Scope* Cactus leaves are diverse; all cacti have foliage leaves; many intermediate stages in evolutionary reduction of leaves are still present; floral shoots often have large, complex leaves whereas vegetative shoots have microscopic leaves. Spines are modified bud scales, some secrete sugar as extra-floral nectaries. Many cacti have juvenile/adult phases in which the flowering adult phase (a cephalium) differs greatly from the juvenile; in some, one side of a shoot becomes adult, all other sides continue to grow as the juvenile phase. Flowers are inverted: the exterior of a cactus ‘flower’ is a hollow vegetative shoot with internodes, nodes, leaves and spines, whereas floral organs occur inside, with petals physically above stamens. Many cacti have cortical bundles vascularizing the cortex, however broad it evolves to be, thus keeping surface tissues alive. Great width results in great weight of weak parenchymatous shoots, correlated with reduced branching. Reduced numbers of shoot apices is compensated by great increases in number of meristematic cells within individual SAMs. Ribs and tubercles allow shoots to swell without tearing during wet seasons. Shoot epidermis and cortex cells live and function for decades then convert to cork cambium. Many modifications permit water storage within cactus wood itself, adjacent to vessels.

Key words: Cactus, epidermis, flower, leaf development, phase change, plant anatomy, shoot apical meristem, structure/function, wood evolution, xerophyte.

INTRODUCTION

The first two objectives of this review are to introduce readers to many of the exotic and extreme aspects of cactus biology, and also to show that even the most bizarre cacti are easy to understand because all have the fundamental tissues and organs of an ordinary dicot. People familiar with *Arabidopsis* will find that cacti have the same basic body organization, just having a bit more cortex, smaller leaves, and axillary buds that develop as clusters of spines. A third objective is to emphasize the diversity of structure, ecology and reproduction in the family. Probably no other plant family exceeds Cactaceae in diversity of structure; its members include trees, vines, dwarfs, giants, epiphytes and geophytes. Many are dimorphic, producing different types of anatomy or morphology at different stages of their lives. The final and main objective is to point out that many research topics in many fields can be studied with this family; there is already a solid foundation of existing knowledge that can be a basis for further studies of morphogenesis, ecology, physiology, evolution and many more areas.

Cactus evolution has been a process of diversification. Starting from some ancestral organization of stems, leaves and roots, cacti have diversified into a multiplicity of body forms. Members of subfamily Pereskioideae (Fig. 1A and Table 1) are shrubs or large trees with thin, broad, ordinary-looking leaves and hard, woody, non-succulent trunks; they are not adapted to dry, hot conditions. Subfamilies Maihuenioideae and Opuntioideae contain

plants with small but still easily visible foliage leaves, and plants vary from being trees to dwarfs (Fig. 1B and C). The largest subfamily, Cactoideae (Fig. 1D), differs from the others by having foliage leaves that are always microscopic: all photosynthesis is carried out by shoot cortex cells covered by a persistent epidermis and stomata, all of which live and function for decades or centuries, as long as the shoot is green. Members of Cactoideae and Opuntioideae occupy almost every terrestrial habitat: hot deserts; cold deserts; grasslands; shady forests; rainforests; and cold, wet or snow-covered alpine zones above the treeline (Mauseth *et al.*, 2002). Several genera of Cactoideae display what appears to be unparalleled in any other group: an absolutely amazing morphogenetic phase change in which the adult body (able to flower) looks nothing at all like the juvenile body (unable to flower). Almost every aspect of shoot morphogenesis changes, each plant produces two totally distinct types of body (Figs 1E and F and 2E).

Various aspects of cactus biology have been reviewed recently, so I will emphasize either newer discoveries or fields that have not received sufficient attention. Two monographs are recommended for numerous excellent photographs and general details of plant form and distribution: Anderson (2001) and Hunt (2006). The older work of Backeberg (1958–1962) lacks many recently discovered species and modern ideas but has much more detail than any other source (4041 pages in six volumes). Natural histories are provided by Rauh (1979) and Mauseth *et al.* (2002; *A Cactus Odyssey* being especially recommended for a less technical, more

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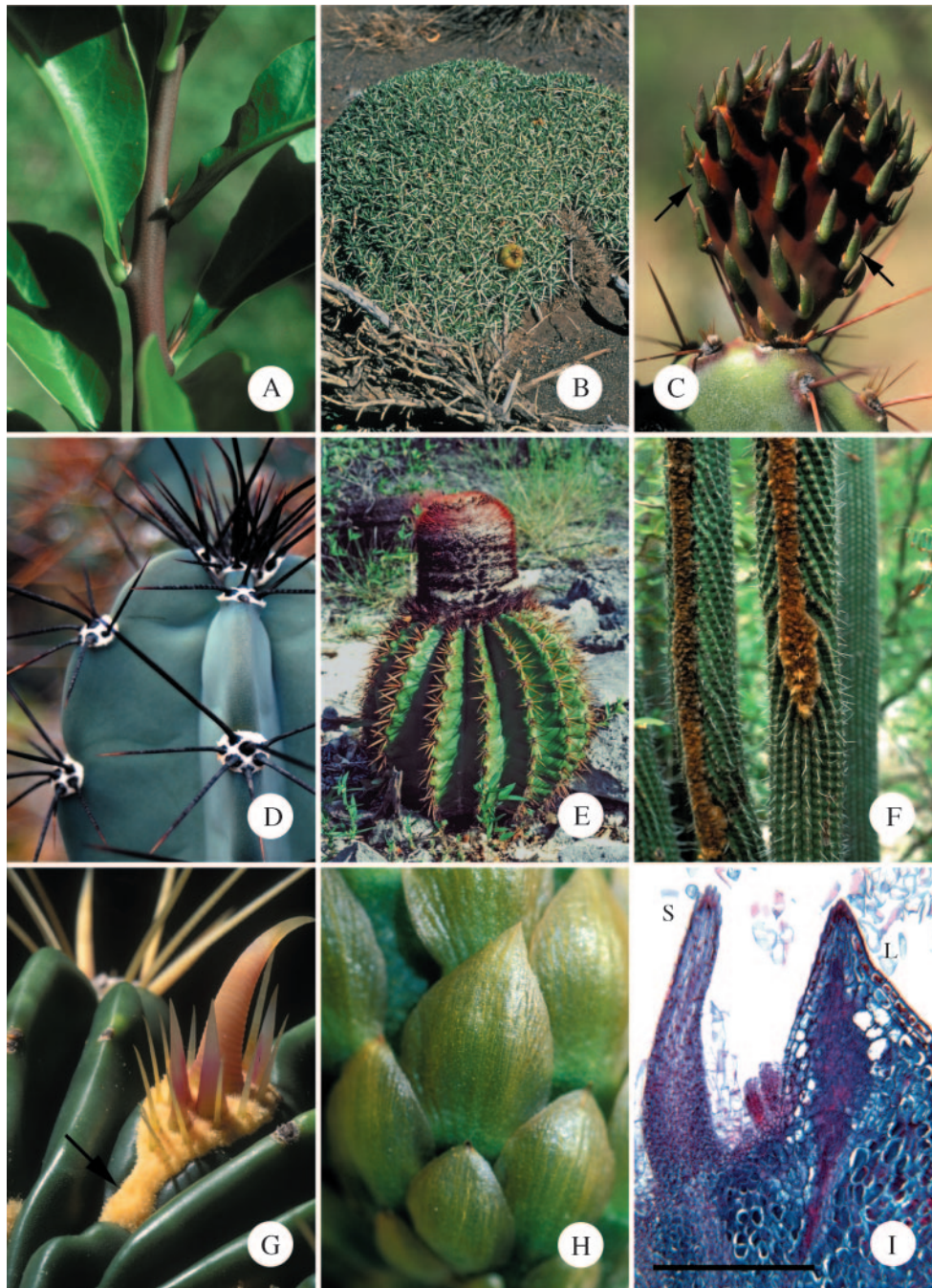


FIG. 1. Cactus shoot structure. (A) *Pereskia sacharosa* with leaves. Stem about 6 mm across. (B) *Maihuenia poeppigii*, a geophyte; all green colour is due to small leaves. The yellow structure is a fruit. The entire plant is about 1 m across. (C) Growing cladode (long-shoot) of *Opuntia violacea*, with leaves still present (two indicated by arrows). Young cladode is emerging from an axillary bud of an older cladode. The spines of the axillary buds of the older cladode are bud scales. Slightly smaller than life size. (D) Shoot tip of *Cereus forbesii*. Three of four ribs are visible; spine clusters (axillary buds, areoles) are located along the rib apex. Spines are bud scales, dormant axillary bud shoot apical meristem is located just above each spine cluster, hidden by a mass of white trichomes. Spines are present even on very young axillary buds thus protecting the shoot apical meristem, which is not the highest point of the shoot (shoot apex is concave). (E) Old plant of *Melocactus intortus* with juvenile portion of shoot (green) produced during the first 10–15 years of the plant's life, and the adult portion (red, the cephalium), which is probably at least 10 years old. This is a single shoot (not a graft of two unrelated plants), produced by a single shoot apical meristem. No new chlorenchyma has been produced for years. (F) Shoots of *Espostoa* with lateral cephalia; flowers are produced only by axillary buds within the adult (cephalium) portion, not from the juvenile (green) portions. Note disrupted phyllotaxy. Shoots are about 5 cm across. (G) Areole (axillary bud) of *Ferocactus*. Spines are modified bud scales. The location of the bud apical meristem is indicated by an arrow, below the mass of trichomes. Trichomes (yellow) are abundant in the areole but absent from the rest of the shoot. Spines and trichomes emerge from a depression about 3 mm deep. About four times life size. (H) Leaves on floral bud of *Browningia candelaris*; the largest scale is about 1 cm across. Vegetative shoots of the same plant have only microscopic foliage leaves. (I) Longitudinal section of fully developed foliage leaf (L) of *Oreocereus trollii*; present are epidermis, stomata (not visible here), vascular tissue, chlorenchyma, dorsiventral asymmetry. Leaf is 450 μm tall. Axillary bud SAM (out of view on left) has produced leaf primordia, one of which is developing as a spine (S). Cells in spine base are meristematic, those in upper portion are elongating into fibres. Scale bar = 300 μm .

TABLE 1. Subfamilies of Cactaceae (see Leuenberger, 1986, 1997; Barthlott and Hunt, 1993; Anderson, 2001; Griffith, 2005; Hunt, 2006)

1. Pereskioideae (Fig. 1A)	Similar to ordinary dicots: leaves broad, thin with reticulate venation; shoots are trees or shrubs (vines in <i>P. aculeata</i>) with slender stems with thin, relatively nonsucculent cortex; shoot epidermis is ephemeral, being replaced by bark while the stem is only 1 or 2 years old. <i>Pereskia aculeata</i> , <i>P. diaz-romeroana</i> , <i>P. grandifolia</i> and <i>P. sacharosa</i> are easy to cultivate; <i>P. diaz-romeroana</i> is self-fertile and produces seeds when only 2–4 years old
2. Maihuenioideae (Fig. 1B)	Two Patagonian species in one genus, <i>Maihuenia</i> (do not confuse with <i>Maihueniopsis</i> in Opuntioideae). Plants are xeric-adapted small shrubs (<i>M. patagonica</i> of hot lowlands) or geophytes (<i>M. poeppigii</i> , with most of body buried, and only the leafy shoot tips visible above ground; of cold highlands)
3. Opuntioideae (Fig. 1C)	A large, diverse group but all members are more highly modified than those of Pereskioideae, all look less like ordinary dicots and are more easily recognized as cacti. Most have green, photosynthetic succulent stems. Although small, opuntiid leaves are green, photosynthetic and always easily visible on young shoots. Stems are flattened cladodes ('pads' or 'ears') in some, have radial symmetry in others, or have cylindrical trunks with cladodes as lateral branches (<i>Consolea</i> , <i>Brasiliopuntia</i>). Only opuntioideae have glochids. Shoots in most are articulated; each stem has a determinate growth period after which the SAM disorganizes and further growth is by several axillary buds. Many shoots easily break apart at these joints, form adventitious roots and establish extensive clones
4. Cactoideae (Figs 1D–I, 2A–I and 3A–D)	A large highly diverse group, none of which would be confused with an ordinary leafy non-succulent dicot. All foliage leaves are too tiny to be visible without aid (except <i>Matucana aurantiaca</i> and several <i>Rhipsalis</i>). Stems vary from long, slender and moderately succulent (<i>Hylocereus</i> , <i>Leptocereus</i> , <i>Selenicereus</i>) to moderately thick to extremely broad and tall (<i>Carnegiea</i> , <i>Pachycereus</i> , <i>Trichocereus</i>) or broad and globose (<i>Ferocactus</i> , <i>Echinocactus</i> , <i>Echinopsis</i> , <i>Eriosyce</i>), to tiny globose (Table 2). Plants may be highly branched or with few or no branches. Many have extreme phase change between juvenile and adult phases (see Cephalia in text)

inclusive account of cactus biology). Cactus structure is reviewed by Buxbaum (1950), Gibson and Nobel (1986), Terrazas Salgado and Mauseth (2002) and Terrazas and Arias (2003). Ecophysiology is summarized by Nobel (1988). Techniques for extracting DNA from even mucilaginous cacti are now available (Griffith and Porter, 2003), and DNA-based phylogenies have been proposed (Nyffeler, 2002; Crozier, 2005; Edwards *et al.*, 2005; Griffith, 2005).

HABIT

In every species, the cactus body organization is fundamentally the same as that of ordinary dicots. Most cactus leaves are microscopically small (Fig. 1I) and the cortex of most species is gigantically enlarged, but still each cactus shoot has the basic dicot organization: all consist of internodes, nodes, leaves and axillary buds produced by shoot apical meristems (SAMs). Without exception their primary body has an epidermis (with stomata), cortex, eustele (single ring of collateral vascular bundles each with primary xylem and phloem) and pith. No cactus is an annual or an herb. All produce a secondary body consisting of secondary xylem (wood), secondary phloem and bark. All genetic programmes that guide basic dicot morphogenesis are probably still present and functional in cacti.

ORGANS OF THE CACTUS SHOOT

Leaves

Evolutionary modification of leaf morphogenesis has been extensive in all cacti, and has resulted in great diversity of leaf types within each individual plant. All cacti produce foliage leaves (microscopically small in most) and spines (modified leaves); some also produce glands (modified spines), most have large, thin leaves on the surface of

their floral shoots (Fig. 1C, D and G–I; see Floral shoots below).

Diversity of cactus leaves is associated with an extreme polymorphism present in all cactus shoots. The green, photosynthetic body of an unbranched cactus is a single shoot known as a 'long-shoot'; if branched, all the green, fleshy branches are also long-shoots (Fig. 1A, C and D). Almost all familiar plants consist only of long-shoots so the term is usually unnecessary and rarely used. But in cacti, each axillary bud immediately produces leaf primordia, which in most other plants would become small, flat, waxy bud scales; in cacti, however, they develop into spines (Fig. 1D, G and I; Boke, 1944, 1952, 1967; Buxbaum, 1950). Many morphologists have considered a cluster of cactus spines to be just an axillary bud; others interpret it as a 'short-shoot', a shoot with extremely short, narrow internodes and without the broad, succulent tissues of the long-shoot. Long-shoot/short-shoot dimorphism is not unusual in seed plants. For example, most of an apple tree (*Malus*) consists of long-shoots which have ordinary photosynthetic leaves with axillary buds enclosed by bud scales, but the axillary buds themselves perennially produce both flowers and photosynthetic leaves on shoots with extremely short internodes: the axillary buds become short-shoots, often called spur shoots. In this case, long-shoots and short-shoots bear leaves that are virtually indistinguishable. In contrast, most of the body of a pine tree (*Pinus*) consists of long-shoots which bear small brown papery scale leaves (easily overlooked); the axillary buds of the scale leaves develop into short-shoots with needle-like leaves. The familiar pine needles are not the leaves of the familiar pine branches (long-shoots) but instead are the leaves of almost invisible short-shoots (Foster and Gifford, 1974).

