×*Pachebergia* (Cactaceae), a nothogenus from western Mexico

×*Pachebergia* (Cactaceae), un notogénero del occidente de México

Salvador Arias^{1*} and Teresa Terrazas²

¹Jardín Botánico, Instituto de Biología, Universidad Nacional Autónoma de México, 04510 México D.F., México

²Departamento de Botánica, Instituto de Biología, Universidad Nacional Autónoma de México, 04510 México D.F., México

*Correspondent: sarias@ibiologia.unam.mx

Abstract. ×*Pachebergia* (*Backebergia* × *Pachycereus*), a new nothogenus from western Mexico, is proposed. Stem and seed morphology of this poorly known taxon from dry to very dry deciduous tropical forest in the Balsas River Basin, Guerrero, are described and illustrated. Its diagnostic morphological characters and relationships with *Pachycereus pecten-aboriginum* and *Backebergia militaris*, its putative parental taxa, are discussed.

Key words: *Backebergia*, Balsas River Basin, hybrid, new nothogenus, *Pachycereus*.

Resumen. Se propone un notogénero nuevo, ×*Pachebergia* (*Backebergia* × *Pachycereus*), del occidente de México. Se describen e ilustran los tallos y la morfología de la semilla de este taxón poco conocido de los bosques subhúmedos y deciduos de la cuenca del Balsas, Guerrero. Se discuten sus caracteres morfológicos diagnósticos y la relación con los supuestos taxones parentales, *Pachycereus pecten-aboriginum* y *Backebergia militaris*.

Palabras clave: *Backebergia*, cuenca del Balsas, híbrido, notogénero nuevo, *Pachycereus*.

Introduction

Reports of spontaneous intergeneric hybrids in cacti are uncommon, but now well documented (Rowley, 1994, 2004), and only 3 nothogenera have been described including columnar cacti of tribe Pachycereeae. The first of those involves a species of *Pachycereus* (A. Berger) Britton et Rose and *Bergerocactus* Britton et Rose from Baja California, with intermediate features between the massive tree-like *Pachycereus pringlei* (S. Watson) Britton et Rose and the shrubby *Bergerocactus emoryi* (Engelm.) Britton et Rose, called ×*Pacherocactus orcuttii* (K. Brandegees) Rowley (Moran, 1962a; Rowley, 1994). A second intergeneric hybrid involves *Bergerocactus emoryi* and *Myrtillocactus cochal* (Orcutt) Britton et Rose, also from Baja California (Moran, 1962b), called ×*Myrtgerocactus lindsayi* Moran. A third hybrid was reported by Glass and Foster (1964), and named ×*Myrtillenocereus*, from Hidalgo state, intermediate between *Myrtillocactus geometrizans* (Martius) Console and *Stenocereus dumortieri* (Scheidw.) Buxb.

Two of the well-known genera of tree-like cacti, often becoming massive, in western Mexico are *Pachycereus*, the cardones, and *Backebergia*, the tiponches, commonly present in dry to very dry tropical deciduous forest. *Pachycereus* occurs from northwestern Baja California state towards the western tip of the state of Chiapas, whereas *Backebergia* is restricted to the central western states of Guerrero, Michoacán, and the southwestern tip of Jalisco (Fig. 1; Cattabriga, 2004). Morphological and molecular data support the recognition of both genera as members of the subtribe Pachycerinae (Arias et al., 2003; Arias and Terrazas, 2006), with *Backebergia* sister to *Pachycereus* s.s.

During a field trip to the Balsas River basin in the summer of 2003, we noticed the existence of a single individual of a tree-like cactus resembling *Backebergia militaris*, but with only golden bristles on the tip of various branches (Mauseth et al., 2005). Vegetative characters were undoubtedly intermediate between 2 other species, *Pachycereus pecten-aboriginum* (Engelm.) Britton et Rose and *Backebergia militaris* (Audot) Bravo ex Sánchez-Mej., species that grow sympatrically on slopes in surrounding deciduous tropical forest. Comparative

Figure 1. Distribution in western Mexico of *Pachycereus pecten-aboriginum* (triangles), *Backebergia militaris* (circles), and *xPachebergia* (star).

analysis of vegetative and seed morphology of the hybrid and the putative parents is presented.

