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Functional morphology and evolution of stem succulence in cacti

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We explored, using a mathematical model, the changes in areole arrangement that have occurred during the evolution of stem succulence in different cactus life-forms. The study was based on field data. The model used two parameters: (a) areole density in the stem and (b) the divergence angle between successive areoles. The stem morphology in different cactus subfamilies is correlated to changes in one or both parameters. Gradual changes in stem compaction and in the divergence angle can explain the apparently complex evolutionary transition from primitive woody and leafy plants to the more evolved, stem-succulent morphologies of cacti.

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Introduction

A remarkable characteristic of the Cactaceae is the great variety of shapes and sizes that the family exhibits along its geographical range, from southern Canada to Patagonia. The family is represented by arborescent, shrubby or creeping individuals with woody or succulent stems. The latter can be jointed, flat, cylindrical or globose in shape, with spines distributed uniformly around the stem or forming longitudinal ribs. Cacti's height can vary from 20 m (e.g. *Pachycereus pringlei* in Baja California), to approximately 1 cm (e.g. *Blossfeldia liliputana* in Argentina; Bravo-Hollis, 1978).

Gibson & Nobel (1986) hypothesized that the ancestors of the family were mesophilous plants inhabiting subtropical regions. The species of the subfamily Pereskioideae show many ancestral morphological and anatomical characteristics (Mauseth & Landrum, 1997), such as a woody stem, developed leaves and a C₃ photosynthetic metabolism. The development of succulence in the stem, the reduction or loss of leaves, and the switch to a CAM photosynthetic pathway were the evolutionary novelties that allowed cacti to colonize new regions. Since then, the family also evolved the striking diversity of forms that can be observed at present, from woody pereskioid trees to leafless succulent species. In previous studies we have looked at this problem at different levels. At a physiological level, we have shown that

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plants belonging to different subfamilies with contrasting morphologies use a C_3 metabolism during the early ontogeny (some weeks after germination, the succulent species shift to their typical CAM metabolism; Altesor *et al.*, 1992). At an anatomical level, Carlquist (1962) described ancestral juvenile traits in the woody anatomy of adult cacti. We have also shown that a retardation in the developmental rate of woody tissues (allometric neoteny) and the maintenance of the juvenile characteristics in the adult stems (paedomorphism) are the important evolutionary mechanisms operating in the development of succulence in the family (Altesor *et al.*, 1994). Thus, cacti show anatomical paedomorphism, with a photosynthetic stem and with paedomorphic vascular bundles surrounded by undifferentiated parenchyma (Fig. 1).

Almost all vascular plants can be conceived as reiterative arrangements of basic stem elements as their architectural units. The simplest expression of these basic units is the stem segment formed by an internode, a node, a leaf and the axillary bud. At this level of organization, three basic morphologic variables modulate the architecture of the whole plant. The first one is the length of the internode, the second one is the relative position of the leaf in any given internode with respect to the leaf in the previous one (known in botany as leaf-arrangement or phyllotaxis), and the third variable is the probability with which the axillary buds generate lateral branches. Although branching patterns are important elements in the evolution of cactoid forms, in this paper we shall concentrate in the first two variables.

In the primary shoot of most dicotyledons, the vascular bundles that run along the stem perform the basic function of connecting the leaves to the rest of the plant (Gibson, 1978). Thus, vascular bundles join leaves along the length of the shoot, and their distribution inside the stem is strongly linked to the external arrangement of the leaves, i.e. to the phyllotactic pattern (Tomlinson & Wheat, 1979). With the appearance of secondary growth, a continuous cambial layer develops (Fig. 1), the

