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SYSTEMATIC ANATOMY AND PHYLOGENY OF MEXICAN COLUMNAR CACTI¹

ARTHUR C. GIBSON² AND KARL E. HORAK²

ABSTRACT

Stem transections of 64 arborescent and fruticose species of columnar cacti were studied to evaluate present systematic treatments of Mexican taxa. Species examined included not only most Mexican taxa, primarily of tribe Pachycereeae, but also related and unrelated taxa from the West Indies and Central and South America. A review of stem biochemical literature on Mexican columnar cacti showed that triterpenes and alkaloids are mutually exclusive, except in *Lophocereus*. In taxa with abundant stem triterpenes all species of *Stenocereus* have silica bodies in the skin, whereas species of *Escontria*, *Myrtillocactus*, and *Polaskia* lack silica bodies. In species which have alkaloids, crystals are generally lacking, but in species closely related to alkaloid-bearing taxa the skin contains abundant calcium oxalate crystals in an unusual pattern. When these and other data on vegetative and reproductive morphology of Pachycereeae are used, two subtribes, Pachycereinae and Stenocereinae, can be clearly defined. Pachycereinae includes taxa that lack funicular pigment cells at anthesis but have either abundant alkaloids or calcium oxalate crystals in the skin, whereas Stenocereinae includes taxa that have abundant triterpenes and funicular pigment cells at anthesis, many which also have silica bodies. Five new combinations are proposed for Mexican species that were assigned to *Heliabravoa*, and *Machaerocereus* and *Rathbunia*, which are submerged into *Polaskia* and *Stenocereus*, respectively. Based on a proposed phylogeny of Pachycereeae, evolutionary trends of vegetative and reproductive features are analyzed. The probable center of early radiation of Pachycereeae is southern Mexico, and geographical isolation has apparently encouraged allopatric speciation of numerous phylads. The assemblage of columnar cacti in the Sonoran Desert is composed of highly specialized species of at least seven distinct phylads, and species are closely related to southern forms and not to sympatric species.

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² Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721.

Nearly all species of columnar cacti have at some time been classified in the comprehensive genus *Cereus* Miller. However, since Britton & Rose (1909, 1920, 1922), who subdivided *Cereus* into numerous small genera and separated some taxa at the subtribal level, most taxonomic monographs of Cactaceae have treated *Cereus* (s. l.) as a form genus. Generic summaries by Bravo (1937), Hunt (1967), and Marshall & Bock (1941) followed the moderate generic concept of Britton and Rose with some modifications, but none expanded very much the subtribal and tribal classification of the columnar taxa. On the other hand, major liberalized classification systems (Backeberg, 1958; Buxbaum, 1958a, 1961, 1962b, 1964–1965, 1968b; Bravo, 1962–1963, after Buxbaum) emphasized the differences between species groups at the generic level and completely rearranged the columnar cacti into as many as eight tribes, all of which are ultimately derived from columnar forms in northern South America and the West Indies that appear to have the primitive features for subfamily Cactoideae. According to all of these authors, *Cereus* (s. s.) is a South American genus found east of the Andean Cordillera. The most conservative approach has been used by Benson (1969a, 1969b, 1970), but only cacti occurring in the United States were treated. Benson (1969a) recognized that *Cereus* (s. l.) is artificial but continued to use the taxon until relationships of the subdivision were better understood.

Even though investigators cannot agree on the nomenclature, classification, and phylogeny of Mexican columnar cacti, all agree that these are autochthonous species. There are about 80 species of arborescent, fruticose, suffrutescent, and procumbent forms, excluding the epiphytes but including several naturally occurring interspecific hybrids. Most species and all but three Britton and Rose genera are found only in North America. Moreover, half of the Mexican species ranging beyond Mexico extend no more than 500 kilometers beyond the border. The genus *Acanthocereus* is widely distributed along the coast of the Gulf of Mexico and occurs in the West Indies and coastal northern South America. *Cephalocereus*, a genus with numerous unresolved taxonomic problems, is wide-ranging from Mexico and Florida to Brazil; North and South American taxa are sometimes treated as separate lines or even several genera (Backeberg, 1960). Species of *Lemaireocereus* (sensu Britton and Rose) outside of Mexico occur in Central America, the West Indies, coastal Venezuela and Colombia, and the western foothills of the Andes to Peru. *Lemaireocereus griseus* (Haw.) Britt. & Rose, the only species of the genus shared between North and South America, is native to Venezuela and its adjacent islands and is probably not a native of Mexico. Patterns of very high endemism in Mexico can also be seen in subfamily Opuntioideae and in tribe Cacteae of Cactoideae. Clearly, the cactus flora of Mexico has evolved relatively independently of the cactus floras of both South America and the West Indies; therefore, Mexico is a reasonable unit for investigation as a secondary center of radiation.

In general, systematic botanists have good reasons to be suspicious of and disappointed with previous taxonomic or putatively phylogenetic treatments of columnar cacti. Gross morphological features of stems, flowers, and fruits and characteristics of growth forms and habits have proved by themselves to be

unreliable indicators of relationships within Cactoideae, in which repeated morphological convergence has occurred. Moreover, characteristics that are used to separate species and genera of cacti often appear minor, based mostly on subjective dogma of each author. Unfortunately, the absolute crossability criterion of the "biological species" is difficult to employ not only because these are long-lived perennials that may not flower for many years, but also because interspecific and intergeneric (infratribal) hybrids occur in cacti, even in nature, probably because morphological and genetic isolating mechanisms are poorly developed and pollinating agents are generally not species specific. In addition, nearly all species of columnar cacti so far analyzed are diploids, $2n = 22$ (see Leuenberger, 1976; Matuda, 1958; Pinkava et al., 1977; Pinkava & McLeod, 1971), thus ruling out the use of cytogenetic information in systematics. Systematic problems have been complicated by a plethora of specific and generic names, often proposed from insufficient materials and lacking adequate justifications for the erection of new taxa. Many of these new names have been incorporated quickly into cactus literature without much critical review. Few species have ever been studied on a population-by-population basis. Finally, systematic anatomy, which has been highly useful in unraveling the taxonomy of other families, has not been carried out with much intensity within Cactaceae.

The only current putatively phylogenetic system of classification that clearly discusses relationships of extant columnar genera is that of Buxbaum (1958a), which has undergone numerous revisions (Buxbaum, 1961, 1962b, 1968b, 1975c). According to the latest revision, tribe Pachycereeae includes nearly all large, nonepiphytic columnar cacti of Mexico, plus other species of these genera found elsewhere. Excluded from Pachycereeae are *Acanthocereus*, *Nyctocereus*, *Peniocereus*, and the epiphytic taxa, assigned by Buxbaum to Hylocereeae, and *Bergerocactus* and *Wilcoxia*, assigned to Echinocereae. Buxbaum now has designated four subtribes, Myrtillocactinae, Pachycereinae, Pterocereinae, and Stenocereinae (once Stenocereinae and Cephalocereinae), within Pachycereeae, and he has chosen Pterocereinae, consisting of *Pterocereus* and *Escontria* of southern Mexico and Guatemala, to represent the primitive subtribe and *Stenocereus stellatus* (Pfeiff.) Riccob. to represent the primitive condition for the other derived subtribes. To date, authors have neither seriously challenged his views on primitiveness, which are the bases for the subtribes, nor carefully studied the membership of each subtribe.

Anatomical descriptions of Mexican columnar cacti are uncommon in the literature. Vegetative anatomy of a small number of unspecified species was described in the familial review of Metcalfe & Chalk (1950), and the study of Preston (1901) included the stem structure of *Carnegiea gigantea* (Engelm.) Britt. & Rose. Ergastic substances in some species have been described (Reichert, 1913; Metcalfe & Chalk, 1950). The most comprehensive study to date was done on wood anatomy (Gibson, 1973), using a comparative approach to demonstrate that quantitative and qualitative features of secondary xylem are convergent within Cactoideae, the changes being correlated with differences and similarities in growth form and habit, size, and degree of succulence. However, the classification system used was somewhat artificial for columnar forms;

therefore, comparisons between species within North America were not as convincing as between clearly unrelated species of North and South America. Numerous low magnification drawings and photographs of flowers, fruits, and seeds, either whole or in longisection, of Mexican columnar cacti have been published, but the anatomy of these structures is poorly known. Buxbaum (1962c, 1963b, 1963d, 1967, 1968b, 1969) has observed that fruit pulp color in some species of Mexican columnar cacti is produced within much enlarged, idioblastic pigment cells of the funicular epidermis, the so-called "pearl cells," whereas other species do not have this feature because the fruit matures dry, the pulp is not colored red, or the color is produced from or within the fruit wall. Buxbaum has assigned all cacti with these funicular pigment cells to tribe Pachycereeae and indicates by his phylogeny (1968b) that the character occurs in all subtribes.

Descriptions of pollen grains have been included in floristic pollen surveys (Martin & Drew, 1969, 1970) and a recent monograph on cactus pollen (Leuenberger, 1976) that reviews all cactus pollen literature. Leuenberger has concluded that most columnar cacti have a similar type of pollen grain, but for each tribe (after Buxbaum) one finds a specific range of exine features.

Because some cacti have been identified as medicinal plants, many species of Mexican columnar cacti have been biochemically investigated. Based on extensive studies of triterpenoid saponins, Djerassi (1957) was able to conclude that about 20 naturally occurring triterpenes, most of them new compounds, are present in stem tissues of columnar cacti. Especially *Escontria*, *Lemaireocereus*, *Machaerocereus*, *Myrtillocactus*, and *Lophocereus schottii* (Engelm.) Britt. & Rose have sufficient amounts of stem triterpenes to isolate and characterize the compounds. Djerassi noted that species possessing triterpenes generally lack alkaloids. Consequently, he suggested that presence of certain triterpenes may be useful in systematic studies. His suggestions and observations were used by Bravo & Cox (1958) and Buxbaum (1962c, 1963d, 1967) to argue that *Myrtillocactus*, *Polaskia*, and *Heliabravoia* are closely related, and Buxbaum (1968b, 1969) has used these data to place *Machaerocereus* into tribe Pachycereeae, which includes all species with copious amounts of triterpenes. However, no worker has yet analyzed Djerassi's findings in an attempt to clarify phyletic lines within the tribe. Moreover, taxonomists have not properly explained the systematic distribution of unusual alkaloids and steroids in some species of columnar cacti (Aguirell, 1969; Aguirell et al., 1971) that lack triterpenes.

Our purpose here is to report the previously unstudied anatomical diversity of the columnar cacti of Mexico, especially structures of stems, and to evaluate the similarities and differences of these structures with respect to data assembled from all sources to determine, if possible, the phyletic position of these taxa. An accurate phylogenetic picture is needed to change the nomenclature of these species. Knowledge of phyletic lines is essential for the study of the origin of physiological adaptations of cacti and to analyze the host preferences exhibited by cactophilic species of *Drosophila*, which feed on yeasts growing in rotting columnar forms.

MATERIALS AND METHODS

A summary of the species examined in this study is provided at the end of this section, including authorities, approximate distributions, and, wherever available, vouchered herbarium specimens in the herbarium of the University of Arizona or Rancho Santa Ana Botanic Garden, Claremont, California. For this study the columnar cacti were defined as those species with cylindrical, ribbed stems that are at least 15 times longer than they are wide. Epiphytic species were excluded because these must be studied as a unit from a wider geographic region. Moreover, adequate materials of *Morangaya*, *Neoevansia*, *Peniocereus*, and *Wilcoxia*, mostly suffrutescent forms, were not available, and a separate study should be devoted to these genera, as well as *Echinocereus* and *Bergerocactus*, to clarify phylogenetic relationships. Most Mexican species have been assigned by Buxbaum to tribe Pachycereeae, and basionyms and most commonly used synonymy are cited not only for species studied but also for other Mexican species (with asterisk).³ Five new nomenclatural combinations are used throughout the text, where justifications are provided, to minimize confusion to the reader. Other than the epiphytic and suffrutescent forms, *Acanthocereus* and *Nyctocereus* of tribe Hylocereeae and *Bergerocactus* presumably of tribe Echinocereae are the only other bona fide columnar cacti endemic to Mexico. Representatives of other tribes were investigated anatomically to determine whether features used in the systematics of tribe Pachycereeae occur in any unrelated columnar cacti. The reader should refer to Backeberg (1959, 1960) and Bravo (1937) for illustrations and general morphological descriptions of the columnar cacti.

Samples were obtained from mature field specimens and from cultivated plants, mostly vegetatively propagated from wild-collected plants. In most cases only one or two samples were available for study of each species.

Materials were liquid preserved in formalin-acetic acid-alcohol fixative (Johansen, 1940). Outer stem samples of ribs and valleys with spines removed were taken from healthy shoot tips just above the level of early periderm formation, so that late-developing features would not be missed. Standard paraffin methods were used to prepare microscope slides, and the thickness of sections varied with the nature of the material. Features of the hypodermis and presence of crystals and mucilage often interfered with proper embedding and sectioning. Sections were stained with safranin and fast green. Microslides were also prepared from unembedded materials of the outer stem of young and old portions to compare with embedded materials and of the vascular cylinder and pith to observe phloem sclerenchyma and pith features. Care was taken to examine fascicular regions with secondary growth because primary phloem fibers often begin to differentiate only after secondary growth has begun in cacti. Freehand sections were made to study fruit walls, but ovules, funiculi, and stamens were mounted in Hoyer's medium (Beeks, 1955), which served as a combined mounting medium and clearing agent.

This study was designed to use qualitative, rather than quantitative, anatom-

³ This list will be more correct when *Cephalocereus* is carefully monographed.

ical comparisons because sufficient numbers of field collections of each species could not be made to do adequate statistical analyses. In a study on cactus anatomy Conde (1975) has already shown that the dimensions of epidermal and cortical structures may be exceedingly variable within a species; however, qualitative features are relatively constant. None of the features used in this study showed marked qualitative differences for the same species between wild and cultivated specimens.

Observations on ergastic substances were made with the aid of polarized light. Starch grains were easily distinguishable, and specific microchemical tests for starch with potassium iodide-iodine (IKI, Johansen, 1940) were used only in special circumstances. Birefringent crystals were assumed to be composed of calcium oxalate or possibly calcium malate (Bailey, 1964). Microchemical tests were made of anisotropic bodies found in the collenchymatous hypodermis and epidermis of certain species to determine if they were silica bodies. Tests included immersing for 1–4 hr unstained thin sections of *Stenocereus gummosus* affixed to microslides in four different solutions: concentrated hydrochloric, nitric, and hydrofluoric acids and dilute sodium hydroxide. These bodies were tentatively identified as silica because they dissolved only in hydrofluoric acid.

Data from the literature on cactus morphology and biochemistry were combined with numerous new anatomical observations on stems and reproductive structures to construct a phylogeny that reflects the similarities and differences of Pachycereeae. Data on 69 variables were entered on computer cards for species of Pachycereeae studied, and 60 were used in the BC-TRY key-cluster analysis system (Tryon & Bailey, 1970), available in the University of Arizona computer center, to check the validity of the phylogeny devised by personal analysis. The agreement was very close in expressing the composition and positions of subtribes and smaller phylads. A list of the variables and scoring procedures is too long to be published here but will be provided to interested readers upon request.

TRIBE PACHYCEREEAE Buxb.

- Backebergia militaris* (Audot) Bravo ex Sánchez Mejorada.* *Cereus militaris* Audot, Rev. Hort. 2: 307. 1845. West central Mexico.
- Carnegiea gigantea* (Engelm.) Britt. & Rose. *Cereus giganteus* Engelm. in Emory, Notes Milit. Recon. 159. 1848. Sonoran Desert. *Gibson* 3233 (ARIZ).
- Cephalocereus alensis* (Weber) Britt. & Rose. *Pilocereus alensis* Weber in Gossel., Bull. Mus. Hist. Nat. (Paris) 11: 508. 1905. Syn. *Pilosocereus alensis* (Weber) Byles & Rowl. Sinaloa to Jalisco, Mexico. *Gibson* 3218 (ARIZ). May include *Pilosocereus guerreronis* (Backeb.) Byles & Rowl. of Guerrero.
- Cephalocereus apicicephalum* Daws.* Allan Hancock Found. Publ. Occas. Pap. 1: 10. 1948. Syn. *Neodawsonia apicicephalum* (Daws.) Backeb. Oaxaca, Mexico.
- Cephalocereus chrysacanthus* (Weber) Britt. & Rose. *Pilocereus chrysacanthus* Weber in K. Schum., Gesamtb. Kakt. 1: 78. 1897. Syn. *Pilosocereus chrysacanthus* (Weber) Byles & Rowl. Southern Mexico. *Gibson* 3188 (ARIZ).
- Cephalocereus collinsii* Britt. & Rose,* Cactaceae 4: 269. 1923. Syn. *Pilocereus collinsii* (Britt. & Rose) Knuth and *Pilosocereus collinsii* (Britt. & Rose) Byles & Rowl. Oaxaca, Mexico.
- Cephalocereus cometes* (Scheidweil.) Britt. & Rose.* *Cereus cometes* Scheidweil., Allg. Gartenzeitung 8: 399. 1840. Syn. *Pilocereus cometes* (Scheidweil.) Knuth and *Pilosocereus cometes* (Scheidweil.) Byles & Rowl. San Luis Potosí, Mexico.
- Cephalocereus gaumeri* Britt. & Rose,* Cactaceae 2: 47. 1920. Syn. *Pilocereus gaumeri* (Britt.

- & Rose) Knuth and *Pilosocereus gaumeri* (Britt. & Rose) Backeb. Yucatán Peninsula, Mexico.
- Cephalocereus hoppenstedtii* (Weber) K. Schum. *Pilocereus hoppenstedtii* Weber, Cact. Pfersdorff. 1864. Syn. *Haseltonia columna-trajani* (Karw.) Backeb. Puebla and Oaxaca, Mexico. Gibson 2332 (RSA; dead seedling).
- Cephalocereus leucocephalus* (Poselg.) Britt. & Rose. *Pilocereus leucocephalus* Poselg., Allg. Gartenzeitung 21: 126. 1853. Syn. *Pilosocereus leucocephalus* (Poselg.) Byles & Rowl. Sonora to Oaxaca, Mexico. Gibson 3206 (ARIZ).
- Cephalocereus nizandensis* (Bravo & MacDoug.) Buxb.* *Neodawsonia nizandensis* Bravo & MacDoug., Anales Inst. Biol. Univ. Nac. México 29: 82. 1958. Oaxaca, Mexico.
- Cephalocereus nobilis* (Haw.) Britt. & Rose. *Cereus nobilis* Haw., Syn. Pl. Succ. 179. 1812. Syn. *Pilosocereus nobilis* (Haw.) Byles & Rowl. Lesser Antiles. Gibson 3207 (ARIZ).
- Cephalocereus palmeri* Rose,* Contr. U.S. Natl. Herb. 12: 418. 1909. Syn. *Pilocereus palmeri* (Rose) Knuth and *Pilosocereus palmeri* (Rose) Byles & Rowl. Tamaulipas and San Luis Potosí, Mexico.
- Cephalocereus purpusii* Britt. & Rose,* Cactaceae 2: 56. 1920. Syn. *Pilocereus purpusii* (Britt. & Rose) Knuth and *Pilosocereus purpusii* (Britt. & Rose) Byles & Rowl. Sonora to Michoacán, Mexico.
- Cephalocereus royenii* (L.) Britt. & Rose. *Cactus royenii* L., sp. pl., ed. 1. 467. 1753. *Pilocereus royenii* L., Illustr. Hort. 11 (Misc.): 74. 1864. Syn. *Pilosocereus royenii* (L.) Byles & Rowl. West Indies. *Heed s. n.*
- Cephalocereus russelianus* (Otto) Rose. *Cereus russelianus* Otto in Salm-Dyck, Cact. Hort. Dyck. 1849: 201. 1850. Syn. *Pilocereus russelianus* (Otto) Rumpl. and *Subpilocereus russelianus* (Otto) Backeb. Venezuela and Colombia. Gibson 3228 (ARIZ). Placement of this species in *Cephalocereus* is tentative.
- Cephalocereus sartorianus* Rose,* Contr. U.S. Natl. Herb. 12: 419. 1909. Syn. *Pilocereus sartorianus* (Rose) Berg. and *Pilosocereus sartorianus* (Rose) Byles & Rowl. Veracruz, Mexico.
- Cephalocereus senilis* (Haw.) Pfeiff. *Cereus senilis* Haw., Phil. Mag. 63: 31. 1824. Syn. *Pilocereus senilis* (Haw.) Lem. Hidalgo and Guanajuato, Mexico. Gibson s.n. (seedling).
- Cephalocereus totolapensis* (Bravo & MacDoug.) Buxb. *Neodawsonia totolapensis* Bravo & MacDoug., Anales Inst. Biol. Univ. Nac. México 29: 74. 1958. Oaxaca, Mexico. Gibson 3234 (ARIZ).
- Escontria chiotilla* (Weber) Rose. *Cereus chiotilla* Weber in K. Schum., Gesamtb. Kakt. 83. 1897. Puebla, Mexico, but also widely cultivated and escaped. Gibson 2356 (RSA), 3181 (ARIZ).
- Lophocereus gatesii* M. E. Jones, Cact. Succ. J. 5: 546. 1934. Southern Baja California, Mexico. McGill s. n.
- Lophocereus schottii* (Engelm.) Britt. & Rose. *Cereus schottii* Engelm., Proc. Amer. Acad. Arts 3: 288. 1856. Syn. *Pilocereus schottii* (Engelm.) Lem. Sonoran Desert. Gibson 3195 (ARIZ); *Heed s. n.*
- Mitrocereus fulviceps* (Weber) Backeb. ex Bravo. *Pilocereus fulviceps* Weber in K. Schum., Gesamtb. Kakt. 476. 1897. Syn. *Pachycereus chrysomallus* (Lem.) Britt. & Rose and *Pseudomitrocereus fulviceps* (Weber) Bravo & Buxb. Puebla, Mexico. Gibson 2531 (RSA).
- Myrtillocactus cochal* (Orc.) Britt. & Rose. *Cereus cochal* Orc., West. Amer. Sci. 6: 29. 1889. Baja California, Mexico. Gibson 3178 (ARIZ).
- Myrtillocactus geometrizans* (Mart.) Cons. *Cereus geometrizans* Mart. in Pfeiff., Enum. Cact. 90. 1837. Central Mexico from San Luis Potosí to Oaxaca. Gibson 3176 (ARIZ).
- Myrtillocactus schenckii* (Purp.) Britt. & Rose. *Cereus schenckii* Purp., Monatsschr. Kakteenk. 19: 38. 1909. Puebla and Oaxaca, Mexico. Gibson 3186 (ARIZ).
- Neobuxbaumia euphorbioides* (Haw.) Buxb.* *Cereus euphorbioides* Haw., Suppl. Pl. Succ. 75. 1819. Syn. *Carnegiea euphorbioides* (Haw.) Backeb., *Cephalocereus euphorbioides* (Haw.) Britt. & Rose, *Pilocereus euphorbioides* (Haw.) Rumpl., and *Rooksbya euphorbioides* (Haw.) Backeb. Veracruz and Tamaulipas, Mexico.
- Neobuxbaumia macrocephala* (Weber) Daws.* *Cephalocereus macrocephalus* Weber in K. Schum., Gesamtb. Kakt. 197. 1897. Syn. *Pachycereus ruficeps* (Weber) Britt. & Rose and *Pilocereus macrocephalus* Weber. Puebla, Mexico.
- Neobuxbaumia mezcalaensis* (Bravo) Backeb.* *Cephalocereus mezcalaensis* Bravo, Anales Inst. Biol. Univ. Nac. México 3: 379. 1932. Syn. *Pilocereus mezcalaensis* (Bravo) Marsh. Puebla, Mexico. One cannot tell from descriptions whether *N. multiareolata* (Daws.)