Material and methods

We revisited the area a number of times between 2003 and 2005 to study the habitat, to search for additional individuals of the hybrid, to determine what species coexist with the hybrid as possible parents, and to locate other sites with similar associations to find new hybrid plants. Morphological features and distribution of *Backebergia* and *Pachycereus pecten-aboriginum* were compiled from fieldwork and supplemented with herbarium material from CHAPA, IBUG, MEXU, NY (Arias et al., 2003; Arias and Terrazas, 2006).

A comparative study of seed morphology of the hybrid and its parents was carried out. For observations with SEM, seeds were removed from fruit and subsequently washed. The dried samples were sputter coated with gold and observed in a SEM (JEOL-JSM-5310LV) microscope. The descriptive seed terminology follows Barthlott and

Hunt (2000) and the mean values are given for seed length and width, and hilum-micropylar region length. No germination experiments were carried out because most species of *Pachycereus* do not germinate if they are stored for more than 15 days under laboratory conditions (Loza-Cornejo, unpublished data), and this was the case with the hybrid since we stored seeds more than 2 months before starting our description.

Results and discussion

According to the morphological characters the plant collected is probably a first generation hybrid, with characters that are intermediate with respect to those exhibited by the parents. In particular, non-reproductive stems (habit, stem color, branch arrangement, and spines) closely resemble those of *Pachycereus pecten-aboriginum* (Fig. 2a, d, g), and reproductive branches seem to be relatively similar to those of *Backebergia militaris* (Fig. 2c, f, i; Table 1).

Backebergia militaris and *Pachycereus pecten-*

Figure 2. Growth habits and details of vegetative and fertile zones. a, *Pachycereus pecten-aboriginum*, adult plant, Michoacán state (Terrazas 466). b, *×Pachebergia apicicostata*, adult plant, Guerrero state (Terrazas 673). c, *Backebergia militaris*, adult plant with apical cephalia, Michoacán (Arias 1336). d, *Pachycereus pecten-aboriginum*, apex of vegetative zone, Jalisco state (Arias 1402). e, *×Pachebergia apicicostata*, apex of vegetative zone. f, *Backebergia militaris*, vegetative zone with constrictions, Michoacán state (Arias 1332). g, *Pachycereus pecten-aboriginum*, apex of fertile zone showing areoles connected by developed grooves, cultivated at Jardín Botánico UNAM. h, *×Pachebergia apicicostata*, apex of fertile zone. i, *Backebergia militaris*, fertile zone represented by typical apical cephalium, cultivated at Jardín Botánico UNAM.

aboriginum flowers are nocturnal and pollinated by bats. In the case of *B. militaris*, the flowers are nearly 4.2-5 cm long and covered by spines, bristles and trichomes of the fertile zone (cephalium) before anthesis; whereas flowers of *P. pecten-aboriginum* are slightly larger (7.2-9.5 cm) and uncovered in the fertile zone. Although flowers of the hybrid are unknown, we suppose that they are also nocturnal and bat pollinated.

Figure 3. Mature fruits in external view and longitudinal section exposing red, juicy pulp. a, *Pachycereus pecten-aboriginum*, Michoacán state (Arias 986). b, *×Pachebergia apicicostata* (Terrazas 673). c, *Backebergia militaris*, Michoacán state (Arias 1338).

The fruit size of the hybrid is intermediate between *B. militaris* and *P. pecten-aboriginum*, but fruit form and wall completely covered with yellow spines and trichomes are similar to those of *P. pecten-aboriginum* (Fig. 3; Table 1).

