

CONVERGENT ADAPTIVE MORPHOLOGY OF A SONORAN DESERT CACTUS (*PENIOCEREUS STRIATUS*) AND AN AFRICAN SPURGE (*EUPHORBIA CRYPTOSPINOSA*)

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Abstract. *Peniocereus striatus* (Cactaceae) and *Euphorbia cryptospinosa* (Euphorbiaceae) both produce slender pencil-like stems with stomata restricted to series of furrows separated by bark-covered ribs. In each species, as the stems dehydrate, the ribs come together to close off the furrows. The unusual structure of these stems in two unrelated succulent genera is a remarkable example of evolutionary convergence. The paper reports on the comparative anatomy of the stems and the adaptive strategies of the slender stems in relation to surface/volume ratios.

Introduction

Convergence in vegetative features between cacti and succulent spurges is well known. In each group, stem succulence represents an adaptive strategy that provides moisture storage over periods of drought. This development has been accompanied by a number of common features, including: reduction of leaf surface to the point where stems provide the major or only photosynthetic surface (i.e., cladophylly); protection of the succulent tissues through spine or thorn development as well as thickened cuticles, cortical collenchyma, crystals, etc.; and development of a wide array of growth habits ranging from arborescent-columnar to smaller globose forms. In addition, both groups have developed means for accommodating stem volume changes during successive dry and wet seasons, either through flattened stems or, in cylindrical and globular forms, through tubercles or ribs.

Development of stem succulence and loss of leaves are also accompanied by a great reduction in potential transpirative surface area in relation to stem volume. This relationship can be most readily expressed as a surface area/volume (s/v) ratio. Because a sphere represents the smallest surface area per unit volume, s/v ratios are lowest in species approaching a spheroidal growth habit (Gibson and Nobel, 1986). The s/v ratio also decreases as the size of a sphere or cylinder increases. It is important to note, however, that no succulent can be perfectly spheroidal, for ribs, tubercles or joints are required to allow for seasonal volume changes.

The calculation of s/v ratios in true cylinders is made by dividing the surface area of a given length of a cylinder (determined by $2 \pi r \times l$) by the volume of the same length of cylinder (determined by $\pi r^2 \times l$) where $\pi = 3.14$, r is the cylinder's radius, and l is the stem length. As

shown in Fig. 1, this equation can be reduced to $2/r$, and the s/v ratio can then be expressed as a surface area (i.e., square cm) associated with a unit of volume (i.e., one cubic cm). In cylindrical objects this ratio ignores the ends of the cylinder. In cylindrical objects we can also simplify the equation by ignoring the length of the cylinder and determining only the circumference of the circle ($2 \pi r$), dividing this by the area of the circle (πr^2). This again reduces to $2/r$ (Fig. 1), which can be expressed as the amount of linear circumference per 1 square unit of area within a circle. Cylinders or circles with small radii then have relatively large surface areas per unit of volume or large circumferences per unit of area. It should be apparent that circumference per area will yield the same ratio as actual surface area to volume.

When considering this in relation to stems, narrow cylinders (small circles) have a relatively large surface area per unit of volume or area and have high s/v ratios. Broad cylinders present relatively less surface area for water loss. Thus, thick stems should have a reduced potential transpirative area per unit volume and should be better adapted to more arid climates. The changes in s/v ratios from narrow to broad cylinders or circles is shown graphically in Fig. 1. It is generally recognized that s/v ratios are significant in determining distribution of succulent plant species in arid regions. Brandegee (1900), Marshall and Bock (1941), and Lindsay (1963) commented on s/v factors in the adaptation of cacti. Felger and Lowe (1967) demonstrated a clinal variation pattern in the s/v ratio between populations of a Sonoran Desert columnar cactus, *Lophocereus schottii* (Engelm.) Britton & Rose, by correlating a decrease in number of ribs and s/v ratios in populations in increasingly arid climates. Their study demonstrated that lower s/v ratios were significant factors allowing adaptation to extreme