Foliage leaves. In all cacti, SAMs (see below) of long-shoots produce leaf primordia (Boke, 1951, 1980;

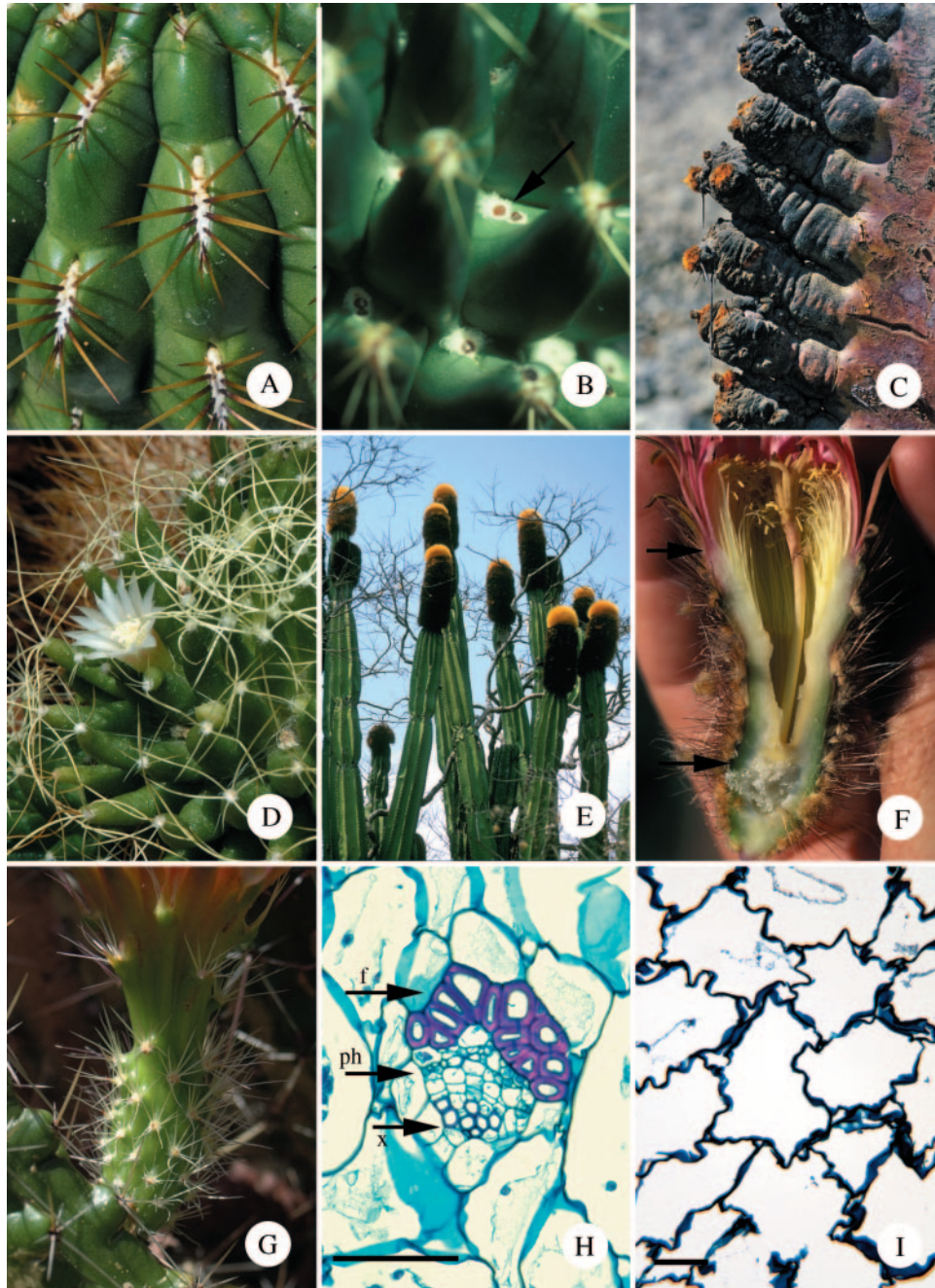


FIG. 2. Specialized features of cacti. (A) Elongated axillary buds of *Oroya peruviana*, with spines in two rows, not in spiral phyllotaxy around the bud SAM, which is located at the top of each areole. Each areole is about 5 mm long. (B) Tubercles of *Coryphantha clavata*, each with an elongate areole containing one or two secretory spines (arrow). Note ordinary non-secretory spines at the tips of each tubercle (out of focus in foreground). Tubercles are about 12 mm long. (C) Elongated areoles of *Neoraimondia roseiflora*. When first formed, these resembled ordinary areoles as in Fig. 1D, but each has flowered numerous times over many years, growing longer each time. Each has bark, cortex, stele and pith. These are about 60 mm long. (D) Dimorphic areoles of *Mammillaria camptotricha*. Each areole SAM has divided into two, one being carried outward with the tubercle apex where it makes only spines, the other remaining at the tubercle base where it produces a flower or a vegetative shoot. The open flower is about 8 mm across. (E) Terminal cephalia of a single, branched plant of *Backebergia militaris*. Green portions are juvenile, cephalia are the adult body. Each shoot tip will be abscised about 4 cm below the cephalium, then one or two axillary buds will grow as new juvenile bodies for several years, then convert to making cephalia. The plant is about 6 m tall. (F) Section of a floral shoot of *Neocardenasia*. The outer portion is a long-shoot with leaves, nodes and internodes. True flower organs occur only along the inner surface (upper arrow indicates boundary between vegetative and floral organs); petals and stamens, although located physically above the ovary and style base, are morphologically lower (proximal). After fertilization, all tissues above the lower arrow will abscise, removing style, stamens, petals and much vegetative tissue. The region below the lower arrow will develop into a true fruit surrounded by a false fruit. (G) External structure of floral shoot of *Echinocereus*. Although referred to as a 'flower,' this is long-shoot tissue with tiny foliage leaves, axillary buds (bud scales are spines), nodes and internodes. True floral structures are present inside this shoot (some petal bases are visible at the top). Almost life size. (H) Cortical bundle in *Lepismium*, with xylem (x), phloem (ph) and a cap of phloem fibres (f). All conducting cells are extremely narrow. Scale bar = 100 μ m. (I) Collapsible cortex in *Haageocereus*. Completely turgid palisade cortex cells are <500 μ m away in the same region. Scale bar = 100 μ m.

Mauseth and Halperin, 1975; Mauseth, 1976, 1977, 1978*d*, 1980*a*, 2004*d*). In *Pereskia*, these develop into large, thin, fully functional photosynthetic foliage leaves with a broad lamina (Fig. 1A; lamina to 23 cm long, 6 cm wide; Bailey, 1960; Leuenberger, 1986; Mauseth and Landrum, 1997). These are the main sites of photosynthesis and persist for months but abscise when plants become dormant. *Pereskia* foliage leaves may be slightly thickened but not remarkably so, and palisade and spongy mesophyll are only weakly differentiated. An extensive reticulate venation of collateral vascular bundles is present. In *Maihueñoideae* and *Opuntioideae*, green photosynthetic leaves are present and all are large enough to be easily visible by the naked eye (Fig. 1C; Mauseth, 1999*a*, 2005; Leuenberger, 1997). They are flattened with a small thick, succulent lamina in *Pereskiaopsis* and *Quiabentia*, but are radially symmetrical in all other *Opuntioideae* and *Maihueña*, and usually are narrow (2–5 mm), short (range 3–12 mm, but 120 mm long in *Austrocylindropuntia subulata*) and ephemeral (persistent in *M. poeppigii*, *Pereskiaopsis*, *Quiabentia* and *Austrocylindropuntia*). Their photosynthesis is probably insignificant except when relatively large and long-lived. If an opuntoid long-shoot is more than 1 or two months old, there may be nothing other than a tiny leaf scar immediately below the cluster of spines.

Long-shoot leaves in all *Cactoideae* have been greatly reduced evolutionarily but most have all the tissue types typical of an ordinary foliage leaf (Fig. 1I; Boke, 1951, 1952, 1957*b*; J. D. Mauseth, unpubl. res.) and thus they probably still have leaf development genes similar to those of other plants (Fleming, 2005). They range from very small (maximum 2.3 mm long in *Matucana aurantiaca*) to microscopic, <500 µm long in most. All but the most miniscule have stomata, at least one vascular bundle, and dorsiventral asymmetry (the vascular bundle is located closer to the adaxial epidermis, and the abaxial mesophyll is slightly aerenchymatous). At least a few have a noticeable lamina (up to 1776 µm wide in *Epiphyllum*) but none has a petiole or abscission zone. The most reduced long-shoot leaves in *Cactoideae* do not develop beyond the leaf primordium stage, but instead remain as just a tiny bump (50 µm tall) of epidermis covering several mesophyll cells; their leaf trace typically runs only to the axillary bud SAM and spines, not to the leaf itself.

Evolutionary restriction of foliage leaf development had consequences other than the obvious ones of reducing the shoot's surface area and surface:volume (S:V) ratio, reducing transpirational water loss, and reducing photosynthetic surface area. It also reduced leaf venation, which is the site of vascular loading and unloading. Ordinary foliage leaves have an extensive set of leaf veins consisting of primary xylem and phloem and having a tremendous length and surface area in contact with living mesophyll. Shoots of *Cactoideae* with their highly reduced foliage leaves have little or no leaf vascular tissue, so water must be unloaded from bundles in the cortex (see Cortical bundles below), from leaf/bud traces or from secondary xylem (wood). But in most non-cactus woody

plants, water is almost never unloaded from or loaded into secondary xylem (roots load water into primary xylem); vessels of wood are surrounded by a matrix of wood fibres or a bit of paratracheal parenchyma, and they do not have extensive surface contact with a voluminous parenchyma capable of absorbing the water they transport. Wood vessels instead transfer water to primary xylem of leaves, flowers, and so on. Loss of leaf venation in cacti almost certainly resulted in selection pressure to alter secondary xylem such that it has increased amounts of paratracheal tissues able to unload, store and transfer water [Fig. 3G; see Secondary xylem (wood) below].

Loss of leaf venation also affected phloem loading; secondary phloem in the central vascular cylinder does not load sugars directly, it only receives them from primary phloem in leaf traces. Because cacti store water in a voluminous cortex, the outer photosynthetic cortex is too distant from the secondary phloem of the central cylinder to allow it to load sugars directly. All loading of sugars apparently must occur in cortical bundles or perhaps leaf/bud traces.

Spines. Cactus spines are the modified bud scales of an axillary bud; alternatively they can be considered the modified leaves of a short-shoot (Mauseth, 1976; Boke, 1980). Differences between the two interpretations are not obvious. Being leaves of an axillary bud, cactus spines almost always occur in clusters, a character which distinguishes this family from all others. Several cacti have only one spine per cluster, and spines are completely absent in *Blossfeldia* (Mauseth, 2006*a*) and some epiphytic rainforest cacti (some *Epiphyllum*, *Lepismium*, *Rhipsalis*; Fig. 3D). Almost as soon as the axillary bud SAM becomes recognizable, it develops zonation typical of any angiosperm, having a uniseriate tunica over a corpus composed of central cells, peripheral zone and pith-rib meristem. It immediately produces leaf primordia; these resemble long-shoot leaf primordia in being small swellings of ground meristem covered by protoderm. As the axillary bud's leaf primordia enlarge, their tip cells vacuolate and elongate, and quickly the young spine consists of three regions: a basal meristem; a zone of elongation/differentiation and an apical zone of mature; and dead lignified fibres (Fig. 1I; Mauseth, 1977).

The spine basal meristem consists of only a uniseriate protoderm surrounding a mass of ground meristem. No vascular tissue or procambium has been reported. Most cell division produces daughter cells aligned parallel to the spine's long axis, but occasional divisions in other planes widen the basal meristem gradually, thus cactus spines taper from a narrow tip to a broader base (Fig. 1G). Spines are frequently circular in transverse section but can be flattened on one side (usually the adaxial side; *Ferocactus latispinus*) or their basal meristem becomes so broad but thin that the spine is flat and papery, mimicking a dry blade of grass (*Leuchtenbergia principis*, *Tephrocactus articulatus*: spines 4 mm wide, 0.3 mm thick, to 15 cm long). Factors that control morphogenesis in spine basal meristems are unknown, but in many cacti these meristems are accessible large masses of uniform