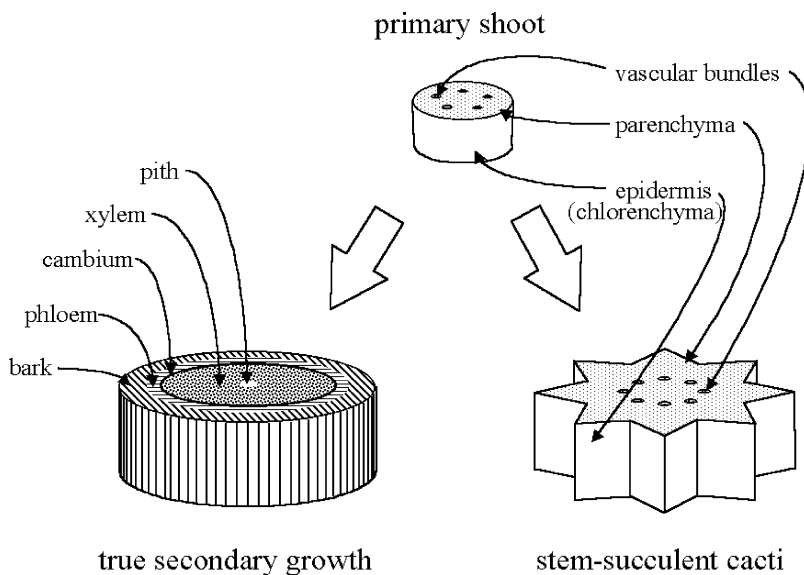


Figure 1. The basic characteristics of primary shoots in most dicots (top) are conductive tissues organized in discrete vascular bundles surrounded by non-specialized parenchyma and a photosynthetic epidermis. With secondary growth (bottom left), the cambial meristem forms a continuous ring that produces xylem towards the centre and phloem towards the exterior. As it grows outwards, phloem is transformed into a non-photosynthetic suberose bark that replaces the photosynthetic epidermis of the primary shoot. In stem-succulent cacti (bottom right) the basic anatomy of primary shoots is maintained in the adult plants.

vascular bundles disappear and the leaves (or the branches that have developed from the axillary buds) become connected to a continuous woody tissue. Cacti, however, commonly retain the bundle arrangement of vascular tissues throughout most of their lives. Additionally, the leaves and the subtended axillary buds are reduced in most cacti to a series of spine-cushions known as areoles, a distinctive feature of the cactus family. Basically, an areole is a transformed axillary bud situated over a tubercle with spines and often with hairs and trichomes. The basic vascular morphology of cacti, however, is similar to that of the seedlings of non-succulent dicots and the vascular bundles run along the stem connecting neighbouring areoles. Additionally, the phyllotactic arrangement of the areoles on the stem is strongly linked to the internal distribution of the vascular bundles (Gibson & Nobel, 1986; Mauseth, 1988).

The evolution of stem succulence imply the need to support large masses of non-specialized parenchyma mechanically sustained by a limited amount of vascular bundles organized in a specific biomechanical configuration (Altesor *et al.*, 1994). It may be hypothesized that selection for a certain biomechanical configuration and, ultimately, for a given internal distribution of the vascular bundles, also implies the selection for a given phyllotactic arrangement. In this case, the way the areoles are arranged externally may reflect how the support tissues are distributed inside the plant.

Even if the probable genetic control of these attributes is unknown, studies in plant molecular genetics have shown that other morphological characteristics of leaf and floral whorls in plants are genetically controlled (e.g. Coen & Meyerowitz, 1991; Pyke, 1994).

Anatomical studies of the primary shoot of plants show that while phyllotaxis is determined by the spatial arrangement of primordia around the apical meristem, internode elongation occurs later, through the action of secondary meristems (Esau, 1977; Mauseth, 1988). Thus, at a meristematic level both phenomena occur in sequentially distinct phases during shoot differentiation, and it is possible to conclude that stem compaction and the phyllotactic divergence angle seem to be genetically and independently controlled by the plant (i.e. one can vary substantially while the other remains constant).

In this paper we explore, through the use of a mathematical model, the changes in the divergence angle between chronologically successive areoles and the changes in internode length that have occurred during the evolution of stem succulence in different cactus life-forms. We do not attempt to analyse the actual physiological mechanisms by which the plants may attain control of the divergence angle and the internode length.