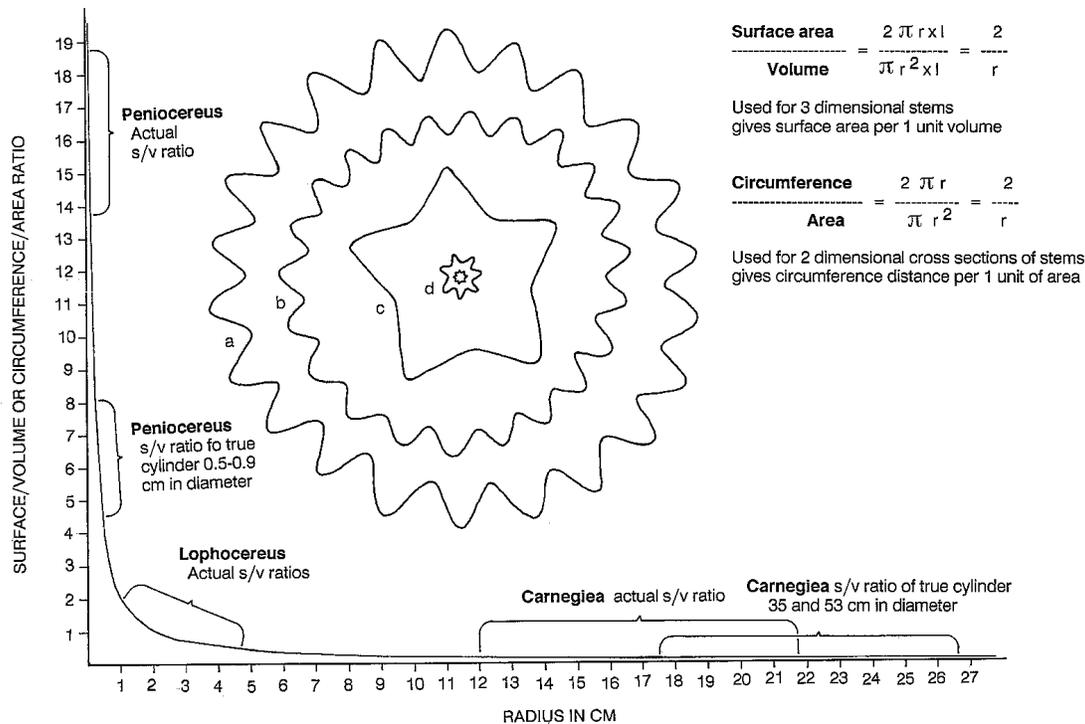


Fig. 1. The relationship of s/v ratios and stem size. Formulas for determining three-dimensional surface/volume ratios and two-dimensional circumference/area ratios are shown at upper right. The curve on the left and bottom margin shows the relation between s/v ratio (ordinate) and stem size (as radius in cm, abscissa). **a–e.** Outlines of various cacti from which s/v ratios have been determined. **a–b.** *Carnegiea gigantea*. **a.** large stem. **b.** small stem. **c–d.** *Lophocereus schottii* showing extreme variation in stem sections from northern (c) to southern (d) populations (after Felger and Lowe, 1967). An outline of the stem of *Peniocereus striatus* is shown within d. The range of s/v ratios for the three cacti is shown along the regression curve as indicated (see text).

xeric environments. Gibson and Nobel (1986) and Nobel (1988) also address the significance of s/v ratios (expressed as v/s ratios) in cacti and agaves.

In most stem succulents, the s/v ratio of an individual plant increases as the plant loses water during droughts—as the plant dehydrates and loses volume, the surface area remains the same, resulting in a progressively less favorable s/v ratio. As an example, consider a stem-joint of *Opuntia*, subgenus *Opuntia* (= *Platyopuntia*) with a fixed surface area losing volume during a period of drought; as it loses water its surface area stays the same while the volume decreases, thus the s/v ratio progressively increases.

We have found in a Sonoran Desert cactus, *Peniocereus striatus* (Brandege) Buxb. [= *Cereus striatus* Brandege = *Wilcoxia striata* (Brandege) Britton & Rose = *Neoevansia striata* (Brandege) Sánchez-Mej. = *Cereus diguetii* Weber = *Wilcoxia diguetii* (Weber) Diguët & Gillaumin] and an east African spurge (*Euphorbia cryptospinosa* P.R.O.Bally) that both species have narrow, furrowed, pencil-like stems, an interesting structural adaptation that results in a significant decrease in s/v ratio with increased water loss. The structural adap-

tation is of interest not only because it allows these species to compensate for an initially unfavorable s/v ratio, but also because it is a remarkable instance of structural convergence between two entirely unrelated succulent plant families (Trager, 1985). As in most instances of structural convergence between unrelated taxa, we have found structural convergences mostly at the macroscopic level. At the microscopic level, each has developed different structural adaptations to their respective xeric environments.

Material and Methods

Stem material of *Peniocereus striatus* was collected 21 Jan 1975 from near Punta Chueca, Sonora, Mexico (Felger s.n., RSA). Material of *Euphorbia cryptospinosa* was obtained from collections of Abbey Garden, Carpenteria, California. Surface area/volume ratios of both desiccated and hydrated stems were determined by grid analysis of photographically enlarged, hand-cut transverse sections. Circumferences were measured with a map line recorder from the same photographs. Both living and FAA (formalin-alcohol-acetic acid) preserved material were used in anatomical studies. Preserved materials were sectioned by standard paraffin

techniques (Johansen, 1940) and stained with safranin-fast green. Material for Scanning Electron Microscope (SEM) analysis was diffusion dried without removal of material from the epidermis, coated with 80-20 gold-palladium and observed with a Cambridge S4-10 SEM.

Results

Peniocereus striatus and *Euphorbia cryptospinosa* are remarkably similar in many aspects of gross vegetative morphology. Both are sparsely branched, sprawling or scandent stem succulents with narrow, cylindrical stems bearing a distinctive series of flat ribs and alternating furrows (Figs. 2, 3). In *P. striatus*, stems range from 5–9 mm in diameter, have 6–9 furrows, and seldom exceed one meter in height, although plants over two meters high are occasionally encountered growing within and receiving support from other shrubs. *Euphorbia cryptospinosa* is more robust, frequently reaching to two meters or more in height, and has stems ranging from 7–12 mm in thickness with 4–9 furrows. Both species tend to grow under and within other shrubs and have brownish-gray stems that appear like dead twigs among the surrounding vegetation. Both species also have tuberous roots that provide water and food-storing capacity; those of *Peniocereus* are extensive and dahlia-like while those of *E. cryptospinosa* are turnip-shaped and seldom exceed the size of a carrot (Bally, pers. comm.). The two plants, however, differ in several fundamental familial characteristics. *Peniocereus* has areolas that bear 8–10 weak acicular spines, some only 1.5–3 mm long, others 10–12 mm long, and nocturnal, funnellform flowers with whitish tepals (Fig. 2a–c). *Euphorbia cryptospinosa* bears only two spines (modified stipules) about 1.5 mm long at each node, is monoecious, and bears clusters of scarlet-colored cyathia in distinct concentric rings near the stem-apex (Fig. 2 e–g).