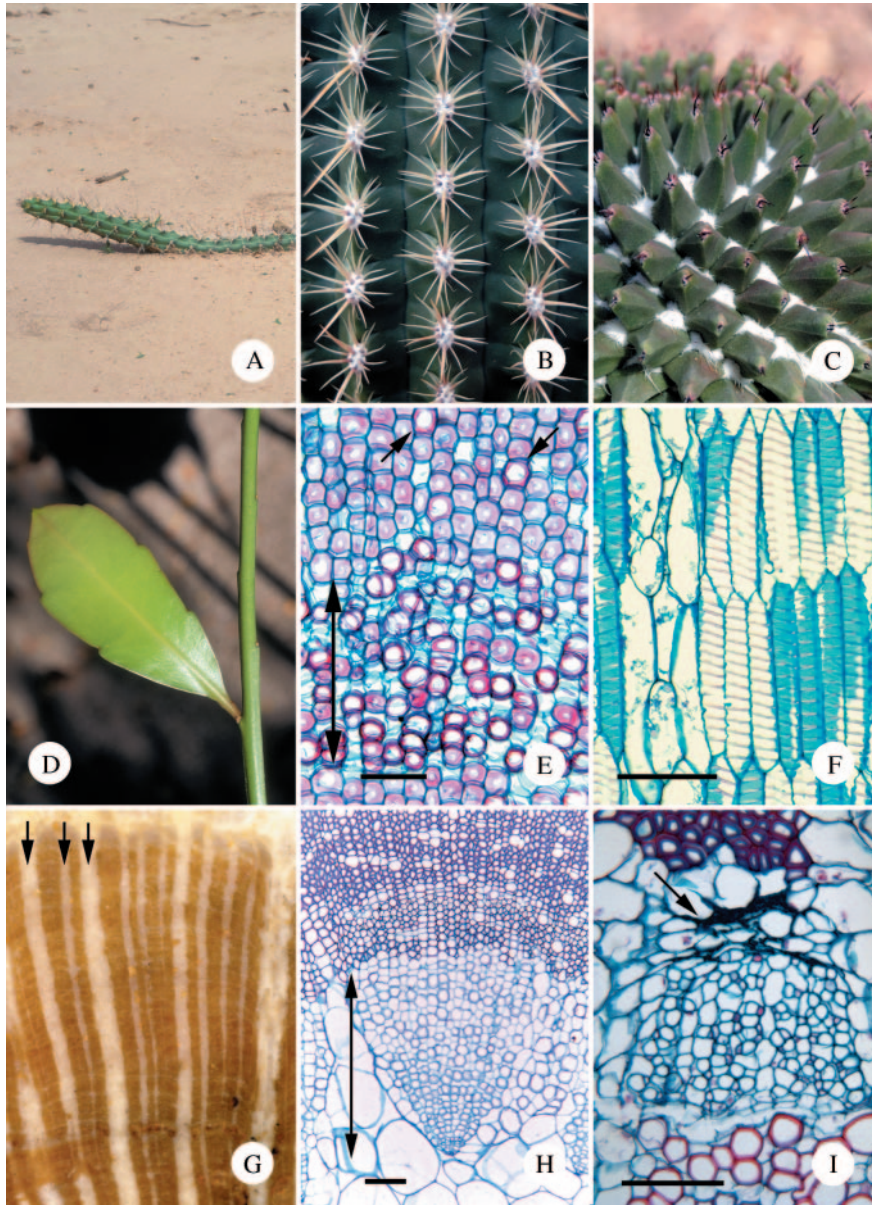


FIG. 3. Cactus structures. (A) Prostrate shoot of *Harrisia pomanensis*. The shoot tip is elevated by reaction cortex near the phloem on the lower side of the shoot. The visible part of the shoot is about 40 cm long; the entire shoot is several metres long, branched and growing in various directions. The lower side has adventitious roots. (B) Three ribs of a columnar cactus, *Coleocephalocereus*. As the shoot loses water and volume, ribs become narrower but do not change surface area. Each spine cluster is an axillary bud; subtending foliage leaves (like those in Fig. 1I) are microscopic. Each areole could potentially produce a vegetative long-shoot (a branch); because this species has lateral cephalia, these are juvenile phase areoles and cannot bloom. Each rib base is about 10 mm across. (C) Tubercles of *Mammillaria magnimamma*, produced in obvious phyllotactic spirals. Tuberculate shoots shrink vertically as well as radially as water is lost. Being a *Mammillaria*, this has divided, dimorphic areoles: areole SAMs at tubercle tips produce only spines; areole SAMs at tubercle bases (hidden by white trichomes) produce floral shoots or vegetative shoots (none are present in the photograph). Each tubercle is about 10 mm long. (D) Dimorphic shoots of *Epiphyllum caudatum*; the branch on the left was initially terete but immediately switched to distichous phyllotaxy with just two tall, thin ribs. The 'midvein' is the central vascular cylinder, the 'blade' is the two ribs and notches along the rib crests are the axillary buds (spines are microscopic). The vertical shoot on the right is terete here, but its tip had also switched to growing as a two-ribbed leaf-like structure. The cladode is about 30 mm across. (E) Wide-band tracheid wood of *Thelocactus bicolor* in transverse section. The double-headed arrow in the lower portion indicates the region with many vessels (dark red, narrower walls), perhaps earlywood. The upper portion of the micrograph is mostly WBTs (perhaps latewood), with two vessels (arrows). In many WBTs, the band-like secondary wall almost occludes the lumen. Scale bar = 100 μ m. (F) Tangential section of WBT wood in *Thelocactus*; WBTs are short and imperforate, and in this species the secondary wall occurs as one or two helices per cell. Blue is the flexible primary wall; despite the thick secondary wall, these cells shorten and lengthen as the water content changes. Cells near the left, lacking wide-bands, are ray parenchyma cells. Scale bar = 100 μ m. (G) Transverse view (macroscopic) of *Consoulea* wood. Rays (white, arrowed) are very wide (1 to 3 mm); vessels within the axial masses (tan) are close to water stored in the rays. These rays interconnect water stored in the pith and cortex. The image is about 30 mm across. (H) Dimorphic wood of *Stenocereus*. The double-headed arrow indicates primary xylem and first-formed secondary xylem, both lacking fibres and instead having WBTs, vessels and xylem parenchyma. After several months, the vascular cambium switched to making fibrous wood (above upper arrowhead), consisting of vessels, xylem parenchyma and xylary fibres but no WBTs. Scale bar = 100 μ m. (I) Transverse section of secondary phloem of *Corryocactus*. The arrow indicates collapsed phloem, below which are abundant sieve tube members and companion cells. A phloem fibre cap is at the top of the image, secondary xylem at the bottom. Scale bar = 100 μ m.

meristematic cells which are active for weeks and thus could be an excellent experimental system. Genes that maintain SAM cells in a meristematic state, such as *WUSCHEL* and *CLAVATA*, may also act in spine basal meristems.

As cells are pushed upward in the meristem, at some point they cross into the spine's zone of elongation and maturation (Mauseth, 1977). All cells in both the surface (protoderm) and centre (mesophyll) develop into fibres. Mesophyll cells elongate greatly and have only a few simple pits in their extremely thick, hard walls. In most spines, cell elongation is uniform throughout, producing a remarkably straight spine, but some have predictable, differential growth rates, elongating more on their adaxial side and thus becoming curved or hooked downward (especially *Ferocactus*, *Mammillaria*, *Parodia*). Once mature, the cells die, but it is not known if they undergo programmed cell death or merely starve as they are pushed far away from the nutrient supply in the basal meristem and separated from it by younger cells that are also sclerifying. Spine protoderm cells also elongate, deposit a sclerified secondary wall then die. Cactus spine epidermis lacks stomata; in a few species some spine epidermis cells elongate outward as trichomes (*Mammillaria plumosa*, *Turbinicarpus*; Sotomayor and Arredondo, 2004). Spines of *Cylindropuntia* are covered by a loose sheath assumed to be deciduous epidermis.

At maturity, cactus spines lack almost all characters of leaves, even of the reduced long-shoot foliage leaves of Cactoideae (Fig. 11; Mauseth, 1977). They have no guard cells, no stomata, no hypodermis, no chlorenchyma (except in the basal meristem), no spongy mesophyll, no phloem and no xylem. Instead they consist of just two cell types that never occur in long-shoot foliage leaves of cacti: libriform fibres and sclerified epidermis. Axillary bud leaf primordia must repress virtually all foliage leaf morphogenesis genes and instead activate genes that normally are only expressed in xylem or phloem fibres.

In tissue culture, cactus leaf morphogenesis is easily controlled by hormones. Cytokinins cause cultured axillary bud SAMs of *Opuntia polyacantha* to convert to long-shoot SAMs and produce primordia that develop as foliage leaves, whereas gibberellins cause cultured SAMs to continue as short-shoot SAMs, producing more spine primordia (Mauseth and Halperin, 1975; Mauseth, 1976, 1977). If cultured SAMs are transferred from one hormone to the other, or given both hormones simultaneously, lateral organs develop combinations of spine and foliage leaf characters (J. D. Mauseth, unpubl. res.).

A single axillary bud usually produces several types of spines, each differing in size, shape, colour and texture, varying in a predictable sequence (Figs 1G and 3B; Buxbaum, 1950). This is an extreme form of heteroblasty. The outermost spines (radial spines) are usually smaller, shorter, more delicate whereas those in the centre (central spines) are more robust and have different pigmentation. Radial and central spines are totally distinctive with no intermediates in many species, but intergrade in others. Spine colour may be important for camouflage (spines often have the colour of dry grass) or for recognition by

pollinators and seed dispersers, but the basis of spine pigmentation is unknown. In a few species, all spines of an axillary bud are similar, differing only slightly from each other (Fig. 2A).

The phyllotactic arrangement of spine primordia around the axillary bud SAM in cacti is unusual and may challenge theories of phyllotaxy and leaf initiation. In most (all?) cacti, spines are produced only on the side of the axillary bud SAM adjacent to the subtending leaf, they are not produced in a radially symmetrical pattern centred on the SAM. An easily observed exotic phyllotaxy is that of *Pelecyphora aselliformis*, *Turbinicarpus pseudopectinatus* and *Oroya peruviana* (Fig. 2A; Boke, 1959); spines occur in two parallel rows, which at first appears to be distichous phyllotaxy, but both rows are located on the same side of the SAM, and all other sides are free of primordia. In some species, spine primordia remain small and quiescent after they are formed and none develops until the full complement is present, but then the most recently initiated primordia develop into spines first, and the first-initiated primordia are the last to enlarge (Boke 1952, 1955, 1957a, b, 1961a, b).

Unusual spines called glochids occur in all members of Opuntioideae (except *Puna clavarioides*; Kiesling, 1984) but no other subfamily. Glochids are short and narrow, occur in high numbers per axillary bud, have retrorsely barbed epidermis cells at their tip, and, unlike all other spines, glochids always abscise from their base (Robinson, 1974). After breaking away, they remain in place unless disturbed because they are so tightly crowded together. An incautious touch results in glochids in skin, clothing, equipment and laboratory. Glochids are modified spines and thus modified leaves; they are initiated by the axillary bud SAM as extremely slender leaf primordia in a phyllotactic pattern; these aspects of SAM function and leaf morphogenesis are unstudied.

Spines provide more than protection from herbivores. When abundant, they shade photosynthetic cortex from intense insolation and UV. Spine epidermis and mesophyll of several cacti have deep fissures as a part of normal development; in *Turbinicarpus klinkerianus*, *Discocactus horstii* and *Opuntia invicta*, radioactive phosphate or safranin dye applied to the spines was absorbed into the cactus body (Schill and Barthlott, 1973; Porembski, 1994); water absorption through such spines may be significant in fog zones. Spines are flammable, increasing damage to cacti during wildfires (Emming, 2005, 2006).

Spines as glands. Spines of several genera are secretory glands but this is almost completely unstudied. Ants are often seen at the glands of some species of *Ancistrocactus*, *Coryphantha*, *Cylindropuntia*, *Ferocactus* and *Opuntia* when they have droplets of clear liquid, presumably sugar and water (Fig. 2B). Ants are attracted to the glands of *Cylindropuntia acanthocarpa* and protect it from insects (Pickett and Clark, 1979), and ant visits to extra-floral nectaries of *Opuntia stricta* increase fruit set (Oliveira et al., 1999). Secretory spines on axillary buds of flowers of *Neoraimondia arequipensis* attract ants to the flower itself.

Glandular spines of *Ancistrocactus scheeri* are short, broad, and taper abruptly to a sharp, narrow spine-like tip; their mesophyll cells are short, blunt, living fibres with thin walls and large intercellular spaces (Mauseth, 1982). Sugars and water secreted by these fibres exude from the top of the glandular spine. After some unknown period, each gland collapses. In *Ancistrocactus* and *Coryphantha*, numerous glandular spines are formed in each axillary bud over a period of at least several months, perhaps >1 year; only one or two glands are active at any time, but any particular axillary bud will be producing secretory product for a protracted time (Dicht and Lüthy, 2005).

Secretory spines in *Calymmanthium substerile* produce a thick white material. This has been seen only in cultivated plants protected from rain. It has not been studied.

Axillary buds

In cactus literature, the region in a long-shoot leaf axil is called an 'areole', not simply an axillary bud. This term is useful because the bud's spines persist even if the axillary bud SAM goes on to produce a flower and fruit. Flowering in most angiosperms causes bud scale abscission, so after the fruit is shed, the region is little more than a set of scars, but in cacti the entire set of spines is still present. Furthermore, some cacti produce spines for a prolonged period, longer than most axillary buds produce bud scales, so these growing structures are more appropriately considered short-shoots rather than merely buds. 'Areole' refers to the region at all stages of its development.

Cactus axillary buds become active immediately and produce spine primordia while still within a few micrometres of the long-shoot SAM, still within its apical depression (Boke, 1944, 1952, 1980; Mauseth *et al.*, 2002). Spine primordia themselves develop immediately, such that many spines project upward, protecting the shoot apex from herbivores (Fig. 1D). Young axillary buds are carried upward and outward with growth of the cortex, and leaf/bud traces elongate as well. Typically, cortex immediately interior to an axillary bud stops expanding slightly earlier than does surrounding cortex, thus the bud becomes located in its own well-like depression (only a few millimetres deep and wide; Figs 1D and G and 2A). This depression is lined by epidermis and hypodermis, both being more delicate and having thinner cell walls than epidermis and hypodermis cells located between areole depressions. In *Blossfeldia liliputana*, stomata are not present anywhere except in the areole depressions (Barthlott and Porembski, 1996; Mauseth, 2006a), and in *Maihuenia poeppigii* (Fig. 1B; Mauseth, 1999a) areole depressions are the only areas in which epidermis does not immediately convert to cork cambium, so in this species, too, areole depressions are the only regions of the stem that have stomata (*M. poeppigii* has persistent macroscopic foliage leaves, *B. liliputana* does not).

The axillary bud SAM produces an abundance of uniseriate, multicellular trichomes along with spine primordia. In most species, it appears as if every single areole epidermis cell becomes either part of a spine primordium or a trichome; there appear to be no ordinary

epidermis cells within the areole. Trichomes in all species die immediately, thus the SAM is protected by an almost impenetrable mass of dead trichomes and spines.

After producing spine primordia and trichomes (and glochids in Opuntioideae), the axillary bud SAM remains capable of further growth, either as a floral bud (Fig. 2G), a vegetative branch (a long-shoot; Figs 1C and 3D), or as a short-shoot. In species that bloom with flowers on new growth near the shoot tip (many species), the axillary bud SAM develops as a floral bud as soon as spine primordium production is completed. If axillary bud SAMs become dormant for 1 or more years after forming spines, the plant blooms with flowers located farther from the shoot apex. In many species of *Hattiora*, *Rhipsalis*, *Schlumbergera* and Opuntioideae, young axillary buds immediately grow out as branches (Buxbaum, 1950), but, in most cacti, branching only occurs from axillary buds that are several to many years old and which are thus located in regions with enough strength to support the weight of branches. Many plants branch only from axillary buds located at the base of the trunk: their SAMs remain dormant for decades, yet develop as normal branches. Many giant columnar cacti and barrel-shaped cacti have few or no branches while growing normally; of their thousands of axillary buds (about 10 000 axillary buds in single shoots of *Trichocereus pasacana*; J. D. Mauseth, unpubl. res.), most do nothing other than produce spines and flowers. However, if these shoots are cut off near their base, one or several axillary buds become active and grow out as branches: they were suppressed by extreme apical dominance.

Axillary buds in some cacti are capable of more than producing only one flower and later one branch. Buds of *Lepismium cruciforme*, *Myrtillocactus*, *Pachycereus gatesii*, *P. marginatus*, *P. schottii* and *Rhipsalis russellii* bear several flowers or fruits simultaneously (Barthlott and Taylor, 1995; Arias *et al.*, 2003), those of *Neoraimondia* (including *Neocardenasia*) produce several flowers per year for many years. Each time a flower is produced the axillary bud becomes slightly longer and the reason for calling it a short-shoot becomes more obvious. With extreme age (how old?), *Neoraimondia* short-shoots become up to 85 mm long, and may even branch; they have pith, secondary xylem and phloem, cortex and bark (Fig. 2C; Rauh, 1957; Mauseth and Kiesling, 1997; Kiesling and Mauseth, 2000).

Other unusual aspects of the growth pattern of *Neoraimondia arequipensis* are worth mentioning here. Their long-shoots are massively succulent, very broad and heavy (40 cm in diameter) and grow to 7 m tall. At that point, a long-shoot stops growing and one of its basal-most areoles grows out as a lateral shoot right at ground level, its eventual weight supported by the soil. Lateral shoots apparently grow rapidly because their apical-most 15 or 30 cm of epidermis has the clean, fresh look of being <1 year old; within a few years, this branch reaches its full length and stops, then another basal areole repeats the process. A typical plant has five to ten giant branches that have stopped elongating and one single branch that is growing: apparently the plant channels most resources to

one branch at a time. But the non-growing branches are not moribund: they are photosynthesizing and their axillary buds all flower perennially (Mauseth *et al.*, 2002). *Neoraimondia* biology has many intriguing aspects but these giant, frost-sensitive plants are not easy to cultivate.

Axillary buds of many Opuntioideae, a few Cactoideae and several *Pereskia* occasionally and sporadically produce a new spine from time to time over many years. These too are short-shoots but always remain only a few millimetres long; their anatomy has not been studied.

Unusual branching of axillary buds. In cacti and most other stem-succulents, cortex below and surrounding an axillary bud grows outward in the form of a cone (tubercle) or ridge (rib; Figs 1D and E and 3B and C; see Ribs and tubercles below). Growth of ribs and tubercles has not been studied, but they appear to have a basal growth zone located proximal to the axillary bud, between it and the stem. Consequently their growth causes the axillary bud to be carried outward along with the tip of the rib or tubercle, so axillary buds and all associated spines, flower parts or branches are located at the apex of a rib or tubercle.

In contrast, in a small subgroup of Cactoideae (e.g. *Coryphantha*, *Mammillaria*), the growth zone is located directly below the axillary bud SAM, which consequently is stretched as the tubercle grows (Boke, 1952, 1953, 1955, 1958, 1961a, b; Dicht and Lüthy, 2005). In *Mammillaria*, the bud SAM always divides dichotomously and one of the two new SAMs is carried outward along with the tubercle tip while the other remains stationary, at the base of the tubercle. Both new meristems become radially symmetrical but have different fates: the distal SAM at the tubercle tip produces only spine primordia, it never flowers or grows as a lateral branch, whereas the proximal one does produce flowers and lateral branches but almost never spines (Fig. 2D). Flowers or new branches of mammillarias emerge from between the crowded bases of the tubercles, not from the tubercle tips and not adjacent to the spines as is typical of most cacti. Remarkably, if tubercle tips are cultured with high levels of cytokinin, the spine-producing SAM can be induced to form a branch with microscopic foliage leaves on long-shoots (J. D. Mauseth, unpubl. res.).