The optimal packing of alternate leaves (or any other set of parts arranged alternately around a circular or cylindrical structure) can be achieved when the divergence angle between chronologically successive leaves is a fraction of a circumference equal to $(3-\sqrt{5})/2$, an irrational constant value which we will refer to as the 'Fibonacci angle' or ' φ ', and which is equal to $137\ 30' 27.95\dots$ " (or $0.38196601\dots$ of a circumference; see Jean, 1984).

The Fibonacci angle is a limiting value of the Fibonacci series ($\{0,1,1,2,3,5,8,13,21,\dots\}$; a mathematical series where the term $f_{n+1} = [f_n + f_{n-1}]$). The limiting value for the ratio (f_{n-1}/f_{n+1}) when $n \rightarrow \infty$, is φ (Niklas, 1992). This means that, in any plant whose phyllotactic angle is φ , leaves that are f_n leaves away from any given one (where f_n is the n th term of the Fibonacci series) will tend to form an helix along the shoot. A set of leaves arranged in a logarithmic spiral row along the stem, is called a contact parastichy. The number of contact parastichies that are visible on a plant with divergence angle equal to φ is a function of the degree of compaction of the stem (i.e. of the internode length). Additionally, because of the numerical proximity of the value of φ with the ratio between terms of the Fibonacci series, it follows that the number of spirals in a contact parastichy will be a Fibonacci number (i.e. a member of the series $\{1,1,2,3,5,8,13,21,\dots\}$; Gibson & Nobel, 1986).

Studies based on mathematical simulations have shown that the organization of plant parts in Fibonacci angles can be obtained as the result of collisions between primordia (Fowler *et al.*, 1992). Douady & Couder (1992, 1993) have shown that Fibonacci patterns emerge naturally from a dynamic system that generates 'punctual particles' (primordia) that migrate outwards from the apical meristem and repel each other, if the frequency with which these points are produced is relatively high. If the frequency between successive points diminishes, then the system may stabilize dynamically into ribbed patterns in Fibonacci numbers. In botanical terms, this means that the physiological signals (inhibitors or hormones) sent by primordia longitudinally along the stem and laterally around the apex may define the type of pattern, ranging from ribs in series of Fibonacci numbers, to areoles uniformly distributed around the stem following a Fibonacci angle. The conclusions of Douady & Couder (1992) are extremely relevant to our study, as they suggest that small changes in the rate of formation of primordia, or, alternatively, changes in the way apical inhibitors diffuse, may dramatically change the phyllotactic pattern. That is, Fibonacci patterns are possibly the result of self-organized, relatively simple dynamic systems.

We used a simulation approach to analyse the changes in the divergence angle between chronologically successive areoles and the changes in internode length that have occurred during the evolution of stem succulence in different cactus life-forms. The hypothesis that guided our analyses was that small changes in phyllotactic parameters, coupled to selection favouring juvenile vascular characteristics of the stem and the evolutionary transformation of leaves into spines, may account for the striking morphological variation of cacti.

Methods

Phyllotaxis

Five cactus species were chosen: *Pereskia lychnidiflora* De Candolle; *Opuntia pilifera* Weber; *Neobuxbaumia tetetzo* (Coultter) Backeberg; *Ferocactus latispinus* (Glass) Taylor, and *Mammillaria collina* Purpus, representing typical and contrasting morphologies within the family (a woody, leaf-bearing cactus, and four fully succulent life-forms which include a cladode-stemmed cactus, a giant columnar cactus, a barrel cactus and a globose cactus, respectively). In several individuals of each species, the internode length and the divergence angle were estimated. Internode length was evaluated through a measure of stem compaction, calculated as the number of areoles per unit stem length. To make plants of different sizes comparable, the unit length of the stem was defined as equal to the diameter, except for *Opuntia*, where the cladode was considered as the unit of the flattened stem. To estimate the phyllotactic fraction, and the value of the divergence angle, the number of contact parastichies in the cladode and globose cacti and the number of ribs in the columnar and barrel cacti were counted. Finally, photographs were taken to make further analyses in the laboratory. *Pereskia lychnidiflora* was observed in the Isthmus of Tehuantepec, (Oaxaca, Mexico), and the other species in the Valley of Zapotitlán (Puebla, Mexico).