- Bravo, Scheinv. & Sánchez Mejorada belongs in *N. mezcalaensis*. Ironically, an analysis of the genus *Neobuxbaumia* by Scheinvar & Bravo (1973), a year after *N. multiareolata* was named, did not discuss this presumed species.
- Neobuxbaumia polylopha* (DC.) Backeb. *Cereus polylophus* DC., Mém. Mus. Hist. Nat. 17: 115. 1828. Syn. *Cephalocereus polylophus* (DC.) Britt. & Rose and *Pilocereus polylophus* (DC.) Salm-Dyck. Hidalgo and Queretaro, Mexico. Gibson s. n. (young plant).
- Neobuxbaumia scoparia* (Poselg.) Backeb.* *Pilocereus scoparius* Poselg., Allg. Gartenzeitung 21: 216. 1853. Syn. *Cephalocereus scoparius* (Poselg.) Britt. & Rose. Veracruz and Oaxaca, Mexico.
- Neobuxbaumia tetetzo* (Weber) Backeb. *Pilocereus tetetzo* Weber, Hort. Paris Engelmann. 1864. Syn. *Cephalocereus tetetzo* (Weber) Bravo and *Pachycereus tetetzo* (Weber) Ochoterena. Puebla and Oaxaca, Mexico. Gibson 3237 (ARIZ).
- Pachycereus grandis* Rose,* Contr. U.S. Natl. Herb. 12: 421. 1909. Central Mexico.
- Pachycereus hollianus* (Weber) Buxb. *Cereus hollianus* Weber in Coult., Contr. U.S. Natl. Herb. 4: 411. 1896. Syn. *Lemaireocereus hollianus* (Weber) Britt. & Rose. Puebla, Mexico. Gibson 3198 (ARIZ).
- Pachycereus marginatus* (DC.) Britt. & Rose. *Cereus marginatus* DC., Mém. Mus. Hist. Nat. 17: 116. 1828. Syn. *Lemaireocereus marginatus* (DC.) Berg. and *Marginatocereus marginatus* (DC.) Backeb. Central Mexico from San Luis Potosí to Guerrero and Mexico, D. F., but also widely cultivated and escaped. Gibson 3185 (ARIZ).
- Pachycereus pecten-aboriginum* (Engelm.) Britt. & Rose. *Cereus pecten-aboriginum* (Engelm.) in S. Wats., Proc. Amer. Acad. Arts 21: 429. 1886. Southern Baja California and mainland Mexico from S. Sonora to Oaxaca. Gibson 3240 (ARIZ). Here is included *Pachycereus tehuantepecanus* MacDoug. & Bravo. The original description (Bravo, 1956b) made comparisons between the new species and *P. grandis*, which overlaps in part of its distribution, but failed to make comparisons with *P. pecten-aboriginum* with which *P. tehuantepecanus* is certainly most closely related. It appears that *P. tehuantepecanus* is a southern disjunct subspecies or race of widespread *P. pecten-aboriginum*.
- Pachycereus pringlei* (S. Wats.) Britt. & Rose. *Cereus pringlei* S. Wats., Proc. Amer. Acad. Arts 20: 368. 1885. Baja California and mainland Mexico from Sonora to Nayarit. Gibson 3197, 3241, 3311 (ARIZ).
- Pachycereus weberi* (Coult.) Backeb. *Cereus weberi* Coult., Contr. U.S. Natl. Herb. 3: 410. 1896. Syn. *Lemaireocereus weberi* (Coult.) Britt. & Rose, *Ritterocereus weberi* (Coult.) Backeb., and *Stenocereus weberi* (Coult.) Buxb. Puebla and Oaxaca, Mexico. Gibson 3235 (ARIZ).
- Polaskia chende** (Gossel.) Gibs. & Horak, comb. nov. *Cereus chende* Gossel., Bull. Mus. Hist. Nat. (Paris) 11: 506. 1905. Syn. *Heliabravoia chende* (Gossel.) Backeb. and *Lemaireocereus chende* (Gossel.) Britt. & Rose. Puebla and Oaxaca, Mexico. Gibson 3180 (ARIZ).
- Polaskia chichipe* (Gossel.) Backeb. *Cereus chichipe* Gossel., Bull. Mus. Hist. Nat. (Paris) 11: 507. 1905. Syn. *Lemaireocereus chichipe* (Gossel.) Britt. & Rose. Puebla and Oaxaca, Mexico. Gibson 3179 (ARIZ).
- Pterocereus gaumeri* (Britt. & Rose) MacDoug. & Miranda. *Pachycereus gaumeri* Britt. & Rose, Cactaceae 2: 71. 1920. Syn. *Anisocereus gaumeri* (Britt. & Rose) Backeb. Yucatán Peninsula and Chiapas, Mexico. Gibson 3213 (ARIZ). Here is included *Pterocereus foetidus* MacDoug. & Miranda, which does not appear to be distinct enough to be recognized as a species separate from *P. gaumeri*. This species is provisionally treated in this tribe.
- Stenocereus alamosensis** (Coult.) Gibs. & Horak, comb. nov. *Cereus alamosensis* Coult., Contr. U.S. Natl. Herb. 3: 406. 1896. Syn. *Rathbunia alamosensis* (Coult.) Britt. & Rose. Sonora to Colima, Mexico west of the Sierra Madre Occidental. Gibson 3182, 3194 (ARIZ); Horak 113.
- Stenocereus beneckeii* (Ehrenb.) Berg. & Buzb. *Cereus beneckeii* Ehrenb., Bot. Zeit. (Berlin) 2: 835. 1844. Syn. *Hertrichocereus beneckeii* (Ehrenb.) Backeb., *Lemaireocereus beneckeii* (Ehrenb.) Britt. & Rose, and *Piptanthocereus beneckeii* (Ehrenb.) Riccob. Guerrero and Puebla, Mexico. Gibson 3208, 3227 (ARIZ).
- Stenocereus chrysocarpus* Sánchez Mejorada,* Cact. Suc. Mex. 17: 95. 1972. Michoacán, Mexico.
- Stenocereus deficiens* (Otto & Dietr.) Buxb. *Cereus deficiens* Otto & Dietr., Allg. Gartenzeitung 6: 28. 1838. Syn. *Lemaireocereus deficiens* (Otto & Dietr.) Britt. & Rose and *Ritterocereus deficiens* (Otto & Dietr.) Backeb. Coastal Venezuela. Gibson 3226 (ARIZ).
- Stenocereus dumortieri* (Scheidweil.) Buxb. *Cereus dumortieri* Scheidweil., Hort. Belge 4:

220. 1837. Syn. *Isolatocereus dumortieri* (Scheidweil.) Backeb. and *Lemaireocereus dumortieri* (Scheidweil.) Britt. & Rose. San Luis Potosí to Oaxaca, Mexico. *Gibson* 3202, 3220 (ARIZ).
- Stenocereus eruca** (T. S. Brandeg.) Gibs. & Horak, comb. nov. *Cereus eruca* T. S. Brandeg., Proc. Calif. Acad. Sci. 2: 163. 1889. Syn. *Lemaireocereus eruca* (T. S. Brandeg.) Britt. & Rose and *Machaerocereus eruca* (T. S. Brandeg.) Britt. & Rose. West central Baja California, Mexico. *Gibson* s. n.
- Stenocereus fricii* Sánchez Mejorada,* Cact. Suc. Mex. 18: 89. 1973. Jalisco to Michoacán, Mexico.
- Stenocereus griseus* (Haw.) Buxb.* *Cereus griseus* Haw., Syn. Pl. Succ. 182. 1812. Syn. *Cereus eburneus* Salm-Dyck, *Lemaireocereus griseus* (Haw.) Britt. & Rose, and *Ritterocereus griseus* (Haw.) Backeb. Coastal Venezuela and adjacent islands, but also naturalized throughout Mexico.
- Stenocereus gummosus** (Engelm.) Gibs. & Horak, comb. nov. *Cereus gummosus* Engelm., Proc. Calif. Acad. Sci. 2: 163. 1889. Syn. *Lemaireocereus gummosus* (Engelm.) Britt. & Rose and *Machaerocereus gummosus* (Engelm.) Britt. & Rose. Baja California, islands of the Gulf of California, and one region in coastal Sonora, Mexico. *Gibson* 3196 (ARIZ), s. n. (2).
- Stenocereus hystrix* (Haw.) Buxb. *Cactus hystrix* Haw., Syn. Pl. Succ. 73. 1819. Syn. *Lemaireocereus hystrix* (Haw.) Britt. & Rose and *Ritterocereus hystrix* (Haw.) Backeb. Greater Antilles. *Heed* s. n.
- Stenocereus kerberi** (K. Schum.) Gibs. & Horak, comb. nov. *Cereus kerberi* K. Schum., Gesamtb. Kakt. 89. 1897. Syn. *Rathbunia kerberi* (K. Schum.) Britt. & Rose. Sinaloa to Michoacán, Mexico. *Gibson* 3189 (ARIZ).
- Stenocereus laevigatus* (Salm-Dyck) Buxb.* *Cereus laevigatus* Salm-Dyck, Cact. Hort. Dyck. 1849: 204. 1850. Syn. *Lemaireocereus laevigatus* (Salm-Dyck) Borg and *Ritterocereus laevigatus* (Salm-Dyck) Backeb. Southernmost Mexico and Guatemala, assuming that the poorly known *Lemaireocereus eichlamii* Britt. & Rose of Guatemala belongs to this species.
- Stenocereus longispinus* (Britt. & Rose) Buxb. *Lemaireocereus longispinus* Britt. & Rose, Cactaceae 2: 89. 1920. Guatemala. *Gibson* 3238 (ARIZ).
- Stenocereus martinezii* (G. Ort.) Buxb.* *Lemaireocereus martinezii* G. Ort., Apuntes para la Pl. Indig. de Sinaloa, Mazatlán. 1929. Sinaloa, Mexico.
- Stenocereus montanus* (Britt. & Rose) Buxb. *Lemaireocereus montanus* Britt. & Rose, Cactaceae 2: 97. 1920. Northwestern mainland Mexico. *Gibson* 3221 (ARIZ).
- Stenocereus pruinus* (Otto) Buxb. *Echinocactus pruinus* Otto in Pfeiff., Enum. Cact. 54. 1837. Syn. *Lemaireocereus pruinus* (Otto) Britt. & Rose. South central Mexico. *Gibson* 3204, 3219 (ARIZ); *McGill* s. n.
- Stenocereus queretaroensis* (Weber) Buxb. *Cereus queretaroensis* Weber in Mathss., Monatschr. Kakteenk. 1: 27. 1891. Syn. *Lemaireocereus queretaroensis* (Weber) Saff., *Pachycereus queretaroensis* (Weber) Britt. & Rose, and *Ritterocereus queretaroensis* (Weber) Backeb. Central Mexico. *Gibson* 3225 (ARIZ).
- Stenocereus quevedonis* (G. Ort.) Buxb.* *Lemaireocereus quevedonis* G. Ort., Mexico Forest. 6: 1. 1928. Sinaloa to Michoacán, Mexico.
- Stenocereus standleyi* (G. Ort.) Buxb. *Lemaireocereus standleyi* G. Ort., Revista Mex. Biol. 7: 121. 1927. Syn. *Ritterocereus standleyi* (G. Ort.) Backeb. Sinaloa, Mexico. *Gibson* 3217, 3331 (ARIZ).
- Stenocereus stellatus* (Pfeiff.) Riccob. *Cereus stellatus* Pfeiff., Allg. Gartenzeitung 4: 258. 1836. Syn. *Lemaireocereus stellatus* (Pfeiff.) Britt. & Rose. Puebla and Oaxaca, Mexico. *Gibson* 2754, 3126, 3205 (ARIZ).
- Stenocereus thurberi* (Engelm.) Buxb. *Cereus thurberi* Engelm., Amer. J. Sci. Arts, ser. 2, 17: 234. 1854. Syn. *Lemaireocereus thurberi* (Engelm.) Britt. & Rose and *Marshallocereus thurberi* (Engelm.) Backeb. Northwestern Mexico and adjacent Arizona. *Gibson* s. n. (2).
- Stenocereus treleasei* (Britt. & Rose) Backeb. *Lemaireocereus treleasei* Britt. & Rose, Contr. U.S. Natl. Herb. 12: 426. 1909. Puebla and Oaxaca, Mexico. *Gibson* 3191 (ARIZ).
- The following are taxa for which taxonomic decisions are not finalized:
- Anisocereus lepidanthus* (Eichl.) Backeb. *Cereus lepidanthus* Eichl., Monatschr. Kakteenk. 19: 177. 1909. Syn. *Escontria lepidanthus* (Eichl.) Buxb. and *Pachycereus lepidanthus* (Eichl.) Britt. & Rose. Guatemala. *Gibson* 3212 (ARIZ).
- Cephalocereus quadricentralis* Daws.,* Allan Hancock Found. Publ. Occas. Pap. 1: 14. 1948.

Syn. *Pilosocereus quadricentralis* (Daws.) Backeb. Oaxaca and Chiapas, Mexico. No description adequately compares this species to others in southern Mexico and Central America.

Cephalocereus tehuacanus (Weing.) Borg.* *Pilocereus tehuacanus* Weing., Z. Sukkulentenk. 3: 58. 1927. Syn. *Pilosocereus tehuacanus* (Weing.) Byles & Rowl. Puebla, Mexico. Same as for *C. quadricentralis*.

Lemaireocereus thurberi (Engelm.) Britt. & Rose var. *littoralis* (K. Brandeg.) G. Linds. *Cereus thurberi* var. *littoralis* K. Brandeg., Zoe 5: 191. 1904. Syn. *L. littoralis* H. E. Gates and *Marshallocereus thurberi* var. *littoralis* Backeb. Cape region, Baja California, Mexico. *Gibson 3000* (ARIZ). This plant closely resembles *Stenocereus thurberi* but is dwarfed in most features and has very gray stems. A relationship to *S. thurberi* is clearly observed, and it is likely that *littoralis* is an interspecific hybrid between *thurberi*, which served as the female, and *S. gummosus* or *Lophocereus schottii*.

Stenocereus chacalapensis (Bravo) Bravo.* *Ritterocereus chacalapensis* Bravo, Cact. Suc. Mex. 2: 50. 1957. Narrow endemic in Oaxaca, Mexico. This species superficially resembles several species of *Stenocereus* and to a certain extent *Pachycereus hollianus* and *Backebergia militaris*. Intensive study is needed to determine to which group *S. chacalapensis* belongs or if this narrow endemic arose as an intergeneric hybrid.

TRIBE CACTEAE

Ferocactus robustus (Link & Otto) Britt. & Rose. Puebla, Mexico. *Gibson 2546* (RSA).

TRIBE CEREEAE

Cereus aethiops Haw. Argentina. *Gibson 3061* (ARIZ).

Cereus dayamii Speg. Argentina. *Gibson 2746* (RSA).

Monvillea cavendishii (Monv.) Britt. & Rose. Southern Brazil to northern Argentina. *Gibson 2757* (RSA).

Stetsonia coryne (Salm-Dyck) Britt. & Rose. Argentina. *Gibson 3056* (ARIZ).

TRIBE ECHINOCEREEAE

Bergerocactus emoryi (Engelm.) Britt. & Rose. Coastal northern Baja California and offshore islands and adjacent California. *Gibson 1970* (RSA).

TRIBE HYLOCEREEAE

Acanthocereus horridus Britt. & Rose. Southern Mexico and Guatemala. *Gibson 3184* (ARIZ).

Acanthocereus pentagonus (L.) Britt. & Rose. Coastal North America around the Gulf of Mexico, sometimes inland. *Gibson 3223* (ARIZ); *Stern 3026* (MARY).

Acanthocereus subinermis Britt. & Rose. Oaxaca, Mexico. *Gibson 3209* (ARIZ).

Harrisia martinii (Labour.) Britt. & Rose. Argentina. *Gibson 2751* (RSA).

Harrisia pomanensis (Weber) Britt. & Rose. Argentina. *Gibson 3059* (ARIZ).

Nyctocereus chontalensis Alex. Oaxaca, Mexico. *Gibson 3216* (ARIZ).

Nyctocereus serpentinus (Lagasca & Rodrig.) Britt. & Rose. Southern Mexico. *Gibson s. n.*

TRIBE LEPTOCEREEAE

Armatocereus (*Lemaireocereus*) *humilis* (Britt. & Rose) Backeb. Colombia. *Gibson 3183* (ARIZ).

Armatocereus (*Lemaireocereus*) *laetus* (H. B. K.) Backeb. Peru. *Gibson 3229* (ARIZ).

Leptocereus quadricostatus (Bello) Britt. & Rose. Puerto Rico. *Heed s. n.*

Samaipaticereus corroanus Card. Bolivia. *Gibson 3210* (ARIZ).

TRIBE TRICHOCEREEAE

Trichocereus spachianus (Lem.) Riccob. Argentina. *Gibson 2755* (RSA).

Trichocereus thelegonus (Weber) Britt. & Rose. Argentina. *Gibson 2761* (RSA).

STEM CHEMISTRY

Table 1 is a summary from the literature of the species of Pachycereeae known to have abundant triterpenoid saponins (glycosides) in stem tissues. Listed

are all species of *Escontria*, *Myrtillocactus*, and *Polaskia* (incl. *Heliabravoia*) and most species of *Stenocereus* (incl. *Machaerocereus* and *Rathbunia*) recognized in this study except *S. deficiens* from South America, which is reported to have only traces of these compounds (Djerassi, 1957). *Stenocereus chacalapensis*, *S. chrysocarpus*, *S. fricii*, *S. laevigatus*, *S. martinezii*, and *S. standleyi* have never been examined for triterpenes, and triterpenes in the rathbunias have not been identified (Bird, 1974). *Cephalocereus senilis* and *Mitrocereus fulviceps* (*Pachycereus chrysomallus*) of Pachycereeae, *Armatocereus* (*Lemaireocereus*) *humilis* of Leptocereeae, and *Trichocereus peruvianus* Britt. & Rose of Trichocereeae also have traces of unidentified triterpenes, and *Armatocereus aragonii* (Weber) Backeb. possesses a mixture of amyrins, simple triterpenoid derivatives from squalene. *Lophocereus schottii*, which has abundant alkaloids and sterols, has a single triterpene, lupeol, but this compound is not present as a glycoside in stem tissues. Lupeol has very recently been isolated from *Stenocereus thurberi* (H. W. Kircher, pers. comm.). Other nonglycosidic triterpenes are calenduladiol, reported from *Stenocereus thurberi* (Bird, 1974), and betulin, found in *S. griseus*. Interestingly, betulin is the probable biochemical precursor of betulinic acid, which occurs in *S. hystrix*, the closest relative to *S. griseus*.

In Table 1 species are arranged so that taxa with similar sets of triterpenes are placed next to each other. Nearly all species have oleanolic acid, but in addition each group of species has one or several common triterpenes. For example, five of the first six species share chichipegenin; eight of the first ten share longispinogenin; three of the four species of *Myrtillocactus* have cochalic acid, longispinogenin, and myrtillogenic acid, the acid of the triol longispinogenin; and the Caribbean and Central American species of *Stenocereus* share erythrodiol. Queretaroic acid is apparently restricted to species of *Stenocereus*.

An analysis of the structures of cactus triterpenes shows that there are two biosynthetic groups (Table 1), those derived from β -amyrin, resulting in the oleanane series, and the lupane series. The least hydroxylated compounds of the oleanane series are erythrodiol, oleanolic aldehyde, oleanolic acid, and maniladiol, and it appears that oleanolic acid and erythrodiol have served as base triterpenes from which a diversity of compounds has arisen. For example, queretaroic, machaerinic, and cochalic acids are diols of oleanolic acid, and treleasegenic acid appears to be the triol of queretaroic acid. In the lupane series, betulinic acid is a monohydroxy acid whereas thurberogenin and stellatogenin are diol and triol lactones, respectively. Biochemists generally agree that compounds with greater numbers of hydroxyl and ester groups (lactones) are more elaborated molecules than those that lack them.

Alkaloids have been identified in relatively few Pachycereeae, in part perhaps because a number of the arborescent species likely to have these compounds have not been investigated. So far, pilocereine has been discovered in both species of *Lophocereus* (Djerassi et al., 1953; Djerassi et al., 1954; West et al., 1975) and in *Pachycereus marginatus* (Djerassi et al., 1954), and two related alkaloids, piloceredine and lophocerine, occur in *Lophocereus schottii* (Djerassi et al., 1958). Simple tyramine alkaloids occur in other species, including carnegine in *Carnegiea gigantea* and *Pachycereus pecten-aboriginum* (see Willaman

TABLE 1. Summary of triterpenes isolated from saponins (glycosides) from stems of Pachycereae. Unless indicated by a footnote, reports are cited in Djerassi (1957).

Taxon	Oleanane Series													Lupane Series					
	Oleanolic Acid	Oleanolic Aldehyde	Erythrodiol	Maniladiol	Chichiengenin	Longispinogenin	Myrtillogenic Acid	Cochalic Acid	Hystrix Lactone	Dumortierigenin	Queretaroic Acid	Treleasegenic Acid	Machaerinic Acid	Machaeric Acid	Gummosogenin	Betulinic Acid	Thurberogenin	Stellatogenin	
<i>Polaskia chende</i>	+ ^a	+ ^b	+ ^b		+ ^a														
<i>P. chichiipe</i>	+				+	+													
<i>Myrtillocactus schenckii</i>	+																	+	
<i>M. geometrizzans</i>					+	+	+	+											
<i>M. geometrizzans</i> f. <i>grandiareolatus</i>	+				+														
<i>M. eichlamii</i> Britt. & Rose	+			+	+	+	+	+											
<i>M. cochal</i>					+	+	+	+											
<i>Escontria chiotilla</i>				+		+													
<i>Stenocereus longispinus</i>	+		+			+													
<i>S. griseus</i>	+		+			+		+											
<i>S. hystrix</i>	+		+			+		+									+		
<i>S. pruinosus</i>	+																		
<i>S. dumortieri</i>										+									
<i>S. stellatus</i>	+																+	+	+
<i>S. treleasei</i>	+											+						+	+
<i>S. thurberi</i>	+											+					+		
<i>S. eruca</i>																	+		+
<i>S. gummosus</i>													+	+	+				
<i>S. queretaroensis</i>	+											+							
<i>S. beneckeii</i>	+											+							
<i>S. montanus</i>	+											+							
<i>S. quevedonis</i>	+					+											+		
<i>S. alamosensis</i>	Present ^d																		

^a In Bravo & Cox (1958).^b Shamma & Rosenstock (1959).^c H. W. Kircher (unpubl. data).^d Bird (1974).

& Schubert, 1961); gigantine (Hodgkins et al., 1967; Agurell, 1969), an isomer of pelletine (Brown et al., 1968), and salsolidine (Bruhn et al., 1970) in *C. gigantea*; anhalonidine in *Pachycereus weberi* (Djerassi et al., 1954); and 3-hydroxy-4-methoxyphenethylamine in *P. pecten-aboriginum* (Agurell et al., 1971). Dopa-

mine, the precursor of these alkaloids, occurs at high concentrations in *C. gigantea* (Steelink et al., 1967) and *Pachycereus hollianus* (Sánchez Mejorada, pers. comm.). An assortment of other alkaloids is known from other columnar cacti (Willaman & Schubert, 1961), but none occurs in species with abundant triterpenes.

Steelink et al. (1967) have determined that the blackening of wounded tissues in *Carnegiea gigantea* results from the successive conversion of dopamine, the most abundant nitrogenous compound, to oxidized quinone, to dopaminochrome, and, finally, to melanin. It is interesting to observe that all six recognized species of *Pachycereus* show reddening and then blackening of wounded tissues, and three of these species have been shown to possess abundant dopaminelike alkaloids. In species with abundant triterpenes, blackening does not occur; instead, in most species with triterpenes the green ground tissues become bright red orange during drying, but the color fades when completely dry. Whether this color reaction is similar to that observed in *C. gigantea* has not been determined. At least in *Stenocereus dumortieri*, *S. pruinosus*, and *S. thurberi* the cortex is yellow when fresh, and *S. thurberi* has bright yellow inner bark. The chemical responsible for this coloration in *Stenocereus* has not been identified but may be a carotenoid because the pigment is extractable with chloroform, not with aqueous solutions (H. W. Kircher, pers. comm.).