Table 1. Summary of the main differences among 3 taxa

Character	<i>Backebergia militaris</i>	<i>×Pachebergia apicicostata</i>	<i>Pachycereus pecten-aboriginum</i>
Branches			
number of ribs	9-11	7-9	8-10(-12)
areole size (mm)	3-5 x 3-4	6-8 x 4-5	7-11 x 4-9
interareolar distance (mm)	4-8	9-11	12-28
constrictions	with bark	absent	absent
Fertile zone			
vegetative structure	podaria	ribs	ribs
spines	all bristle-like	all bristle-like	some bristle-like, some rigid
spine color	yellow to black	yellow	brown to black
bark	present	absent	absent
Fruit			
size (cm)	2.1-3 x 1.4-2.1	2.8-3 x 3.2-3.4	4.3-5.5 x 4-6
spines and trichomes	not covering fruit wall	covering fruit wall	covering fruit wall
form	oblong	globose	globose
dehiscence	longitudinal	apical	apical
Seed			
size (mm)	3.8-5.1 x 2.5-3.8	4.3-4.7 x 2.6-3.4	3.3-4.7 x 2.2-3.4
anticlinal boundaries	evident	inconspicuous	inconspicuous

In addition the fruit developed in areole below the apical region where the areoles were covered by large bristles a pattern different from *B. militaris*, in which flowers and fruits always develop within the cephalium (Vázquez-Sánchez, 2001). The modifications observed in the apical region are intermediate with the ones occurring in the cephalium of *B. militaris*, lacking interareolar space and developing periderm.

The comparative seed morphology is also congruent with the hypothesis that *P. pecten-aboriginum* and *B. militaris* are the putative parents (Table 1, Appendix 1), because the seed is larger than 3 mm, oval to wide oval in the 3 taxa. Seeds of most species included in the genus *Pachycereus sensu* Barthlott and Hunt (1993) are larger than 3 mm, smaller in few species (Arias and Terrazas, 2004). Testa relief with flat walls is a common character in all species of Pachycereinae, as is the case in the hybrid herein described (Fig. 4), whereas species classified in Stenocereinae show convex relief in different degrees. Micro-relief is minutely rugose in *P. pecten-aboriginum*, in *B. militaris*, and in the hybrid, as in the other species of Pachycereinae, a clear difference with members of Stenocereinae, which show different degrees of striation probably of cuticular origin (Arias and Terrazas, 2004; Arroyo-Cosultchi et al., 2006; Barthlott and Hunt, 2000). Moreover, mean values for seed length and hilum-micropylar region (HMR) length are clearly intermediate and seed width larger in the hybrid than in the putative parents (Table 1, Appendix 1); however, the minimum and maximum seed values for the hybrid showed a narrower

interval than in the putative parents (Table 1).

The only other species of cacti which grow sympatrically with the hybrid and the putative parents are *Stenocereus fricii* Sánchez-Mej. and *S. queretaroensis* (F.A.C. Weber) Buxb. The possibility that either of these 2 species of *Stenocereus* could be one of the parents has been rejected, because the hybrid does not display any character that could be considered as intermediate between it and either species. These species of *Stenocereus* have seeds smaller than 3 mm with convex and striate relief (Arroyo-Cosultchi et al., 2006), and their stem architecture as well as their fruit form and spination are different (Arreola-Nava and Terrazas, 2003).

Based on these evidences we propose the following:

×Pachebergia S. Arias et Terrazas **nothogen. nov.** (*Backebergia* Bravo × *Pachycereus* (A. Berger) Britton et Rose)

Genus hybridum inter *Pachycereum* (A. Berger) Britton et Rose et *Backebergiam* Bravo intermedium.

×Pachebergia apicicostata S. Arias et Terrazas **nothosp. nov.** (*Backebergia militaris* (Audot) Bravo ex Sánchez-Mej. × *Pachycereus pecten-aboriginum* (Watson) Britton et Rose).

Planta arborescens, ramis ad 4 m altis, sine peridermide in crescentiae constrictionibus; areolae 6-8 mm longae, 4-5 mm diametro, spinis radialibus 7-9, 1-1.6 cm longis, spina centrali 1, 1-2.5 cm longa. Zona fertilis distincta, 9-costata, spinis setosis numerosis, 3-5 cm longis,

Figure 4. Scanning electron microscope (SEM) photographs of complete seeds (left column) and cell shape in lateral region (right column). a, b, *Pachycereus pecten-aboriginum*. c, d, *Pachycereus pecten-aboriginum*. e, f, *Backebergia apicicostata*. Scales: a, c, e = 1 mm; b, d, f = 50 μ m.

flavis, apicem ramorum obtegentibus; areolae intervallo separatae.