Number of ribs in barrel and columnar cacti

In 44 and 95 randomly selected individuals of *F. latispinus*, and *N. tetetzo*, respectively, the ribs were counted. *Ferocactus* is a barrel species with helicoidal ribs, while *Neobuxbaumia* is a giant columnar species with longitudinal ribs. In *Ferocactus* the number of ribs was counted at the top of the stem of large adult plants. In *Neobuxbaumia* the ribs were counted at eye height, ca. 1.7 m from the ground. To

evaluate if variation in rib numbers from plant to plant could be considered a random process around an allometric mean, or if, alternatively, the number of ribs is dependent on some other factor rather than plant size, the resulting distribution of rib numbers was tested for randomness by comparing it against a theoretical Poisson distribution.

Vascularization

Plant 'skeletons' (i.e. the remains of the vascular system from dead plants) were selected from two contrasting species. The distribution of vascular bundles inside the stem can be easily observed in these dried structures, as the external photosynthetic epidermis and the internal succulent parenchyma rot quickly once the plant dies, and only the lignified vascular tissues remain. To measure the vascularization a cylindrical opuntoid species (*O. fulgida* Engelmann from the Sonoran Desert) was chosen. Its vascular tissues stems are better preserved under field conditions and allow easier measurements than the flat-stemmed *O. pilifera*. The vascularization of a giant columnar cactus (*N. tetetzo*) was also measured.

Simulation studies

A computer program was written to simulate the distribution of areoles around a cylindrical stem section. Each areole was considered as a discrete unit whose occurrence is mathematically regulated by two simple neighbourhood functions: (a) the distance from any given areole to its lateral neighbours, and (b) the longitudinal separation from the older predecessor along the stem. Thus, our model was based only on two parameters: (a) stem compaction (a function of internode length), and (b) the angle between successive areoles. The model allows either to enter a particular divergence angle, or to choose from a set of predefined angular values, including ϕ (the Fibonacci angle). The model also allows to choose angular values from any pair of terms of the Fibonacci series (f_{n-1}/f_{n+1}). For example, the terms (f_4/f_6) = (3/8) yield an angular divergence of 0.375 of a circumference, or $135^\circ 00'00''$. Because these angles are not irrational numbers, they will generate sets of areoles that form longitudinally ribbed plants: the value (3/8) will generate stems with eight ribs, as the ninth areole will appear exactly above the first one ($135^\circ \times 8$ is 1080° , an exact multiple of 360°). Simulations were done by supplying the model with the phyllotactic values measured in the field. In cases where the estimation of the divergence angle in the field had been difficult, the model was used to obtain the parameter estimate that repeated the architecture observed in the field. Stem compaction was measured successfully in all plants.

Results

Phyllotaxis

The Fibonacci angle ϕ gave the best description of the areole arrangement in the ancestral-like species *P. lychnidiflora*, in the cladode-stemmed *O. pilifera*, and in the globose *M. collina*. While the generating angle in these three species was uniformly $(3-\sqrt{5})/2$, large between-species differences were observed in the degree of stem compaction. The less compacted form was *P. lychnidiflora*, followed by *O. pilifera*. *Mammillaria collina* was the most densely compacted species of this group (Fig. 2). The columnar and barrel forms (*N. tetetzo* and *F. latispinus*) also had high values of stem compaction. Additionally, they presented divergence angles different from ϕ , allowing the alignment and fusion of tubercles to form the ribs.