Numerous structural similarities also exist at the microscopic level (Fig. 3). In both taxa, ribs are covered with thickened, suberized, translucent periderm and stomata are entirely restricted to the furrows. The outermost cortex contains layers of collenchyma that are much thicker under the ribs than under the furrows. Collenchyma tissue in both species contains a reddish pigment that darkens the outer stems, aiding in camouflage. The inner mass of cortex consists of parenchymatous water-storage tissue, while starch is stored in the pith.

Although the degree of this convergence is remarkable, the species differ in many anatomical details. The rib periderm of *P. striatus* ranges from 35–50 μm in thickness and consists of tabloid cells 35–140 μm long and 30–40 μm wide, with moderately thickened walls (Fig. 3 d). Rib periderm in *E. cryptospinosa* is slightly

thicker (50–75 μm) and consists of longer, fiber-like cells to 450 μm in length, 25–50 μm maximum width, with uniformly thin walls (Fig. 3i). In both species phellem (true bark) of successive seasons is eventually lost, falling away by means of an abscission layer comprised of thin-walled, non-collapsed cells that are the last-formed cells of the previous season's growth. Also in both taxa the consistent radial orientation of the phellem cells of successive seasons indicates that either the same phellogen is active over several seasons or new phellogens are derived from the phelloderm (Fig. 3d, i). The underlying lamellar collenchyma tissue present in both taxa consists of one or two layers (to 50 μm thick) of cells of dimensions similar to those of their respective phellem cells. Interior to the collenchyma tissue, parenchymatous cortex tissue contains chloroplasts that are more numerous under the ribs than under the adjacent furrows.

Structure of the furrow region is distinct from that of the ribs, as the epidermis is persistent and is not replaced by more rigid periderm. While the basic structure of the two species is again similar, minor structural differences are also apparent in the furrows. In *P. striatus* the outer epidermal walls are much thicker (14 μm) than the inner (3 μm) walls, with a thin cuticle measuring only 2 μm in thickness (Fig. 3d). Epidermal cell walls of *E. cryptospinosa* are also thickened but are considerably thinner (2–6 μm), while the cuticle is thicker (4 μm) (Fig. 3i). The furrows of *P. striatus* are glabrous, while those of *E. cryptospinosa* are beset with short, blunt, biseriate trichomes to 80 μm long (Figs. 3h, 4a–b).

A remarkable adaptation was noted in stomata. Stomata in both species are restricted to the furrow areas, have paracytic subsidiary cells, and average 88 stomata per mm^2 in *E. cryptospinosa* and 48 stomata per mm^2 in *P. striatus*. SEM studies revealed that stomata along the furrow margins in desiccated stems of *P. striatus* were completely sealed over by an undetermined substance that could be removed by washing with water (Fig. 4e–f). This phenomenon could be significant in that it may reduce the number of potentially transpirational stomata during periods of drought.

The internal volume of all succulents change during consecutive wet and dry seasons. Expansion and contraction of stem volume in nearly all cases is accompanied by alteration in the shape of the plant, e.g., ribs narrow, tubercles flatten or narrow, or, in platyopuntias, the entire stem flattens. In all of these plants, surface area remains approximately constant while the internal volume decreases, resulting in gradually increasing s/v ratios. Stem structure of *P. striatus* and *E. cryptospinosa*, however, provides a notable exception to this tendency. Because their stems consist of alternating ribs