Type: MEXICO. Guerrero: Mun. Coyuca de Catalán, ca. 30 km southwest of Ciudad Altamirano, in tropical deciduous forest, 300 m, 25-May-2003, T. Terrazas, S. Arias, M. Vázquez, and J. Mauseth 673 (holotype: MEXU; isotype: CHAPA). Figures 2b, e, h, and 3b.

Tree with few branches, 5 m tall; trunk well defined, 1 m tall, ca. 30 cm diameter, without spines. Branches of first order 4 m tall, 16-20 cm diameter, slightly arched at the base, dark green, the apex green glaucous when growing; constricted without bark; ribs 7-9, 3-3.5 cm high, angulate in cross section; areoles elliptic, 6-8 x 4-5 mm, distance between them 1-1.5 cm; radial spines 7-9, acicular, rigid, gray, divergent, 1-1.6 cm long; central spine 1, acicular, porrect, round, gray with black tip, 1-2.5 cm long. Fertile zone well differentiated in the taller branches; branches 15-18 cm diameter, dark green; ribs 9, 2-2.5 cm tall; areoles

orbicular, 8-10 x 7-9 mm, with abundant yellow trichomes 2 cm long; spines yellow, all bristle-like, abundant, with reddish base, 3-5 cm long, without color change up to the fertile zone; trichomes and bristles not covering the epidermis; interareolar spaces present. Flower unknown. Fruit globular, 2.8-3 cm long, 3.2-3.4 cm diameter; scales dry, black, 4 x 1 mm; areoles with abundant yellow trichomes and numerous yellow bristles 1.4-3.5 cm long; trichomes and bristles covering the epidermis; pulp red, scarce, dry at fruit maturity; seeds 4.40 x 3.25 mm, ovoid, black, glossy; testa with elongate cells, the periclinal wall flat, without micro-relief.

Additional specimens examined.

1. *Backebergia militaris* (Audot) Bravo. MEXICO. **Michoacán:** Buenavista Tomatlán, Terrazas 391 (CHAPA); La Huacana, Arias 1332, 1336, 1337, 1338, 1339 (MEXU). 2. *Pachycereus pecten-aboriginum* (Engelm.) Britton et Rose. MÉXICO. **Baja California Sur:** La Paz, Terrazas y Arias 478 (CHAPA). **Jalisco:** Autlán de Navarro, Arias y Gama 1402 (MEXU). **Michoacán:** Nocupétaro, Arias et al. 986 (MEXU); Apatzingán, Terrazas 466 (CHAPA). **Oaxaca:** Santo Domingo Tehuantepec, Arias 1353 (CHAPA); San Pedro Pochutla, Arias et al. 1351; Santa Jalapa, Arias et al. 1353 (MEXU). **Sinaloa:** El Fuerte, Arias et al. 1322 (MEXU); Huatabampo, Arias et al. 1321 (MEXU). **Sonora:** Álamos, Terrazas et al. 419a, 419b (CHAPA); Guaymas, Terrazas et al. 415 (MEXU).

Acknowledgements

To Fernando Chiang for Latin translation and useful comments, and Michael Nee for his revision and nomenclatural comments. Field work was supported by Consejo Nacional de Ciencia y Tecnología grant 33064-V (T.T.). We are grateful to Gabriel Arroyo-Cosultchi for assistance with seed data, to Berenit Mendoza for SEM, Susana Gama for maps, and Julio César Montero for art work.