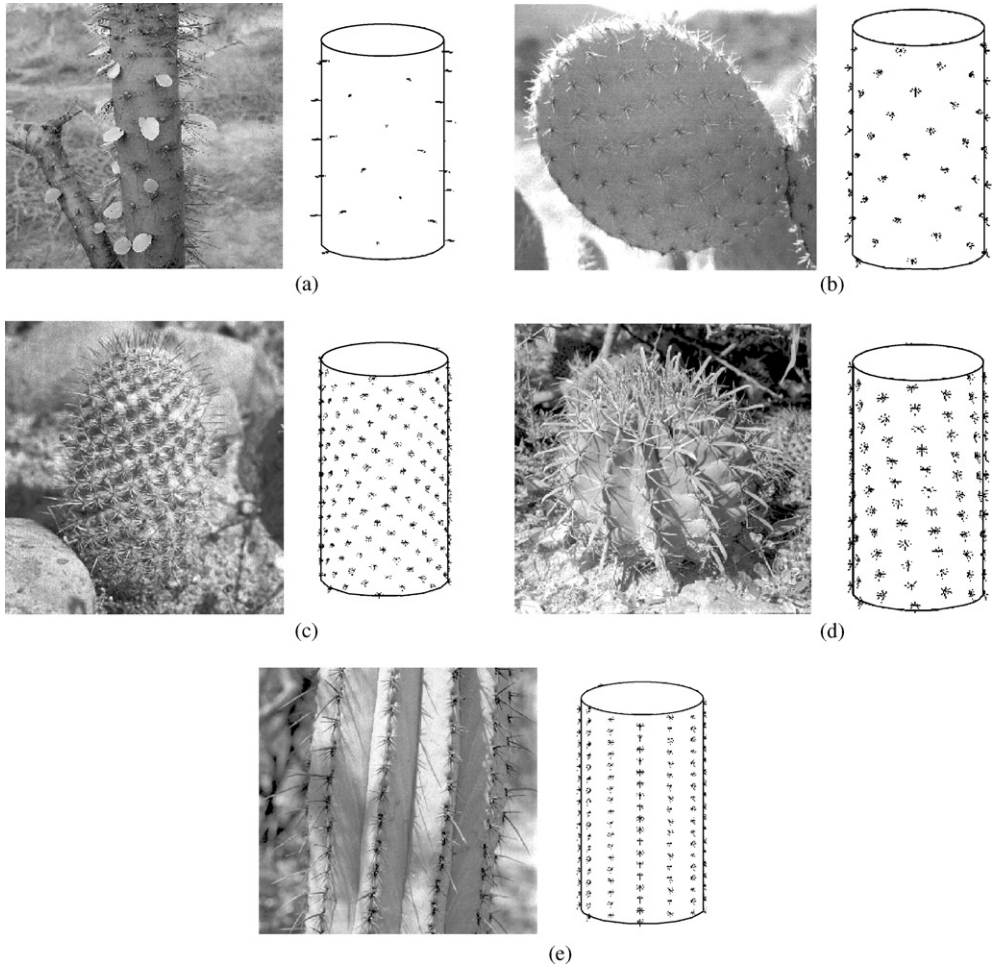


Figure 2. Modelled phyllotactic patterns for (a) *Pereskia lichnidiiflora* (divergence angle(d.a.) = $137^{\circ} 30'27.95...''$; stem compaction s.c. = 16 areoles per unit diameter), (b) *Opuntia pilifera* (d.a. = $137^{\circ} 30'27.95...''$; s.c. = 40 areoles), (c) *Mammillaria collina* (d.a. = $137^{\circ} 30'27.95...''$; s.c. = 300 areoles). (d) *Ferocactus latispinus* (d.a. = $138^{\circ} 03'36''$; s.c. = 50 areoles), and (e) *Neobuxbaumia tetetzo* (d.a. = $138^{\circ} 27'41.54...''$; s.c. = 90 areoles).

Number of ribs in barrel and columnar cacti

In *latispinus*. 49% of the plants had 13 ribs in the upper section of the stem, 42.2% had eight ribs and 6.8% had five ribs (Fig. 3). The number of ribs in this species corresponded in all cases to numbers of the Fibonacci series, and their distribution departed very significantly from the expected distribution under the assumption of a random process of rib generation around an allometric mean. Ribs in this species, as in many other barrel cacti, are not longitudinally arranged but slightly helicoidal.

In *N. tetetzo* 29% of the sampled plants had 13 ribs, 26.9% had 14 ribs, 19.3% had 12 ribs, 7.5% had 15 ribs, 5.4% had 8 ribs, and the remaining 11% were distributed among 7, 9, 10, 11, 16, 17 and 19 ribs (Fig. 3). The observed distribution showed two peaks significantly above the expected random distribution, and that also correspond to Fibonacci numbers (8 and 13), or to numbers very near them (12 and 14). In this species the ribs are longitudinally, not helicoidally, arranged.