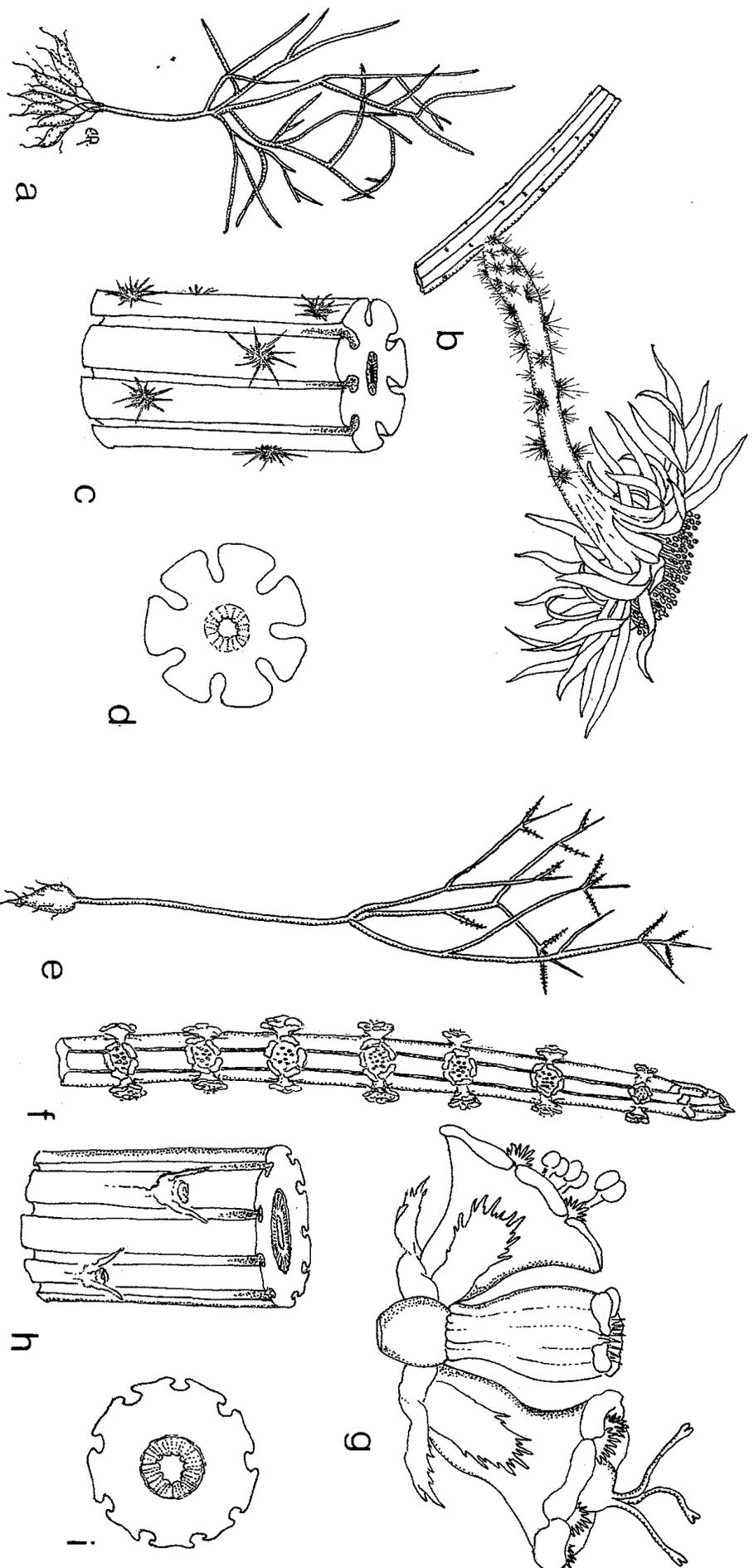


Fig. 2. Illustrations of *Peniocereus striatus* and *Euphorbia cryptospinosa*. **a-d.** *P. striatus*. **a.** Growth habit, showing cluster of tuberosous roots and branched stems. **b.** Stem with characteristic flower. **c.** Cross section of stem showing central xylem and stomata-containing furrows. **e-i.** *E. cryptospinosa* (redrawn from Bally's original illustration). **e.** Growth habit showing a single turnip-like storage root and branched stems). **f.** Distal portion of stem showing arrangement of cyathia. **g.** Triad of cyathia with anthers (left) and gynoecium (right). **h.** Portion of stem showing paired stipular spines at nodes and distinctive furrows. **i.** Cross section of stem, showing central xylem and stomata-containing furrows.

Table 1. Data on surface/volume ratios in stems of *Peniocereus striatus* and *Euphorbia cryptospinosa* as measured from stem cross-sections.

	Outer surface	Volume (area)	S/V ratio	S/V ratio with initial total surface	Percent reduction in S/V ratio
<i>Peniocereus striatus</i>					
Hydrated	26.7 mm	19.4 mm ²	1.38		
Desiccated	15.9	12.4	1.28	2.15	40%
Hydrated	25.8	13.7	1.87		
Desiccated	17.0	8.0	2.12	3.21	34%
<i>Euphorbia cryptospinosa</i>					
Hydrated	20.2	9.8	2.06		
Desiccated	11.4	6.7	1.71	3.07	44%

with rather rigid, thickened periderm and much less rigid furrows, decrease in internal volume results in a folding or contraction of the furrow areas into the stem until adjacent ribs contact one another, essentially closing the furrows. The stomata then are largely separated from the atmosphere by the thickened, non-transpiring periderm-covered ribs (Fig. 5).

Data presented in Table 1 show changes in stem circumference and stem area in turgid and desiccated stems of *P. striatus* and *E. cryptospinosa*. In both species, volume (measured as stem cross-sectional area) decreased, as expected, when desiccated. However, unlike other succulents, the effective surface area (measured as circumference of the exposed area) decreased significantly between turgid and desiccated stems. This decrease was caused by the reduction of effective exposed surface area as the ribs close off the furrows. If the furrows were not closed off, the surface area in desiccated stems would have remained approximately unchanged and the s/v ratios would be 34–44 percent greater than those encountered. In these taxa, therefore, the s/v ratio does not increase with desiccation as in other succulents but may even decrease when turgid stems become desiccated. It is of great importance that the exposed surface in the desiccated state primarily consist of impermeable periderm; therefore, actual water loss is even less than might be expected from the s/v ratio alone.

Discussion

The morphological similarities of *P. striatus* and *E. cryptospinosa* represent an extreme example of convergent adaptive strategies in unrelated succulent plants. Both species grow within other shrubs, relying on the shrubs for support. Their dull brown, narrow stems appear like dead twigs and presumably provide protection from herbivores through camouflage. The spines, therefore, are superfluous and in both species are poorly developed.

The stems in both species have ribs separated by distinct furrows and are quite small in diameter, resulting in very high s/v ratios. However,

the combination of thickened suberized periderm covering the ribs and a mechanism that seals the stomata-bearing furrows in desiccated plants appears to provide an effective barrier to transpiration. Although the thin stems provide little volume for water storage, both species have enlarged storage roots. The dahlia-like storage roots of *P. striatus* are extensive and provide a significant storage reservoir for both water and starch.

While these species have achieved a remarkable similarity in gross morphology, each is distinct at the microscopic level, indicating different structural adaptations. In desiccated stems of *P. striatus*, stomata at the margins of the furrows were sealed over by an unknown, water-soluble material (Fig. 4e). We have also observed a similar phenomenon in *Calabanus bookeri* (Lem.) Trel. (Nolinaceae), where similar water-soluble material fills stomata-containing furrows in the leaves. Furrows of *E. cryptospinosa*, on the other hand, contain series of short, blunt trichomes or papillae (Fig. 3a–b) that are similar in size and appearance to those found in such diverse species as *Yucca brevifolia* Engelm., *Phoradendron diguetianum* Tiegh., *P. flavescens* (Pursh) Nutt. These papillae would be expected to provide reduced air movement within the furrows, thereby reducing transpiration by preventing mixing of dry air with the more humid air within the furrows.