EXTERNAL SHOOT MORPHOLOGY

Growth form and habit are particularly difficult to summarize for columnar cacti because even within a single tribe one often finds a nearly continuous series of designs from tall arborescent to procumbent species. The following is a useful but somewhat artificial classification design of Mexican Pachycereeae:⁴

- I. Tall arborescent (> 7 m).
 - A. Solitary (unbranched) columnar; stems very thick with extremely wide pith—*Cephalocereus hoppenstedtii* (25), *C. senilis* (25), *C. totolapensis* (28), *Neobuxbaumia mezcalaensis* (15), and *N. polylopha* (29).
 - B. Excurrent columnar with relatively few ascending or spreading stems; stems very thick with extremely wide pith—*Carnegiea gigantea* (18; also IA), *Neobuxbaumia macrocephala* (24), and *N. tetetzo* (15).
 - C. Columnar with well-developed trunk and numerous straight, very long, ascending stems; stems thick to very thick with wide to extremely wide pith, respectively—*Backebergia militaris* (8), *Mitrocereus fulviceps* (14), *Pachycereus grandis* (10), *P. pectenaboriginum* (11), *Stenocereus chacalapensis* (7), *S. chrysocarpus* (7), and *S. dumortieri* (6).
 - D. Large candelabra with a massive trunk and numerous very long, ascending stems arising from several main, massive branches; stems thick with wide pith—*Pachycereus weberi* (10).
 - E. Decurrent with a large trunk, having erect or spreading stems that are often branched (similar to IB and IC); stems thick with very wide pith—*Neobuxbaumia scoparia* (19) and *Pachycereus pringlei* (13).
 - F. Decurrent with prominent trunk, having erect or spreading stems that are often branched; stems moderate in thickness with moderate pith 2–4 cm diam.—*Cephalocereus leucocephalus* (12) and *Stenocereus griseus* (10).

⁴ Approximations of each growth habit are based on the largest and most typical design of a species, not on atypical varieties and forms. Mode rib number for each species is indicated in parentheses.

- II. Small arborescent and large fruticose (4–7 m).
- A. Solitary columnar or with few ascending branches; stems moderate in thickness with narrow pith—*Neobuxbaumia euphorbioides* (9) and *Pachycereus hollianus* (11).
 - B. Decurrent and divaricate with short trunk, forming a nearly flat-topped crown; stem moderate in thickness with pith narrow to 3 cm diam.—*Escontria chiotilla* (7), *Myrtillocactus cochal* (7), *M. geometrizzans* (6), *M. schenckii* (8), *Polaskia chende* (7), and *P. chichipe* (9).
 - C. Decurrent with short trunk and numerous erect or spreading stems that are long and sometimes branched (similar to IF); stems mostly moderate in thickness with varying amounts of pith development—*Cephalocereus* spp. (7–9), *Pterocereus gaumeri* (3), *Stenocereus fricii* (5), *S. laevigatus* (6), *S. pruinatus* (5), *S. queretaroensis* (7), and *S. standleyi* (4).
 - D. Large fruticose with very short trunk and numerous, mostly unbranched, ascending stems (similar to IF and IIC); stems moderate to relatively thick with well-developed pith except in *S. stellatus*—*Cephalocereus* spp. (7–12), *Lophocereus schottii* (7, but very variable; see Felger & Lowe, 1967), *Stenocereus martinezii* (9), *S. montanus* (8), *S. quevedonis* (8), *S. stellatus* (10), *S. thurberi* (15), and *S. treleasei* (20).
 - E. Small candelabra (as in ID); stems relatively thick with relatively wide pith—*Pachycereus marginatus* (5). Wherever cultivated, this species assumes a growth habit similar to IIA.
- III. Miniature arborescent and fruticose (< 4 m).
- A. Excurrent with a few spreading stems; stems thick with wide pith—*Cephalocereus nizandensis* (25), *C. purpusii* (12).
 - B. Ascending stems from a short base (similar to IID); stems moderate to somewhat slender with relatively narrow to moderate pith—*Cephalocereus apicicephalum* (23), *Lophocereus gatesii* (13).
 - C. Spreading or arching stems from a common base; stems moderate to relatively slender with narrow pith—*Stenocereus alamosensis* (7), *S. beneckeii* (7), *S. gummosus* (8), and *S. kerberi* (4).
- IV. Procumbent—*Stenocereus eruca* (11).

Detailed descriptions and illustrations of the growth habits classified above as well as those of other species in the study are not presented here because many readily available accounts include these data (Backeberg, 1959, 1960; Bravo, 1937; Britton & Rose, 1920; Marshall & Bock, 1941). There too the reader may find in-depth information on the features of stem areoles. One characteristic that needs to be emphasized is the presence of red-colored glandular trichomes in young areoles of *Stenocereus beneckeii*, *S. chrysocarpus* (Sánchez Mejorada, 1972), *S. martinezii*, *S. montanus*, *S. queretaroensis*, *S. quevedonis*, and *S. thurberi*. Shreve & Wiggins (1964) have observed in *S. thurberi* that minute viscid droplets are exuded from these hairs that coalesce to form a waxy mass.

ANATOMY OF THE SHOOT

ORIGIN OF GROUND TISSUES

Ontogeny of succulence in columnar cactus stems below the shoot tip has never been described. Enlargement of the pith results from divisions in various planes of cells produced from the rib meristem, and at maturity the vacuolate, isodiametric cells are loosely packed, showing no radial or longitudinal lineages of cells. The inner cortex is formed in the same manner at the pith but from derivatives of the flanking (generative) meristematic zone (after Boke, 1941); however, the much-enlarged outer cortex, including succulence in the ribs, is produced principally by a subprotodermal meristem, the initials of which divide periclinally to produce cells in radial files. Derivatives of this meristem greatly

enlarge radially but often remain in files for several to many years. These cells sometimes divide again, mostly periclinally; but eventually cells round up with increased vacuolation, and large intercellular spaces are created. Cell divisions of cortical ground tissue then cease. If present, mucilage cells differentiate as idioblasts where divisions of pith or cortical cells are no longer observed.

SKIN

The "skin" by our definition is the tough, xeromorphic, but also flexible, covering on a cactus stem consisting of the epidermis, covered by a cuticle, and, in most Cactaceae, a collenchymatous hypodermis. In columnar cacti the epidermis and hypodermis are fully formed several millimeters from the shoot apex within the apical depression. Thereafter, major qualitative changes are usually not observed in the numerous cell layers in the skin until the first phellogen is initiated, commonly from epidermis. This regular pattern helps to standardize sampling methods.

Most cacti have a single-layered epidermis derived from a uniseriate protoderm, but many Pachycereeae have a multiple epidermis (Table 2). In one form of multiple epidermis, each epidermal cell, functioning as a mother cell, undergoes periclinal, anticlinal, and oblique divisions to produce a cluster of cells of various sizes (Fig. 1). In *Lophocereus schottii*, *Neobuxbaumia tetetzo*, *Polaskia chende*, *P. chichipe*, *Stenocereus stellatus*, and *S. treleasei*, each cluster, containing up to ten cells, is distinct and raised, forming a minutely bullate surface. Thicker deposits of cuticle clearly separate adjacent clusters (Fig. 2). *Armatocereus humilis* (Leptocereeae), *Cephalocereus russelianus*, and *Lophocereus gatesii* (Fig. 3) have similar but fewer-celled clusters; and in the latter, cells are often curiously nipped. In *Escontria*, *Myrtillocactus*, nearly half the species of *Stenocereus*, *Samaipaticereus corroanus*, and *Trichocereus thelegonus*, large epidermal cells commonly proliferate by periclinal (Fig. 4), anticlinal, and oblique divisions, forming two to several smaller daughter cells. Late-formed walls are generally thinner than original walls. Because such divisions occur after the cuticle has been deposited, the epidermal surface cannot expand and remains flat. In *Carnegiea gigantea* (Fig. 5), *Myrtillocactus cochal*, *M. geometrizzans*, *Pachycereus pecten-aboriginum*, and *Stenocereus thurberi*, four species with thick skins, the epidermis is distinctly biseriate; and *Pachycereus pringlei* often has a triseriate epidermis. All the walls of these multiple epidermises have the same relative thickness, and the layers appear to be derived from separate cell layers. Developmental data are needed to determine whether multiple layers arise from original tunica layers or from layers produced by the subprotodermal meristem.

Outer periclinal epidermal walls are typically flat to slightly convex and smooth, but in some species walls are strongly convex or papillate, e.g., in *Nyctocereus chontalensis*. The two species of *Cereus* examined have irregular outer walls. In *Escontria chiotilla*, *Mitrocereus fulviceps*, *Myrtillocactus schenckii*, and *Pachycereus marginatus* (Fig. 6), the outer periclinal walls have conspicuous hornlike projections; and in *Myrtillocactus cochal*, *M. geometrizzans*, and *Pachycereus hollianus*, projections are present but less prominent.

TABLE 2. Anatomical features of the skin. Species of Pachycereaceae are arranged within each group so that plants with closely similar skin anatomy are placed together.

Taxon	Maximum Cuticular Thickness (μm)	Cuticular Features (see text)	Type of Multiple Epidermis (see text)	Epidermal		Epidermis		Hypodermal Thickness, Range of Diameters (μm)	Hypodermal Silica Bodies, Range of Diameters (μm)	Hypodermal Solitary Prismatics, Maximum Length (μm)
				Silica Bodies, Range of Diameters (μm)	No./Cell, Maximum Length (μm)					
Pachycereaceae with abundant triterpenes										
<i>Escontria chiotilla</i>	30	horns; rough	internal divisions					395-570		
<i>Myrtillocactus schenckii</i>	23	horns; rough	internal divisions					680-790		
<i>M. goemetrizans</i>	15	horns; rough	internal divisions					395-510		
<i>M. cochal</i>	15	horns; rough	internal divisions					695-790		
<i>Polaskia chichipe</i>	1.3	smooth	bullate clusters					<50		
<i>P. chende</i>	2.2	smooth	bullate clusters					<30		
<i>Stenocereus stellatus</i>	1.1	smooth	bullate clusters					170-370	12-21	
<i>S. treleasei</i>	1.1	smooth	bullate clusters					130-180	9-18	
<i>S. thurberi</i>	2.9	smooth	multiple layers			3-12		180-395	9-24	
<i>Lemaireocereus thurberi</i>										
var. <i>littoralis</i>	3.5	smooth				3-9		70-125	6-12	
<i>Stenocereus gummosus</i>	2.6	smooth				9-18		190-285	12-35	
<i>S. eruca</i>	3.5	smooth						90-170	12-21	
<i>S. hystrix</i>	3.2	smooth	internal divisions			3-6		180-270		
<i>S. longispinus</i>	3.5	smooth	internal divisions			3-6		340-380	6-12	
<i>S. deficiens</i>	2.9	smooth	internal divisions			6-12		180-215		
<i>S. pruinosus</i>	2.9	smooth				6-15		285-340	6-12	
<i>S. dumortieri</i>	2.9	smooth				6-9		240-370	12-18	
<i>S. quereтарыensis</i>	1.1	smooth	internal divisions			3-6		230-285	6-9	
<i>S. montanus</i>	2.1	smooth	internal divisions			6-9		190-230	3-6	
<i>S. beneckeii</i>	2.4	smooth; epicutular wax				3-9		170-230		
<i>S. standleyi</i>	2.9	smooth	internal divisions			6-12		170-210	6-12	
<i>S. kerberi</i>	1.1	smooth				3-9		160-210	6-12	
<i>S. alamosensis</i>	1.5	smooth				3-9		100-170		

TABLE 2. Continued

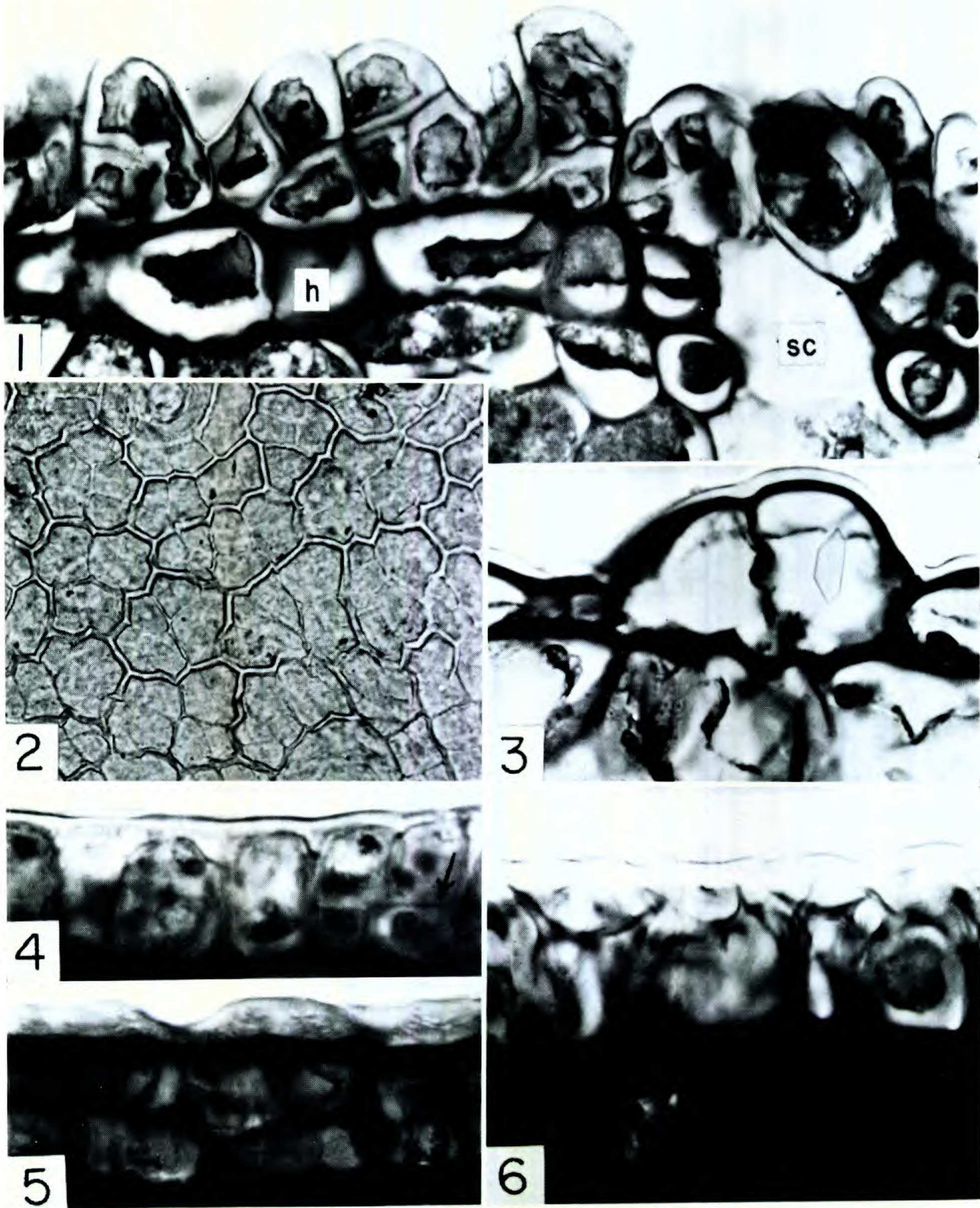
Taxon	Maximum Cuticular Thickness (μm)	Cuticular Features (see text)	Type of Multiple Epidermis (see text)	Epidermal Silica Bodies, Range of Diameters (μm)	Epidermis Prismatics: No./Cell, Maximum Length (μm)	Hypodermal Thickness, Range of Diameters (μm)	Hypodermal Silica Bodies, Range of Diameters (μm)	Hypodermal Solitary Prismatics, Maximum Length (μm)
Pachycereae lacking abundant triterpenes or not analyzed chemically								
<i>Pachycereus pringlei</i>	43	wavelike ridges	multiple layers			530-860		
<i>P. pecten-aboriginum</i>	18	rough	multiple layers			210-250		
<i>P. weberi</i>	9.0	1 ridge/cell				625-730		
<i>P. marginatus</i>	15	horns; rough				280-340		
<i>P. hollianus</i>	5.8	small horns; rough				<50		
<i>Lophocereus schottii</i>	12	smooth;	bullate clusters			90-145		
		epicuticular wax						
<i>L. gatesii</i> ^a	2.6	smooth with nipples	small bullate clusters		few, 12	50-60		
<i>Mitrocereus fulviceps</i>	12	reticulate			few, 24	600-675		125
<i>Carnegiea gigantea</i>	15	ridges; horns radiating striations	multiple layers			510-680		
<i>Neobuxbaumia tetetzo</i>	7.5	smooth;	bullate clusters		many, 15	150-180		
		epicuticular wax						
<i>N. polylopha</i> ^a	2.6	smooth			many, 18	120-180		
<i>Pterocereus gaumeri</i>	3.9	smooth				90-200		
<i>Cephalocereus russeletianus</i>	5.8	smooth	small bullate clusters		many, 12	55-80		
<i>C. totalapensis</i>	1.3	smooth	small bullate clusters		many, 12	110-135		
<i>C. hoppenstedtii</i> ^b	n.a.	n.a.	n.a.		many, 30	n.a.		
<i>C. senilis</i> ^a	0.9	smooth			few, 12	40-55		38
<i>C. chrysacanthus</i>	20	rough			many, 12	110-185		33
<i>C. leucocephalus</i>	4.2	smooth			many, 15	220-275		29
<i>C. alensis</i>	7.0	nearly smooth				90-125		44
<i>C. royenii</i>	8.5	nearly smooth			many, 15	90-140		24
<i>C. nobilis</i>	2.2	smooth			many, 6	75-90		
<i>Anisocereus lepidanthus</i>	0.9	smooth			many, 6	<50		

TABLE 2. Continued

Taxon	Maximum Cuticular Thickness (μm)	Cuticular Features (see text)	Type of Multiple Epidermis (see text)	Epidermal Silica Bodies, Range of Diameters (μm)	Epidermis Prismatics: No./Cell, Maximum Length (μm)	Hypodermal Thickness, Range of Diameters (μm)	Hypodermal Silica Bodies, Range of Diameters (μm)	Hypodermal Solitary Prismatics, Maximum Length (μm)
Columnnar and other cacti assigned by Buxbaum to tribes other than Pachycereeae								
<i>Acanthocereus horridus</i>	2.9	smooth			one, 15	65-90		
<i>A. pentagonus</i>	3.5	smooth			one, 30	100-125		
<i>A. subinermis</i>	2.6	smooth			one, 18	130-155		
<i>Armatocereus humilis</i>	9.0	smooth	bullate clusters		one, 24	135-190		
<i>A. laetus</i>	12	rough;				340-450		
		epicuticular wax						
<i>Bergerocactus emoryi</i>	3.9	slightly rough			many, small	65-80		
<i>Cereus aethiops</i>	3.9	rough				120-175		
<i>C. dayamii</i>	4.8	rough				250-340		
<i>Ferocactus robustus</i>	3.4	smooth				65-90		
<i>Harrisia martinii</i>	5.8	slightly rough				35-55		
<i>H. pomanensis</i>	3.5	nearly smooth				110-130		
<i>Leptocereus quadricostatus</i>	3.5	smooth			one, 24	130-155		
<i>Monvillea cavendishii</i>	1.1	smooth				55-70		
<i>Nyctocereus chontalensis</i>	2.9	smooth;				35-55		
		epicuticular wax						
<i>N. serpentinus</i>	2.9	smooth				55-70		
<i>Samaipaticereus corroanus</i>	3.9	smooth	internal divisions			110-155		
<i>Stetsonia coryne</i>	6.3	slightly rough				110-135		
<i>Trichocereus spachianus</i>	5.6	smooth	internal divisions			100-125		
<i>T. thelegonus</i>	2.6	smooth	internal divisions			110-125		

^a Quantitative measurements were taken from seedlings or very young plants, which do not have fully developed skin features.

^b This species is represented only by a skin clearing from a dead specimen.



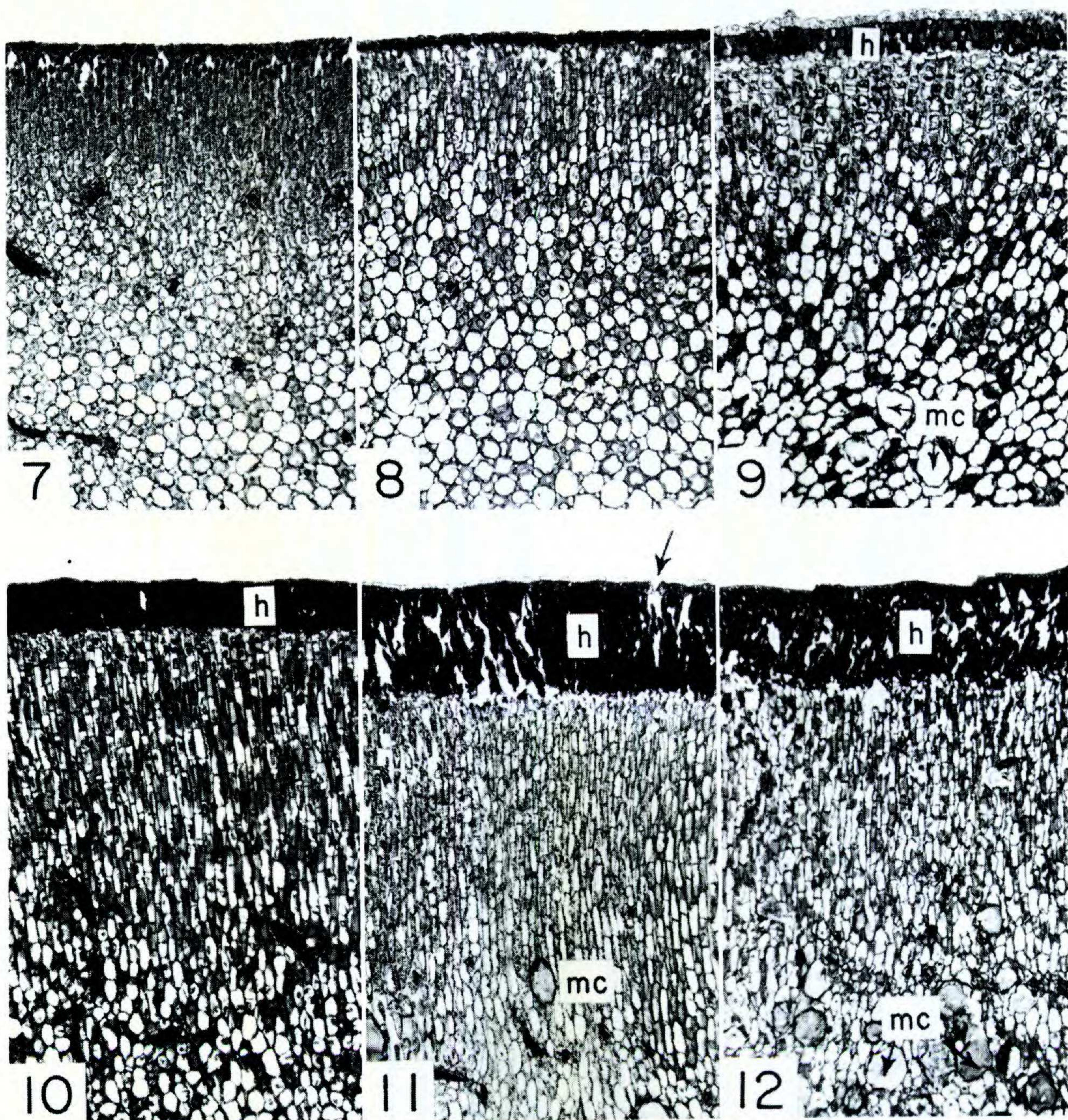
FIGURES 1-6. Skin features of Pachycereeae.—1-2. *Polaskia chende*.—1. Transection of stem surface, showing minutely bullate epidermal cells covered by thin cuticle and with very thin hypodermis (h). Note around substomatal chamber (sc) hypodermis is bilayered. $\times 560$.—2. Surface view of cleared skin, showing groups of proliferated epidermal cells separated by thicker deposits of cuticle. $\times 170$.—3. *Lophocereus schottii*; transection of skin, which has small bullate clusters, prominent cuticle, and occasional, strongly flattened calcium oxalate crystals that have hexagonal faces. $\times 560$.—4. *Stenocereus hystrix*; transection of epidermis with internal periclinal divisions of the original single layer (arrow). Small silica bodies are barely visible in these cells. $\times 560$.—5. *Carnegiea gigantea*; transection of epidermis showing multiple layers of cells covered by a very thick cuticle. $\times 560$.—6. *Pachycereus marginatus*; transection of outer skin in which the outer epidermal walls are hornlike, extending into the thick cuticle. $\times 560$.