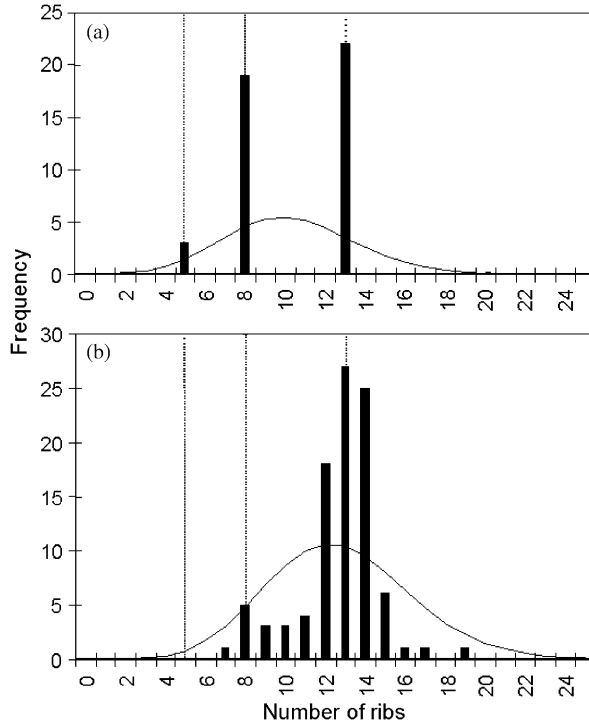


Figure 3. Frequency distribution (bars) of rib numbers in selected barrel and columnar cacti, and the expected Poisson distribution (lines). (a) Distribution of rib numbers in *Ferocactus latispinus* in the upper section of the stem. (b) Distribution of rib numbers in *Neobuxbaumia tetetzo* at eye-level height. Both distributions departed significantly from the Poisson random model ($\chi^2 = 81.8$, df. = 7, $p < 0.001$; and $\chi^2 = 85.9$, df. = 11, $p < 0.001$, respectively). In both plots, the vertical dotted lines indicate Fibonacci numbers (5, 8, 13).

Vascularization

The woody bundles of the skeletons of *O. fulgida* and *N. tetetzo* showed a high resemblance with the corresponding computer-generated images of the vascular bundles connecting the areoles (Fig. 4). In the case of *O. fulgida* (which like *O. pilifera* also has a divergence angle of φ), the vascular bundles were arranged in a two-way set of helices, both in Fibonacci numbers (eight bundles spiralling in one way, and 13 in the other). In the case of *Neobuxbaumia* the bundles were organized longitudinally along the stem, underlying the external ribs (Fig. 4).

Discussion

According to the evolutionary classification of phyllotactic patterns of Church (1920) and Jean (1988), in plants with alternate leaves the spiral pattern is considered primitive whereas whorled and other non-spiral patterns are considered derived or secondary. This evolutionary criterion coincides with the result of our model. The lowest compaction of areoles was found in *P. lychnidiflora*, a species with a Fibonacci divergence angle (φ). This species belongs to a subfamily (Pereskioideae) presenting