While these species would initially appear to have very unfavorable s/v ratios, the ability of desiccated plants to effectively reduce transpirative surfaces by means of mechanical changes in the stem shape has helped these species adapt to arid conditions. *Peniocereus striatus* occurs in the Sonoran Desert of coastal Sonora and Baja California where rainfall averages are less than 130 mm per year (Hastings and Turner, 1969a, 1969b). This is a much more arid region than one would expect for such a slender-stemmed plant. *Euphorbia cryptospinosa* occurs in the thorn scrub, desert grassland savanna and semi-desert scrub vegetations in Kenya and the adjacent Somali Republic, regions receiving between 150–400 mm rainfall annually (Griffiths, 1972).

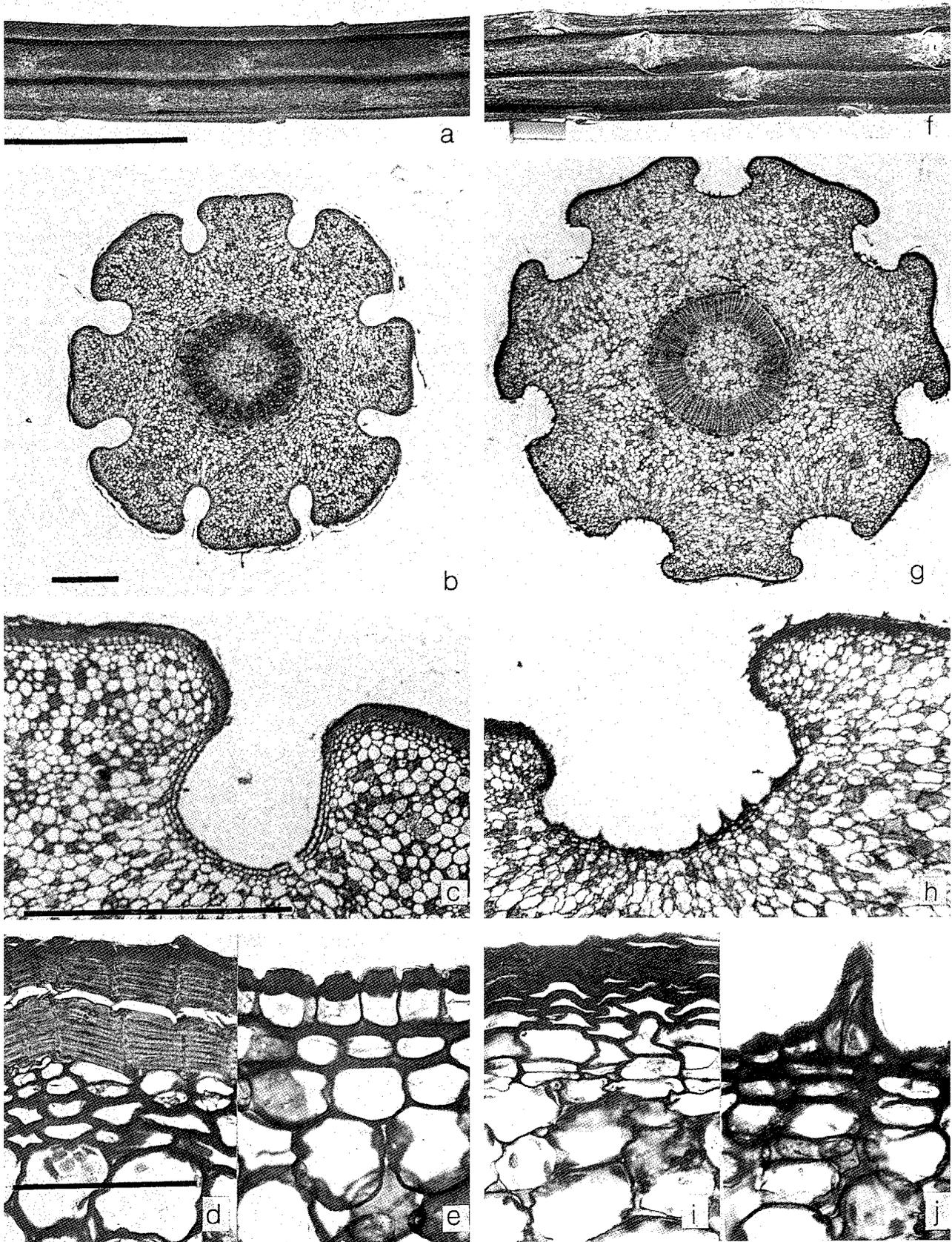


Fig. 3. Comparative stem structure and anatomy of *Peniocereus striatus* and *Euphorbia cryptospinosa*. **a-e.** *P. striatus*. **a.** Stem showing furrows and nearly spineless nodes. **b.** Cross section of stem showing central xylem and furrows alternating with outer bark-covered ridges. **c.** Enlargement of furrow area showing a stoma in the furrow and the thicker ridges. **d.** Periderm of the ridge, consisting of thickened, tablet-shaped outer bark cells that retain their vertical orientation from year to year. **e.** Epidermis of furrow area showing the thickened tangential and thin radial walls. **f-j.** *E. cryptospinosa*. **f.** Stem showing furrows and paired spines at nodes. **g.**

The stem structure displayed by *P. striatus* and *E. cryptospinosa* occur in other taxa as well. Other closely related, probably congeneric, cacti also have narrow, furrowed stems, namely *Neoevansia lazaro-cardenasii* (J.L. Contr. et al.) D.R. Hunt, *Peniocereus viperinus* (Weber) Buxb., and *N. zapilotensis* (Meyrán) Buxb. Elsewhere within the Cactaceae, a similar series of furrows and ridges are found in species of *Selenicereus*, a genus of trailing to climbing cacti ranging from Texas to northern South America. Stems of *S. murrillii* Britt. & Rose have 7–8 periderm-covered ribs and the stomata are restricted to the furrows as in *Peniocereus*. Bally (pers. comm.) notes that two other species of *Euphorbia* have similar stem morphology (*E. erlangeri* Pax and *E. migiurtinorum* Chiov.) and that other closely related species also have 4-angled stems.