In *Coryphantha* and *Ancistrocactus*, growth of the tubercle below the axillary bud causes the SAM to elongate but not divide dichotomously. Perhaps it acts as if forming a crest because it produces leaf primordia along its entire length. These leaf primordia develop into extrafloral nectaries (glandular spines; Fig. 2B; see Spines as glands above). In addition, radial growth of the tubercle cortex upward below the elongate SAM is inhibited, so the nectaries are located in a groove running along the tubercle's adaxial side (Boke, 1961b).

Phase change, heteroblasty and the transition from juvenile to adult

Seedlings of most angiosperms produce leaves and stems that differ at least slightly from those produced

when the plant is older. This is called 'heteroblasty,' but additional characters differ between seedlings and older plants, and the term 'phase change' is more inclusive (Howell, 1998). Phase change is occasionally associated with conversion from the juvenile state (incapable of flowering) to the adult state (able to flower). In classic examples such as *Citrus* and *Hedera*, the juvenile/adult transition occurs simultaneously with phase change, but in many species, phase change is completed before the juvenile/adult transition occurs: the plant grows with its mature phase morphology for one to several years before becoming old enough to flower.

All cacti undergo phase change. Compared with older plants, seedlings have narrower primary stems with fewer cortex and pith cells; more delicate epidermis and hypodermis; shorter ribs or tubercles (and species with ribbed adults may have tuberculate seedlings); shorter, more delicate spines. Most produce wide-band tracheids (WBTs; see Wide-band tracheids below; Fig. 3E, F and H) in their primary and secondary xylem (Loza-Cornejo *et al.*, 2003; Mauseth, 2004c). As the seedling ages, each successive bit of growth becomes more robust, its characters progressively more similar to those of an older plant. Species that will grow to have slender shoots stop producing WBT wood and switch to making fibrous wood instead (see Dimorphic wood below). These changes are not accompanied by a juvenile/adult transition because almost no cactus can bloom before it is 1 year old (in many cases, several years or decades old), so most cacti grow with their mature morphology for years even though they are still juvenile.

The juvenile/adult transition is accompanied by no obvious morphological changes in most cacti, but in others there are stunning changes in anatomy, morphology and physiology. The differences between juvenile and adult phases are much more extensive and dramatic than those of any other group of plants. Once old enough to flower, these cacti produce an adult body called a cephalium.

Terminal cephalia. *Melocactus* and *Discocactus* (do not confuse with *Disocactus*) have terminal cephalia. Young plants grow as juveniles with unbranched globose to short cylindrical shoots with prominent ribs and areoles, each with a small number of stout spines (Fig. 1E; Mauseth, 1989). Most of the green shoot surface is unobscured, visible and photosynthetic because ribs are large, areoles small and spines are few. The juvenile phase lasts several to many years, varying with species and growing conditions, and the biochemical trigger to become adult is unknown: plants of *M. matanzanus* (commercially available) grown with fertilizer, water and full sunlight become adults while only 3 years old, during which time they have produced about 160 leaves and areoles. As a plant converts from juvenile to adult, almost all aspects of its growth change. The adult shoot—the cephalium—is produced by the same SAM that produced the juvenile shoot (juvenile shoot and cephalium are the two ends of one shoot) (Niklas and Mauseth, 1981; Mauseth, 1989). Phyllotaxy becomes very high, and the adult SAM

produces small, closely spaced tubercles rather than prominent ribs as it did while it was juvenile. Spine number per areole increases greatly and cephalium spines are short and slender. Trichomes are produced in abundance. Because areoles are so closely spaced and the density of spines and trichomes is so high, the surface of the adult shoot is completely hidden under an impenetrable, solid mass (about 1.0 cm thick) of spines and dead trichomes (Mauseth *et al.*, 2002). No light penetrates this mass, photosynthesis is impossible, and there are no stomata, no guard cells, no ordinary epidermis cells. The adult SAM becomes smaller, produces a narrower cortex free of chloroplasts but with cortical bundles and closely spaced leaf/bud traces. Cephalium pith is also narrow, so the entire adult region is much narrower than the juvenile. The transition is abrupt with little or no intermediate tissues. Adult shoot secondary xylem consists of WBTs and vessels, and that of the juvenile shoot consists of an inner region of fibrous wood surrounded by an outer, more recently produced layer of WBT wood; apparently the juvenile/adult transition also affects the vascular cambium such that once the SAM begins producing adult morphology at the shoot's apex, the cambium begins producing wood with adult morphology throughout the shoot.

Axillary buds in the cephalium produce flowers. Being located on a tiny tubercle below a thick layer of spines and trichomes, each flower bud is remarkably well protected from predation. During anthesis flower buds elongate and petals curve outward just above the spines. Ovules and nectaries, still located at the base of the mass of spines, are accessible to pollinators through a petal-lined flower tube. Flowers close after just 1 d, the perianth withers and remains in place, protecting the ovary. When ready, the mature fruit swells, pushing itself up above the mass of spines, becoming visible to seed dispersers (Cortes Figueira *et al.*, 1994).

A cephalium in this position is a terminal cephalium because it is at the apex of the shoot, not because it terminates the plant's growth. Instead, the plant continues its growth for many years, but as with any other species that undergoes a juvenile/adult transition, all further growth is with the adult organization (the cephalium is not an inflorescence, is not ephemeral). The cephalium becomes longer every year, every year there are more flowers and fruits, but every year the juvenile portion merely becomes older—and it is the only photosynthetic tissue the plant has. Because the shoot is produced by one single SAM and does not branch, no new photosynthetic cortex can be added, so the ratio of photosynthetic tissue to heterotrophic tissue decreases every year. Melocacti easily become 20 or 30 years old in cultivation, continuing to rely on the same, old chlorenchyma cells they produced when they were juveniles. Under normal conditions, melocacti never branch, but if a mature plant is decapitated, an axillary bud of either the cephalium or the juvenile body will grow out as a lateral branch with juvenile characters. At some point this switches to adult growth, a new cephalium. All 33 species of *Melocactus* have this morphology; no known species

retains intermediate stages in cephalium evolution (Taylor, 1991).

Discocacti resemble melocacti, but their cephalia grow more slowly and even old plants that have bloomed for years have only extremely short cephalia. Discocacti grafted onto hardy rootstocks are easy to cultivate.

Plants of *Backebergia militaris* (*Pachycereus militaris*) are giant columnar cacti, up to 5 m tall (Fig. 2E). They grow as juveniles with broad stems and prominent ribs until at least 3–4 m tall, then they add several ribs and soon switch to producing tubercles (Cattabriga, 2004; Mauseth *et al.*, 2005). In this short transition region, spines are shorter, narrower, more brittle and translucent. Production of trichomes increases. The adult body is only slightly narrower than the juvenile, and the thick layer of long, densely packed spines causes the cephalium to appear broader than the juvenile body. Unlike *Melocactus*, the adult body of *B. militaris* does have a few cells that become ordinary epidermis cells, and stomata are present; the outer cortex is weakly chlorophyllous, but certainly little light penetrates the spines. Just as in *Melocactus* and *Discocactus*, each year the cephalium becomes longer, whereas the juvenile body remains the same length.

Backebergia, however, periodically abscises its cephalia, which releases one of the uppermost axillary buds on the juvenile portion from apical dominance. The bud grows out as a new lateral branch with juvenile morphology and fresh chlorophyllous tissue. Once the branch becomes 2–3 m long, it too converts to adult growth and becomes topped with a terminal cephalium. This process occurs repeatedly, resulting in giant, highly branched plants. *Backebergia militaris* cannot tolerate frost but small plants grow readily in a greenhouse. Adult portions of *Pachycereus schottii* have more and longer spines than do juvenile portions.

Terminal, temporary cephalia occur in *Arrojadoa*, *Cephalocereus* (*Neodawsonia*) *apicicephalum* and *Stephanocereus leucostele* (Table 2). After the shoot has bloomed with a set of flowers emerging from a cephalium encircling the shoot tip, its SAM returns to vegetative growth and then makes a segment (many centimetres long) of green stem incapable of flowering. In the following year, it makes another terminal, temporary cephalium. The shoot alternates between non-flowering zones and ring-shaped flowering zones, which remain recognizable for years, long after all flowers and fruits have matured and abscised; internal anatomy is not known.

Stephanocereus luetzelburgii, a poorly known species, grows as a broad column until about 20 cm tall, then it switches to growing as a much narrower column, perhaps accompanied by a juvenile/adult transition (Taylor and Zappi, 2004).

Lateral cephalia. Lateral cephalia are regions with adult characters located on one side of the shoot, not at its apex (Fig. 1F). They have been studied in *Cephalocereus* (Vásquez Sánchez *et al.*, 2005) and *Espositoa* (including *Vatricania*; Buxbaum, 1952, 1959; Rauh, 1957; Mauseth, 1999b; Mauseth *et al.*, 2002). A seedling grows as a

TABLE 2. Genera with at least some species with unusual features; especially noteworthy species are indicated (for illustrations and more examples, see Anderson, 2001; Mauseth et al., 2002; Hunt, 2006)

Broad stems	<i>Carnegiea gigantea</i> , <i>Cephalocereus</i> , <i>Coryphantha</i> (<i>C. elephantidens</i>), <i>Echinocactus</i> (<i>E. grusonii</i> , which is easy to obtain and cultivate), <i>Echinopsis</i> (<i>E. [Soehrensia] bruchii</i>), <i>Ferocactus</i> , <i>Gymnocalycium</i> (<i>G. saglionis</i>), <i>Neobuxbaumia</i> (<i>N. macrocephala</i> , <i>N. tetetzo</i>), <i>Oreocereus</i> (<i>O. celsianus</i>), <i>Pachycereus</i> (gigantic plants), <i>Trichocereus</i> (<i>T. pasacana</i> , <i>T. terscheckii</i>)
Cephalia	Terminal cephalia: <i>Backebergia</i> (<i>Pachycereus</i>) <i>militaris</i> , <i>Discocactus</i> , <i>Melocactus</i> Terminal but temporary cephalia: <i>Arrojadoa</i> , <i>Cephalocereus</i> (<i>Neodawsonia</i>) <i>apicicephalium</i> , <i>Stephanocereus</i> Lateral cephalia: <i>Coleocephalocereus</i> (<i>Buiningia</i>), <i>Espostoa</i> (<i>Pseudoespostoa</i> , <i>Thrixanthocereus</i> , <i>Vatricania</i>), <i>Espostopsis</i> (<i>Austrocephalocereus</i> , <i>Gerocephalus</i>), <i>Facheiroa</i> , <i>Micranthocereus</i> (<i>Siccobaccatus</i>) Pseudocephalium: <i>Cereus mortensenii</i> , <i>Pilosocereus</i>
Climbing by adventitious roots	<i>Hylocereus</i> , <i>Selenicereus</i> , <i>Weberocereus</i>
Determinate shoots	<i>Hatiora</i> , Opuntioideae (all species), <i>Rhipsalis</i> , <i>Schlumbergera</i>
Dwarf shoots	<i>Ariocarpus agavoides</i> , <i>A. scaphirostris</i> , <i>Astrophytum asterias</i> , <i>Blossfeldia liliputana</i> , <i>Copiapoa hypogaea</i> , <i>C. laui</i> , <i>C. tenuissima</i> , <i>Echinopsis chamaecereus</i> (<i>Chamaecereus silvestrii</i>), <i>Epithelantha</i> , <i>Eriosyce esmeraldana</i> , <i>E. krausii</i> , <i>Eriosyce occulta</i> , <i>Escobaria duncanii</i> , <i>E. minima</i> , <i>Frailea</i> , <i>Maihuenia poeppigii</i> (<i>Maihuenioideae</i>), <i>Maihueniopsis</i> (<i>M. clavarioides</i> : height above soil level = 0.0 cm), <i>Mammillaria luethyi</i> , <i>M. saboae</i> , <i>Mila</i> , <i>Parodia nothominuscula</i> , <i>P. subterranea</i> , <i>P. tenuicylindrica</i> , <i>Pediocactus</i> (tiny plants but difficult to cultivate), <i>Pterocactus</i> (Opuntioideae), <i>Rebutia</i> , <i>Sclerocactus</i> (difficult), <i>Turbinicarpus</i>
Leaf production rapid	<i>Aporocactus flagelliformis</i> , <i>Cleistocactus</i> , <i>Espostoa</i> , <i>Hylocereus</i> , <i>Pilosocereus</i> , <i>Selenicereus</i> (vigorous grower)
Leaf production slow	<i>Ariocarpus</i> , <i>Lophophora</i> , <i>Pediocactus</i> , <i>Sclerocactus</i>
Extremely few branches	<i>Ariocarpus</i> , <i>Astrophytum</i> , <i>Blossfeldia</i> , <i>Carnegiea</i> , <i>Cephalocereus</i> , <i>Ferocactus</i> , <i>Mammillaria</i> , <i>Melocactus</i> , <i>Neobuxbaumia</i> , <i>Oreocereus celsianus</i> , <i>Pachycereus</i> , <i>Trichocereus pasacana</i> , <i>T. terscheckii</i> . Some species of <i>Ferocactus</i> , <i>Mammillaria</i> and <i>Pachycereus</i> are highly branched
Prostrate columnar	<i>Cereus kronleinii</i> , <i>Echinopsis hahniana</i> , <i>Haageocereus decumbens</i> , <i>H. icensis</i> , <i>H. tenuis</i> , <i>Harrisia pomanensis</i> , <i>Praecereus saxicola</i> , <i>Stenocereus eruca</i>
Ribs only two	<i>Discocactus</i> , <i>Epiphyllum</i> , <i>Hatiora</i> (<i>Rhipsalidopsis</i> , <i>Epiphyllopsis</i> , <i>Pseudozygocactus</i>), <i>Lepismium</i> , <i>Pseudorhipsalis</i> , <i>Rhipsalis</i> (<i>R. elliptica</i> , <i>R. pachyptera</i> , <i>R. russellii</i>), <i>Schlumbergera</i> ('Christmas cacti', commonly called <i>Zygocactus</i>), <i>Selenicereus anthonyanus</i>

juvenile green column with prominent ribs and stout, sparse spines on all sides for several years. When old enough to undergo the juvenile/adult transition, development of only some ribs on one side is altered, all tissues being added to the other ribs on the rest of the body continue to develop with juvenile characters; as the shoot continues to grow from one single SAM, some leaf primordia and their associated node and internode tissues develop with adult morphology, the rest develop with juvenile characters. Adult characters are similar to those in *Melocactus*: cortex is thin and non-chlorophyllous; short, small tubercles with long, slender spines are produced instead of large ribs and stout spines; and there are also abundant trichomes and bark. Only areoles in the cephalium produce flowers; other areoles at the same level (thus with the same age) but in juvenile regions do not. Differential growth of cortex and ribs/tubercles disrupts phyllotaxy but the SAM is not affected and continues to grow for years, simultaneously producing reproductive adult tissues and chlorophyllous juvenile tissues. Lateral cephalia occur in numerous genera (Table 2).

In *Pilosocereus*, areoles that produce flowers simultaneously produce copious amounts of long trichomes, giving the shoot the appearance of having a cephalium. However, internal portions of the shoot are not affected, and once the trichomes break off after several years, that portion of the shoot looks like any other; such regions are pseudocephalia. *Cephalocleistocactus* produces exceptionally long spines on just one side, giving the impression of a weakly formed lateral cephalium, but flowering is not restricted to those

areoles. All areoles are adult, so the role of the cephalium-like region is unknown.

Other types of phase change. The juvenile/adult transition of *Browningia candelaris* is more or less the opposite of producing a terminal cephalium. Juvenile plants grow as vertical, unbranched determinate columns with prominent ribs and abundant long spines. Once the shoot reaches about 2 m tall, it stops growing and five to ten apical areoles grow out as lateral branches. These are slightly narrower than the juvenile shoot (the trunk), have many low ribs with short weak spines that could almost be overlooked. These branches constitute the adult body and are the only part that bears flowers (Mauseth et al., 2002).