Mature epidermal cells are commonly squarish to slightly tabular in transection, but in *Ferocactus robustus* cells are large and palisadelike. In surface view, the ground mass epidermal cells may have straight to wavy anticlinal walls, depending on the species, but cells are never markedly elongate.

Stomatal apparatuses superficially appear paracytic, similar to those of *Pereskia* (Bailey, 1964); however, meristemoid development needs to be described for columnar cacti. Guard cells are most commonly transverse to the long axis of the shoot (Metcalf & Chalk, 1960). In columnar cacti, stomata are not deeply sunken except in *Escontria chiotilla*, *Pachycereus pecten-aboriginum*, and *P. pringlei*; in fact, guard cells often appear above the level of the ground mass cells in many species.

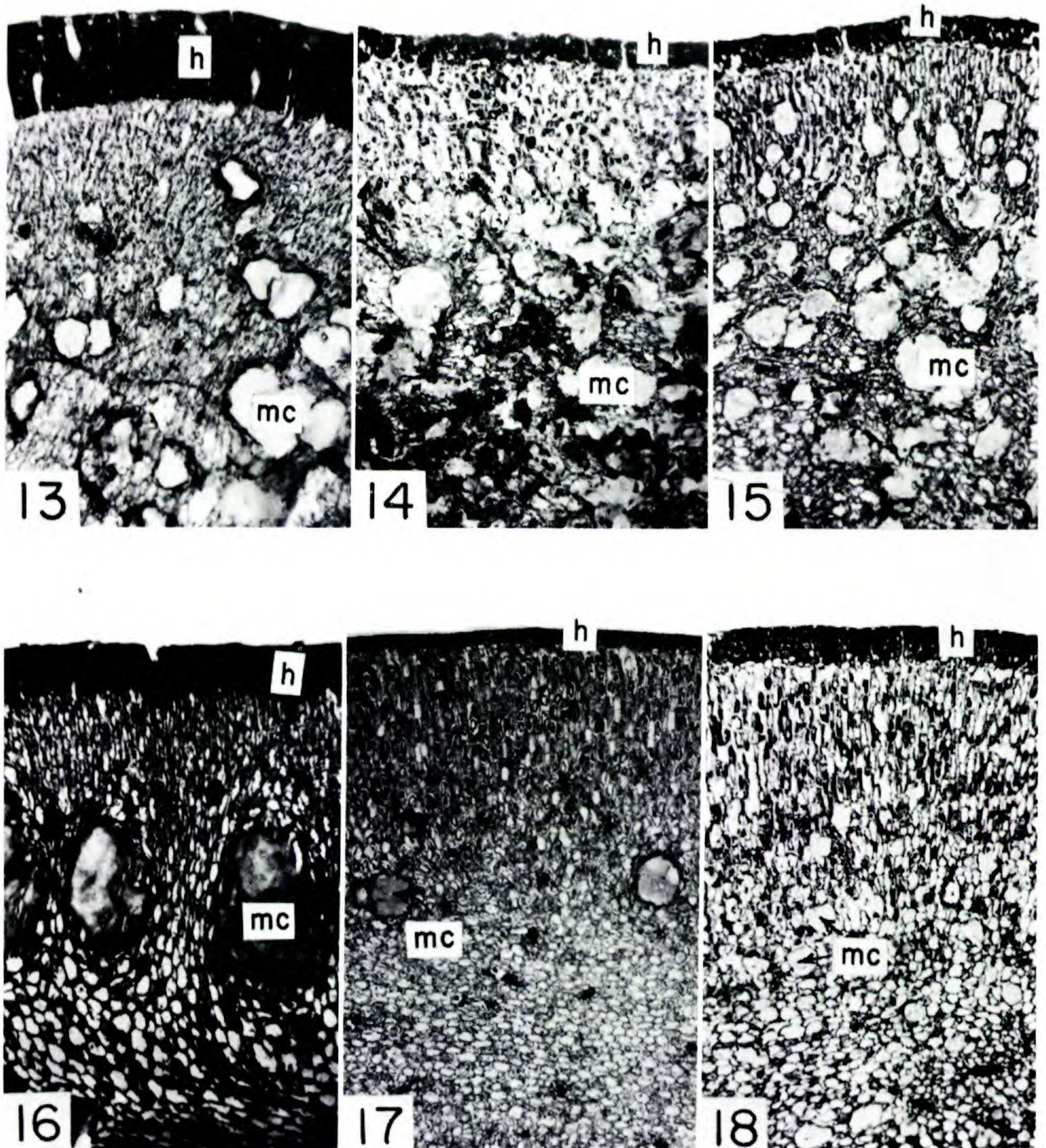
In transection, the cuticle proper (sensu Esau, 1965) in the majority of species is relatively thin and smooth and follows cell contours (Table 2); and within each genus closely related species have a cuticle of very similar thickness and characteristics. Species with hornlike projections from the outer periclinal walls have a thick, rough cuticle that completely covers the projections (Fig. 6), the taller the horns the thicker the cuticle. A thick to very thick, often rough cuticle is characteristic of numerous Pachycereeae that lack triterpenes. The most interesting cuticles are those with regular surface reliefs such in *Pachycereus weberi*, which has one central cuticular ridge above each cell; *P. pringlei* has a series of wavelike ridges opposite vertical anticlinal walls; *Carnegiea gigantea* has a series of parallel striations or ridges radiating from each stomatal apparatus, much as found in *Pereskia* (Bailey, 1964); and *Mitrocereus fulviceps* has a highly reticulate ridge system opposite anticlinal epidermal walls. Epi-cuticular wax is generally not observable with light microscopy in liquid-preserved materials of these species but is definitely present in *Armatocereus laetus*, *Cephalocereus chrysacanthus*, *Lophocereus schottii*, *Neobuxbaumia tetetzo*, *Nyctocereus chontalensis*, and *Stenocereus beneckeii*. Preliminary observations indicate that these crystalline surface structures are relatively diverse in form and distribution and may be useful for systematic purposes when studied intensively with scanning electron microscopy.

Beneath the epidermis lies a collenchymatous hypodermis (Figs. 1, 7–18), the so-called pseudohypodermis of Metcalf & Chalk (1950), which ranges in thickness from one cell in *Anisocereus lepidanthus*, *Pachycereus hollianus*, young specimens of *Lophocereus gatesii* and *Pachycereus pecten-aboriginum*, *Polaskia chende* (Figs. 1, 8), and *P. chichipe* (Fig. 7) of Pachycereeae and *Harrisia martinii* of Hylocereeae to 12 or more cells in *Carnegiea gigantea* (Fig. 11), *Myrtillocactus cochal* (Fig. 13), *M. schenckii*, *Pachycereus pringlei*, and *P. weberi* (Fig. 12) of Pachycereeae and *Armatocereus laetus* of Leptocereeae. Hypodermal thickness in Table 2 is in micra, a rough indicator of the number of cell layers. Species with the thinnest hypodermises generally also have the thinnest hypodermal walls, e.g., in *Lophocereus gatesii* (Fig. 3) and *Polaskia* (Fig. 1); single-layered hypodermis is often composed of tangentially flattened cells with lamellar primary thickenings. In species with more than one collenchymatous layer, cells are mostly isodiametric and lack intercellular spaces. The hypodermis of *Pachycereus weberi* (Fig. 12) is unusual in that



FIGURES 7-12. Transections of stems of Pachycereeae, showing thickness of hypodermis (h) and distribution of mucilage cells (mc) in the outer rib. $\times 12$.—7. *Polaskia chichipe* with thin hypodermis and no mucilage cells.—8. *Polaskia chende* with thin hypodermis and no mucilage cells.—9. *Lophocereus schottii* with relatively thin hypodermis and a few scattered mucilage cells.—10. *Pachycereus marginatus* with medium hypodermis and no mucilage cells. Note the elongate chlorenchymatous cells of the outer rib.—11. *Pachycereus pringlei* with very thick hypodermis, sunken stomates (arrow), and few, scattered mucilage cells far from the hypodermis. Note elongate chlorenchyma cells.—12. *Pachycereus weberi* with very thick hypodermis and scattered mucilage cells far from the hypodermis.

cells are markedly elongate in the radial plane and are retained in their original radial files. Hypodermal cells have prominent primary pit-fields, the so-called conspicuous intercellular pitting of Conde (1975). In species with very thick skins, hypodermis may be twice as thick in the valleys as on the flat surfaces of the ribs and thinnest in the vicinity of each areole. Collenchyma in columnar cacti is capable of undergoing decrease in wall thickness and dedifferentiation



FIGURES 13-18. Transsections of stems of columnar cacti, showing relative thickness of hypodermis (h) and distribution of mucilage cells (mc) in the outer rib. $\times 12$.—13. *Myrtillocactus cochal* with thick hypodermis and scattered large mucilage cells throughout the rib.—14. *Stenocereus standleyi* with relatively thin hypodermis and abundant, closely packed mucilage cells throughout the rib.—15. *Stenocereus beneckeii* with relatively thin hypodermis and numerous, closely spaced mucilage cells.—16. *Stenocereus thurberi* with medium hypodermis and very large mucilage cavities located around the outer rib cortex.—17. *Acanthocereus horridus* with relatively thin hypodermis and a few, widely spaced mucilage cells far from the hypodermis.—18. *Cereus dayamii* with a relatively thin hypodermis and relatively small, well-spaced mucilage cells throughout the rib.

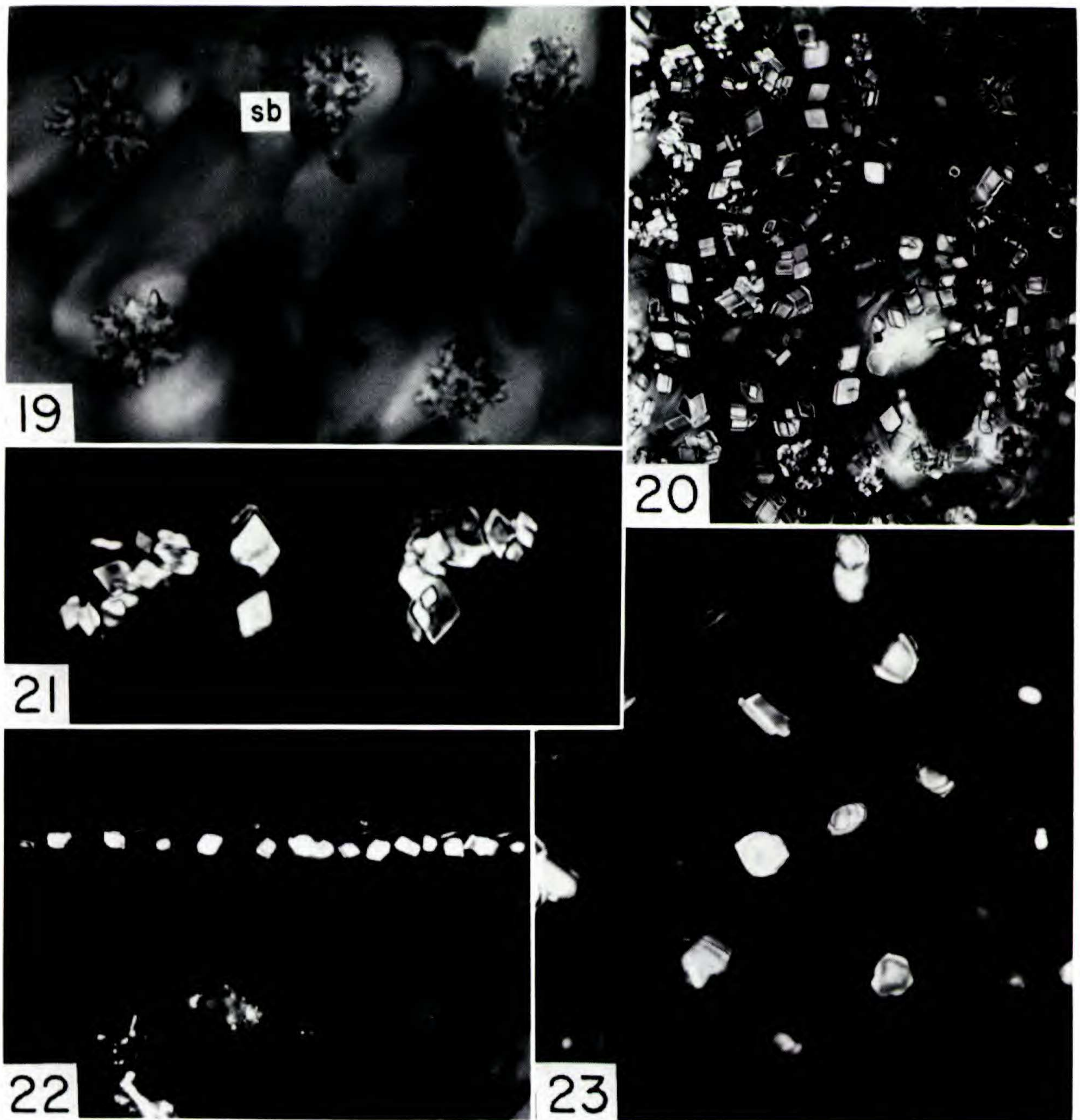
into parenchyma for initiation of phellogen. No cactus hypodermis has ever been found with lignified walls at maturity (Conde, 1975; Gibson, unpubl. data).

Collenchyma is interrupted at regular intervals by substomatal canals that

extend from the guard cells to the chlorenchyma. In species with a single-layered hypodermis, two collenchymatous cells are generally found beneath the guard cells (Fig. 1).

Among the species examined from North and South America, 17 species (Table 2), namely, all species of *Stenocereus* included in this study and "*Lemaireocereus thurberi* var. *littoralis*," have silica bodies in the skin (Fig. 19). They are found in both the epidermis and hypodermis of 13 species, only in the hypodermis of two species, and only in the epidermis of three species. In stained microslides of *Stenocereus alamosensis*, *S. beneckeii*, and *S. kerberi*, hypodermal silica bodies are small and infrequent and can easily be overlooked; therefore, absence of these structures in hypodermis of several other species of *Stenocereus* is not certain. Only one silica body is present per cell, and they are absent in the stomatal guard cells. In species of *Stenocereus* with more than one epidermal layer, every epidermal cell contains a silica body. Size and morphology of silica bodies vary between species (Table 2), between specimens, and even from outer to inner portions of the skin of the same rib. In our materials, *S. gummosus* has the largest silica bodies, which have very prominent branched projections (Fig. 19). Large spheroidal hypodermal silica bodies with short but prominent arms are found in *S. stellatus*, *S. thurberi*, and *S. treleasei*, but of these species only *S. thurberi* has epidermal silica bodies. These inclusions in other species of *Stenocereus* are often irregular in shape and have shorter, narrower, and more numerous projections. Size of hypodermal silica bodies generally decreases from the outside to the inside of the skin, and in some species the innermost hypodermis possesses few, if any, silica bodies.

One-third of the species investigated have prismatic calcium oxalate crystals in the skin (Table 2), and the occurrence of silica bodies and calcium oxalate crystals in the skin is mutually exclusive. Half the species of Mexican Pachycereeae that lack triterpenes have many small rhomboidal crystals in each ground-mass epidermal cell (Figs. 20–21). These crystals are extremely similar in size and shape in seven species of *Cephalocereus* (including the type, *C. senilis*), in *Mitrocereus*, and in *Neobuxbaumia*. *Mitrocereus fulviceps* is unusual in that these crystals are found in many, but not all, epidermal cells. *Carnegiea* has numerous small birefringent bodies in each epidermal cell that are probably prismatic crystals. *Anisocereus lepidanthus* has crystals that tend to be squarish or rectangular in outline and are smaller than those in *Cephalocereus*; and *Lophocereus gatesii* has few, extremely flat crystals that are hexagonal on the largest facets (Fig. 3). In contrast, crystals in the epidermis of *Acanthocereus* (Fig. 22), *Armatocereus*, and *Leptocereus* are generally large, rhomboidal, and solitary. Large prismatic calcium oxalate crystals, usually one per cell, are found in the hypodermis of four species of *Cephalocereus* (Fig. 23), including one of the two species that lacks epidermal crystals, and *Mitrocereus fulviceps*. Stellate druses occur in every cell of the outermost hypodermal layer in *Monvillea cavendishii* of Cereeae. *Stetsonia coryne* is the only species other than Pachycereeae that has hypodermal crystals, and these are extremely large and do not closely resemble those of Pachycereeae in shape.



FIGURES 19-23. Ergastic inclusions in skin of columnar cacti.—19. *Stenocereus gummosus*; transection of hypodermis in which large silica bodies (sb) with prominent arms are found, 1 per cell. $\times 450$.—20. *Cephalocereus hoppenstedtii*; surface view of cleared skin of a dead specimen in polarized light, showing few to many prismatic calcium oxalate crystals in each ground-mass epidermal cell. $\times 140$.—21. *Cephalocereus totolapensis*; transections of epidermis in polarized light, showing numerous prismatic, calcium oxalate crystals in each ground-mass epidermal cell. $\times 500$.—22. *Acanthocereus pentagonus*; transection in which a large prismatic, calcium oxalate crystal occurs in each ground-mass epidermal cell. $\times 140$.—23. *Mitrocereus fulviceps*; transection of valley of stem in which one calcium oxalate crystal occurs in each hypodermal cell. Numerous prismatic crystals are found occasionally in epidermal cells of this species on the ribs. $\times 350$.

Wild-collected plants differ from cultivated plants of the same species in having thicker cuticle, hypodermis, and hypodermal walls; more numerous epidermal proliferations; and slightly larger or more numerous ergastic inclusions. Therefore, anatomical differences between species of the same genus may not be as clear as indicated in Table 2; nevertheless, data in the table can be used to identify sterile materials correctly to genus and often to species. Broad sampling

of natural populations will be needed to obtain maximum and minimum values for skin features.

CORTICAL GROUND TISSUE

A variety of textures of cortical (including rib) ground tissue may be observed when fresh stems of cacti are cut. In columnar cacti cortical textures range from firm or even hard and nonmucilaginous to firm, very spongy, or soft but highly mucilaginous. Some species are so mucilaginous that specimens with the skin removed slip easily from the hands. This range of textures, which includes all degrees of mucilage accumulation, corresponds at the anatomical level to differences between species in number, size, and distribution of idioblastic mucilage cells and crystal-bearing cells. In Pachycereeae the simplest condition, where neither mucilage nor crystalliferous cells are present in the cortex, is found in *Pachycereus hollianus*, *P. marginatus* (Fig. 10), *Polaskia chende* (Fig. 8), *P. chichipe* (Fig. 7), and *Pterocereus gaumeri*; *Anisocereus lepidanthus* is nonmucilaginous but has large solitary prismatics scattered throughout the cortex. As discussed in the previous section, all of these species except *P. marginatus* have a one-layered or thin hypodermis, and all but *A. lepidanthus* lack crystals in the skin. Other species of *Pachycereus* and *Mitrocereus fulviceps* have moderately sized and widely spaced mucilage cells in the ribs, generally 1 mm or more from the hypodermis (Figs. 11–12), and of these species only *P. weberi* has a significant number of scattered mucilage cells in the cortex. Cells bearing large to very large aggregates of cuboidal or rhomboidal crystals occur in the cortex of these arborescent Pachycereeae but are unusually abundant in the cortex of *M. fulviceps*, giving this ground tissue a granular texture. Large nests of crystal aggregates are also present in *Neobuxbaumia* and *Cephalocereus totolapensis*, which have moderately sized mucilage cells widely spaced throughout the cortex. Both species of *Lophocereus* have nearly nonmucilaginous cortical ground tissue, the few scattered mucilage cells occurring at the base of the ribs (Fig. 9). All other Pachycereeae examined have abundant mucilage structures. For the species listed in Table 1, which also includes all species with silica bodies in the skin, three designs of mucilage-cell distribution are observed: (1) medium to relatively large mucilage cells that are generally evenly spaced in the main stem and the ribs but are not abundant near the hypodermis, as in *Escontria* and *Myrtillocactus* (Fig. 13); (2) medium to large mucilage cells that are abundant and often closely packed throughout the main stem and rib cortex and are generally found near the hypodermis, as in most species of *Stenocereus* (Figs. 14–15); and (3) extremely large mucilaginous sacs located beneath the hypodermis, only in *S. thurberi* (Fig. 16). The remaining species, belonging to *Cephalocereus* and *Carnegiea gigantea*, have abundant moderately sized mucilage cells distributed throughout the cortex, much as in *Stenocereus*. Many species of *Stenocereus* have large aggregates of cuboidal crystals near the stele and scattered crystal aggregates in the center of the rib.

Of the other 20 species examined, *Ferocactus robustus* of Cacteeae, *Monvillea cavendishii* and *Stetsonia coryne* of Cereaeae, and *Harrisia pomanensis* and species of *Nyctocereus* of Hylocereeae are nonmucilaginous. In *S. coryne* small to mod-

erately sized crystal aggregates are present throughout the cortex, and within the ribs individual cells or groups of cells form lignified secondary walls in old stems. *Harrisia pomanensis* has large crystal aggregates, mostly in the ribs, whereas *Nyctocereus serpentinus* has them restricted to regions near the stele. In contrast, *N. chontalensis* has abundant delicate stellate druses of acicular crystals, primarily in the ribs; similar acicular crystals are also observed in *Eccremocactus* and *Hylocereus*, epiphytes of the same tribe (unpubl. data). In species of *Acanthocereus* of Hylocereeae, widely spaced cortical mucilage cells are observed near the stele and in two species occasionally in the ribs (Fig. 17). *Acanthocereus pentagonus* and *A. subinermis* have some stellate druses scattered throughout cortical ground tissue. *Leptocereus quadricostatus* of Leptocereeae has relatively few scattered mucilage cells in the cortex, but nearly every parenchyma cell contains either a large solitary crystal or a crystal aggregate, giving this tissue a hard, granular texture similar to that of *Mitrocereus fulviceps*. The mucilage cells of *Samaipaticereus corroanus* are restricted to the ribs, and crystals are generally absent. In species of *Armatocereus*, which undoubtedly are related to Pachycereeae, cortical mucilage of *A. humilis* is similar to that of *Myrtillocactus* and cortical mucilage of *A. laetus* to that of the large arborescent species of *Pachycereus*. Other columnar cacti have highly mucilaginous stems with numerous mucilage cells, evenly distributed throughout the cortex (Fig. 18), much as in *Cephalocereus* and most species of *Stenocereus*. The most mucilaginous are *Bergerocactus emoryi* and *Trichocereus thelegonus*, which have large mucilage cells near the hypodermis. Even though the patterns of mucilage cells of *Cereus* are superficially similar to those of Pachycereeae, the ground tissues of these taxa are dissimilar in texture and anatomical appearance. In-depth comparisons between unrelated species with similar mucilage cell and crystal patterns are premature because tissue morphology is undoubtedly affected by differences in age and chemical composition.