In most succulents, the plants undergo gradual desiccation during dry periods, the surface area remaining the same while the internal volume decreases. This causes a gradual increase in s/v ratio. Loss of water is associated with the physiological requirements of photosynthesis and growth. To grow, the plants open their stomata to uptake carbon dioxide but in the process lose water. If this were a continuous process, the plant would continue to lose water at an accelerated pace as the surface area increases relative to the internal volume. However, most succulents have Crassulacean Acid Metabolism (CAM) (Gibson and Nobel, 1986), open their stomata only at night to reduce water loss, and, when desiccation reaches some point, cease to open their stomata and internally recycle their carbon dioxide. So there is a point where succulents stop, or at least strongly limit, this desiccation cycle.

Stem succulents vary greatly in s/v ratios. Figure 1 illustrates the change in s/v ratios in true cylinders of increasing diameter shown as a regression curve. Keep in mind that one can consider s/v ratios in a three-dimensional structure, or, by ignoring the length of the structure and considering just a cross-sectional surface, one can produce a two-dimensional correlate of s/v: circumference/area. Both s/v ratio and circumference/area ratio measure the same thing, and the formulae of each reduces to a simple $2/r$, which is the quantity expressed in the regression curve. The regression curve shows that narrow cylinders with a radius under 2 cm have rapidly increasing s/v ratios as the cylinders narrow, while broad cylinders over 5 cm in ra-

dus show only slight changes in s/v ratio as the cylinder radius increases. Cacti and *Euphorbia*, however, rarely are true cylinders, for most species have raised surface areas associated with ribs or tubercles that permit changes in volume with changes in hydration.