Several species, especially *Lepismium* (*Pfeiffera*) *ianthothele* appear to be neotenous: their adult bodies strongly resemble the seedling phase of other lepisiums (Barthlott and Taylor, 1995).

Dwarfism, gigantism

Evolutionary dwarfism of shoots appears common in cacti. The ancestors of cacti were probably woody, non-succulent trees or large shrubs; this body form occurs in *Pereskia* (Pereskioideae), *Maihuenia patagonica* (Maihuenioideae), *Pereskiaopsis* (Opuntioideae) and Cactoideae (*Leptocereus*, *Calymmanthium*, *Acanthocereus* and many others). However, many clades now have genera or species whose plants consist of dwarf shoots <10 cm tall, often <3 cm (Kiesling, 1995; Table 2). These have WBT wood (see Wide-band tracheids below), a type of wood characteristic of seedlings, so dwarfism may be linked to neoteny.

In contrast, many species of *Pachycereus* (*P. fulviceps*, *P. weberi*), *Trichocereus* (*T. atacamensis*, *T. pasacana*, *T. terscheckii*), *Cephalocereus senilis* and *Neobuxbaumia tetetzo* are gigantic. Within Opuntioideae, *O. echios* of the Galapagos Islands must be the result of tremendous evolutionary increase in body size from a smaller ancestor. Griffith (2004a, b) has pointed out that all subfamilies of Cactaceae except Pereskioideae also contain small, dwarf geophytic plants, thus it is theoretically possible that very small body size is basal in the family.

Floral shoots

Most cactus flowers are inside out, with perianth located physically above stamens, both located above carpels, all buried deeply within a shoot (Fig. 2F; Boke, 1963, 1964, 1966, 1968; Leuenberger, 1986). When a cactus axillary bud produces a flower, it first initiates several to many leaf primordia, nodes and internodes, then switches to producing the primordia of petals (there are often no distinctively sepal-like structures), stamens and carpels. All primordia are present in an ordinary acropetal sequence while the bud is microscopic (Ross, 1982). When cell enlargement occurs, it stops earlier in the centre of the bud than in peripheral regions, so the ovary is elevated little, stamens are elevated a bit more and petals are elevated most. All floral organ primordia become located on the inside of a conical depression in the end of the elongating floral shoot (Fig. 2F). At the rim-like apex of the depression are the first-formed, most proximal perianth primordia and the last-formed, most distal leaf primordia; on the outside of the floral shoot are progressively older leaves and areoles in ordinary phyllotactic sequence (Fig. 2F and G). The object we see when viewing a cactus 'flower' from the side is really just a long-shoot (not flower) surmounted by petals. The true flower (except for the petals) is completely hidden inside the long-shoot. Floral shoots are >10 cm long in many cacti and reach 30 cm in *Epiphyllum crenatum* and *E. oxypetalum* (Anderson, 2001): ovary and ovules are 30 cm below the uppermost leaves. After pollination and fertilization, the true fruit develops inside the base of the long-shoot, which itself develops as a false fruit; just as in an apple fruit, the boundary between inner true fruit and outer false fruit is not readily apparent. Only the region immediately exterior to the ovary converts to false fruit, all the distal long-shoot tissue is abscised along with the style, stamens and perianth (most cacti have dozens of stamens and petals, an important consideration for the ABC model of floral morphogenesis).

Each node of the floral branch often has a scale-like leaf and an axillary cluster of spines. In *Cylindropuntia fulgida* ('chain fruit cholla'), *C. leptocaulis*, *Pereskia sacharosa* and a few others, the axillary buds on the 'flower' produce floral shoots which later become 'fruits' whose axillary buds repeat the process. Axillary buds on the false fruits of *C. leptocaulis* even produce non-floral branches. *Calymmanthium substerile* goes one step farther: the apical rim with the last leaves and the first petals does not grow radially as the floral shoot elongates, so it

remains just a tiny hole. During anthesis, the flower's expansion actually rips the floral shoot open such that petals, stamens and style elongate through ruptured, dying long-shoot tissues (Mauseth *et al.*, 2002).

The long-shoot nature of the exterior of a cactus 'flower' is important because in many genera its nodes bear large, thin photosynthetic leaves (Fig. 1H). They are referred to as 'scales' or 'bracts' but they develop from leaf primordia, have a lamina (23 mm long, 14 mm wide in *Browningia candelaris*; Mauseth *et al.*, 2002) with extensive leaf venation, axillary buds, and some have an abscission zone. Thus almost all 'leafless' cacti (subfamily Cactoideae) have not only microscopic long-shoot foliage leaves (see Leaves above) but also large, relatively ordinary leaves as well (they differ from petals, which are pigmented and lack axillary buds and spines). Many cacti are adapted to mesic habitats in which virtually all associated plants have photosynthetic leaves, and rain-forest epiphytic cacti occur in very moist habitats. Yet none of these uses floral leaf genes to produce large, photosynthetic leaves on their vegetative body. As most cacti evolved to be exclusively stem-photosynthetic, they gave up the beneficial capacity that drought-deciduous plants have; modern cacti (other than pereskias, maihuebias and some Opuntioideae) cannot have an extensive photosynthetic surface area (large leaves) during rainy seasons and then abscise that extra surface area during drought. Many *Euphorbia* and *Pachypodium* combine stem-succulence with stem-photosynthesis and drought-deciduous leaves; it seems as if cacti should have the genetic capacity to do this also, but instead remain 'leafless' except when flowering.

TISSUES OF THE CACTUS SHOOT: PRIMARY BODY

Shoot apical meristems

Evolutionary modification of one aspect of plant biology often affects other aspects. Such interactions are extensive in cacti, and the co-evolution involving SAMs, increased cortex succulence and decreased branching is especially interesting. All cacti with relatively narrow stems (diameter <1.0 cm) have SAMs between 90 and 300 μm , a rather ordinary size for seed plants (Boke, 1941; Gifford, 1954; Mauseth, 1978d, 2004d). However, all cacti with greatly enlarged stems (due to having a very thick cortex, which is possible due to having cortical bundles; see Cortex below) have exceptionally large SAMs, up to 2565 μm (>2.5 mm) diameter in *Echinocactus platyacanthus* (also *E. grusonii*, which is commercially available and easy to cultivate). The only other plants with such large SAMs are cycads, which also have broad-diameter primary bodies and high phyllotaxy (Foster, 1940). The exceptionally broad cortex makes cactus shoots exceptionally heavy per unit length; e.g. a 1.0-m-long section of *Trichocereus pasacana* shoot weighs about 32 000 g (J. D. Mauseth, unpubl. res.) while an equal length of *Arabidopsis thaliana* would weigh <0.5 g. Almost certainly, this increased weight

caused selection of mutations that decrease branching, and many cacti with broad stems have few or no branches (Cody, 2002; Table 2).

Related to reduced branching is a reduced number of SAMs that produce the shoot system. In non-succulent trees such as *Pinus* or *Acer*, each plant is highly branched, each has thousands of twigs and thus thousands of SAMs. Even if each SAM is of ordinary size with only a few hundred cells, the shoot is being produced by hundreds of thousands of apical meristem cells. In contrast, sparsely branched cacti have only a few SAMs, and unbranched cacti have just one single SAM that produces the entire shoot body (reminder: the bulk of cactus shoots consists of primary tissues derived directly from a SAM, not secondary tissues produced by cambia). If unbranched cacti had a SAM of ordinary size with just a few hundred meristem cells, each cell would have to undergo tens of thousands of rounds of cell division, and the number of copy-error mutations created with each replication would accumulate to unacceptable levels (Klekowski, 1988) before a cactus shoot had reached maturity. But because sparsely branched cacti have gigantic SAMs, each with thousands of cells, the number of rounds of cell division required of each meristem cell is reduced, as is the risk of introducing copy-error mutations.

The evolution of SAMs up to 2500 μm in diameter from ancestors whose SAMs were much smaller must have required extensive modification of genes that control shoot apex morphogenesis. SAM genes in *Arabidopsis thaliana* and other model plants probably play the same roles in cacti but must have evolved to interact over much greater distances and greater volumes of meristematic cells (Mauseth, 2004d).

Rate of leaf production and length of plastochron vary tremendously in the family, although studies are needed. SAMs in *Ariocarpus*, *Lophophora*, *Pediocactus* and *Sclerocactus* may produce only one to five leaf primordia per year (Table 2), but plants of *Cleistocactus*, *Espostoa* and several other genera probably have the highest leaf production rates and the shortest plastochrons in the entire plant kingdom. Shoots of *C. strausii* have up to 30 ribs, each with leaves and axillary buds (spines clusters) located every 3 mm; a shoot may grow 300 mm per year, which is 100 leaves per rib, and 3000 leaves on all 30 ribs. The growing season is about 9 months or 270 d, thus each SAM produces about 11 leaves per day with a plastochron of 2.2 h (J. D. Mauseth, unpubl. res.).

Cactus SAMs are located in depressions at the shoot tip, they are not the most apical point physically (Fig. 1D). Newly formed cortex cells grow upward slightly sooner than do newly formed pith cells, so cortex actually protrudes beyond the SAM. The apical depression may be as much as 3.0 cm deep and 20 cm wide in large globose cacti such as *Echinocactus* or *Echinopsis*, so newly formed epidermis and leaf primordia are carried upward and outward by growth of subapical tissues. Following a row of leaf primordia in its phyllotactic spiral from oldest to youngest, you would follow them up the outside of the shoot, across the ring-shaped top of the shoot and then down the inside of the apical depression.

Indeterminate SAMs and monopodial growth. The orderly nature of ribs and phyllotactic spirals of tubercles indicates that shoot growth is monopodial and indeterminate in most Cactoideae. Cactus SAMs become dormant in winter or dry seasons but never form terminal buds and, in almost all cases, the first-formed nodes and internodes of one year grow to be as wide as those of the previous year, so columnar cacti tend to have uniform, straight ribs and globose cacti have uniform spirals of tubercles. Seasonal growth increments along a shoot's length can occasionally be identified due to constrictions of the ribs or markings in their cuticle (Otis and Buskirk, 1986). In *Backebergia militaris* immature portions of ribs in the dormant shoot apex form a bit of bark, which prevents them from expanding fully in the following growing season: the shoot's longitudinal growth increments are marked by constrictions (Fig. 2D; Mauseth *et al.*, 2005). Constricted monopodial shoots are especially pronounced in *Armatocereus*, whose shoots consist of vertically aligned segments, strongly resembling the jointed bodies of an *Opuntia* or *Cylindropuntia* (but these latter have determinate shoots and sympodial growth). Demographic studies may be possible with *Armatocereus*; each segment demarcated by a constriction indicates a single growth episode. In *A. procerus*, they may be correlated to episodic El Niño rains rather than annual growth cycles (Mauseth *et al.*, 2002).

Determinate SAMs and sympodial growth. In contrast to the evolution of giant SAMs in many Cactoideae, SAMs in Opuntioideae evolved to be determinate, functioning briefly before being replaced by a branch derived from an axillary bud (Fig. 1C). This is almost universal in Opuntioideae; only *Pereskopsis*, *Brasiliopuntia*, *Consolea* and *Tacinga* have any indeterminate shoots. Plants of *Pereskopsis* are highly branched shrubs with many indeterminate shoots (Arias Montes, 1996); those of *Brasiliopuntia* and *Consolea* have a single indeterminate, radially symmetrical trunk but all branches are determinate, laterally flattened cladodes. Another species, *Tacinga funalis*, has radially symmetrical, indeterminate shoots. All other opuntioide genera grow with determinate SAMs only (Mauseth, 2005). The jointed cylindrical stems of chollas (*Cylindropuntia*) are each determinate shoots; the flat 'pads' or 'ears' of prickly pears (genus *Opuntia* or subgenus *Platyopuntia*) are determinate cladodes. Less familiar opuntioide genera such as *Maihueiniopsis*, *Pterocactus* and *Tephrocactus* consist of sympodial sets of globose determinate shoots (Kiesling, 1982, 1984; Hunt and Taylor, 2002; Mauseth *et al.*, 2002; Griffith, 2005). Typically, the SAM has finished producing all internodes, nodes, leaf primordia and axillary buds while it is still <1.0 cm long. Apparently their SAMs convert to masses of large parenchyma cells at maturity. In contrast, a seedling's epicotyl SAM persists longer, although it too is ultimately determinate; this needs study (Table 3).

Determinate SAMs are associated with unusual branching patterns and shoot polymorphism in several rainforest epiphytes in Cactoideae (Barthlott and Taylor, 1995). In *Hattiora salicornioides*, each determinate shoot

TABLE 3. Resources for research on cacti (these lists do not include all possible sources or journals)

Sources of plant material	Huntington Botanical Garden (San Marino, CA), Desert Botanical Garden (Phoenix, AZ), Le Jardin Exotique (Monaco), Städtische Sukkulentensammlung (Zurich), plus numerous commercial nurseries
Reviewed journals	<i>Bradleya</i> , <i>Haseltonia</i> , <i>Desert Plants</i>
Natural history journals	<i>British Cactus and Succulent Journal</i> , <i>Cactus and Succulent Journal</i> (USA), <i>Kakteen und andere Sukkulente</i> (Germany), <i>Quepo</i> (Peru), <i>Succulentes</i> (France, Monaco)

has one narrow, long basal internode (1 mm by 3–4 mm) followed by four to six broad, short internodes (3 mm × 1 mm), followed by five to eight internodes that form a concave disc at the shoot apex; shoots are shaped like inverted beer or wine bottles (common name: ‘drunkard’s dream’). Its SAM disorganizes into a plate of parenchyma, and three to five of the axillary buds in the topmost flat disc become active simultaneously, forming a whorl of shoots identical to the one to which they are attached. This pattern repeats indefinitely. In *Rhipsalis mesembryanthemoides*, an axillary bud near the base of a shoot grows out as a long (20 cm) determinate shoot; almost all its axillary buds grow out as short (1.5 cm) determinate shoots which do not branch under ordinary circumstances but which bear flowers. Once the long shoot stops growing, one of its basal-most branches grows out as another long shoot. In *Rhipsalis burchellii*, a basal axillary bud grows out as a long (60 cm) determinate shoot. Once it stops growing, several apical-most axillary buds grow out as a whorl of shorter determinate shoots, and when they stop, several apical-most axillary buds on each of them grow out as a whorl of even shorter determinate shoots. This repeats until the last determinate shoots grow to be only about 6.0 cm long, then the pattern repeats as one of the basal-most axillary buds on the original long shoot grows out as another very long determinate shoot.

Dichotomous branching of SAMs. Dichotomous branching occurs in at least two species of *Mammillaria* (*M. perbella* and *M. parkinsonii*; Boke, 1976) and one *Echinocereus* (*E. reichenbachii*; Boke and Ross, 1978) and sporadically in several other genera. For several years, plants grow as unbranched short columnar shoots with radial symmetry and a set of intersecting phyllotactic spirals of tubercles. At some point in time, the shoot apex becomes oval rather than round and phyllotaxy becomes abnormal. The shoot apex becomes even more elongate and gradually the phyllotaxy resolves itself into two separate sets of phyllotactic spirals, each set centred on the ends of the oval-shaped apex: the apex has divided into two separate SAMs, each producing ordinary radially symmetrical shoots. After several years, both apices of *M. perbella* divide dichotomously again, this time perpendicular to the previous division.

During dichotomous branching the SAM temporarily switches to bilateral symmetry, and, if viewed in median longitudinal section, it is extremely broad due to a lateral expansion of the central cell zone and pith-rib meristem. The peripheral zone appears unaffected (Boke, 1976; Boke and Ross, 1978). Cells in the centre of the broadened SAM begin dividing regularly, giving rise to a layered pattern typical of a peripheral zone, and leaf primordia are formed in the centre of the broad apex. At this point, the SAM has divided into two separate meristems. If the SAM is viewed in a median longitudinal section perpendicular to that described above, it appears normal throughout the process.