In cactus stems, cortical ground tissue is bright green directly beneath the translucent skin and paler toward the inside. Chlorenchyma is densest and chloroplasts are largest in the first subskin layers. Particularly in stems where mucilage cells are not found close to the skin or are completely absent from the ribs, the files of chlorenchymatous cells are well developed (Figs. 7-8, 10-12) and remain intact even after bark forms on the green stems. In the arborescent species of *Pachycereus* (Figs. 10-12) and in *Stetsonia coryne*, chlorenchymatous cells are markedly elongate in the radial direction.

In Cactoideae, cortical ground tissue is vascularized by an elaborate system of bundles, which are more or less independent in development from the principal primary vascular system of the shoot. To date, the three-dimensional nature of this system in columnar cacti has not been studied. In Pachycereeae, the most extensive systems occur in the most succulent plants. Mucilage cells generally are not found any closer to the hypodermis than are the cortical bundles, and throughout the cortex mucilage cells are nearly always next to the phloem of these bundles. The close proximity of mucilage structures to phloem suggests that in these species sugars for mucilage production are directly supplied from the phloem. Cortical vascular bundles generally lack primary phloem fibers,

even in old stems, but such fibers are conspicuous and precocious in *Acanthocereus horridus*, *Bergerocactus emoryi*, and *Stenocereus stellatus*.

STELE

In transection the stele of most columnar cacti consists of a ring of several dozen to over 200 collateral bundles surrounding a pith. Within a tribe, the number of bundles present is a function of stem diameter, number of ribs, and diameter of the pith; those species with the widest pith and most ribs have the most stelar bundles. Bundles of the vascular cylinder occur in sets, being concentrated opposite the stem valleys and not the ribs; therefore, the number of sets of bundles is equal to the number of stem valleys (or ribs), and the sets are separated by parenchyma. Largest bundles of each set occur in the center, and bundle size decreases gradually away from this point. In Pachycereeae, each set is solidly joined by secondary growth so that the first-formed system is a ring of parallel rods, one per valley (Gibson, 1978). This design accommodates late expansion of the pith. These rods may fuse into a solid cylinder of wood when pith enlargement stops, giving the vascular cambium time to become completed across the parenchymatous regions. However, in arborescent species with extremely wide pith, e.g., in *Carnegiea gigantea* and *Pachycereus pringlei* (categories IA–IC and IE of the earlier section), rods of wood are discrete for many years, generally being separate to near the trunk or base (solitary columnar forms) of mature trees. This pattern of wood formation as rods is characteristic of only Pachycereeae (Gibson, 1978); in fact, each tribe of Cactoideae appears to have its own basic architectural design of primary vasculature and wood skeletons even though external features are convergent.

Primary phloem fibers are found in all columnar cacti in this study; however, comparisons between specimens with similar amounts of secondary growth show that phloem-fiber formation is precocious in some species. Species in the following genera show relatively late differentiation of phloem fibers: *Anisocereus*, *Armatocereus*, *Carnegiea*, *Cephalocereus*, *Escontria*, *Lophocereus*, *Mitrocereus*, *Myrtillocactus*, nonmucilaginous species of *Pachycereus*, *Polaskia*, *Pterocereus*, and *Stenocereus dumortieri*, *S. thurberi*, and *S. treleasei*. This list includes all of the species of Pachycereeae with nonmucilaginous or slightly mucilaginous stems. Precocious development of primary phloem fibers, well in advance of secondary growth, is found in species with many different growth habits, e.g., *Acanthocereus*, *Bergerocactus*, *Stenocereus stellatus*, and *Pachycereus weberi*; so there appear to be no strong correlations between plant size and degree of development of phloem fibers. Nevertheless, fibers differ in length, width, and wall thickness between species, and some correlations may exist between design of the plant and tissues and the nature of phloem fibers. No sclerenchyma occurs in secondary phloem of columnar cacti.

One avenue of evolution for succulence in columnar cacti has been the enlargement of pith. As indicated in a previous section, size of the pith is generally correlated with type of growth form and habit; and, in general, species with the most extreme growth habits in a genus, e.g., very large arborescent species, have the widest pith of the phylad. Pith typically has a vascular system; but this

system is poorly developed in *Leptocereus quadricostatus* (Leptocereae) and completely lacking in *Ferocactus robustus* (Cacteae) and in *Acanthocereus*, *Nyctocereus chontalensis*, and *Peniocereus* (Hylocereae). Of the Pachycereae with medullary systems, pith mucilage cells are absent in all species of *Anisocereus*, *Lophocereus*, *Mitrocereus*, *Neobuxbaumia*, *Pachycereus*, *Polaskia*, and *Pterocereus*, and also in *Cephalocereus russelianus* and *C. totolapensis*. As noted before, these species have little or no mucilage in the cortex. Mucilage cells are relatively few, small, and scattered in the pith of other species of *Cephalocereus* as well as in *Escontria* and *Myrtillocactus*. Walls of pith cells in *Pachycereus weberi* are surprisingly thick but still unglified. Other Pachycereae have mucilaginous pith, especially in *Stenocereus*. In *Stenocereus*, *S. deficiens*, *S. dumortieri*, and *S. pruinosus* have the fewest and smallest mucilage cells. In tribes other than Pachycereae, pith mucilage cells are generally abundant and well spaced except in species that lack mucilage in the cortex. Species of *Acanthocereus* have numerous, widely spaced mucilage cells in the pith but lack medullary vasculature, showing that mucilage cells can differentiate apart from vascular bundles. In general, however, medullary bundles are present where pith mucilage occurs.

STORAGE OF STARCH IN THE STEM

Some estimates of the general distribution of starch in a stem can be made by staining transections of entire cactus stems with IKI. Although amount of starch probably varies in different parts of the plant and in different seasons, some definite distributional trends were observed in the specimens examined. In stems without mucilage cells in the cortex and pith and with relatively narrow pith, starch grains accumulate most often in the inner cortex, primary phloem, medullary rays, and outermost cell layers of the pith; whereas in species with large pith containing numerous mucilage cells, starch grains in the pith are not only very abundant but also very large. Exceptions are *Pterocereus* and *Anisocereus*, which have extremely large compound starch grains concentrated in the narrow pith; *Stenocereus thurberi*, which has numerous large starch grains in the ribs as well as in the pith; and species of *Armatocereus*, and certain species of *Cephalocereus*, *Myrtillocactus schenckii*, and *Pachycereus marginatus*, which show no concentration of starch in any specific tissue. Thus, enlargement of the pith seems paralleled by increased utilization of pith for starch storage. However, some species with narrow pith apparently have arisen from species with larger pith yet still store starch in the pith, e.g., in certain narrow-stemmed taxa of Hylocereae. An intensive study of these ergastic substances may provide important systematic information.

MORPHOLOGY OF REPRODUCTIVE STRUCTURES

GENERAL FEATURES

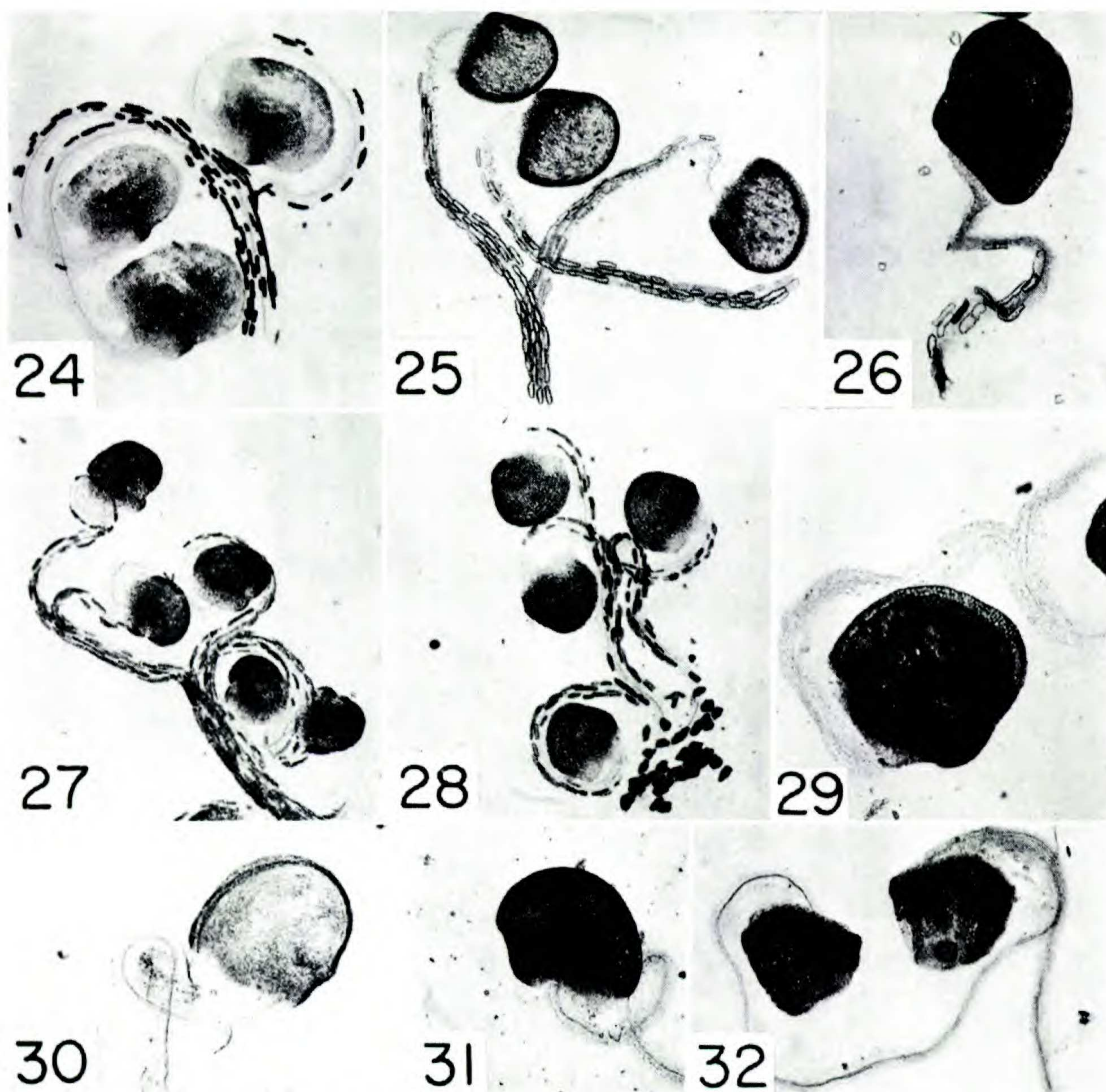
Boke (1964) has conclusively shown that epigyny in cacti has resulted from the pulling downward of the ventral sutures of numerous carpels with axile placentation so that the bases of the carpels are not at the bottom of the locule

and placentation appears parietal. Therefore, in the typical epigynous cactus flower the ovary is covered by stem tissue and the floral tube actually begins above the level of the multicarpellate locule. Buxbaum (1953) has coined the term "pericarpel" for the stem tissue covering the ovary that later becomes the outer pericarp. Cactus flowers are always solitary, borne on axillary buds (areoles), but a few species have long-lived condensed spur shoots on which several flowers may arise from several axillary buds of areolar spines.

In columnar cacti no external distinction can be seen between the pericarpel and floral tube because nodes on both are produced in the same helical phyllotactic sequence. The leaf bases (podaria) are most commonly enlarged and often decurrent, especially on the floral tube, and their laminae are often very reduced. Axillary buds of these primordia most commonly have tufts of soft trichomes and may have either rigid spines or more flexible bristles. The size and morphology of podaria, laminae, and areolar features change in a graded series from older to younger nodes, the younger primordia becoming weakly differentiated sepaloïd and petaloïd perianth parts. Color of the flower also grades from the darkest, generally greenest, shades on the podaria of the floral tube toward the inner perianth parts. Adnate to the floral tube are 100 to several thousand helically arranged stamens, which have long filaments and basifixed anthers that dehisce tricolpate pollen grains through longitudinal slits. A nectary chamber forms below the stamens around the lower part of the style. The unilocular multicarpellate pistil generally has numerous branched funiculi, each bearing four or more anatropous ovules, and a long, thick style with a multipartite papillate stigma. After pollination, the floral tube and style shrivel but often are long persistent on the developing fruit, and the ovary with attached pericarpel matures into a large berry, often with red-colored pulp containing hundreds of dark brown or black seeds. During maturation of the fruit the diameter of the ovary increases several fold, and the external pericarpel features often change markedly, providing an interesting array of characteristics for classification.

TRITERPENE-BEARING PACHYCEREEAE

As noted in the introduction, Buxbaum (1962c) first observed in *Myrtillocactus* special pigment cells in the edipermis of funiculi which he termed pearl cells ("Perlzellen") because at maturity these cells are enlarged, looking like a string of colored pearls. In species that have these intensely colored cells, the pigment first appears before anthesis (Figs. 24–28). Only some of the cells of the epidermis contain the pigment, the rest remain colorless. This is in sharp contrast to pigmentation of the pulp in other species (Figs. 29–32), e.g., *Carnegiea gigantea* and *Lophocereus schottii*, in which the pigment is manufactured late in the ontogeny of the fruit and diffuses from the ovary wall via vascular strands into the cells of the pulp. Even though the chemistry of Buxbaum's pearl cells has not been studied, there are reasons to suspect that the pigment present at anthesis is not water soluble because it does not diffuse out of the cells when mounted in Hoyer's medium, fresh in water, or preserved in FAA, a fixative that includes water and ethanol. Similar pigment cells are found in the epidermis



FIGURES 24-32. Funiculi with anatropous ovules at or slightly after anthesis, mounted in Hoyer's medium. Differences in ovule size are not proportional to the final differences in seed size because ovules are not at the same stage of development. $\times 25$.—24-28. Branches of funiculi with epidermal pigment cells.—24. *Stenocereus alamosensis*.—25. *Polaskia chende*.—26. *Escontria chiotilla*.—27. *Stenocereus thuberi*.—28. *Myrtillocactus cochal*.—29-32. Branches of funiculi with no pigment cells at anthesis.—29. *Stenocereus beneckeii*.—30. *Cephalocereus hoppenstedtii*.—31. *Lophocereus schottii*.—32. *Pachycereus hollianus*.

of the perianth parts, inner floral tube, filaments, style, stigma, and, sometimes, the anthers of the same species that have the funicular pigment at anthesis, but this same pigment also colors floral parts of other Pachycereeae that lack the funicular pigments, e.g., *Lophocereus*.

To date, Buxbaum has reported special funicular pigment cells in *Heliabravoa* (1967, here as *Polaskia chende*), *Machaerocereus* (1968b, 1969), *Myrtillocactus* (1962c, 1972), *Polaskia s.s.* (1963d), *Rathbunia* (1975c, here as *Stenocereus*), and most species of *Stenocereus* (1963b, 1969). Buxbaum (1963b) observed that these pigment cells are absent in *S. beneckeii*, *S. laevigatus*, and *S. weberi*, which he considers primitive species of the genus. Our observations confirm Buxbaum's list but also add *Escontria* and *Lemaireocereus thurberi* var. *littoralis*.

Both *Stenocereus marginatus* and *S. weberi*, here assigned to *Pachycereus*, lack these cells in our material, and *S. beneckei* lacks them in the immature flowers we have seen. No material of *S. laevigatus* was available for study; nevertheless, it is clear that only species with abundant stem triterpenes have these unusual funicular pigment cells in Pachycereeae and in Cactaceae as a whole. These are also the only reported cases of silica bodies in the stem.

Polaskia.—2 spp. (Backeberg, 1960; Bravo & Cox, 1958; Buxbaum, 1963d, 1967). Flowers borne at shoot tips, 1 per areole, diurnal, to 5 cm long, slightly wider than long when fully open; ovary and floral tube covered by numerous small but discrete podaria, each bearing a small but evident lamina, the areoles with conspicuous tan trichomes and light-colored bristles in *P. chende* but essentially naked in *P. chichipe*; floral tube short and narrow, to 1 cm long above the ovary; perianth spreading and inner parts pale pink (*P. chende*) or rotate to reflexed and yellowish green (*P. chichipe*), minutely serrulate along the upper margins; stamens numerous; style with 12 strongly papillate stigma lobes, exerted beyond the stamens; nectary chamber open; at anthesis, immature fruit 1.0–1.5 cm thick, the wall nonmucilaginous; red pigmentation present in the pericarpel and absent from the ovary wall and beneath the locule; locule spherical, about 4 mm thick. Fruit globular, 4 cm (*P. chende*) or 2.5 cm (*P. chichipe*) thick, generally lacking laminae but having clusters of short spines rather than bristles, some long trichomes persistent in *P. chende*; pericarp with few mucilage cells; pulp of mature fruit somewhat mucilaginous, sweet and red. Seeds very small, well spaced, pyriform-ovoid and subtruncate, with tan sublateral hilum; testa dull black and reticulate punctate.

Escontria.—1 sp. (Bravo, 1937; Buxbaum, 1970a; Marshall & Bock, 1941). Flowers borne at shoot tips, 1 per areole, diurnal, 3.5–4.0 cm long, narrowly cylindrical-funnelform; ovary and floral tube covered by wide imbricated, chartaceous, yellowish but translucent scales (laminae) with minutely serrulate upper margins; floral tube about 1 cm long above the ovary; perianth erect, the parts narrow, yellow, minutely serrulate; stamens numerous; style with about 8 stigma lobes, included; nectary chamber somewhat closed; at anthesis, immature fruit about 1.5 cm thick, the wall usually nonmucilaginous; red pigmentation present in the thick pericarpel and absent from the ovary wall and beneath the locule; locule shieldlike in longisection, 6 mm or more wide. Fruit globular, 5 cm thick, covered by chartaceous scales of the original pericarpel and lacking trichomes or spines; pericarp with abundant mucilage cells; pulp of mature fruit deep purple red, sweet. Seeds very small (smallest of any Pachycereeae), similar to those of *Polaskia* but with more rugose testa.

Myrtillocactus.—4 spp. (Buxbaum, 1962c, 1972). Flowers several per areole, produced on old spur shoots on all green stems, diurnal, no more than 3 cm long, slightly wider than long when fully open; ovary and floral tube with few, low podaria, each with a small lamina, the spines and trichomes hidden or absent; floral tube extremely short and slightly flaring; perianth spreading to rotate, the parts grading from pale pinkish white in the center to purplish green on the outside; stamens relatively few; style with up to 6 stigma lobes, exerted when perianth rotate; nectary chamber very small, narrow, completely open;

at anthesis, immature fruit oblong, not more than 5 mm thick, the wall of the ovary and pericarpel relatively mucilaginous; red pigmentation present in the pericarpel and absent in the ovary wall and beneath the locule; locule oblong, 1–2 mm thick. Fruit oblong, to 2.5 mm long, mostly smooth with small laminae, each subtending a small tuft of light-colored trichomes and, sometimes, a very short, often inconspicuous spine; pericarp with abundant mucilage cells; pulp deep purple red and sweet. Seeds very small, widely spaced, similar in structure to those of *Escontria*.

Stenocereus.—ca. 22 spp. (Backeberg, 1960; Benson, 1969a; Bravo, 1937, 1956c; Britton & Rose, 1920; Buxbaum, 1955, 1963b, 1963d, 1968b, 1969; Gates, 1957; Martin, 1973; Sánchez Mejorada, 1972, 1973a; Shreve & Wiggins, 1964). Flowers borne mostly at shoot tips, except in *S. dumortieri* where borne far down the ribs, and in *machaerocerei* and *rathbunias*, where borne mostly on old areoles, 1 per areole, diurnal or nocturnal, 5–22 cm long, tubular-campanulate, funnelform, funnelform-campanulate, and narrowly salverform; ovary and floral tube with numerous podaria, often with long-decurrent bases on the floral tube, each usually bearing small laminae; podaria of ovary often with tan, brown, or red trichomes, and clusters of short spines, but those of the floral tube often naked or nearly so, the lower floral tube and pericarpel of several species (e.g., *S. stellatus* and *S. treleasei*) more typically with light-colored bristles; floral tube well developed, 2.5–10 cm long above the ovary; perianth commonly wide spreading or reflexed at anthesis, the inner parts typically white, cream, pale pink, or lavender changing to darker shades to purple red outside and on the floral tube, but *rathbunias* pink changing to terracotta red; stamens numerous to very numerous (largest flowers), often with very long filaments; style with multilobed stigma, up to 14 stigma lobes, generally exerted from the floral tube and stems when the perianth is spreading; nectary chamber open or partially enclosed by the bases of the filaments, extending nearly a third the length of the floral tube in *machaerocerei*; at anthesis, immature fruit globular, 1–3 cm thick, the wall often mucilaginous; red pigmentation absent completely or present only in the ovary wall and not in the pericarpel; locule spherical to ovoid, 5–10 mm wide and at least half the diameter of the ovary, with the funiculi often markedly branched. Fruit globular to ovoid, 3–9 cm thick, generally lacking trichomes but typically having small laminae and clusters of long spines at maturity, the spines deciduous in some species; pulp of mature fruit red, sweet, edible. Seeds either brown or blackish brown, dull, verrucose, with a large basal hilum or glossy black with very fine punctae, 1.5–3.0 mm long.

This diagnosis indicates that *Stenocereus* is a very diverse genus, with a broad range of floral designs. Few, if any, features clearly define this genus, except that the flowers have small scales on the pericarpel, a long floral tube, and edible, ovoid to globose fruits that are very spiny at or just before maturity.

OTHER PACHYCEREEAE

To date, chemical investigations of other Pachycereeae have found that glycosidic triterpenes either are absent or are present only in trace amounts. Lupeol, a sapogenin (aglycon), is found in *Lophocereus*, in which alkaloids are

particularly abundant. None of the species here assigned to *Backebergia*, *Carnegiea*, *Cephalocereus*, *Lophocereus*, *Mitrocereus*, *Neobuxbaumia*, *Pachycereus*, and *Pterocereus*, has special epidermal funicular pigment cells at anthesis. Instead, at anthesis the pericarpel is chlorophyllous, the ovary wall is greenish white to white, and the tuniculi and ovules are white. Red pigmentation of the fruit appears very late in development when a water-soluble betalain first is produced within the fruit wall and then occurs in the locule. Certain species have white pulp in ripe fruits, and green-fruited species occur in *Neobuxbaumia*.

Lophocereus.—2 spp. (Backeberg, 1960; Buxbaum, 1970b; Lindsay, 1963; Shreve & Wiggins, 1964). Flowers borne at shoot tips where flowering areoles become highly branched and produce long, gray white bristles, nocturnal, 2.5–4 cm long, broadly funnelform and nearly as wide as long when fully open; ovary and floral tube with very low podaria with small laminae but no conspicuous trichomes or spines; floral tube short, generally less than 1.5 cm long above the ovary; perianth widely spreading or rotate, the inner parts white to light or dark pink (*L. schottii*) or burnt coral (*L. gatesii*); stamens relatively few; style with 5–6 white stigma lobes, slightly exerted beyond the stamens; nectary chamber small and essentially open; at anthesis, immature fruit oblong, less than 1 cm thick, with a few scattered mucilage cells in the wall; locule oblong, to 6 mm wide. Fruit globular to oblong, 1–3 cm thick, glabrous, nearly spineless, with persistent laminae, bursting irregularly; pulp red and juicy. Seeds glossy, black, with a prominent raphe and a swollen collar around the hilum, 2 mm long.