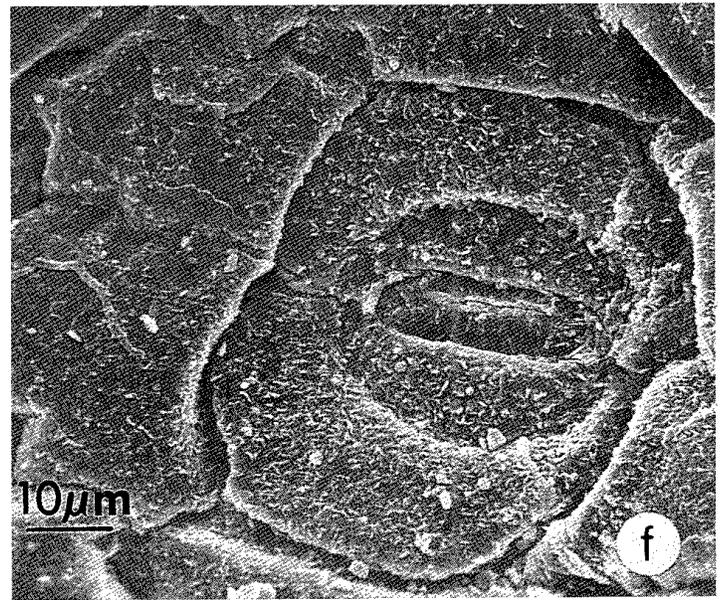
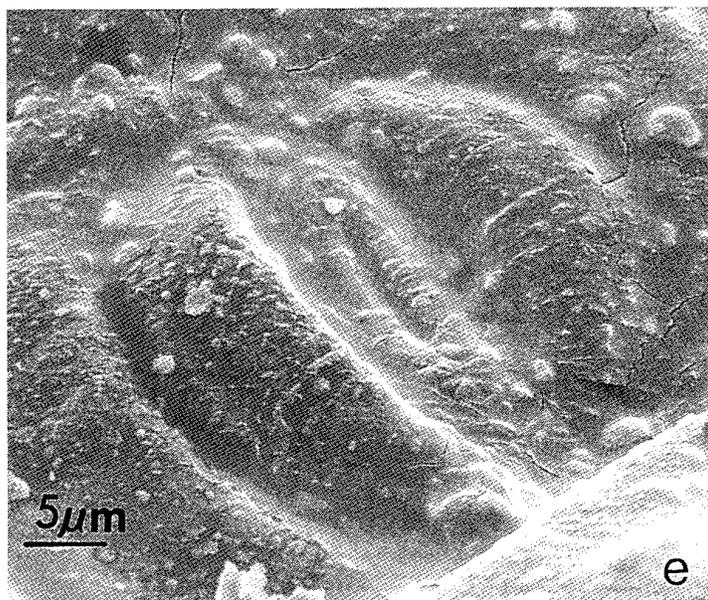
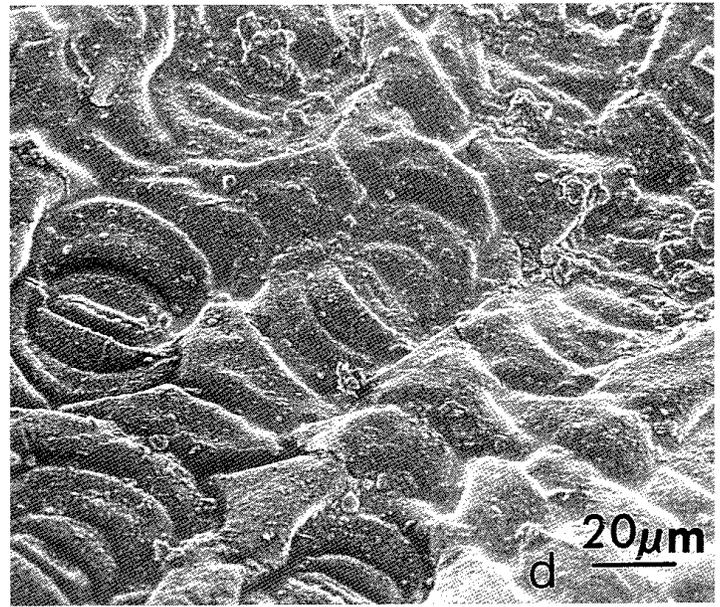
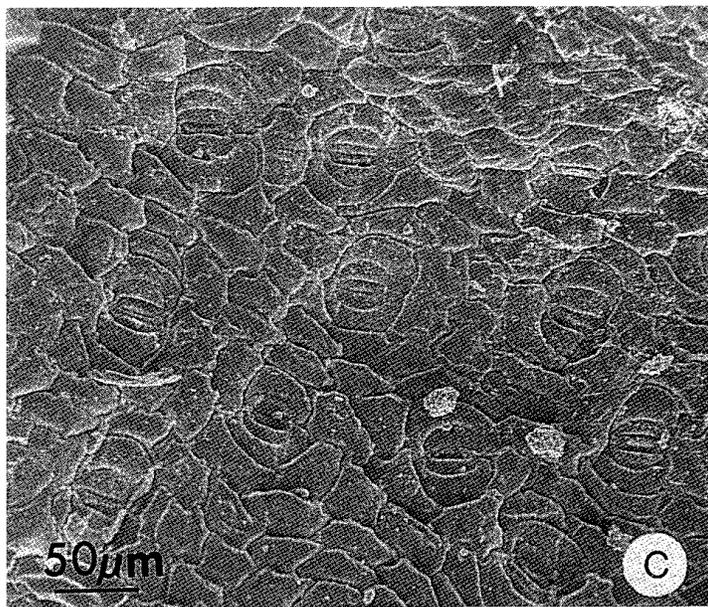
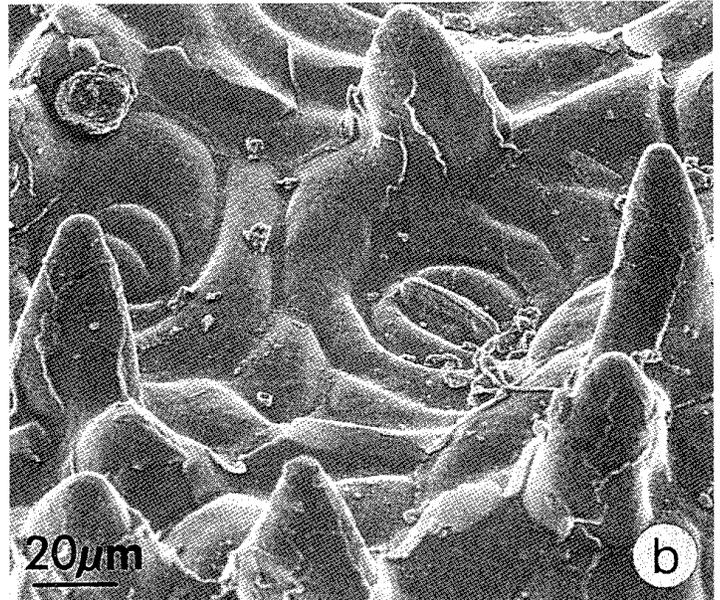
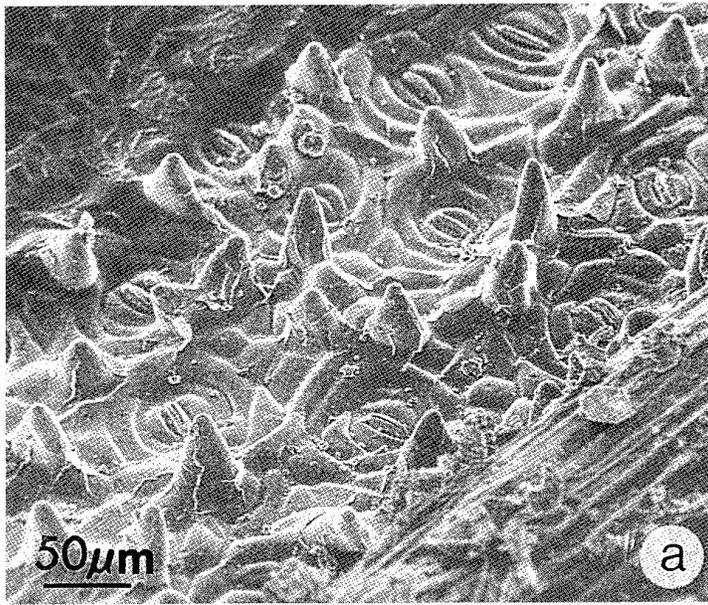
Figure 1 also shows stem outlines of two species of cacti to compare with *Peniocereus*. The saguaro, *Carnegiea gigantea* (Engelm.) Britt. & Rose, is shown in the outer two outlines, one of an older stem (Fig. 1a), the other of a young stem (Fig. 1b). Each stem has 22 ribs, and the stems have low s/v ratios, ranging from 0.1–0.17 square cm per unit volume. The ratios for this species were determined from cross sections, one 35 cm in diameter, the other 53 cm in diameter. If each stem were true cylinders with these diameters, the s/v ratios would be smaller still, about 0.07–0.11 square cm per unit volume. When these values are compared to the measured s/v ratios, one can see that the presence of ribs has only a minor effect on the s/v ratio in this large-stemmed cactus. This favorable s/v ratio is achieved at the expense of limiting photosynthetic tissue and replacing it with large volumes of non-photosynthetic, water-storing tissue.