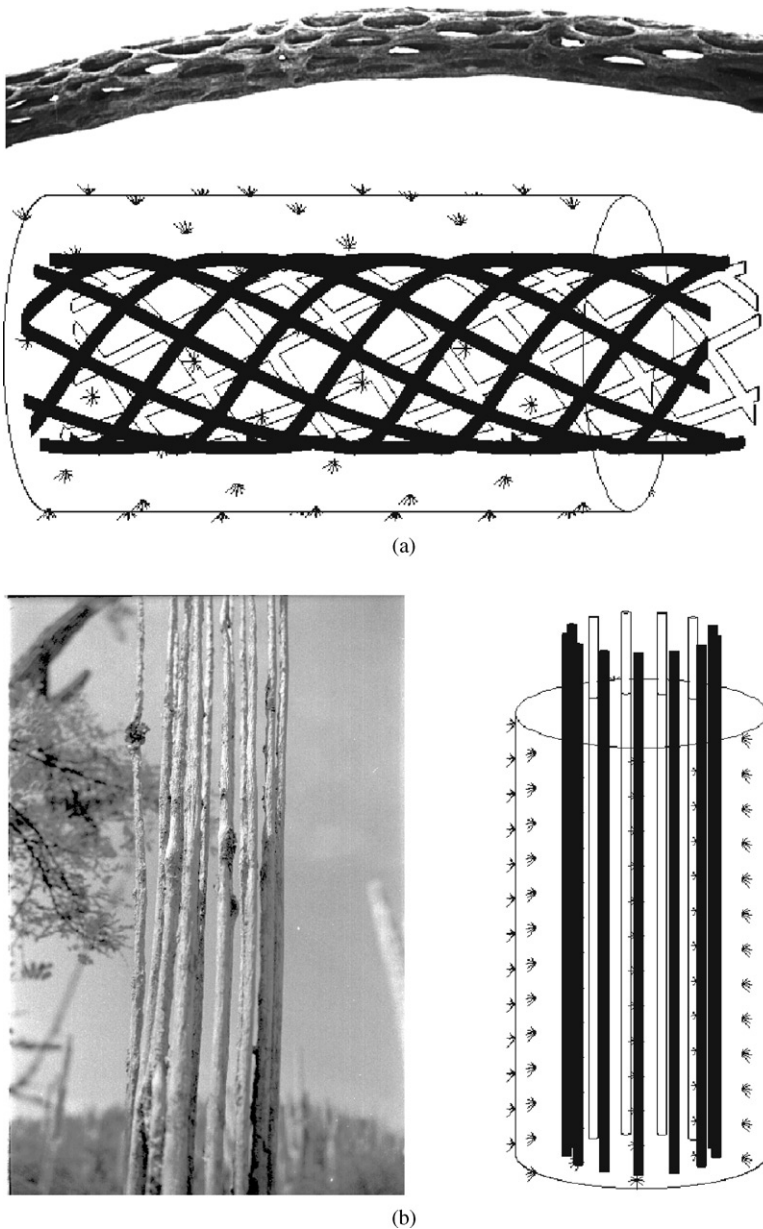


Figure 4. (a) Model of vascular skeleton of *Opuntia fulgida*, generated by computing lines ('bundles') that connect neighbouring areoles (divergence angle (d.a.) = $137^{\circ} 30' 27.95...''$; stem compaction = 40 areoles per unit diameter). (b) Model of vascular skeleton of *Neobuxbaumia tetetzo* (d.a. = $138^{\circ} 27' 41.54...''$; s.c. = 90 areoles). A small change in the phyllotactic angle predicts the formation of vascular ribs.

ancestral stem characteristics. Increasing stem-compaction through the simple shortening of the internodes without modifying the divergence angle, generates the apparently complex spiral phyllotactic patterns of some of the stem-succulent cacti, such as *O. pilifera*. The highest degree of stem compaction was present in the globose forms of the subfamily Cactoidae, exemplified in this study by *M. collina* (Fig. 2). The

dense spiral phyllotaxis of these globose plants allows a most efficient packing of the areoles, and results in a dense reticule of spines that uniformly covers the plant. Spines in these plants are important as a means of self-shading (Nobel, 1978) and of defence against predators (McAuliffe, 1984).

The rib numbers of *F. latispinus* correspond to terms of the Fibonacci series (Fig. 3). It was also observed that seedlings usually had three ribs, followed by small plants with five ribs, intermediate plants with eight, and large plants with 13 ribs. These results agree with data reported by Gibson & Nobel (1986) for other 15 species of *Ferocactus*. According to our model, the divergence angle in *F. latispinus* corresponds approximately to $138^{\circ} 04'$ (Fig. 2). The variation in the mathematical value of the divergence angle is not quantitatively very large from the Fibonacci value ($\phi = 137^{\circ} 30'27.95\dots'$) that generated the non-ribbed spiral phyllotaxis in the case of the first three species. The small parametric difference was enough to produce a very important change in the architecture of the whole plant.