Pachycereus.—6 spp. (Backeberg, 1960; Bravo, 1937, 1956a, 1956b; Britton & Rose, 1920; Buxbaum, 1963a, 1963b; Shreve & Wiggins, 1964). Flowers borne at shoot tips in most species but far down the ribs in *P. marginatus* and on old areoles in *P. weberi*, 1 per areole, except in *P. marginatus* which may have 2 per areole, diurnal or nocturnal, 4–12 cm long, broadly cylindrical, cylindrical-funnelform, or funnelform; ovary and floral tube covered by numerous, relatively low podaria, with small to medium-sized laminae, the areoles with tufts of tan, beige, or golden trichomes, particularly in *P. grandis*, *P. pecten-aboriginum*, and *P. pringlei*, with small light-colored bristles on the pericarpel and floral tube in *P. grandis*, *P. hollianus*, and *P. pecten-aboriginum*, present but inconspicuous only on the floral tube of *P. marginatus* and *P. weberi*, and essentially absent in *P. pringlei*; floral tube thickened, about half as long as the flower; perianth generally short, the parts spreading very far from the tube except in *P. weberi*, the parts white or ivory white in most species but sometimes rose in *P. marginatus* and purplish in the outer parts of *P. pecten-aboriginum*, minutely serrulate along the upper margins in several species; stamens numerous, particularly in large flowers; style with numerous stigma lobes, exerted above the level of the stamens except in *P. marginatus* and *P. weberi*; nectary chamber open or nearly so; at anthesis, immature fruit globular, 1–2 cm thick, seemingly wider in species with copious tan to golden trichomes that cover the pericarpel as a thick carpet, the wall thick and nonmucilaginous; red pigmentation absent; locule spherical, shieldlike (*P. hollianus*), or squarish (*P. marginatus*); ovules and funiculi generally not filling the locule, and in *P. pringlei* each branched funiculus with its numerous ovules widely spaced and discrete. Fruit globular or ovoid, 4–8

cm thick, burlike with long golden spines or bristles and trichomes (*P. grandis*, *P. pecten-aboriginum*, and *P. pringlei*), covered with abundant clusters of golden spines that are deciduous at maturity, or with fewer clusters of shorter, thinner spines or bristles and light-colored trichomes; pulp eventually red, burlike fruits generally dry and open by apical splits; fleshy fruits not very mucilaginous. Seeds mostly glossy black, comparatively large, 2–4.5 cm long, the raphe prominent in all species but especially in *P. hollianus* and *P. marginatus*; hilum typically oblique, with a thick collar in *P. marginatus*; testa thin.

Like *Stenocereus*, *Pachycereus* is a genus with diverse reproductive features. *Pachycereus marginatus* has small, tubular, white or rose-colored flowers, with some trichomes and virtually no bristles, small lightly armed fruits, and large seeds. *Pachycereus hollianus*, the type species of *Lemaireocereus*, has broadly cylindrical flowers 7–10 cm long, with a short ivory white perianth, having conspicuous tufts of trichomes and numerous bristles, large ovoid fruits with numerous bristles, large ovoid fruits with numerous bristles, large ovoid fruits with numerous light-colored trichomes, bristles, and spines, and black shiny seeds with a prominent raphe. Flowers of *P. weberi* are funnellform, 8–10 cm long, with small tufts of coffee brown trichomes; the fruits are large, oblong, and naked at maturity because spine clusters are deciduous, and the seeds are large, black, and shiny without a prominent raphe. The remaining species have large cylindrical-funnelform flowers covered with copious tannish trichomes, burlike fruits (less so in *P. pringlei*), and very large, black, shiny seeds with a small raphe.

Backebergia.—1 sp. (Bravo, 1961; Buxbaum, 1975b). Flowers produced within a dense terminal head of golden spines and bristles, 1 per areole, nocturnal, 6–7 cm long, tubular; ovary and floral tube with podaria having fairly conspicuous laminae, conspicuous tufts of long tannish brown trichomes, especially on the pericarpel, and 1–several golden bristles per areole, especially on the floral tube; floral tube 3 cm long, relatively thick; perianth parts golden green, relatively short, mostly erect; stamens relatively few; style short with relatively few short stigma lobes, included; nectary chamber large but open, with a slight apical constriction; at anthesis, immature fruit 1.5 cm thick; red pigmentation completely absent, the walls green; locule semicircular in outline, with a small apical point, ca. 9 mm wide; ovules and funiculi not filling the locule. Fruit ovoid, 3.5 cm thick, covered by long trichomes and long mostly erect bristles; splitting irregularly, pulp wine red, juicy. Seeds shiny, black, 5 mm long, ca. 4 mm thick, with a prominent raphe and thin testa.

Mitrocereus.—1 sp. (Backeberg, 1960; Britton & Rose, 1920; Buxbaum, 1953, 1971a; Hertrich, 1934). Flowers borne at shoot tips, 1 per areole, the flower often subtended by long trichomes and bristles, nocturnal but remaining open the next day, 7–8 cm long, broadly cylindrical-funnelform; ovary and floral tube with podaria bearing large leaflike laminae, but these hidden by copious, long tannish brown trichomes and some light-colored bristles; floral tube ca. 5 cm long, very thick; perianth parts rose red but when spreading cream-colored in the center; stamens numerous; style long, thick, with few very short stigma lobes, long exerted beyond the stamens and perianth; nectary chamber very large, well hidden by enlargement of the bases of the lowermost stamens; at anthesis, im-

mature fruit 2.5 cm thick, the walls with numerous, well-spaced mucilage cells; red pigmentation completely absent, the walls green; locule semicircular in outline with a small apical point, ca. 10 mm wide; ovules and funiculi not filling the locule, the funiculi often with papillate epidermal cells near the ovules. Fruit obovoid, greenish, 4 cm thick, lanate, with some bristles; pericarp mucilaginous, splitting lengthwise into 8 or more segments; plup white, relatively dry. Seeds shiny, black, larger than but similar in structure to those of *Pachycereus hollianus*, having a prominent raphe.

Cephalocereus.—20–30 spp. (Backeberg, 1960; Bravo, 1937; Bravo & MacDougall, 1959, 1963; Britton & Rose, 1920; Buxbaum, 1962a, 1971b; Marshall & Bock, 1941). Flowers borne near shoot tips, often in dense clusters, 1 per areole, nocturnal or diurnal, generally 3–8 cm long, but longer when the ovary is elongate, e.g., in *C. russelianus* (possibly not a member of this genus), funnel-form or funnellform-campanulate, the flowering areole typically with numerous long soft white trichomes; ovary and floral tube often without prominent podaria but generally with noticeable laminae, especially in species referred to as *Neodawsonia*, the areoles sometimes with short trichomes but mostly lacking spines and bristles; floral tube often thickened and half as long as the flower; perianth parts generally spreading or reflexed, light pink to dark rose red; stamens numerous; style thickened, with up to 12 stigma lobes, commonly exerted slightly beyond the stamens; nectary chamber partially or completely closed; at anthesis, immature fruit globular or slightly flattened, but in certain species markedly oblong, rarely more than 2 cm thick, the wall thick and generally mucilaginous; red pigmentation absent, the walls green; locule mostly shieldlike or cordate in outline, with an apical point; funiculi with papillate epidermal cells in *C. hoppenstedtii* and *C. senilis*. Fruit usually depressed-globular, sometimes oblong, to 5 cm thick, completely naked, with small laminae only, or, in a few species, with small trichomes and spines; pericarp usually mucilaginous; pulp generally red, except in *Neodawsonia*, where sometimes white. Seeds poorly described, shiny, black or black brown, with very fine sculpturing, small.

Neobuxbaumia.—6 spp. (Backeberg, 1960; Bravo et al., 1970, 1971a, 1971b, 1973; Buxbaum, 1957; Dawson, 1952; Poindexter, 1949; Scheinvar & Bravo, 1973; Vail, 1960). Flowers borne mostly at shoot tips but produced on old areoles in *N. polylopha*, 1 per areole, nocturnal, 4.5–7.5 cm long, funnellform to funnellform-campanulate; ovary and floral tube with relatively large podaria and small to medium laminae, the trichomes and bristles usually inconspicuous or absent at anthesis, the podaria specialized as extrafloral nectaries at least in *N. polylopha*; floral tube relatively long and thick; perianth generally spreading, whitish to purple red; stamens numerous; style often with relatively few stigma lobes, included; nectary chamber typically large and closed for species where descriptions are available; at anthesis, immature fruit globular to ovoid-pyriform, 1–2 cm thick, the wall thick and mucilaginous, especially in the pericarpel; red pigmentation absent in the wall; locule either shieldlike or oblong, less than 1 cm wide; ovules and funiculi generally absent from the center of the locule, as in *Pachycereus pringlei*. Fruit globular to ovoid-pyriform, often with a persistent floral tube, rarely more than 4 cm thick, the podaria greenish, generally con-

spicuous but laminae may be absent, with some white trichomes and thin spines in some species, e.g., *N. mezcalaensis* and *N. tetetzo*, dehiscent but with 1–several apical splits; pulp generally dry, white. Seeds shiny, dark brown or black, with very fine sculpturing, obliquely reniform, up to 2 mm long.

Carnegiea.—1 sp. (Backeberg, 1960; Benson, 1969a; Bravo, 1937; Buxbaum, 1958b; Shreve & Wiggins, 1964). Flowers borne at shoot tips, 1 per areole, nocturnal but remaining open the next day, 10–12 cm long, 5–6 cm wide, funnel-form; ovary and floral tube covered by relatively large podaria with conspicuous laminae, the areoles with whitish trichomes on the pericarpel and lower floral tube; floral tube 6–7 cm long, green, fused to the base of the style above the ovary for 1 cm; perianth commonly reflexed at anthesis, the inner and outer parts pure white; stamens extremely numerous, the filaments long and white; style with about 10 stigma lobes, exerted beyond the stamens; nectary chamber small and open, above point of fusion of style and floral tube; at anthesis, immature fruit globular to oblong, 1.5–2 cm thick, the walls with abundant mucilage cells; red pigmentation completely absent, the walls green; locule markedly oblong, 6–8 mm wide, packed with ovules. Fruit obovoid to ellipsoid, green tinged with red, 5–7 cm long, to 5 cm thick, with tufts of white trichomes and inconspicuous white bristlelike spines; pericarp mucilaginous, splitting lengthwise along 3 lines; pulp red. Seeds shiny, black tinged with red, the sculpturing merely slightly bulging epidermal walls, 1.5 mm long; testa relatively thin.

Anisocereus.—7 sp. (Backeberg, 1960; Buxbaum, 1970a).⁵ Flowers 1 per areole, 7 cm long, cylindrical-funnelform; ovary and floral tube covered with conspicuous green laminae, those of the pericarpel and lower floral tube subtending areoles with trichomes and thin spines; floral tube 5 cm long, relatively thick; perianth parts orange red, relatively short, spreading; stamens numerous; style with relatively few stigma lobes, slightly exerted beyond the stamens; nectary chamber with a slight apical constriction but mostly open; at anthesis, immature fruit 1.5 cm thick; locule relatively wide. Fruit almost dry; pulp whitish. Seeds shiny, black brown, 3 mm long.

Pterocereus.—1 sp. (Backeberg, 1960; Glass & Foster, 1973; MacDougall & Miranda, 1954).⁵ Flowers often borne on old areoles, 1 per areole, nocturnal with fetid odor, 8–9 cm long, cylindrical; ovary and floral tube covered by podaria with large imbricated, recurved, green leaflike laminae, trichomes, and spines; floral tube 4.5 cm long, relatively thick; perianth parts numerous, yellowish green, strongly spreading or recurved at anthesis; stamens numerous; style with several short stigma lobes, approximately at the upper level of the uppermost stamens; nectary chamber fairly large and closed; at anthesis, immature fruit globular, 2.5–3 cm thick, the wall thick and lacking mucilage; red pigmentation absent, the walls green; locule shieldlike, 8 mm wide. Fruit becoming dry, 3–4 cm thick.

POLLEN GRAINS OF PACHYCEREEAE

As summarized by Leuenberger (1976), all Pachycereeae examined to date have very similar pollen grains, having the following features. *Size*: maximum

⁵ Existing descriptions are very incomplete.

diameters 79–47 μm ; minimum diameters 73–41 μm . *Structure and sculpture of exine*: tectate-perforate; finely anulopunctate; columellae 0.6–1.0 μm high, irregularly dispersed or reticuloid and numerous, 40–80 per 50 μm^2 ; spinules 2.5–0.8 μm high, isolateral or slightly concave. *Apertures*: almost exclusively tricolpate with occasional hexacolpate grains in tricolpate samples. Although Leuenberger does not advocate use of pollen data for classification of species within Pachycereeae, certain patterns do appear in his tables: (1) pollen grains of the two species of *Polaskia* are perfectly spherical and very similar to each other; (2) pollen grains of *Escontria* and *Myrtillocactus* are strikingly similar in exine features; (3) pollen grains of *Stenocereus* resemble those of *Polaskia* but are slightly larger and have fewer spinules and higher columellae; (4) pollen grains of *S. gummosus* very closely resemble those of *S. stelatus*; and (5) pollen grains of all species that lack stem triterpenes are very similar, being most similar to those of *Polaskia* among the triterpene-bearing species. The most divergent pollen grains in the tribe are those of *Lophocereus*, which have the tallest spinules and widest perforations.

SPECIES OF OTHER TRIBES OF CACTOIDEAE

Because most species of other tribes of columnar cacti are not included in this study, there is no need to summarize the reproductive features for species examined outside tribe Pachycereeae.

Most species have flower, fruit, seed, and pollen characteristics that closely overlap patterns in Pachycereeae. The seeds and pollen grains, as well as flower and fruit structure, of *Bergerocactus emoryi* (Benson, 1969a, 1969b; Moran, 1965; Shreve & Wiggins, 1964) indicate that this species is closely related to, if not derived from, tribe Pachycereeae and not Echinocereae but also may represent a connection between Pachycereeae and Echinocereae. *Bergerocactus* and *Echinocereus* lack pearl cells at anthesis (Buxbaum, 1975). In tribe Cactae reproductive features of the genera with primitive features, e.g., *Echinocactus* and *Ferocactus*, are not unlike those of *Polaskia* and *Pachycereus hollianus*, which co-occur with these same species. Even though external features of flowers of *Machaerocereus* are superficially similar to those of Hylocereeae and Trichocereae, other features of flowers, fruits, and seeds show that these taxa are not closely related (Buxbaum, 1968b). Tribe Cereae has flowers and pollen grains similar to those found in Pachycereeae; however, phylogenetic reconstructions of the tribe (Buxbaum, 1968a, 1968c, 1968d; Leuenberger, 1976, after Buxbaum) clearly show that the species with flower and fruit characteristics similar to Pachycereeae, e.g., *Cephalocereus*, are the most highly derived phylads of the tribe, a result of convergent evolution. Although none of the genera of Leptocereae and Browningeae are adequately described, published illustrations of their flowers (Buxbaum, 1963e, 1965, 1966; Rauh, 1958) are strikingly similar to flowers of *Polaskia* and *Pachycereus*, especially flowers of *Armatocereus* and *Samaipaticereus* (Leptocereae), and *Browningia* and *Castellanosia* (Browningeae) of northwestern South America; in fact, species of *Armatocereus* were originally included in *Lemaireocereus* by Britton & Rose (1920).

POLLINATION

Few data are published on pollination of Mexican columnar cacti, and accounts often emphasize bat pollination (Alcorn et al., 1959, 1961, 1962; Howell, 1972; McGregor et al., 1959, 1962; Moran, 1962b; Porsch, 1939; Vogel, 1968). Bat pollination is probably very widespread in Pachycereeae in that many species are ideally suited for bat visitation. Their flowers typically open at night; are mechanically strengthened, funnelform-campanulate to campanulate; and have great numbers of anthers, a large stigmatic surface, and large, basal and hidden nectary chamber. The flowers are positioned near the tips of the branches, often held above the neighboring vegetation, and flower color is often white or light rose. In addition, some species also have strong fetid nocturnal odors, e.g., *Pterocereus gaumeri* (Glass & Foster, 1973), which has yellow green flowers covered with large leafy primordia. Flowers that are campanulate and open during the day may attract bird and insect visitors (Moran, 1961).

Flowers adapted for hummingbird visitation, including those of *Myrtillocactus*, *Pachycereus marginatus* (Beutelspacher & Martínez, 1973), *Polaskia chende*, *Stenocereus alamosensis*, *S. beneckeii*, and *S. stellatus*, have diurnal anthesis, a pinkish to red short narrow floral tube and perianth parts, and an open nectary chamber; and in *Myrtillocactus*, *Pachycereus marginatus*, and *S. alamosensis* flowers are produced on old areoles along the stem rather than clustered at the tips. Hummingbirds have been observed visiting native populations of *Myrtillocactus cochal*, *M. geometrizzans*, and *S. alamosensis*.

Although hawkmoth pollination has not been observed in Pachycereeae, we suspect that the long salverform pinkish flowers of machaerocerei, the narrow tubular pinkish flowers of *Stenocereus standleyi*, and the short tubular, rotate pinkish flowers of *Lophocereus*, which all open at night, are preferred by hawkmoths. Their nectary chambers are completely open.

Many species of cacti are visited by small insects foraging either on the copious pollen or nectar (e.g., Shreve & Wiggins, 1964), but the effectiveness of these small insects as cactus pollinators has rarely been measured (Alcorn et al., 1961; McGregor et al., 1959).

Closely related species often differ markedly in flower shape, length, color, and time of anthesis. For example, *Stenocereus alamosensis*, a northern desert species with diurnal flowers, and *S. standleyi*, a species of more mesic habitats with nocturnal flowers, are morphologically very similar; likewise *Lophocereus* with small clustered nocturnal flowers, *Pachycereus marginatus* with small tubular diurnal flowers, and *P. weberi* with funnelform nocturnal flowers are closely related to judge from all evidence of stem structure and chemistry. One may conclude from these and other examples that within Pachycereeae dependence upon relatively large, highly mobile animal vectors for outcrossed pollination has resulted in a radiation of floral designs. Therefore, differences between species that are pollination strategies in particular geographical regions must not be overweighed. Between geographically isolated species, one should expect to find not only differences in flower size, shape, position, color, and time of opening but also differences in the type and size of appendages on the exterior of the flower, e.g., to attract certain types of pollinators or to prevent injury

(spination) to animal vectors. The degree of development of primordia at anthesis, which is stressed in the classification of Britton & Rose (1920), may not be valid for delimiting genera.

DISCUSSION

Comparative anatomy is useful in reconstructing phylogenies but is not automatically reliable by itself since internal tissues, like external structures, experience convergent and parallel evolution. Anatomical features are not necessarily conservative, because characters that affect the fitness of a plant are likely to be acted on by natural selection. Therefore, any worker is pleased to uncover sets of anatomical and other taxonomic features in otherwise similar taxa that are so unusual for flowering plants that the combination of features can clearly define a natural group (Thorne, 1958, 1963). The sets of anatomical, morphological, and biochemical features discussed above not only clarify the limits of subtribes within Pachycereeae but also help determine with reasonable certainty where dichotomies have occurred between related phylads and species pairs.

One natural group of Mexican columnar cacti has become clearly defined through observations in this study. Subtribe Stenocereinae (sensu Buxbaum) first included only *Stenocereus* (i.e., all species of *Lemaireocereus* except *L. hollianus*), *Carnegiea*, and *Lophocereus*; but later *Machaerocereus* and *Rathbunia* from the tribe Echinocereae (Buxbaum, 1968b, 1969, 1975c) and subtribe Cephalocereinae were added to form one large subtribe (Fig. 33). We propose to emend and redefine this subtribe to include instead the taxa that have: (1) abundant stem triterpenes and no alkaloids (Table 1); (2) pigment cells in the epidermis of the funiculus in the flower; (3) generally small seeds (3 types); and (4) strong similarities in growth habit and vegetative and reproductive morphology and anatomy. Included here are all species that have silica bodies in the skin and the species of *Stenocereus* (s. l.) having areoles with red glandular trichomes. Many, but not all, species of *Lemaireocereus* (sensu Britton & Rose, 1920) are included here, as well as the genera *Escontria*, *Machaerocereus*, *Myrtillocactus*, and *Rathbunia*. We have in effect combined some members of all four subtribes of Buxbaum into one and have excluded *Carnegiea*, *Lophocereus*, and the Cephalocereinae, which have biochemical or morphological features more typical of a different subtribe. Because features such as presence of stem triterpenes, skin silica bodies, special funicular pigment cells, and areoles with red trichomes are apparently unlinked in any biological functions, their consistent occurrence together denotes monophyly: it is highly unlikely that this unique set of features, absent from other Cactaceae, has evolved more than once.

Within subtribe Stenocereinae two groups of genera are identifiable, those without and those with skin silica bodies. The first group consists of *Escontria*, *Myrtillocactus*, and *Polaskia*, the seven species with the smallest seeds in the tribe. All five records of chichipegenin (Table 1) occur in *Myrtillocactus* and *Polaskia*, and five species from all three genera have longispinogenin. These taxa are all trees 4–7 m tall with a distinct trunk to 1 m high; *M. cochal* tends to have the flattest crown. In addition, all species have relatively small flowers, and

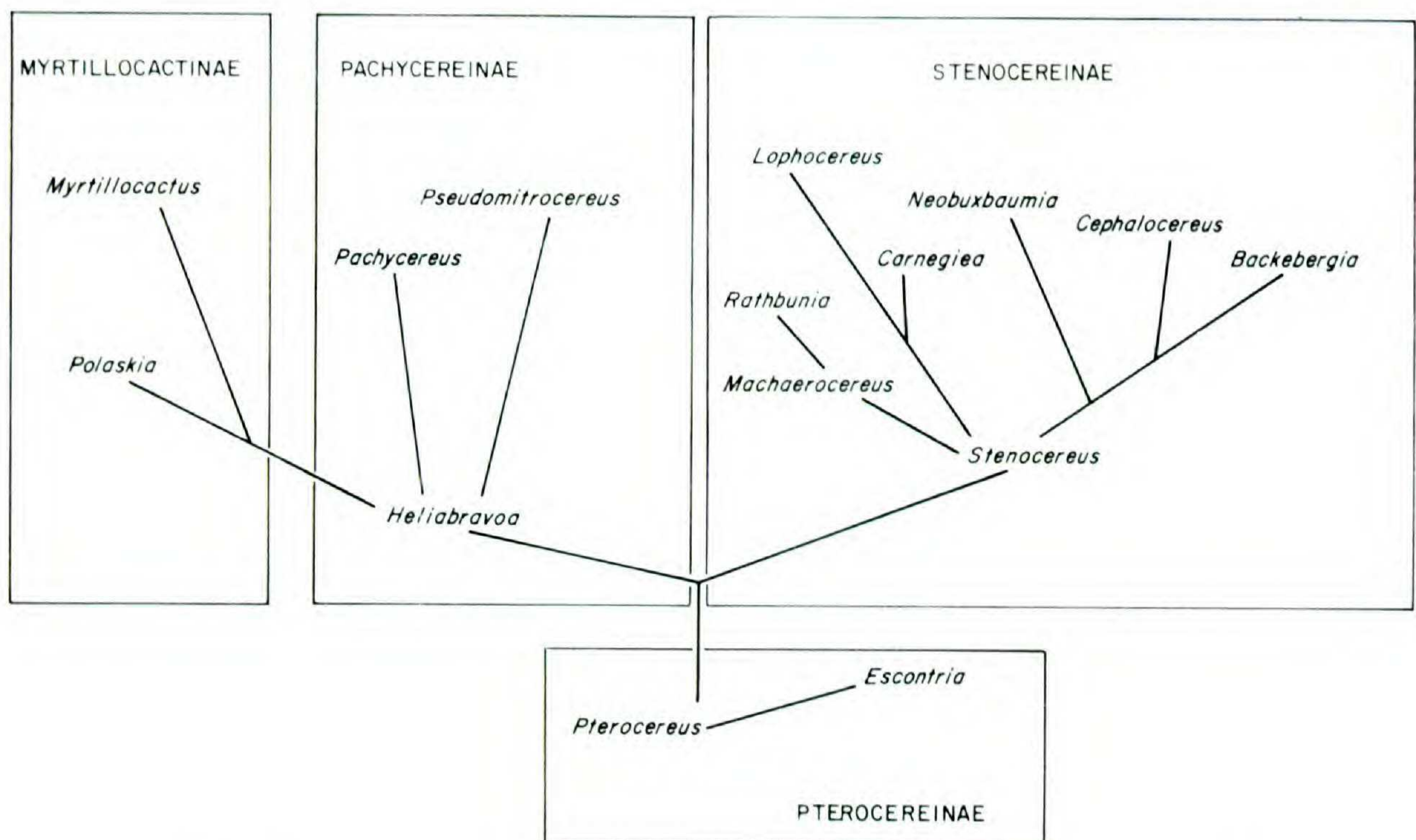


FIGURE 33. Approximate phylogenetic relationships of Pachycereeae according to Buxbaum (after Leuenberger, 1976).

pigmentation in the female part of the flower is restricted to the pericarpel and does not occur on the sides of or below the locule. The two species of *Polaskia* are obviously closely related to each other in the following ways: (1) stems light, bright green, a color uncommon in this tribe; (2) the sharply acute ribs bear morphologically similar areoles and spines; (3) rib number similar but generally higher in *P. chichipe*; (4) skin very thin, with a smooth cuticle, bullate multiple epidermis, and 1(-2)-layered hypodermis with lamellar primary thickenings; (5) cortex and pith lacking mucilage and crystal cells, and pith very narrow and lacking abundant starch; (6) external and internal structures of the flowers similar even though the number of primordia and trichomes on the pericarpel and short floral tube differ; (7) seed size and shape and testal surface features nearly identical; (8) pollen grains very similar, more so to each other than to other species of Pachycereeae; and (9) stem triterpenes very similar and biochemically very simple. *Escontria* and *Myrtillocactus* also show close relationships to each other in the following respects: (1) horns present on the outer epidermal walls, and these covered by a thick, rough cuticle; (2) hypodermis thick and lacking crystals; (3) mucilage cell patterns of the cortex and pith nearly identical; (4) both species with relatively narrow pith; (5) testal surface features of seeds strikingly similar; and (6) pollen grains nearly identical. Flowers of *Myrtillocactus* more closely resemble flowers of *Polaskia chende* than those of *Escontria* and may be viewed as very small versions of the former with almost no development of pericarpel vesture and armature and with stronger development of mucilage of the fruit. Nevertheless, *Myrtillocactus* is unusual because more than one flower occurs per areole, an uncommon feature in Pachycereeae found elsewhere in *Lophocereus*. Buxbaum (1962c, 1963d, 1967) has

repeatedly noted the relatedness of *P. chende* (as *Heliabravo*), *Myrtillocactus*, and *Polaskia* for some of the reasons cited above, but he (1970) has compared *E. chiotilla* with *Pterocereus* and *Anisocereus*.