Literature cited

Arias, S. and T. Terrazas 2004. Seed morphology and variation in the genus *Pachycereus* (Cactaceae). Journal of Plant

- Research 117:277-289.
- Arias, S. and T. Terrazas. 2006. Análisis filogenético con base en caracteres morfológicos en *Pachycereus* (Cactaceae). *Brittonia* 58:197-216.
- Arias, S., T. Terrazas and K. Cameron. 2003. Phylogenetic analysis of *Pachycereus* (Cactaceae, Pachycereeae) based on chloroplast and nuclear DNA sequences. *Systematic Botany* 28:547-557.
- Arreola-Nava, H. J. and T. Terrazas. 2003. Especies de *Stenocereus* con aréolas morenas: clave y descripciones. *Acta Botanica Mexicana* 64:1-18.
- Arroyo-Cosultchi, G., T. Terrazas, S. Arias and H. J. Arreola-Nava. 2006. The systematic significance of seed morphology in *Stenocereus* (Cactaceae). *Taxon* 55:983-992.
- Barthlott, W. and D. R. Hunt. 2000. Seed diversity in the Cactaceae subfamily Cactoideae. *Succulent Plant Research* 5:1-173.
- Cattabriga, A. 2004. *Backebergia militaris*. *Cactus and Company* 8:131-162.
- Glass, C. and R. Foster. 1970. Mexico logbook. *Cactus and Succulent Journal* (Los Angeles) 42:268.
- Mauseth, J. D., T. Terrazas, M. Vázquez-Sánchez, and S. Arias. 2005. Field observations on *Backebergia* and other cacti from Balsas Basin, Mexico. *Cactus and Succulent Journal* (Los Angeles) 77:2-13.
- Moran, R. 1962a. *Pachycereus orcuttii* – a puzzle solved. *Cactus and Succulent Journal* (Los Angeles) 34:88-94.
- Moran, R. 1962b. The unique *Cereus* of Rosario Bay. *Cactus and Succulent Journal* (Los Angeles) 34:184-188.
- Rowley, G. 1994. Spontaneous bigeneric hybrid in Cactaceae. *Bradleya* 12:2-7.
- Rowley, G. 2004. Intergeneric hybrid in Cactaceae - 2004 update. *British Cactus and Succulent Journal* 22:64-65.
- Vázquez-Sánchez, M. 2002. El cefalio de *Pachycereus militaris* (Audot) Hunt (Cactaceae): morfología y anatomía. Tesis, Facultad de Estudios Superiores de Iztacala, Universidad Nacional Autónoma de México. Tlalnepantla, Estado de México. 48 p.

Appendix 1. Seed morphology descriptions

Pachycereus pecten-aboriginum (Fig. 4a, b) (Arias 986 MEXU; Terrazas 415, 419a, 419b 478 CHAPA). Seed oval, 3.35-4.78 x 2.24-3.44 mm, black-brown, glossy, the periphery slightly keeled; border slightly expanded around hilum; cells gradually smaller toward hilum, in lateral region isodiametric-polygonal, anticlinal boundaries inconspicuous, straight; interstices uncommon on lateral region, minutely pitted in peripheral regions; relief flat; micro-relief minutely rugose; HMR medium size, 1.34-2.27 mm, oblique, superficial.

×Pachebergia apicicostata (Fig. 4c, d) (Terrazas et al. 673 MEXU). Seed oval, 4.30-4.78 x 2.64-3.46 mm, black-brown, glossy, the periphery slightly keeled; border slightly expanded around hilum; cells gradually smaller toward hilum, in lateral region isodiametric-polygonal, anticlinal boundaries inconspicuous, straight; interstices uncommon on lateral region, minutely pitted on peripheral regions; relief flat; micro-relief minutely rugose; HMR medium size, 1.42-1.60 mm, oblique, superficial.

Backebergia militaris (Fig. 4e, f) (Arias 1332, 1336, 1338, 1339 MEXU; Terrazas 391 CHAPA). Seed oval, 3.81-5.13 x 2.57-3.80 mm; black, glossy, the periphery keeled in the dorsal and apical region; border slightly expanded around hilum; cells gradually smaller toward hilum, in lateral region isodiametric-polygonal, anticlinal boundaries evident in all regions, straight; interstices uncommon on lateral region, minutely pitted in peripheral regions; relief flat; micro-relief minutely rugose; HMR medium size, 0.79-1.75 mm, oblique, finely impressed.