The giant columnar species *N. tetetzo* presents longitudinal ribs in numbers which do not always coincide with the Fibonacci series. Once a plant develops a longitudinal arrangement of areoles, there is no adaptive reason why it should show ribs in Fibonacci numbers, other than a phylogenetic trend. Any number of ribs proportionate to the size of the plant will serve the adaptive purpose of providing mechanical support. Accordingly, our model can simulate ribbed cacti with any number of ribs, by simply changing the phyllotactic angle slightly. The fact that *N. tetetzo* presents ribs in Fibonacci numbers more frequently than in any other number, is likely to be the result of some sort of evolutionary memory of the plant, more than an adaptive consequence. That is, if the hypothesis that results from our analysis, in the sense that ribbed morphologies have derived from ancestral Fibonacci patterns by joining adjacent contact parastichies is true, then it could be expected that some columnar plants would still produce ribs preferentially in Fibonacci numbers. In support of this idea, we have observed that the seedlings of *N. tetetzo* are not ribbed but follow a Fibonacci helicoidal pattern during their very early ontogeny (less than 6 months of age). This means that the same transition that the adult individuals of the species have made in evolutionary time can also be observed within one individual during the early ontogeny. The columnar forms, and to a lesser degree the barrel ones, face the problem of erect growth, together with the loss of mechanical resistance that results from the development of succulence. Vascular bundles organized in longitudinal ribs seem to have emerged through natural selection as a solution to this problem. All giant columnar cacti are ribbed, with vascular bundles forming separate wooden rods that run under the external ribs of the plant. Additionally, the separated bundles allow the change of volume of the plant, and facilitate the accumulation of water in the tissues (Nobel, 1978). Thanks to this system, some giant columnar cacti can absorb water up to a 10% of their standing mass in only 4 days after a rainfall (Nobel, 1988). Thus, the evolutionary transition to columnar growth seems to have been directed by the change from a reticulate phyllotaxis generated by a Fibonacci divergence angle (ϕ), to a ribbed system of parastichies generated by a divergence angle that allows the development of areoles immediately above previously existing ones.

This morphology, however, seems to have some ecological costs. The less-protected space between ribs in columnar cacti allows the attack of predators such as goats that seek the parenchyma as a source of food, or the excavation by woodpeckers that nest in the giant stems (McAuliffe & Hendricks, 1988; Merlin, 1999). Additionally, the longitudinal arrangement of vascular bundles seems to eventually encounter mechanical limitations as the plants grow in size. Very frequently, giant columnar cacti break or fall under their own weight (Zavala-Hurtado & Díaz-Solis, 1995).

Mechanical damage, in turn, facilitates the microbial infection of the plants (Steenbergh & Lowe, 1977). In the *N. tetetzo* stands of the Tehuacán valley, most of

the adult plant mortality (*ca.* 80%) is due to the physical collapse of the larger individuals, brought down by their sheer weight. The second most important cause (*ca.* 20%) is due to the attack of pathogens that infect the plant mostly through wounds between ribs (Díaz-Maeda, 1991). Similar mortality trends have been reported for *Carnegiea gigantea* in the Sonoran Desert (Steenbergh & Lowe, 1977).

Summarizing, two morphological variables seem to have changed together with the development of stem succulence in cacti and the replacement of leaves for spines. On one hand, stem compaction and the development of spiny areoles seem to have played an important role during the transition from woody and leafy ancestral species into the modern stem-succulent plants. On the other hand, the transformation from non-ribbed to ribbed species seems to have been accompanied by relatively small changes in the phyllotactic angle, from the ancestral Fibonacci value (ϕ) to other values that permitted the evolutionary transformation of contact parastichies into true ribs. Our simulation model shows that small changes in the phyllotactic divergence angle can produce dramatic transformations in both the external morphological appearance and in the internal arrangement of vascular bundles. These changes, in turn, may have an extraordinary effect on the mechanical properties of the whole plant.

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