In *Lophocereus schottii*, a narrower columnar cactus from Sonora, there is a great variation in stem size ranging from large stems in the northern Sonoran Desert, often with 5 ribs (Fig. 1c), to small stems in thorn scrub in southern Sonora with 7(–10) ribs (Fig. 1d). Studies by Felger and Lowe (1967) have shown that s/v ratios for the species range from 0.27–1.97 square cm per unit volume. They demonstrated that plants from southern Sonora have narrower stems with more ribs and higher s/v ratios (Fig. 1d), while the more northern plants, in the arid Sonoran Desert, have larger stems with fewer ribs and much lower s/v ratios (Fig. 1c). The study was the first to record clinal changes in surface/volume ratio from less arid to strongly arid habitats and it showed that such surface/volume factors can be critical to the success of a species.

When we look at the s/v ratio of *Peniocereus striatus*, we see that it has a very unfavorable s/v ratio for a cactus. Its slender, pencil-like stems present a large surface area per unit volume. If *Peniocereus striatus* were a true cylinder, 0.5–0.9 cm in diameter, the s/v ratios would be 4.4–8.0 cm² surface per cm³ volume. But because of the ribs and furrows, the actual s/v ra-

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Cross section of stem showing inner xylem core and furrows alternating with outer bark-covered ridges. **h.** Enlargement of furrow area showing short hairs in the furrow. **i.** Periderm of the ridge area is less organized and consists of variously collapsed cells. **j.** Epidermis of furrow area showing the biserial nature of the hairs and adjacent epidermal cells. Magnifications of paired structures the same; bar in 3a is 10 mm long, in b–c is 1 mm long, in d is 0.1 mm long.



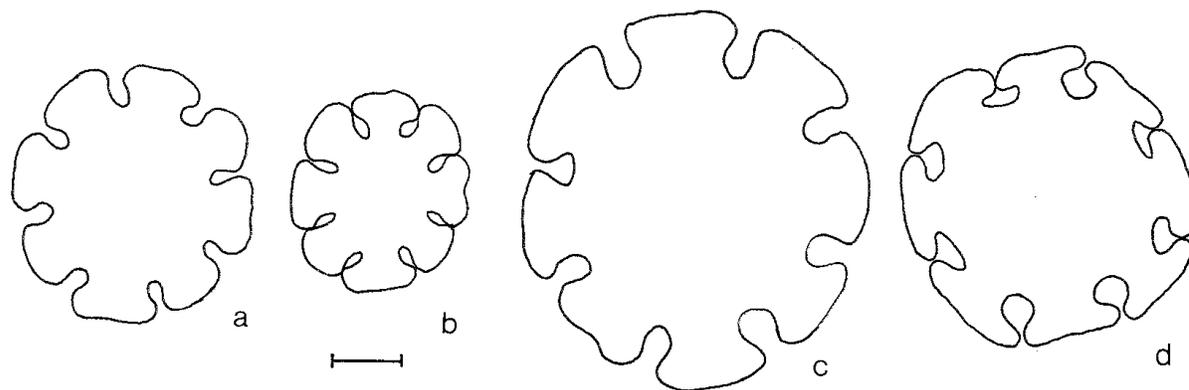


Fig. 5. Outlines of hydrated vs. desiccated stems of *Peniocereus striatus* and *Euphorbia cryptospinosa*. **a-b.** *P. striatus*. **a.** Hydrated stem showing furrows open. **b.** Desiccated stem showing furrows closed. **c-d.** *E. cryptospinosa*. **c.** Hydrated stem showing furrows open. **d.** Desiccated stem showing furrows closed. Magnifications as indicated by bar.

tios are 13.8–18.7 cm² surface per cm³ volume. (Note that this number differs from that presented in Table 1 by a magnitude of 10 because data in Table 1 are presented in mm). For a perennial desert succulent such a high s/v ratio is unfavorable, and one would not expect such a plant to exist in such as true desert habitat. But as we have seen, *Peniocereus striatus* has restricted its transpirative surface area to the furrows; covering the ribs is a periderm that excludes water-loss over much of the stem. When the stem becomes desiccated, it decreases its effective surface area by closing off the furrows so that the s/v ratios remain relatively constant (see Table 1). The plant compensates for the lack of water storage capacity with extensive storage roots. In addition, its weak, narrow stems typically grow within other shrubs and this, to some extent, shades the plant and allows the plant to escape from browsing by mimicking the twigs of the support plant.

In summary, this paper has presented two themes. It has documented the morphological and anatomical convergence between a highly specialized cactus and a similarly specialized species of *Euphorbia*. It has discussed surface/volume ratios in cacti and the concept that succulent plants with larger stems have more favorable s/v ratios. It has shown that a slender-stemmed growth habitat, like that of the two subject species, results in a very unfavorable s/v ratio but that the plants may compensate for this through mechanisms that close the stomata-containing furrows as the plants become desiccated.

Acknowledgments

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Fig. 4. Scanning electron micrographs of stem features of *Euphorbia cryptospinosa* and *Peniocereus striatus*. **a-b.** *E. cryptospinosa*. **a.** Stomatal furrow of young stem showing small hairs and location of stomata within the furrow. **b.** Magnification of the same. **c-e.** *P. striatus*. **c.** Stomatal furrow of young stems showing position of stomata within the furrow. **d.** Magnification of the same showing most stomata covered with an unknown water-soluble material. **e.** Close up of stomata sealed with the water-soluble material. **f.** Stomata from stem washed with distilled water before observation showing loss of water-soluble coating material. Magnification as indicated by bar.