Perhaps related to dichotomous branching is formation of crested shoots. A SAM becomes extremely broad in one plane as described above, but instead of dividing, it continues to broaden (Boke and Ross, 1978). SAMs as much as 1 m wide are known, and despite having dimensions on the order of 50 µm tall × 200 µm thick × 1000 000 µm wide, they produce leaf primordia, nodes, internodes and axillary buds. Phyllotaxy is irregular in most crests. Crested cacti are often propagated by cuttings; many can be obtained for research. Colour-based chimeras are also now available commercially.

Cortex

Cortical bundles. A key innovation in the evolution of many cacti (in particular Cactoideae) must have been the acquisition of cortical bundles, a network of collateral bundles that vascularizes the cortex and permitted it to evolve to a thickness not found in any other plant of any kind (Fig. 2H). Although several cactus clades have narrow shoots with a relatively thin cortex, most Cactoideae have cortexes that range from extremely broad to extraordinary compared with shoots of all non-cactus plants; the cortex is 300 mm thick in *Echinocactus platyacanthus* (compared with 0.048 mm in *Arabidopsis thaliana*), and a range of 10–70 mm is common in Cactoideae (mean thickness is 19.9 mm; Mauseth, 2000).

Cortical bundles apparently were not an early step in cactus evolution. They are completely absent from subfamilies Pereskioideae, Maihuenioideae and Opuntioideae; they are present in all Cactoideae except *Blossfeldia liliputana* (Boke, 1980; Mauseth and Sajeve, 1992; Mauseth and Landrum, 1997; Mauseth, 1999a, b; Terrazas and Arias, 2003; Mauseth, 2005, 2006a). DNA cladograms suggest *B. liliputana* is the earliest-divergent member of Cactoideae (Nyffeler, 2002; Crozier, 2004, 2005), so presence of cortical bundles is a synapomorphy for the rest of Cactoideae.

Cortical bundles are critically important for the evolution of a broad cortex because, even if a stem has a thick, wax-covered cuticle, it gradually loses water to dry desert air, so epidermis, hypodermis and outer regions of cortex must be kept hydrated by some means. If the cortex is unvascularized (as it is in almost all vascular plants; Howard, 1979), then water must move from the central vascular cylinder to epidermis by diffusion, which is slow over distances of more than a few millimetres

(Barcikowski and Nobel, 1984), thus limiting any increase in cortex thickness. But with the evolution of cortical bundles, water can be transported rapidly in bulk and distributed throughout the outermost regions of the stem, keeping chlorenchyma, hypodermis and epidermis hydrated no matter how distant they are from the xylem in the central ring of bundles. Similarly, as cortex evolved to be thicker, the chlorenchyma and the sugars it produces became located farther from central cylinder phloem, but cortical bundles allow mass flow of phloem sap across the thickest cortex. In contrast, other stem-photosynthetic succulents, such as euphorbias and stapelias, lack cortical bundles and never have a truly thick, truly voluminous cortex similar to that common in Cactoideae (Mauseth, 2004a, b). Although they are excellent examples of evolutionary convergence with cacti, their shoots are not as wide, they never have giant globose or columnar primary bodies; the euphorbia that are broad achieve their width by accumulation of wood.

The molecular genetic basis of cortical bundle morphogenesis is not known, but these bundles greatly resemble leaf venation (Fig. 2H; Mauseth and Sajeve, 1992). Cortical bundles are collateral, slender with just a few narrow conducting cells, they have a similar spacing between veins, they form a network (three dimensional whereas leaf venation is two dimensional), and in many species they end in a cluster of short, broad terminal tracheids. Also like leaf veins, cortical bundles never extend to the epidermis or hypodermis but instead lie just at the base of the photosynthetic tissues, the palisade mesophyll of leaves, the palisade cortex in cacti (see below in this section). Cortical bundles may have evolved by means of mutations that allowed cortex cells to ectopically activate genes normally expressed only in leaves.

Unlike leaf veins, cortical bundles must remain functional for decades, as long as the cortex is photosynthetic and the epidermis is permitting gas exchange (cactus epidermis lives for years; see Epidermis below). A vascular cambium arises in each cortical bundle and produces abundant secondary phloem and, in most cases, at least a bit of secondary xylem (Mauseth and Sajeve, 1992). As is typical of all vascular plants, sieve tube members and companion cells collapse after they stop conducting, and old cortical bundles in the trunks of old plants have large masses of collapsed phloem. Typically, little secondary xylem is produced in cortical bundles, and it usually consists of just narrow vessel elements. In a few species, cortical bundles are especially complex, having phloem fibre caps (reviewed in Terrazas Salgado and Mauseth, 2002; Terrazas and Arias, 2003).

At least some species of subfamily Opuntioideae have leaf/bud traces that ramify somewhat, sparsely vascularizing a restricted region of cortex between the stele and the leaf and its axillary bud (Gibson, 1976; Mauseth, 2005).

Cortex ground tissues. In all stem-photosynthetic, stem-succulent cacti (i.e. all except *Pereskia*, *Maihuenia*, and a very few Cactoideae), stem cortex consists of three

regions: (1) an outermost chlorophyllous, photosynthetic palisade cortex; (2) a lightly- or non-chlorophyllous region in the centre of the ribs or tubercles (rib centre cortex); and (3) a non-chlorophyllous inner cortex located between the stem's ring of vascular bundles and the bases of the ribs or tubercles. Cells of the outermost, photosynthetic cortex are arranged in rows (palisades) perpendicular to the stem surface (Sajeve and Mauseth, 1991). Palisade cells have little cell-cell contact, so there are extensive intercellular spaces and free surface area, permitting rapid diffusion and uptake of carbon dioxide. Palisade cortex is always much thicker than that of leaf palisade mesophyll; the range is at least 540 µm (five cells per palisade), in various *Haageocereus* species, up to 4845 µm (26 cells) in *Discocactus alteolens* (J. D. Mauseth, unpubl. res.); systematic studies correlating thickness with phylogeny and ecology are needed. Cactus cortical bundles do not penetrate deeply into palisade cortex despite its thickness but instead end within its base, leaving as much as 1000 µm of palisade chlorenchyma unvascularized.

Palisade cortex develops by orderly cell divisions with periclinal walls such that all cells within each palisade appear to be derived from just one or two progenitor cells. In cacti with tubercles (see Ribs and tubercles below), palisade cortex is developed more or less equally all the way around the tubercle; adaxial, abaxial and lateral sides appear similar. Mucilage cells and druses are present in the palisade cortex of many species.

Cortex in the centre of ribs or tubercles is rather nondescript. It usually consists of larger, more rounded cells not aligned in rows. Chloroplasts may be sparsely present. This region stores water adjacent to the chlorenchyma; its cells swell and widen the ribs or tubercles as the shoot absorbs water, and they shrink as water is gradually lost during drought. In cacti with slender stems bearing just three or four tall, narrow ribs (*Acanthocereus*, *Calymmanthium*, *Dendrocereus*) or just two ribs (which makes the shoot a leaflike cladode; Fig. 3D and Table 2), most of the shoot's water-storage capacity occurs in the centre cortex of the ribs. In cacti with broad stems bearing many low ribs, the inner cortex between the stele and the rib bases is the more voluminous water-storage region (Mauseth, 2000). Both leaf traces and cortical bundles traverse the rib/tubercle centre cortex.

Cortex between the stem's central vascular cylinder and the bases of the ribs or tubercles is inner cortex, and it is usually the main site of water storage. Many Cactoideae facilitate transfer of water stored in the inner cortex to the chlorenchymatous palisade cortex by constructing their respective walls differently (Mauseth, 1995). In some regions of inner cortex, called collapsible cortex, cells have thin, undulate or plicate walls that fold easily as the cell gives up water, thus allowing the entire cell to shrink readily without plasmolysing (Fig. 2I). In contrast, walls of chlorenchyma cells are thicker and straighter, with little tendency to buckle (Sajeve and Mauseth, 1991). Theoretically as a plant loses water during drought, water-storage cells give up water easily, chlorenchyma cells are more resistant and thus water would be transferred to

them; although cacti probably rarely have enough water to keep their shoots fully hydrated, not all tissues suffer dehydration equally. Instead, palisade chlorenchyma appears to remain turgid even as inner cortex cells shrink. Collapsible cortex cells are lacking in Opuntioideae but do occur in some non-cactus stem-succulents (Mauseth, 2004a, b, 2005).

Many long, slender shoots in Cactoideae have reaction cortex, a tissue that elevates the tips of prostrate shoots (J. D. Mauseth, unpubl. res.). A few species of Cactoideae have shoots that always grow horizontally but their shoot tips are upturned, not pointed horizontally (Fig. 3A; Mauseth *et al.*, 2002). A region of inner cortex about 10–20 cm proximal to the shoot tip and adjacent to stele phloem on the convex side of the shoot is especially turgid (reaction cortex is hard, like the flesh of a firm apple) and generates the force necessary to elevate the shoot tip. The outermost inner cortex on the same side of the shoot and all the cortex on all other sides is softer and less turgid. As the tip continues to grow, progressively more distal regions act as reaction cortex and more proximal ones stop. The high turgidity that constitutes the reaction cortex affects cells only transiently and migrates distally as rapidly as the shoot tip elongates, generating a particular bending force. Reaction cortex never enables the shoot to grow upright, it only elevates the tip.

Secretory structures in cortex. Several secretory structures are common but not universally present in cactus cortex. Depending on the species, crystalliferous cells with calcium oxalate druses range from absent to abundant, small to large, and distributed uniformly throughout the cortex to being more prominent in certain areas. Crystal sand is very rare and only *Jasminocereus thouarsii* is known to have tiny crystals in its walls (Mauseth, 1996). Mucilage cells follow the same pattern as druses, varying from absent to abundant, distributed uniformly or in particular regions. Mucilage cells may contain druses or crystal sand or neither. Mucilage is secreted across the plasmalemma then trapped by the wall in many cases; as mucilage accumulates, the protoplast shrinks and ultimately undergoes programmed cell death (Mauseth, 1980b; Trachtenberg and Fahn, 1981; Trachtenberg and Mayer, 1982). In a few species, mucilage passes through the wall and accumulates in intercellular spaces; adjacent cells remain alive and without any obvious mucilage within themselves (Mauseth, 2005); this has not been studied in detail. All species of *Consolea*, *Nopalea*, *Opuntia* and *Tunilla* (all are Opuntioideae with flattened cladodes) have wide (660 µm × 3600 µm) canals filled with mucilage cells floating freely in extracellular mucilage, unattached by middle lamellas; the canals are lined with a multilayered epithelium. Mucilage-cell canals occur just exterior to the primary phloem, grow wider as inner epithelium cells detach and float into the lumen (Mauseth, 1980c, 2005). Large mucilage cell canals also lie at the base of the ribs in *Uebelmannia gummifera* (Nyffeler, 1997, 1998). Many species of *Mammillaria* have epithelium-lined canals that ooze a milky white or semi-milky, cloudy liquid when the plant is cut or

damaged (Boke, 1960; Mauseth, 1978b, c; Wittler and Mauseth, 1984a, b; Lüthy, 1995). The secretory product is the result of modifications of many organelles as well as the primary cell wall, and cells degenerate completely at maturity, forming a long, branched, tubular lumen. Surrounding epithelium cells convert to secretory cells, lyse and thus add to the secretory product and widen the lumen.

Ribs and tubercles

Having a folded surface, rather than a smooth one, affects a shoot's strength, flexibility, ability to swell without tearing and its surface-to-volume ratio. The shoot surface is folded longitudinally into ribs, or both longitudinally and transversely into tubercles, in almost all stem-succulent plants, cacti and non-cacti alike (Figs 1D, E and G, 2A, B and D and 3B and C; Porembski *et al.*, 1991; Mauseth, 2000, 2004a, b). Tubercles occur in sets of intersecting phyllotactic spirals but ribs run vertically and unite nodes that are not members of the same phyllotactic series.

Unlike animals, plants generate epidermis cells only at apical meristems and in lateral organ primordia (leaf, flower parts), never in regions of mature nodes and internodes. If a shoot with a smooth cylindrical or spherical surface were to absorb too much water, its surface would tend to increase, but due both to its inability to generate new cells and the inextensibility of mature epidermis cells, the shoot's surface would be torn open. But by having a plicate surface, as water is absorbed and shoot volume increases, rib bases merely spread apart, increasing the rib's volume without requiring an increase in surface area. As rib bases widen, the inner cortex can also expand: shoots change volume but not surface area so there is no damage to epidermis or hypodermis (Mauseth, 2000).

Tubercles are associated with short, broad shoots, whereas ribs typify long or columnar shoots. Whereas ribs allow the inner cortex to expand and shrink radially without damaging the shoot surface, tubercles allow the entire shoot to shorten or lengthen as water content changes. But shoots can shrink and lengthen only if they completely lack fibres in both xylem and phloem, thus tubercles occur only on shoots sufficiently short and broad to be supported by turgor pressure rather than fibrous wood (see Wide-band tracheid wood below). Ribs rather than tubercles may be more functional on long or columnar shoots by providing mechanical support. Large cacti have a tough hypodermis (see Hypodermis below), and ribs project the hypodermis outward as a continuous pleated sheet farther from the centre of the shoot, giving it greater leverage in resisting shoot flexion (Niklas *et al.*, 2000, 2003). A tuberculate surface is so flexible it could not strengthen a long, slender shoot and indeed such shoots in cacti always have ribs, never tubercles. Rather surprisingly, many short, globose cacti have ribs rather than tubercles and thus cannot shrink longitudinally.

Any degree of plication increases a shoot's S:V ratio over that of a smooth cylindrical or spherical form, but

beyond that, the relationship is complex (Nobel, 1988; Mauseth, 2000). Rib height affects both rib volume and surface (taller ribs have more volume and more surface than do shorter ribs with the same base width). But if two shoots differ only in the number of ribs (both have equal rib height), the one with the greater number of ribs must have proportionally narrower rib bases, so tissue volume of all ribs is equal in the two shoots (but the one with more ribs has greater surface). As rib height and number increase, self-shading increases as well. Many rainforest epiphytic cacti have only two ribs (Fig. 3D; distichous phyllotaxy; Table 2) giving the shoots a leaflike appearance with a very high S:V ratio. In contrast, up to 120 narrow ribs occur in *Echinofossulocactus* (Mauseth, 2004d).

The number of ribs or phyllotactic spirals present is related to the diameter of the SAM (Mauseth, 1978a, d, 1979, 2004d). SAMs typically enlarge after seed germination or the initial outgrowth of a branch, and as their basal diameter increases, they have more room available for leaf primordium initiation. Seedlings often have few phyllotactic spirals or few ribs but add more as the stem enlarges; a cactus seedling has a narrow diameter and low phyllotaxy because it is being produced by a narrow SAM with only a few layers of cells in its peripheral zone and pith-rib meristem, but that same SAM produces a much wider stem when the plant is several months or years older because the meristem itself has grown wider and added more layers of cells to its peripheral zone and pith-rib meristem. The numbers of phyllotactic spirals of tubercles in globose stems are usually Fibonacci numbers, and seedlings may progress from 3 + 5 to 5 + 8 to 8 + 13 and so on as the SAM enlarges. SAM size stabilizes at some point and phyllotaxy then remains constant and is typically easy to see and count in non-seedling plants. In young plants with enlarging SAMs, irregularities in phyllotaxy occur with the changes.

In cacti with ribs, rib number is not at all restricted to the Fibonacci series and can increase by as few as one or two ribs at a time. A seedling may have four ribs then increase to five then six and so on. In genera with low rib numbers (*Epiphyllum*, two; *Hylocereus*, three; *Acanthocereus* and *Dendrocereus*, four), the number stabilizes quickly while the plant or lateral branch is still young, but genera with many ribs (*Browningia*, *Pachycereus*, up to 20 ribs; *Carnegiea*, *Cephalocereus* and *Trichocereus*, up to 30) might add more ribs after they are many years old and many metres tall. Phyllotactic spirals are often not at all easy to identify in columnar cacti. Species with ribbed adults often have tuberculate seedlings.