Stenocereus is a monophyletic taxon in which vegetative and reproductive features have undergone extensive evolution. All species studied here have silica bodies in the skin and highly mucilaginous stem cortex, but within the genus the distributional patterns and shapes of these features reveal smaller lines of radiation, paralleled by patterns observed in distribution of stem triterpenes.

Stenocereus stellatus and *S. treleasei*, species of southern Mexico, are the only known taxa to produce both stellatogenin and thurberogenin in the stem. Cactus taxonomists have consistently placed these species next to each other from similarities in growth habit, flowers, and fruits (Backeberg, 1960; Bravo, 1937); in fact, Backeberg includes only these species in *Stenocereus*. *Stenocereus treleasei* has a higher rib number than *S. stellatus*, fewer central and radial spines, and shorter flowers, with larger tufts of trichomes. This study also shows that their stem anatomy is nearly identical, especially the structure of the skin, in which the large silica bodies are found only in the hypodermis. The flowers of both species are similar in areolar features to *Polaskia chende* and in floral design to *Pachycereus marginatus*.

Stenocereus pruinosus is certainly closely related to the *stellatus* group to judge from superficial similarities in growth habit, stem anatomy, and seeds; but *S. pruinosus* is clearly distinct chemically and has longer, more funnelliform flowers and has fruits with tan-felted areoles and numerous persistent yellow spine clusters. The general features of the shoot, especially those of the areoles, flowers, and fruits are also characteristic of *S. chrysocarpus* (Sánchez Mejorada, 1972), which has longer flowers and larger fruits. That species, however, has red glandular trichomes in the areoles in addition to the normal tan ones, and in this way is similar to *S. queretaroensis*. Studies of the stem anatomy and chemistry of *S. chrysocarpus* are needed to evaluate its relationships.

Another phylad within *Stenocereus* consists of *S. griseus*, *S. hystrix*, and *S. longispinus*, which have similar external features of stems and reproductive structures and also similar sets of unusual stem triterpenes (Table 1). *Stenocereus laevigatus* may also belong to this phylad, but its anatomy and chemistry are still unknown. Stem anatomy of *S. hystrix* and *S. longispinus* shows that this phylad belongs in the genus because silica bodies are present, and the seeds of this phylad are very similar to those of *S. pruinosus* and *S. stellatus*. The species are native to the West Indies, Guatemala, and southernmost Mexico, and in all likelihood this phylad is an early radiation from Mexican stock. The flowers appear to be adapted for nocturnal pollination by bats, which are particularly common in the ranges of these species.

Stenocereus dumortieri, which has been called *Isolatocereus dumortieri* (Backeberg, 1960), is certainly a highly specialized species of the genus and the largest species related to *S. pruinosus* and *S. chrysocarpus*. Ribs are few, bluish green or glaucous, and bear areoles that are very closely spaced. Spines are thinner than in most stenocerei, and the cortex is bright yellow, more so than in *S. pruinosus*. Moreover, *S. dumortieri* has a unique oleanane triterpene, dumorti-

erigenin, an unusual lactone compound that is probably derived biochemically from oleanolic acid. The flowers and fruits are most similar to those of the *stellatus* group, and their seeds also resemble those of *S. stellatus*, *S. hystrix*, and *S. pruinus*. From these data, *S. dumortieri* appears most closely related to *S. pruinus*.

Stenocereus beneckeii, *S. martinezii*, *S. montanus*, *S. queretaroensis*, *S. quevedonis*, and *S. thurberi* appear to represent a phylad that has speciated in Mexico in Nueva Galicia and west of the Sierra Madre Occidental. All these species have red trichomes in stem areoles, and of the five species that have been chemically studied, four have queretaroic acid, a triterpene found in no other cacti. *Stenocereus martinezii*, which has never been studied chemically or critically described, is so similar to *S. thurberi* that their relationship is inescapable. All these species have similar external rib features, e.g., strongly sinuate margins, and *S. montanus* and *S. queretaroensis* have similar stem anatomy. *Stenocereus thurberi* has stem chemistry and skin silica bodies most similar to *S. stellatus*; however, its flowers and seeds are unlike those of *S. stellatus*, and the large mucilage sacs in the outer cortex are distinctive among columnar cacti examined, though other species from Sinaloa may share this feature. *Stenocereus queretaroensis* is closest to *S. stellatus* in vegetative anatomy and morphology but differs in having funnelliform flowers. The seeds have not been described. Diurnal and nocturnal flowers occur in this phylad, and flower shape, length, and color are also variable, presumably in response to natural selection for preferred pollinators.

The recently described *Stenocereus fricii* (Sánchez Mejorada, 1973a) is difficult to compare to other stenocerei because no chemical and anatomical data are available. The growth habit most closely resembles that of *S. stellatus* and the previous phylad with red glandular trichomes, e.g., *S. montanus* and *S. quevedonis*. However, *S. fricii* has cream-colored felt on the areoles and has flowers and fruits similar to those of *S. pruinus* and *S. chrysocarpus*.

When Britton & Rose (1909) established the genus *Rathbunia*, several species of *Stenocereus*, then *Lemaireocereus*, had not been yet described, including species from Sinaloa and Nueva Galicia. Consequently, the conspicuous red tubular flowers of *Rathbunia* were quite distinctive from typical funnelliform flowers in *Lemaireocereus*. When *L. standleyi* was described from Sinaloa, the distinctions between these genera were diminished. This species has strongly sinuate rib margins that bear well-developed clusters of numerous radial and central spines in areoles that generally lack trichomes. Comparisons of *S. standleyi* with rathbunias show very few differences, either superficially or anatomically; rathbunias appear to have fewer and smaller silica bodies. Flowers and fruits of these taxa are closely similar even though the flowers of *S. standleyi* are lighter in color, more funnelliform, and nocturnal, whereas those of rathbunias are red, tubular, and diurnal. In addition seeds of both are about 2 mm long, shiny, and black, with minute punctae, a seed type uncommon in Stenocereinae. All these observations support a conclusion that *standleyi*, *alamosensis*, and *kerberi* belong in the same genus, the principal difference in the flowers having arisen by adaptation to different pollinators. *Rathbunia* thus must be transferred to *Steno-*

cereus. More study is needed of these northern species of *Stenocereus*, especially the morphs of *S. standleyi*, to determine to what other species they are related. Likely close relatives are *S. quevedonis* and *S. montanus*.

Even with information on stem anatomy and chemistry, placement of *Stenocereus deficiens* is difficult, and we prefer to remain uncommitted on this Caribbean species until the flowers and fruits are better described.

Machaerocereus is clearly related to *Stenocereus*, as seen by Britton & Rose (1909) when they placed the species in *Lemaireocereus* before establishing *Machaerocereus* (1920). Justification for this segregation was that the growth habit of *Machaerocereus* is more lax than in *Lemaireocereus*; spine clusters are well developed and bear a strongly flattened, downward-pointing central spine; and the perianth is very elongate and relatively long persistent. Although the triterpenes of each *Machaerocereus* species is different (Djerassi, 1957), these taxa have similar hypodermal silica bodies and seeds, and the flowers and fruits are quite similar, though the parts are darker colored in *gummosus*. On the basis of gross similarities in vegetative form, stem anatomy, triterpene chemistry, and seed structure, machaerocerei are more closely related to *S. stellatus* than to other cacti examined. However, *S. fricii* from Nueva Galicia, Mexico (Sánchez Mejorada, 1973a), also has several vegetative and reproductive similarities to *Machaerocereus*. Regardless whether machaerocerei are most closely related to *S. fricii* or *S. stellatus*, the morphological gap is not great enough to recognize *Machaerocereus*. Therefore, we recommend assigning *eruca* and *gummosus* to *Stenocereus*. The floral divergence of machaerocerei is, of course, overemphasized by the strong dependence of this phylad for nocturnal pollination by, presumably, hawkmoths.

Backeberg (1960) recognized seven genera for the species here included in *Stenocereus*, but none of the segregates is strongly defensible. Both *Marshallocereus* and *Ritterocereus* are artificial phylads, composed of species from several separate lines, and *Hertrichocereus*, *Isolatocereus*, *Machaerocereus*, and *Rathbunia* are extreme forms. For example, *Hertrichocereus* (= *S. beneckeii*) has markedly glaucous stems, and *Isolatocereus* (= *S. dumortieri*) has flowers produced for long distances from shoot tips. Such segregates tend to confuse workers not familiar with cactus taxonomy and overemphasize differences between species, obscuring the fact that they are monophyletic. We support Buxbaum's (1963d) conclusion that such names are unnecessary and should not be used.

The genus *Pachycereus* has been difficult to circumscribe since Britton & Rose (1909) first proposed it to include arborescent cacti with trichome-covered flowers and burlike fruits. Their treatment of *Pachycereus* in 1920 recognized ten species in a more broadly defined genus. Since 1920 various workers have shown that their genus was artificial; *P. orcuttii* is really an intergeneric hybrid between *P. pringlei* and *Bergerocactus emoryi* (McGill & Pinkava, 1974; Moran, 1962a, 1963); *P. columna-trajani* and *P. ruficeps* are synonyms of species belonging to other genera of Britton and Rose; and *P. chrysomallus* of Britton and Rose is the plant now recognized as *Mitrocereus fulviceps*, which was inadvertently included in synonymy of another distinctive species, now called *Backe-*

bergia militaris (Sánchez Mejorada, 1973b). Two other species have been removed from *Pachycereus* by most authors and assigned to *Pterocereus* or to *Pterocereus* and *Anisocereus* (Backeberg, 1960) or *Escontria* (Buxbaum, 1970a). *Lemaireocereus hollianus*, the type of its genus, has been transferred to *Pachycereus* by Buxbaum (1961), especially on seed characteristics, and *P. marginatus* has been transferred to *Lemaireocereus* (Berger, 1929) and to *Stenocereus* (Buxbaum, 1961). Another arborescent species, *L. weberi*, has been placed in *Pachycereus* by Backeberg (1960). Therefore, only three species, *P. grandis*, *P. pecten-aboriginum*, and *P. pringlei*, have consistently been retained in the genus.

Confusion on the generic limits of *Pachycereus* can be resolved only after the phylogenetic relationships of the species are clearly understood. The genus is composed of several divergent phylads; consequently, no set of taxonomic features satisfactorily defines the genus. Species appear to lack crystals in the skin, and they have stem alkaloids that form red and then black pigments after wounding. Moreover, all species have large black shiny seeds, generally with a conspicuous raphe. The two species that lack stem mucilage, *Pachycereus hollianus* and *P. marginatus*, also are the only species in the subtribe that have outer epidermal-cell horns, a feature found only in the other subtribe in *Myrtillocactus* and *Escontria*. Although this feature may have evolved convergently, it is more likely that it developed in parallel from a common ancestor. These two species of *Pachycereus* are not similar in vegetative morphology or anatomy, but the flowers are closely similar, having very short perianth parts that barely extend beyond the floral tube, and the floral tube and pericarpel have axillary tufts of tannish trichomes. Especially *P. hollianus* has prominent bristles at anthesis, the ones in *P. marginatus* appearing only on the floral tube. The mature growth form (Backeberg, 1960) and skin anatomy of *P. marginatus* resemble those in *P. weberi*, which is the most massive Mexican cactus. In this regard and in the presence of some mucilage cells in the cortex, *P. weberi* is more highly derived. The flowers of *P. weberi* are funnelform with a conspicuous white perianth, and with axillary tufts of tannish trichomes and bristles. Both *P. marginatus* and *P. weberi* bear flowers far down the ribs from the shoot tips, and the flowering areoles typically bear numerous gray white bristles, an uncommon feature in Pachycereeae, otherwise found only in *Lophocereus*. Stem anatomy of *P. weberi* is extremely similar to that of *P. pecten-aboriginum* and *P. pringlei*, but in *P. pringlei*, as in *P. grandis* and *P. pecten-aboriginum*, the flowers generally have conspicuous tufts of tan axillary trichomes. The latter two species have bristles at anthesis, which are generally lacking at anthesis in *P. pringlei*. The seeds are very large, black, and glossy in the four largest species of the genus; and in *P. grandis*, *P. pecten-aboriginum*, and *P. pringlei* the fruits are burlike, covered with golden trichomes and long stiff bristles. In both *P. marginatus* and *P. weberi* the trichomes and bristles are deciduous at maturity, but in *P. hollianus* both spines and bristles are retained at maturity.

Closely related to *Pachycereus*, in particular to *P. marginatus*, are the two species of *Lophocereus*, *L. gatesii*, and *L. schottii*. The growth habit of *L. schottii* can be obtained by shortening the base of a mature specimen of *P. marginatus*. All aspects of the external shoot morphology show the clear relation-

ships of these two genera. Flowers of *Lophocereus* differ from those of *Pachycereus marginatus* in being smaller, more numerous per areole, and adapted for nocturnal pollination, probably by hawkmoths, whereas flowers of *P. marginatus* are pollinated in the day by hummingbirds. The fruits of *Lophocereus* are almost spineless, yet the seeds within the red pulp are strikingly similar to those of *P. marginatus*. With all of these features in common, the occurrence of the same alkaloid in only these taxa is convincing proof of their relationship, even though the epidermis differs just as it differs between *Polaskia* and *Myrtillocactus*. Stems of *Lophocereus* do not blacken after wounding.

Backebergia militaris is tentatively recognized in this treatment as a distinct genus but has not been anatomically or biochemically studied. Strong similarities in growth habit, external shoot morphology, and flower and fruit structure (Bravo, 1961; Buxbaum, 1975b) between *B. militaris* and *Pachycereus* not only show a relationship but raise the question whether the species cannot be included in *Pachycereus*. The flowers and fruits have numerous long bristles and golden trichomes, but as in no other species of *Pachycereus*, the flowers are borne terminally within a dense crown of golden spines.

Pachycereus gaumeri and *P. lepidanthus* have been moved to other genera (see Glass & Foster, 1973) because the floral tube of each is covered with prominent leaflike scales. In *Pterocereus gaumeri*, the stems have three or four high, very acute ribs bearing widely spaced areoles with a few short spines, and the stem has a thin, crystalless skin and a densely packed, nonmucilaginous cortex, similar to that of *Pachycereus marginatus* and *Polaskia*. In *Anisocereus lepidanthus*, the stems have seven to nine extremely low ribs, with closely spaced areoles and conspicuous thin spines, and the stem is nonmucilaginous but less compact, appearing more like stems of *Cephalocereus*. Moreover, *A. lepidanthus* has prismatic crystals in the skin. For these reasons we have chosen to segregate these species from *Pachycereus* and from each other as two genera, *Pterocereus* and *Anisocereus*. Though these species probably share some common ancestry, the gap between them is difficult to determine without adequate data on flowers, fruits, seeds, and stem chemistry. If they do belong to Pachycereeae, they certainly are older derivatives than any other extant genus. Buxbaum (1961) expressed the same point of view when establishing the primitive subtribe Pterocereinae to include these species. However, he made this decision because of leafy appendages on the floral tube, feeling that a leafy floral tube must be the primitive condition. On the contrary, there is no convincing evidence that the tribe arose from ancestors with floral tubes having very large leaves, and it is probable that increased leafiness is correlated with dependence on nocturnal pollination by bats, especially in *Pterocereus*, in which flowers are dull in color and produce fetid nocturnal odors (Glass & Foster, 1973).

Sorting out the relationships and phylogeny of the remaining species is not completely possible at this time because data on stem chemistry and stem anatomy are unavailable for most species. *Carnegiea gigantea* seems closely related to *Pachycereus* when chemical data are used but more closely related to *Neobuxbaumia* based on similarities in growth habit, vegetative morphology, and flower and fruit structure. Not surprisingly, several species of *Neobux-*

baumia have *Pachycereus* synonyms, and the only other species ever placed in *Carnegiea* was *N. euphorbioides*. *Carnegiea* has traditionally been considered a very isolated genus, unrelated to any sympatric species in the Sonoran Desert. Workers should have compared features in *C. gigantea* with those of *N. mezcaltensis* and *N. tetetzo*, whose vegetative and reproductive structures are remarkably similar to *Carnegiea* except that these species of *Neobuxbaumia* have slightly smaller flowers and fruits. On the mature fruits, both *C. gigantea* and *N. tetetzo* have a conspicuous ring of white trichomes at the base, small persistent tufts of white areolar trichomes, and a few, hardly noticeable whitish bristles. Moreover, seeds of *Carnegiea* and *Neobuxbaumia* are relatively small and glossy black to reddish black, and the testa is noticeably thin in comparison to those of other cactus seeds. *Neobuxbaumia polylopha* has most unusual reddish purple, strongly angular flowers with pronounced podaria that function as external nectaries. Certainly Dawson (1952) was correct in pointing out the closeness of *Carnegiea* and *Neobuxbaumia*.

Mitrocereus fulviceps resembles *Backebergia*, *Neobuxbaumia*, and *Pachycereus* in growth habit and rib features; and the stem anatomy is not unlike that of *Neobuxbaumia*, although *M. fulviceps* has fewer epidermal cells with crystals and great densities of crystal aggregates in the pith and cortex. However, the reproductive features of *Mitrocereus* show no close relationships to any single genus. The flowers are extremely wide and are similar in longisection to those of *Cephalocereus senilis*; but the pericarpel has copious shaggy trichomes and flexible golden bristles more typical of *Backebergia*. Fruits split open in the same fashion as *Carnegiea* and *Neobuxbaumia*, and the pulp is white and of the same consistency as in certain species of *Neobuxbaumia* but not *Carnegiea*. Seeds closely resemble those of *Backebergia* and *P. hollianus*. Based on these meager superficial comparisons, phylogenetic placement of *Mitrocereus* is most defensible between *Backebergia* and *Neobuxbaumia*, near the divergence of Mexican species of *Cephalocereus*.

Classification of species currently assigned to *Cephalocereus* and its numerous segregate genera is still a major unresolved systematic problem. As a single genus, in which species typically have unarmed flowers and fruits and flower-bearing areoles with long wooly trichomes, the type is *C. senilis*. This species is highly derived, with a solitary columnar arborescent growth habit and a large lateral pseudocephalium in which the flowers are produced. Observations in this study indicate that all eight species of cephalocerei, including the type and *C. hoppenstedtii*, its closest relative, but excluding *C. russelianus*, have numerous small prismatic calcium oxalate crystals in each epidermal cell, regardless of the features of the external shoot. This crystal pattern also occurs in *Neobuxbaumia* and, to a lesser degree, in *Mitrocereus*. We conclude that *Cephalocereus* should include those species of cephalocerei from mainland North America, the West Indies, and coastal northern South America that have this crystal pattern. We cannot determine whether *C. russelianus* and its relatives are a related South American phylad. Because most species of cephalocerei were not examined in this study, we cannot determine whether certain South American taxa, particu-

larly species in Brazil, belong to this tribe. Buxbaum (1958a, 1968d) has concluded that these species belong in tribe Cereeae and not in Pachycereeae.

Authors have the choice of emphasizing differences or similarities, with liberal or conservative schemes, respectively. We feel use of too many generic names confuses the reader by overstating the importance of small differences in cactus structure. In a very liberal classification of cactus genera one loses appreciation for the interrelationships of taxa by segregation without significantly improving their systematics. Conversely, use of a single genus, *Cereus*, for all columnar cacti obscures interesting evolutionary trends. Even though sufficient comparisons between North and South American species have not been presented here, it is clear that for Mexican species, gaps between phyletic lines, based on morphology, anatomy, and biochemistry, are as evident as between genera and subtribes in other plant families. A single genus for all columnar cacti is therefore not systematically justifiable, and we recommend the abandonment of the name *Cereus* for Mexican species.

PHYLOGENY OF MEXICAN PACHYCEREEAE

The most useful phylogeny of Pachycereeae has been that of Buxbaum (Fig. 33), who employs data on stem triterpenes, funicular pigments, and seed morphology to assign genera to the tribe. Evidence summarized here supports the following conclusions of Buxbaum: (1) *Polaskia chende* (syn. *Heliabravo*), *P. chichipe*, and *Myrtillocactus* are closely related, and *P. chende* has retained many primitive features; (2) *P. chende* is closely related to *Stenocereus*, particularly *S. stellatus*, and *Pachycereus*, especially *P. hollianus*; (3) *Machaerocereus* is directly derived from *Stenocereus*; (4) species of *Stenocereus* from the West Indies and Central America are derived from southern Mexican taxa (Buxbaum, 1963b); and (5) *Anisocereus lepidanthus* (as *Escontria* in Buxbaum, 1970a), *Pachycereus marginatus*, *Pterocereus gaumeri*, and *Stenocereus stellatus* are all old taxa of the tribe. Buxbaum (1963b) has also concluded with ample justification that *Hertrichocereus*, *Marshalllocereus*, and *Ritterocereus* of Backeberg (1960) are unnecessary segregates of *Stenocereus* because these genera are too narrowly defined. Data presented here do not support Buxbaum's placement of *Stenocereus benecke* next to either *Pachycereus weberi* or *Lophocereus*; of *P. weberi* very close to *Carnegiea gigantea* (Buxbaum, 1963b); of *Pachycereus* as nearest neighbor to *Mitrocereus*; of *Stenocereus dumortieri* near *Pachycereus marginatus*; or of *P. weberi* and *P. marginatus* in *Stenocereus*. Moreover, *Escontria* sensu Buxbaum (1970a) is artificial, misinterpreted from similarities of primordia on the floral tube. Although Buxbaum has never emphasized presence of stem triterpenes and funicular pigment cells to construct subtribal phylogenies, in his diagram all of these genera are directly connected except *Escontria* (Fig. 33). According to his phylogeny, it follows that species lacking triterpenes have evolved from triterpene-bearing species numerous times.

In order to construct phylogenetic systems, authors must propose and justify what are the primitive features for the higher taxonomic subdivisions. Characters of nonsucculent species of *Pereskia* are presently regarded as primitive for cacti as a whole (Gibson, 1975), and if Pachycereeae are directly or indirectly related

to the pereskias, one must expect that relatively nonxeromorphic features are primitive for columnar cacti, i.e., very thin cuticle; little or no hypodermis; no mucilage structures in the cortex, pith, or flowers; few, if any, crystals; narrow pith; and highly lignified wood; and the stem would probably have few ribs because at some time in the past the line arose from cylindrical stems. The plants should have the growth habit of a "normal" small tree, as in *Pereskia*, and have few spines that are not strongly dimorphic. All these features sharply describe *Polaskia chende*, which we regard as the closest extant species to the ancestral stock. Interestingly, *P. chende* has a growth habit, flowers, and fruits that are intermediate in characters between *Stenocereus* in subtribe Stenocereinae and *Pachycereus* in Pachycereinae. Moreover, the triterpenes present in stems of *P. chende* are biochemically very simple in comparison to compounds found in the rest of the subtribe.

Any feature regarded as primitive may be secondarily derived in other species. The single evolutionary trend that appears to be unidirectional in Pachycereeae is the acquisition of abundant mucilage cells from nonmucilaginous forms. Based on intuitive reasoning, one expects that mucilage is so important to a succulent plant that, once attained, this feature with associated anatomical structures is difficult to eliminate through natural selection. Interestingly, the absence of stem mucilage in species of Pachycereeae is usually correlated with thin hypodermis, narrow pith, and relatively few ribs, but some species with thin hypodermis or few ribs are found to have abundant mucilage. Therefore, the character of mucilage cells probably is not directly linked to other morphological features, at least in columnar cacti.

When all the phylads described and justified in the previous sections are brought together and species which lack mucilage are placed near the base of a phylogenetic tree (Fig. 34), a great number of taxonomic problems may be resolved. For example, *Pachycereus hollianus*, *P. marginatus*, and *P. weberi* have been assigned in the past by various authors to *Lemaireocereus* or *Stenocereus*, and by their position one can see that they are, indeed, fairly closely related to *Stenocereus*. Similarities between growth habits of some taxa are observed between early phylads of the closely related subtribes, thus giving some justification for using growth habit in classification of these plants.

EVOLUTIONARY TRENDS OF FEATURES WITHIN PACHYCEREEAE

If the proposed phylogeny is accurate, the following points may be advanced to explain diversity of features within the tribe Pachycereeae.

1. Stem chemistry. The presence of abundant triterpenes and alkaloids in cacti has probably served throughout time to discourage foraging on succulent tissues by animals. Living specimens of columnar cacti of Mexico, even those with few spines, are generally not food plants for vertebrate predators (Kircher & Heed, 1970). Cactophilic species of *Drosophila* are found only in rotting parts of cacti, not in uninfected tissues. One may wonder whether secondary plant substances are in any way able to inhibit the growth of microorganisms, providing a defense primarily against bacteria and fungi. Unfortunately, sufficient data are not available to determine whether diversity of compounds is a response

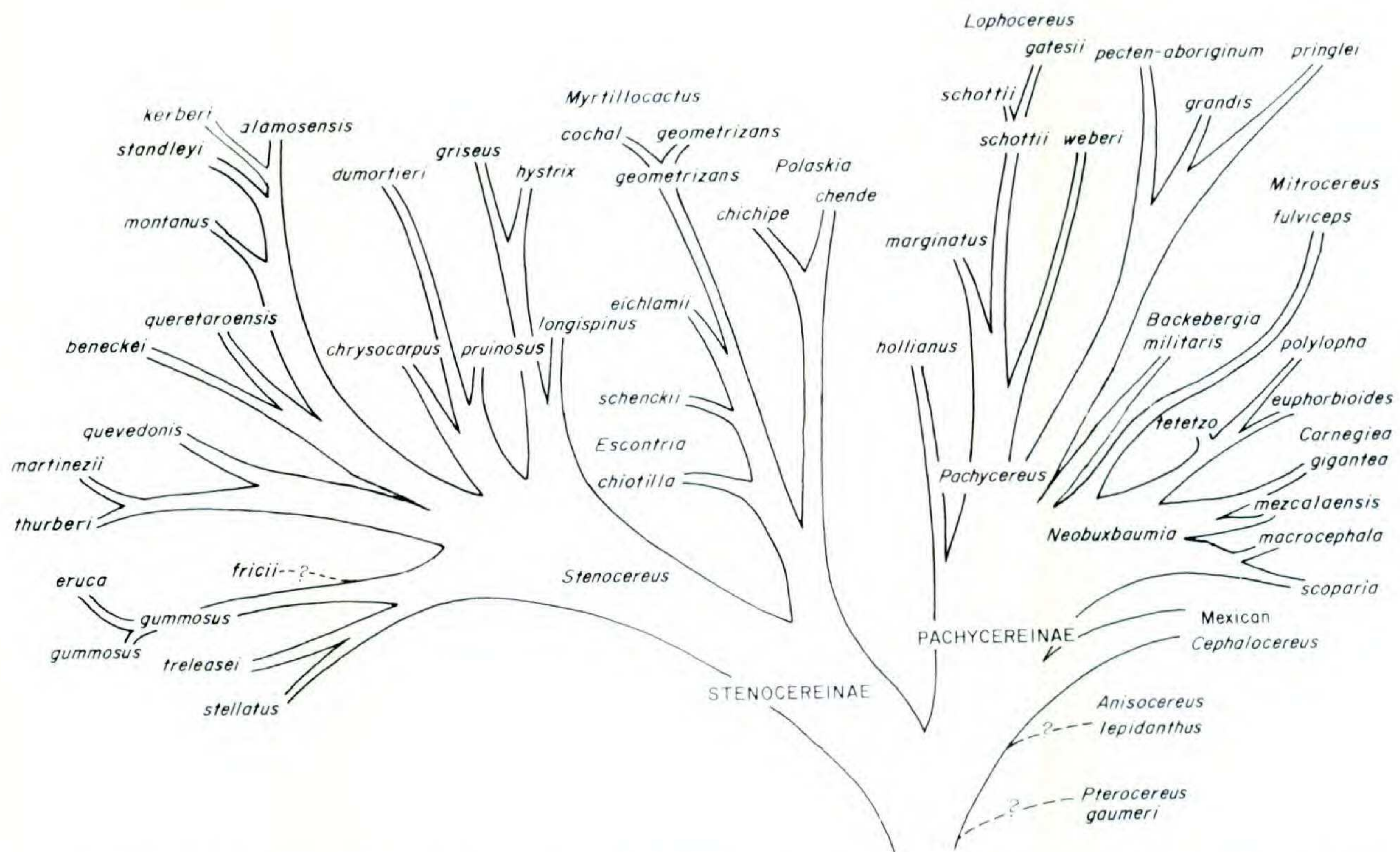


FIGURE 34. Proposed phylogeny of Mexican Pachycereae (excluding poorly known species) based on current observations. Steps used in the construction of the phylogeny are those outlined by Throckmorton (1965) for *Drosophila*. In this phylogeny, primitive features are found closest to the center of the phylogenetic tree. Primary variables stressed in this phylogeny are stem chemistry, funiculus pigmentation, seed morphology, growth form, rib morphology and anatomy, and flower morphology.

through natural selection for better defense against microorganisms or insects. However, it is clear from other summaries on plant chemicals (Hegnauer, 1963, 1964, 1966) and Ponsinet et al. (1968) on cactoid Euphorbiaceae that triterpenes are particularly common in many stem and leaf succulent angiosperms, another example of convergent evolution of succulent plants. Presence of abundant alkaloids may be linked to rapid callus formation after wounding.

2. Growth habit and form. Tall tree species have evolved apparently in response to bat pollination in both subtribes, whereas shorter growth habits seem to have evolved for pollination by hummingbirds or hawkmoths. In Pachycereinae taller species have evolved through an increase in length of the trunk, an increase in the erectness and length of primary branches, and a decrease in the number of secondary branches. In Stenocereinae, some species have converged to arborescent forms with shorter trunks and narrower stems than arborescent Pachycereinae. Species shorter than their original stock have mostly arisen by a decrease in the length of the trunk and of primary branches.

Species with the primitive features tend to have relatively few, acute ribs, whereas more specialized growth habits tend to have rounded ribs that range in number from four to more than 50. This diversity is attributable to at least two major factors. Firstly, number of ribs is partially determined by the diameter of the stem, which is strongly correlated with plant height. Therefore, the

thicker the stem, the more ribs that are needed to cover the surface. This increase in rib number is certainly influenced by changes in phyllotactic patterns on the shoot apex. Secondly, rib number and stem thickness have been shown to be adaptations of plants to different geographical situations (Felger & Lowe, 1967). Populations of a single species vary widely in rib number, and those in the coldest (or highest latitudes) habitats tend to have the lowest surface-volume ratio to protect adult plants or seedlings against low winter temperatures. No one has tried to explain what determines the highest ratios in southernmost habitats. One cannot wholly discount that there may be advantages for carbon fixation and water conservation in certain growth forms or habits. Ribs do, of course, increase the photosynthetic area of the stem but at the same time decrease the amount of stem illuminated with direct sunlight because of the shadow effect. On the other hand, valleys between ribs may have thicker boundary layers and slightly cooler temperatures and, therefore, lower transpiration rates. Ribbing of the stem is important to accommodate diurnal (Schroeder, 1975) and seasonal (MacDougall & Spalding, 1910) expansion and contraction of the stem. Therefore, differences in rib number and stem thickness between closely related species may be a physiological response to different regional climates.

3. Spination of ribs. Length and strength of spines have generally increased in the highly specialized Pachycereeae; species with primitive features tend to have few, short spines.

4. Stem succulence and mucilage production. All species in the tribe have abundantly succulent stems, but there is also a trend for the increase in diameter and starch-storing ability of the pith. Moreover, within each subtribe mucilage production has evolved first in the cortex and then in the pith, with an overall increase in the amount in the main stem cortex and ribs. Especially in Pachycereinae, increase in size of pith is closely correlated with increase in plant height and total stem diameter.

5. Skin. On a broad scale, relative thickness of the cuticle is unreliable for predicting whether a species grows in an arid or semiarid habitat. Species with vastly different skin thicknesses are sympatric, e.g., in the Sonoran Desert; rather, trends in cuticle thickness appear to follow systematic lines. Sampling here is insufficient to determine evolutionary changes in cuticle thickness within phyletic lines or in different habitats for a single species, but in a study with adequate sampling (Conde, 1975), no trend in cuticle thickness was observed in populations of five species of *Opuntia*.

Glaucous stems have evolved convergently several times within Pachycereeae and numerous other times in other Cactoideae. Occurrence of glaucous stems is not correlated with specific habitats.

In several Pachycereeae, especially relatively old taxa, epidermal cells proliferate to form a minutely bullate surface. This feature is found at the base of our phylogenetic tree in both subtribes. Other early lines have horns on the outer epidermal walls, a feature not known in other Cactaceae.

Unlike other xerophytes, columnar cacti generally do not have sunken stomates. Only in several species are the stomates well below the level of other epidermal cells, particularly species with very thick cuticle. Pachycereeae are

probably CAM plants (not yet demonstrated) so that retaining stomates at the level of the stem surface may facilitate gaseous exchange during periods of nocturnal carbon fixation.

Thickness of the skin varies greatly within Pachycereeae and even within a single species. One clear evolutionary trend is an increase in thickness of the skin, especially the hypodermis, within each subtribe. However, species with vastly different thicknesses are often sympatric, suggesting that thickness alone is not an ecological adaptation. Skin is obviously important to deter predators, to conserve water, and to insulate the plant. Therefore, we would expect that certain physiological properties of the skin have also evolved in this tribe, e.g., the ability of protoplasts and proteins to withstand very high temperatures. One might also expect to find that the physiological ability of seedlings and mature plants to withstand coldest winter temperatures has evolved in the tribe.

Many species have crystals in the skin, probably as a mechanical deterrent to herbivores to increase the toughness and reduce the palatability of the skin. Because these crystals presumably arose millions of years ago, speculation as to the probable herbivores excluded is unwarranted. Crystals certainly can interfere with feeding of insects with chewing or sucking mouth parts. Diversity of patterns within phylads sheds no light on the probable functions of these crystals but does serve as a useful systematic tool.

6. External morphology and size of flower. As pointed out in a previous section, divergence in floral design is one of the most conspicuous evolutionary trends in Pachycereeae. These species seem to have depended on relatively large, highly mobile animal vectors for outcrossed pollination throughout their evolutionary history. The result has been a radiation of floral designs in each subtribe. In addition to visitation by small insects, members of this tribe are undoubtedly attractive to bats, hummingbirds, or hawkmoths.

Flowers of Pachycereeae with the primitive features are generally 4–5 cm long and have a relatively small ovary at anthesis. Flower size has generally increased in nearly all phylads with concomitant increases in numbers of anthers and stigma lobes and size of ovary and locule. Nevertheless, there are no unidirectional trends in the evolution of flowers, and development of features appropriate for one type of pollinator appears to have been opportunistic and not predetermined by the structure of the stock. Flowers of *Myrtillocactus* and *Lophocereus* certainly show a reduction from the primitive size, and these genera have also converged to produce more than one flower per areole.

7. Seeds. Seed size and testal morphology range widely within the tribe, but features are fairly constant within genera. The smallest seeds in each subtribe tend to occur in the species with other primitive features. Buxbaum (1955) has previously observed that seeds of this tribe lack perisperm and endosperm and that evolution of the embryo has been toward an increase in succulence of the hypocotyl-root axis and a reduction in size of the cotyledons. The increase in seed size is therefore related not only to attraction of bird dispersers for the seeds but also to an increase in embryo size which improves chances of seedling establishment. Fruits that split open at maturity are certainly adapted to attract

animals toward the dark colored seeds, some of which are very large, as in *Mitrocereus* and *Pachycereus*.

EVOLUTIONARY HISTORY OF PACHYCEREEAE

The probable center of origin of Mexican Pachycereeae appears to have been southern Mexico. Over half the Mexican Pachycereeae occur in Puebla and Oaxaca, and all the species whose stems lack mucilage cells and have a thin hypodermis occur in this same region and in neighboring states to the south. Moreover, the least specialized features of a genus or phylad occur near or in Puebla or Oaxaca, and the most specialized, such as the most mucilaginous stems, are farthest away. Lines of speciation radiate out from southern Mexico into northwestern mainland Mexico and Baja California and into the West Indies. For example, a group of species with red glandular areolar trichomes has evolved in Nueva Galicia and on the western side of the Sierra Madre Occidental. Therefore, the ten species of columnar cacti that occur in the Sonoran Desert are highly derived end products of a variety of phylads from the south, and the sympatric species are not closely related.

At least one author (Friedrich, 1974) has suggested that interspecific hybridization has been an important evolutionary factor in Cactaceae, but this is probably not the case for tribe Pachycereeae. The genera defined here do not include species with abnormal characteristics that might have come from unrelated taxa; rather, each phylad appears to have produced species via allopatric speciation. Two naturally occurring hybrids, \times *Pachgerocereus orcuttii* (Moran, 1962a), from *Pachycereus pringlei* and *Bergerocactus emoryi* and \times *Myrtgerocactus lindsayi* (Moran, 1962c, 1963) from *Myrtillocactus cochal* and *B. emoryi* are evolutionary deadends with very limited distributions, and *Lemaireocereus thurberi* var. *littoralis*, whether or not it is a hybrid, is also very restricted. Less than one-third of the Mexican columnar cacti have been cytologically examined, but from data already collected, polyploidy appears to be uncommon in these species. Therefore, one may assume that changes in base number and in level of ploidy have not been important in the evolution of these columnar species.

Although cacti in general are noted for their ability to root from stem cuttings, most Pachycereeae reproduce in nature only from seeds. No studies have determined whether seeds of these species are ever apomictic.

Several authors (Axelrod, 1960, 1970; Turner, 1972) have suggested that cacti in general and Mexican columnar cacti in particular have old, if not pre-Tertiary, origins. We feel that the family is probably no older than the Miocene, and certainly did not radiate significantly before the Miocene. Evidence for this conclusion must be indirect because verifiable fossils for this family are no older than the Late Pleistocene (ca. 30,000 yr; Van Devender, 1973), when many extant species are recognizable. When the family as a whole is analyzed, about 30% of the extant species, including five species of Pereskioideae, are autochthonous endemics of the Andean Cordillera, which arose only in the Miocene (Solbrig, 1976). Other recent habitats with endemic species are the islands off the coast of Mexico, the Galapagos Islands, and certain islands in the

West Indies. In addition, many of the North American species of Opuntioideae are obviously recent in origin, and *Mammillaria*, the largest cactus genus, with about 20% of the total species, has speciated predominantly in Mexico after very local geographical isolation. Very recent geographical isolation of populations has caused taxonomic problems for genera in North and South America for which no one can agree on the gaps between species. Bird dispersal of seeds from juicy fruits also has promoted geographical isolation of populations in this family. Moreover, once a cactus population is established, plants are likely to survive long periods because they are succulents or, in a few cases, they have the ability to reproduce apomictically. Cactus flowers are attractive to numerous pollinators because they have copious pollen and nectar; therefore, obtaining a new pollinator after arriving in a new area is probably not a major problem. In addition, a number of species appear to be self-compatible. Consequently, many aspects of these organisms are favorable for speciation.

Opinions that Mexican columnar cacti are bradytelic relicts certainly were based on and biased through analyses of the northernmost species, the ultimate derivatives of phylads derived from tropical southern Mexico. When the phylogeny is reconstructed using all available features, morphological gaps between species are small indeed; in fact, character evolution has been very gradual from one species to another. To account for the total number of Mexican Pachycereeae from an initial population, one can propose successful dichotomies on the average of every three million years. This amount of time for speciation is not only realistic but also, in some cases, overgenerous. Speciation in northern Mexico has been encouraged by geographical isolation from the south, e.g., *Carnegiea* and *Lophocereus*; during periods of climatic change, e.g., *Stenocereus alamosensis* and *S. thurberi*; or by habitat isolation within the Sonoran Desert, e.g., *L. gatesii* in southern Baja California. Analyses of paleofloras in Mexico may help us to make intelligent guesses on the age of habitats in which extant species occur and may suggest a time of radiation.

If the phylogeny presented here is relatively correct, flowers have converged a number of times to bat, hummingbird, and hawkmoth pollination since the radiation of the tribe in Mexico. The families of these animals that act as pollinating agents are mostly Tertiary in age, and, in some cases, probably post-Miocene, e.g., the phyllostomatid bats (Koopman & Jones, 1970). Because these cacti have radiated to utilize these large pollinators, it is not likely that the cactus radiation occurred before the pollinators were present. Other organisms that use cacti are species of *Drosophila*, which feed within the rots of columnar cacti and platyopuntias (Fellows & Heed, 1972; Richardson et al., 1977). Throckmorton (1975) suggested that the lineage giving rise to the cactophilic *repleta* and *nannoptera* groups arrived perhaps by mid-Oligocene and radiated later during Oligocene and Miocene times in mountains and developing deserts. Because species of *Drosophila* often feed on only one or a limited number of cactus species, it is reasonable to assume that the timing of the evolution of columnar cacti and their *Drosophila* was relatively synchronous.

Because few species of the West Indies and northern South America have been studied here, no conclusions on the phylogenetic relationships of tribe

Pachycereeae to other columnar forms is justifiable. Nevertheless, similarities observed in available materials suggest that Pachycereeae are most closely related to Browningeae and *Armatocereus* and *Samaipaticereus* (Leptocereeae), all of northwestern South America. *Armatocereus* is very close to Pachycereeae, but Mexican Pachycereeae are likely not closely related to the very specialized species of *Armatocereus* of Central America. We have no way to determine whether progenitors of Pachycereeae migrated through Central America to Mexico or seeds were long-distance dispersed from northern South America. Moreover, data are lacking to determine whether Mexican species of *Cephalocereus* have evolved directly from other Mexican Pachycereinae or originated in northern South America.

ADDENDUM: ADDITIONAL COLLECTIONS

In June, 1978, the senior author collected in Nueva Galicia, Mexico, seven more columnar cacti, including one genus and four species not sampled in the initial study plus three more collections of stenocerei. The additional species provide a test for predictions embodied in the proposed phylogeny.

Backebergia militaris (Gibson 3433, ARIZ). Stems eventually blackening when cut; skin hard, extremely brittle; epidermis uniseriate, covered by thick ($18\ \mu\text{m}$), rough cuticle; stomates not sunken; hypodermis thick ($380\text{--}450\ \mu\text{m}$); silica bodies and crystals absent in skin; outer cortex in ribs composed of radially elongate chlorenchyma, as in *Pachycereus*; mucilage cells abundant in ribs, cortex of axis, and pith; phloem fibers very late in development; starch storage mainly in pith.

Pachycereus grandis (Gibson 3440, ARIZ). Stems blackening immediately when cut; skin hard, brittle; epidermis biseriate, covered by very thick ($35\ \mu\text{m}$), rough cuticle; stomates slightly sunken; hypodermis thick ($400\text{--}460\ \mu\text{m}$); silica bodies and crystals absent in skin; outer cortex in ribs composed of markedly elongate chlorenchyma developing secondary walls in age; mucilage cells essentially absent; phloem fibers late in development; starch storage not abundant.

Neobuxbaumia mezcalaensis (Gibson 3412, ARIZ). Stems remaining green when cut; skin hard, brittle; epidermis uniseriate, covered by cuticle $3.5\ \mu\text{m}$ thick and thick epicuticular wax; stomates not sunken; hypodermis moderately thick ($150\text{--}210\ \mu\text{m}$); several small prismatic crystals of calcium oxalate in epidermis and solitary large ones in hypodermis, as in *Cephalocereus*; mucilage cells absent; phloem fibers apparently absent; starch storage abundant in cortex of axis and pith, starch grains largest in pith.

Stenocereus quevedonis (Gibson 3441). Stems turning orange when cut; epidermis mostly biseriate, covered by relatively thin ($3\ \mu\text{m}$), smooth cuticle; stomates not sunken; hypodermis moderately thick ($210\text{--}250\ \mu\text{m}$); silica bodies in epidermis ($3\text{--}6\ \mu\text{m}$) and hypodermis ($12\text{--}18\ \mu\text{m}$), resembling those of *S. thurberi*; mucilage cells large, not close to hypodermis, large and abundant throughout stem; starch storage dispersed throughout ground tissue.

Stenocereus kerberi (Gibson 3359, ARIZ); *Stenocereus* aff. *montanus* (Gibson 3381, ARIZ); and *S. pruinosus* (Gibson 3429, ARIZ). Features as described in text; silica bodies present in skin.

Backebergia militaris certainly belongs next to *Pachycereus*. The skin of *Backebergia* resembles those of arborescent *Pachycereus*, and the outer cortex has the distinctive elongate chlorenchymatous cells. However, unlike *Pachycereus*, *B. militaris* is highly mucilaginous. A relationship of *Backebergia* to *Lophocereus* is also undeniable. Not only do young stems of *Backebergia* have a similar external appearance and color in fresh-cut tissue but also the smell of fresh and rotting cortex is strongly reminiscent of *Lophocereus*. The eventual blackening of the stem of *B. militaris* is indicative of its inclusion in *Pachycereinae*. Presently, the chemistry of *B. militaris* is being studied by H. Kircher (sterols and fatty acids) and J. McLaughlin (alkaloids; many present).

These observations give further confidence to the previous treatment and discussion of other genera. No exceptions have been found where silica bodies are absent in any species of *Stenocereus*. Crystal patterns in *N. mezcalaensis* confirm its close relationships to *Mitrocereus* and *Cephalocereus*, and *Pachycereus grandis* has anatomical features common with *P. pecten-aboriginum* and *P. pringlei*.

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