Some species with low number of ribs switch between producing ribs and tubercles. In full sunlight, *Acanthocereus* has long, four-ribbed stout shoots with large formidable spines, and it grows much like a thicket of blackberries: shoots lean against neighbouring brush and low branches of trees. If a shoot of *Acanthocereus* bends enough for its tip to touch soil (especially if shaded), it typically produces several centimetres of

terete (not ribbed) stem with spirals of low tubercles, very small weak spines and adventitious roots. At some point (after becoming well-rooted?) the branch curves upward and resumes growth as a stout, four-ribbed shoot again. Similar sun/shade forms occur in *Harrisia* and *Monvillea* (J. D. Mauseth, unpubl. res.). *Selenicereus wittii* has amazing two-ribbed shoots that press themselves tightly against trees at high water line in Amazonian inundation forests; the exposed side of the two ribs has a thick cuticle and deep chlorophyllous palisade cortex, the side that adheres to the tree has adventitious roots, thin cuticle and is weakly chlorophyllous (Barthlott *et al.*, 1997). Shoots of *Epiphyllum* always grow out initially as terete, smooth shoots with neither tubercles nor ribs, but after they reach a specified length, their SAM switches from spiral phyllotaxy to distichous, and all further growth is as a two-ribbed leaf-like cladode: individual shoots are terete at one end, flat at the other (Fig. 3D).

The cortex of Pereskioideae, Maihuenioideae and most Opuntioideae is much simpler than that in Cactoideae. Pereskias and maihuenias have a thin cortex <3 mm thick and with a more or less uniform consistency; it never grows out as ribs or tubercles, it never has a palisade cortex, and it has so few intercellular spaces that photosynthetic absorption of carbon dioxide would be difficult (Fig. 1A; Boke, 1954; Sajeve and Mauseth, 1991). Most Opuntioideae have a thick, chlorophyllous palisade cortex overlying a less or non-chlorophyllous inner cortex (Mauseth, 2005). Those with laterally flattened cladodes (Fig. 1C) lack surface plications but Opuntioideae with radially symmetrical stems often have low, flat tubercle-like projections (those with short or globose shoots) or elongate rib-like ridges that are not united vertically into continuous ribs (those with more elongate shoot segments). No member of Opuntioideae is known to have cortical bundles but some have slightly ramified leaf traces (Gibson, 1976; Mauseth, 2005). Mucilage, druses and crystal sand are common.

Epidermis

In most cactus species, the epidermis of stems persists for decades as a living, transparent tissue capable of facilitating gas exchange. Whereas stem epidermis in most seed plants is ephemeral [lasting only as long as an herb lives (about 6 weeks for *Arabidopsis thaliana*, a few months for *Zea*) or dying when bark is formed on a perennial plant], cactus epidermis is present and alive as long as green colour is visible in the underlying cortex. Furthermore, when cacti do form bark at the base of old trunks, the cork cambium arises by renewed cell division in epidermis cells; despite having been exposed to UV radiation, heat and dry air for decades, epidermis cells and nuclei are sufficiently healthy to come out of cell cycle arrest, begin dividing and producing cork cells and sclereids (see Secondary body below; Mauseth, 1996; Mauseth *et al.*, 1998). Furthermore, whereas stomata are rare or absent in stem epidermis of *Pereskia* (Eggli, 1984), they are abundant in stem epidermis of most other cacti (Sajeve and Mauseth, 1991). The evolution of a persistent

stem epidermis with a high density of stomata—necessary for shoot-based photosynthesis—must have preceded the evolution of the ‘leafless’ condition.

Other features of cactus stem epidermis have been reviewed previously (Gibson and Horak, 1978; Terrazas Salgado and Mauseth, 2002; Loza-Cornejo and Terrazas, 2003), but several points are important. In some species, distribution of stomata is restricted and precisely controlled; in *Maihuenia* (plants with small persistent leaves) and *Blossfeldia* (dwarf, globose ‘leafless’ cacti), stem stomata occur predominantly in the depressions in which axillary buds are located (Barthlott and Porembski, 1996; Mauseth, 1999a, 2006a), and in *Peniocereus* (slender, ribbed shoots) stomata are restricted to the depressions between ribs (Loza-Cornejo and Terrazas, 2003); in these shoots, many cortex chlorenchyma cells are not close to any stoma. Epidermis cell walls tend to be thin, not thickened and not lignified. Cuticle thickness varies but has not been studied systematically for correlations with habitat; it is often thinner (1.0–10 µm) than one would expect of a xerophyte, and the same was found for non-cactus stem-succulents in *Euphorbia*, *Stapelia* and similar drought-adapted plants (Mauseth, 2004a, b; Terrazas *et al.*, 2005); it may be that thick cuticles are more characteristic of non-succulent xerophytes (Fahn and Cutler, 1992). Studies are needed to determine if the cuticle and waxes of long-lived epidermis cells are eroded and become thinner with age or if epidermis cells synthesize more throughout their long life. Similarly, the ‘self-cleaning’ features found in some other taxa (Neinhuis and Barthlott, 1997) would be beneficial in perennial epidermis of cacti; research is needed. Shoot epidermis protects internal tissues from UV-B radiation in alpine plants (Körner, 2003), and Darling (1989) reported UV-opacity in epidermis/hypodermis of *Carnegiea*, but, considering the long functional life spans of cactus shoot epidermis, hypodermis and photosynthetic cortex, more studies are needed.

Long, multicellular uniseriate trichomes are abundant at every node of every cactus (no known exceptions), but internode epidermis almost universally lacks any sort of outgrowth (Fig. 1D and G). Almost every epidermis cell within an axillary bud develops into a trichome while the bud is young (see Axillary buds above), but all internode epidermis cells (those that lie between axillary buds, constituting the bulk of the long-shoot surface) instead develop into flat or cube-shaped or slightly bulging cells. The exceptions are shoots of *Astrophytum* (easily recognizable because they do have tufts of short, white hairs all over their bodies) and various microscopically small projections in *Ariocarpus fissuratus*, *Monvillea spegazzinii*, *Opuntia tomentosa* and *Peniocereus* (Mauseth *et al.*, 1998; Mauseth, 2005). Multiple epidermis (produced by periclinal divisions in epidermis cells) is common, but often occurs only in small patches surrounded by ordinary unistratose epidermis.

Hypodermis

A hypodermis of several layers of cells with extremely thick, hard walls is present in most species (Gibson and

Horak, 1978; Mauseth *et al.*, 1985, 1998; Mauseth and Ross, 1988; Mauseth, 1996, 1999b; Mauseth and Kiesling, 1997; Terrazas Salgado and Mauseth, 2002; Loza-Cornejo and Terrazas, 2003; Terrazas and Arias, 2003). However, most studies have been of species with medium to very large shoots; a recent study of dwarf cacti with small, soft bodies found that either there was no hypodermis or it was composed of just a few layers of cells with thin walls (Mauseth, 2006a). A large number of cactus species have adults whose disc-shaped or globose shoots are small enough (about 4 cm in height or 6 cm diameter; Table 2) that lack of mechanically strong hypodermis tissues may actually be common. Similarly, the slender shoots of *Maihuenia* and *Pereskia* lack a hypodermis (Mauseth and Landrum, 1997; Mauseth, 1999a). A tough, elastic surface layer is thought to resist the expansion of a turgid cortex and thus provide rigidity and strength; it may be that in cacti this is important to support a broad cortex, not the shoot as a whole. A tough hypodermis also provides protection against predators, including parasitic plants (Mauseth *et al.*, 1984, 1985, 2006).

Hypodermis cells, when present, often have such extremely thick walls that almost no lumen remains; it can be impossible to even identify the number of layers of cells present in a mature hypodermis. However, hypodermis cells remain alive even when very old, such as in the trunks of giant columnar cacti (Mauseth, 1996, 1999b; Mauseth and Kiesling, 1997). Chemistry of thick hypodermis walls has not been studied; in many species they do not stain with safranin (thus they are probably not lignified), whereas in others they stain intensely. Typically hypodermis walls are so brittle they fracture during microtoming, even after use of various softening agents. Gibson and Horak (1978) reported that no cactus hypodermis has ever been found with lignified walls at maturity, but they gave no documentation; this tissue needs further study. Remarkably, attack by the parasitic dicot *Ligaria cuneifolia* (Loranthaceae) causes thick-walled, mature hypodermis cells of *Corryocactus brevistylus* to resume cell division and act as a cork cambium (J. D. Mauseth, unpubl. res.). Crystals, typically druses but also prisms, or silica bodies are present in the hypodermis of many but not all species; druses are especially common in hypodermis of Opuntioideae (Mauseth, 2005), but are not universally present as has been claimed. Tannins are often present. Various features of cactus hypodermis have been reviewed elsewhere (Terrazas and Loza-Cornejo, 2002; Terrazas Salgado and Mauseth, 2002; Loza-Cornejo and Terrazas, 2003).

Pith

Pith ranges from narrow to moderately broad (1–2 mm diameter in slender stems of rainforest epiphytes (*Epiphyllum*, *Rhipsalis*; Fig. 3D) to 145 mm in *Denmoza*; unpubl. res.) but is typically not voluminous relative to the cortex of the same stem (Mauseth, 2000). Medullary bundles are present in many Cactoideae, but are absent from all other subfamilies (Mauseth, 1993b). Like cortical bundles, medullary bundles often have

considerable secondary phloem and only a trace of secondary xylem; they almost always lack fibres. Pith matrix consists predominantly of parenchyma but may have mucilage cells, druses or laticifers. Surprisingly, the perimedullary zone (outermost pith adjacent to protoxylem and medullary rays) of some Opuntioideae consists of WBT (Mauseth, 2006b), a cell type associated with xylem rather than ground tissue such as pith or cortex (see Wide-band tracheid wood below).

Pith and innermost regions of medullary rays in trunks of *Pereskia lychnidiflora* undergo cell division and expand (dilatate), reaching a diameter of 5 cm even after the trunks have become woody (Bailey, 1963b).

Primary vascular tissues

All cactus stems, even the most flattened cladodes in Opuntioideae, have a single ring of collateral vascular bundles (a eustele, typical of all non-monocot seed plants). These primary vascular tissues have few or no unusual features in Cactaceae (Bailey, 1961; Gibson, 1976; Mauseth, 2004c). Tall, slender shoots that will form fibrous wood (all *Pereskia*, most non-cladode Opuntioideae, most nonspherical Cactoideae) have a cap of fibres (usually nucleate and septate) immediately exterior to the primary phloem. Species that will have nonfibrous wood in their adult bodies lack phloem fibre caps. Primary phloem consists of a small number of sieve tube member/companion cell pairs and either sparse or abundant nonconducting phloem parenchyma. Vascular cambium is formed while the vascular bundle is young and primary phloem is quickly replaced by secondary phloem (Bailey and Srivastava, 1962).

Primary xylem consists of narrow tracheary elements and associated matrix. Protoxylem has a matrix of parenchyma; metaxylem has a matrix of either parenchyma (plants with globose stems) or fibres (usually plants with long, slender stems). In almost every species, primary xylem contains a mix of both vessel elements and WBTs (see next paragraph). WBTs have not been found in stem primary xylem of *Pereskia*, *Leptocereus*, *Dendrocereus*, *Epiphyllum* and *Rhipsalis* and several others (Mauseth, 2004c).

Wide-band tracheids. WBTs are short, broad tracheids whose secondary wall occurs only as a set of rings (annular pattern) or one or two helices (Fig. 3E and F; helical pattern; Müller-Stoll and Süß, 1970; Mauseth *et al.*, 1995; Mauseth, 2004c) (WBTs have also been called ‘vascular tracheids,’ which is now used for a different type of tracheary element; Carlquist, 1988). ‘Wide-band’ indicates that secondary wall deposition continues until the annular or helical walls protrude deeply into the tracheid lumen, in many cases almost occluding it. WBTs never have scalariform, reticulate or pitted walls; they never have perforations. Their annular or helical secondary walls are the patterns typically associated with protoxylem, which differentiates while an organ is still elongating and thus its tracheary elements must be extensible. The other wall patterns (reticulate, scalariform and pitted) are stronger and less extensible

and are more typical of metaxylem and secondary xylem, which differentiate after organ elongation has stopped.

WBTs have a combination of features, some ordinary, some unexpected. An annular or helical secondary wall is not unusual but being so wide that it almost prevents conduction is unusual. Having this wall pattern in protoxylem is not unusual, but WBTs occur instead of fibres in metaxylem and secondary xylem of many cacti, resulting in an unusually weak wood. WBTs are never the sole tracheary element in cactus xylem but instead are accompanied by vessels: having xylem lacking fibres and dominated by tracheids rather than vessels is unusual in angiosperms.

Perhaps the key benefit of having WBTs is that they are reversibly extensible: as a cactus loses water during drought, the annular or helical walls permit WBTs to shrink, thus reducing their volume. As long as lumen volume shrinks to match that of the remaining water in the tracheid, cavitation will not occur. During a prolonged drought, WBTs might shrink greatly in length (small, disc-shaped or globose shoots, with tubercles instead of ribs, often shrink until their apices are at or below ground level) but will probably remain uncavitated and thus capable of conduction once drought ends. Such a mechanism is functional only if the shoot has no other mechanical tissues that resist shrinkage; stems with WBTs in their primary and secondary xylem typically lack fibres in both xylem and phloem (see also Wide-band tracheid wood and Dimorphic wood below).

TISSUES OF THE CACTUS SHOOT: SECONDARY BODY

All cacti are woody plants, all develop a vascular cambium that produces both secondary xylem (wood) and secondary phloem, and all produce bark from a cork cambium. Although many cacti have soft parenchymatous bodies, none is truly an herb (a plant that lacks a vascular cambium). Many dwarf cacti whose globose shoots never grow larger than 2 or 3 cm in diameter (Table 2) produce only a small amount of delicate wood that decomposes quickly after the shoot dies, but they do have wood.

Secondary xylem (wood)

Diversification of wood in Cactaceae has been extraordinarily extensive. All modifications are easy to understand, all are variations on the standard organization of wood and the vascular cambium typical of ordinary woody plants; despite occasional statements to the contrary, no cactus has anomalous secondary growth of any kind. In fact, despite the fact that many cacti are highly derived, the pereskias are the largest trees with ordinary vascular cambium and ordinary wood in the Caryophyllales.

Several important wood features are universal in Cactaceae. No cactus produces heartwood: even in samples collected from the base of pereskias and old columnar cacti, pith cells are alive, as are primary xylem parenchyma, all ray cells and all xylary fibres (cactus

wood fibres do not undergo programmed cell death; Mauseth *et al.*, 1984, 1998; Mauseth and Ross, 1988; Mauseth and Plemons, 1995; Mauseth and Plemons-Rodriguez, 1997, 1998; Mauseth, 1993*a*, 1996, 1999*a, b*, Mauseth and Kiesling, 1997; Mauseth and Landrum, 1997). No cactus has tyloses. Growth rings are detectable in only a few genera that have woods lacking fibres (Fig. 3E; Mauseth *et al.*, 1998; Mauseth, 2006*a, b*). All woods consist of a ray system produced by short ray initials and an axial system produced by long fusiform initials (for a possible exception, see WBT wood with tracheids in the rays below); primary rays extend from pith to vascular cambium and secondary rays are initiated within the axial system by conversion of fusiform initials to ray initials. Vascular cambium was studied by Bailey and Srivastava (1962).

Woods with a fibrous matrix. Short globose cacti are so broad relative to their height that turgid cortex and pith are their main skeletal support, but all tall cacti or ones with slender shoots rely on strong wood just as any non-succulent woody plant does (Bailey, 1963*a–c*, 1964; Gibson, 1973, 1977; Gibson and Horak, 1978; Mauseth and Ross, 1988; Mauseth, 1996, 1999*b*, 2006*b*; Mauseth and Landrum, 1997; Terrazas, 2000; Soffiati and Angyalossy, 2003; Terrazas and Arias, 2003; Terrazas *et al.*, 2005). Tall, slender cactus shoots all have a hard fibrous wood similar to that found in the majority of dicot trees. Most cells produced by fusiform initials mature into xylary fibres with thick, lignified walls that give the wood great strength. Xylary fibres in cacti are living, nucleate and usually septate. Wall thickness and hardness vary from taxon to taxon, but these fibres are extraordinarily hard in *Cylindropuntia*, the pendant epiphytes in *Epiphyl-lum* and *Rhipsalis* and the scandent, sprawling stems of *Acanthocereus*, *Selenicereus* and *Hylocereus*.

Vessels and paratracheal parenchyma are embedded within the fibre matrix. Vessel diameter varies over a small range within each shoot, which improves conductive safety (Stevenson and Mauseth, 2001, 2004; Mauseth and Stevenson, 2004), and vessel width is influenced by water availability during development (Arnold and Mauseth, 1999). Vessels are rather narrow in fibrous woods of cacti (Gibson and Horak, 1978; Mauseth and Plemons-Rodriguez, 1997), and occur singly or in small clusters of two to about ten; wood is diffuse-porous. There are no growth rings in any cactus with fibrous wood. Axial parenchyma is exclusively scanty paratracheal, consisting of just a few slender parenchyma cells in direct contact with one side of a vessel (not completely encircling a vessel or cluster of vessels). Apotracheal parenchyma (a mass of axial parenchyma cells, none of which actually contact a vessel) does not occur.

Rays in fibrous wood are multiseriate and consist mostly of parenchyma cells. Perforated ray cells occur in at least 16 species in seven genera of Pachycereeae (large North American cacti; Terrazas, 2000). Ray cells may have just thin, primary walls or thickened, lignified, pitted secondary walls (but not so thick as to resemble sclereids). Ray sclerification correlates with wood hardness: species

with very hard wood with extremely thick-walled xylary fibres often have sclerified ray cells, but species with softer, weaker woods with thin-walled xylary fibres often have non-sclerified ray cells. Individual rays are often sclerified in some regions, parenchymatous in others.

Fibrous wood like this has little capacity to store water within itself and is not particularly adapted to xeric habitats (Carlquist, 1988). When vessels are under tension and close to cavitation, little water is available in either scanty paratracheal parenchyma or narrow, partially lignified rays; water stored in cortex or pith is abundant but not immediately accessible to vessels. However, fibrous wood is present in all slender, long shoots that require mechanical stiffness (both upright erect cacti and pendant species), and such cacti occur in many habitats, ranging from the severely xeric coastal deserts of Chile and Peru to rainforests (Mauseth *et al.*, 2002).

A common modification is an increase in the ray system as a percentage of total wood volume. This has occurred in several ways, first by increasing the height and width of masses of ray initials which thus produce large rays (Fig. 3G). But in quite a few cacti, even many with hard, fibrous wood, primary xylem rays dilate; after ray cells are several years old, they undergo cell division and enlarge, widening rays and pushing axial masses of fibres and vessels farther apart. Pith usually dilates as well, but expansion is rather limited if the wood's fibre matrix is strong (Bailey, 1963*b, c*). Alternatively, the percentage of wood composed of rays is increased by keeping rays narrow but increasing their number, which requires that axial masses of fibres and vessels become narrower. This has a double benefit of increasing water-storage capacity within wood itself and also placing every vessel closer to ray parenchyma. However, such wood is heavy and weak; it occurs in species whose shoots are small even when mature (Mauseth and Plemons-Rodriguez, 1997, 1998).

Wide-band tracheid wood. Virtually all cacti with broad globose or disc-shaped shoots (Table 2) have an axial system in which vessels occur in a matrix of WBTs and parenchyma but which lacks xylary fibres (Fig. 3E and F; Gibson, 1977; Mauseth, 1989, 2006*a, b*; Mauseth *et al.*, 1998; Terrazas Salgado and Mauseth, 2002; Terrazas and Arias, 2003). Rays consist entirely of parenchyma cells with no wall thickening or lignification. Wide-band tracheid wood can contract during drought because none of its component cells has strong lignified walls running longitudinally, and phloem too lacks both secondary sclereids and fibre caps. In addition, vessel elements have pseudohelical pitting in which pits are so broad that each almost completely wraps around the vessel; cells appear to have helical secondary walls (Mauseth and Fujii, 1994). The pseudohelical wall is weak in the direction of the cell's longitudinal axis, so these vessel elements, just like WBTs, can be pulled into a longer shape when living parenchyma cells around them absorb water and elongate, and they can contract as parenchyma cells around them shrink during drought. As long as WBTs and vessel elements shrink such that their lumen volume continues to

match the volume of water remaining within them, they will not cavitate.

Wide-band tracheid wood can be either ring-porous or diffuse porous. When viewed in transverse section, ring-porous WBT wood appears to have annual growth rings, although typically the shoots are older than a count of rings would indicate (Fig. 3E; controlled studies are needed). The innermost portion of each ring is a narrow band only several cells thick radially, consisting predominantly or exclusively of vessels and parenchyma. In some species there may be a few WBTs present as well. The outermost, much thicker portion of each ring resembles latewood and consists predominantly of WBTs with a small amount of axial parenchyma and, in some species, a few vessels. WBT wood in Tribe Cactaceae (North American globose cacti) has little axial parenchyma; consequently the WBTs have a somewhat hexagonal shape and form a closely packed, orderly mass. In Tribe Notocactaceae (South American globose cacti), the regularity of latewood WBTs is disrupted by more abundant axial parenchyma and vessels, so these WBTs tend to appear more circular in cross-section and their arrangement is not as orderly.

Shoots having WBT wood range from large, heavy, giant globose stems to tiny dwarf spheres. In the smallest dwarf cacti (in both Opuntioideae and Cactoideae), medullary rays (parenchyma located between each vascular bundle) are wide and interfascicular cambia may not form within them, so the vascular cambium consists of just fascicular cambium in narrow vascular bundles (Mauseth, 2006a). This may contain only fusiform initials and thus produce only axial elements (WBTs, vessel elements and axial parenchyma), and only a tiny amount of wood is produced (<500 µm radially even in mature plants). It is easy to mistakenly assume that these are not woody plants. But in other species, the fascicular cambium contains both fusiform and ray initials so the shoots have narrow secondary rays and broad medullary rays. In shoots that are somewhat larger, a weak interfascicular cambium may form across the medullary rays, producing parenchymatous xylem and phloem rays. In the largest, heaviest shoots with WBT wood, the vascular cambium forms as a complete ring (fascicular and interfascicular, as is typical in most woody plants) and is very active, producing a considerable amount of secondary xylem (but <5 cm thick).

In many cacti, wood at the junctions of a shoot and its branches must be especially hard and fibrous otherwise the branches would twist or break off. But in many Opuntioideae, structural failure of junctions between determinate shoots is essential for vegetative reproduction (Fig. 1C). Wood at these junctions has fewer fibres and more parenchyma than it does in the rest of the shoot (Nobel and Meyer, 1991; Bobich and Nobel, 2001; Bobich, 2005).

WBT wood with tracheids in the rays. In Opuntioideae, wood has tremendous diversity (Gibson, 1977, 1978a, b; Mauseth, 2006b). Some species have ordinary fibrous wood, others have WBT wood, but there are two

variations in Opuntioideae in which WBTs are located in the rays themselves. In one type, the distinction between ray system and axial system is not clear because WBTs occur in both; axial regions are defined by the presence of vessels (and by sieve tube members in corresponding regions of secondary phloem), and rays are areas with no vessels (and corresponding regions of secondary phloem lack sieve tube members). These same species also have WBTs in their perimedullary zones (see Pith above). Ray WBTs can be distinctly larger than axial WBTs in the same shoot. In the second variation in Opuntioideae, WBTs occur only in rays, not in the axial system; rays are very wide, consisting of WBTs and parenchyma, the fusiform initial-derived axial systems consist of just one or two rows of vessels and a few axial parenchyma cells.

Research is needed on vascular cambia of species with WBT wood. In most cacti, just as in non-succulent dicots and conifers, differences between rays and axial system are obvious, but this is not so true in cactus WBT wood. Cells derived from fusiform initials—WBTs, vessel elements and axial parenchyma—are very short, whereas cells derived from ray initials—ray parenchyma—are somewhat elongated. WBTs derived from ray initials in Opuntioideae obscure this even further. In very broad rays, marginal ray cells next to the axial system are fully as long as axial cells and only the cells in the centre of the ray are definitely shorter; there is a gradual intergradation of length between fusiform initials and ray initials in these species. Finally, in many Notocactaceae, what appear to be uniseriate or biseriate rays will often contain one or two WBTs somewhere, further complicating the concept of ray and axial cells in derived cacti.

Parenchymatous wood. Very rarely, the axial system consists of just vessels with pseudohelical secondary walls in a matrix of parenchyma; there are neither fibres nor WBTs. Rays also consist of just parenchyma, so this wood is a mass of parenchyma with vessels running through it. Each vessel is in contact with at least one paratracheal parenchyma cell. Parenchymatous wood is obviously extremely weak and has never been found as the only type of wood in a shoot; instead, it occurs in some cactus roots and as the second phase of a dimorphic wood (see next paragraph; Mauseth and Stone-Palmquist, 2001; Stone-Palmquist and Mauseth, 2002).

Dimorphic and monomorphic wood. Shoots that produce two distinctly different types of wood have dimorphic wood, those with a single type have monomorphic wood (Mauseth and Plemons, 1995; Mauseth and Plemons-Rodriguez, 1997, 1998; Mauseth and Stone-Palmquist, 2001; Stone-Palmquist and Mauseth, 2002). Most plants (all non-cactus woody plants?) produce just a single type of wood in any given shoot. In contrast, the epicotyl of many cactus seedlings grows into a shoot that produces two distinctly different types of wood: newly formed vascular cambium in the seedling's shoot produces WBT wood for several weeks or months but then undergoes a phase change and switches to producing fibrous wood (Fig. 3H; Loza-Cornejo *et al.*, 2003; Mauseth, 2004c).

Timing of the phase change is related to the shape of the adult shoot: phase change occurs early in slender seedlings that quickly need the mechanical support of a strong wood. It occurs when shoots have grown to a height of only 100–165 mm in *Cephalocereus senilis*, *Cleistocactus fieldianus*, *Stenocereus thurberi*, and is even earlier in others, occurring when shoots are only 30 mm or less tall in *Neobuxbaumia polylopha*, *Rauhocereus riosanensis*, *Weberbauerocereus albus* (all grow to have shoots many metres tall). If an older shoot is examined in transverse sections, wood produced right at its base will have an innermost WBT wood and all the rest will be fibrous wood; if the section is taken higher in the shoot (200 mm or higher in these examples), all wood will be fibrous wood. In species whose adult shoots are always globose or disc-shaped, turgor in the cortex and pith is always adequate for skeletal support so fibrous wood is unnecessary; they have monomorphic WBT wood, they never undergo the phase change to producing fibrous wood in their shoots (their roots, which must be strong enough to prevent them from rolling, do have fibrous wood; Stone-Palmquist and Mauseth, 2002).

Between these two extremes is late phase change, in which the first phase lasts for years. Young plants in these species are globose but ultimately grow tall enough to require the strength of fibrous wood, then phase change occurs. A transverse section near the base of these shoots reveals a thick accumulation of WBT wood and much less fibrous wood, although all subsequent growth is fibrous wood. Because the WBT phase is so protracted, even transverse sections 1 m or more above the root/shoot junction will have first-phase WBT wood (Mauseth and Plemons, 1995). Transition may be abrupt with purely WBT wood followed by purely fibrous wood, but it is not uncommon to find small groups of fibres scattered among the outermost WBTs, those produced a few weeks before the shoot definitely switches to making fibrous wood. Once a layer of rigid fibrous wood is deposited, the WBT wood can no longer avoid cavitation by shortening.

The WBT → fibrous wood dimorphism is possible only because the first wood of almost all cactus epicotyls is WBT wood (first-formed wood of branches has not been studied). Seedlings of non-cactus woody plants produce an ordinary wood with a matrix of tracheids in conifers and basal angiosperms, of fibres and vessels in eudicots. But when WBT wood evolved as the first-formed wood of cactus seedlings, it was problematic because this type of wood is not strong enough to support slender or large, columnar shoots and thus a phase change to fibrous wood was necessary, resulting in wood dimorphism. It is not known what selective pressure results in WBT wood in seedlings, but it is absent from *Pereskia* and a few Cactoideae (*Leptocereus*, *Neoabbottia*, and the epiphytes *Epiphyllum* and *Rhipsalis*; Mauseth, 2004c). Consequently, these species do not have wood dimorphism; they produce only fibrous wood all their lives, just as most non-cactus woody plants do.

Two other types of wood dimorphism (fibrous → WBT) and (fibrous → parenchymatous) occur in some cacti (*Samaipaticereus corroanus*, *Werckleocereus*

[*Weberocereus*] *glaber*; Mauseth and Plemons, 1995). These shoots produce a strong self-supporting wood while young and growing vertically, but at some point they become top-heavy and topple into the branches of surrounding trees. Their weight is then supported by the tree, not by their own wood, and these cactus shoots switch to producing WBT wood or parenchymatous wood.

A fibrous → WBT dimorphism appears to occur as part of a juvenile-to-adult transition in *Melocactus intortus* (see Phase change, heteroblasty and the transition from juvenile to adult phase above). The very innermost, basal wood is seedling WBT wood as would be expected, but then the shoot switches to producing fibrous wood during the rest of its juvenile growth. Once its SAM undergoes the juvenile/adult transition and begins producing the adult body (the cephalium), the vascular cambium throughout the entire plant also switches and begins producing WBT wood. Transverse sections through the cephalium reveal only monomorphic WBT wood, sections through the top of the juvenile portion reveal fibrous → WBT dimorphism, and at the very base is a WBT → fibrous → WBT trimorphic wood (Mauseth, 1989).

Secondary phloem

Secondary phloem seems to have few noteworthy features. It consists of both phloem rays and an axial system with sieve tube members and companion cells (Fig. 3I; Bailey, 1961; Srivastava and Bailey, 1962; Mauseth and Ross, 1988; Mauseth, 1989, 1996, 1999a, b; Mauseth and Kiesling, 1997; Terrazas *et al.*, 2005). Phloem rays consist exclusively of parenchyma with thin walls. In some species, sieve tube members and companion cells constitute most of the volume of the phloem axial system, there is only sparse non-conducting parenchyma present. Consequently, when sieve tube members and companion cells collapse, almost all the phloem collapses. Such phloem can accumulate for years without becoming voluminous. In other species, non-conducting parenchyma is more abundant such that even after sieve tube members collapse, the phloem retains significant volume and, as it accumulates it may become several millimetres thick. In those species that have fibrous wood, non-conducting phloem parenchyma cells usually become secondary sclereids after surrounding sieve tube members collapse (Mauseth, 1996; Terrazas *et al.*, 2005). In species with non-fibrous woods, secondary sclereids are not formed (Mauseth, 2005, 2006a). In most cacti, there is so little accumulation of secondary xylem that secondary phloem, cortex, hypodermis and epidermis are not pushed far outward. There is little circumferential stretching, consequently there is little or no dilatation growth.

Bark

With few exceptions, cork cambium of cacti arises from epidermis cells (Mauseth and Ross, 1988; Mauseth, 1989, 1996, 1999a, b; Mauseth and Kiesling, 1997; Terrazas Salgado and Mauseth, 2002). Unlike most other seed

plants, cacti form only this one cork cambium, it is not replaced by a new one formed later, deeper within the cortex or secondary phloem. Because the one and only cork cambium is superficial, cactus bark consists simply of alternating bands of cork cells and sclereids (both produced by the cork cambium); it never contains hypodermis, cortex, primary or secondary phloem as is typical of bark in many seed plants. The water-storing cortex is never shed. Lenticels appear to be absent. Phelloderm occurs in 12 species of *Stenocereus* (Terrazas et al., 2005).

Cork cambium arises in cortex in short-shoots of *Neoraimondia*. These shoots produce flowers perennially, eventually becoming several centimetres long (see Axillary buds above). All their protoderm cells develop into spine primordia, flower primordia or trichomes, leaving no ordinary epidermis cells available to act as cork cambium (Mauseth and Kiesling, 1997).

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