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Comparative stem anatomy of three species of *Coryphantha* (Cactoideae-Cactaceae)

Anatomía comparativa del tallo de tres especies de *Coryphantha* (Cactoideae-Cactaceae)

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Abstract

Background: The genus *Coryphantha* has the second largest number of species of the tribe Cacteae-Cactaceae. Morphologically, it has been reported that the stem presents mainly globose, ovoid and cylindric variations. However, at the anatomical level, descriptions are scarce and focused on particular tissues (epidermis or xylem). The aim of this work is to contribute to the anatomical knowledge of the genus.

Questions and/or Hypotheses: What are the anatomical characteristics that differentiate one species from another? Does the presence of crystals allow differentiation between species?

Study species: *Coryphantha clavata*, *Coryphantha cornifera* and *Coryphantha radians*.

Site and years of study: San Luis Potosí and Querétaro, Mexico; 2017, 2020.

Methods: Three individuals per species were collected, and conventional histological techniques were applied. Anatomical descriptions were made for different tissues, and structural characteristics were measured for each species.

Results: The species exhibited the greatest differences in the epidermis and hypodermis, such as the presence of subepidermal stomata (*C. radians*), three-layered hypodermis (*C. clavata*), and non-collenchymatous hypodermis (*C. cornifera*). Crystals were not observed in the epidermises but instead in the hypodermes, which exhibited crystal shapes of druses (*C. cornifera* and *C. radians*), prisms and round bodies (*C. clavata*). In the cortical tissue, *C. clavata* had abundant mucilage cells. The observed xylem and phloem tissues exhibited characteristics similar to those of other *Coryphantha* species.

Conclusions: The anatomical characteristics of the epidermis and hypodermis are considered of high systematic value and could be used to distinguish between species of the genus.

Key words: Cacteae, crystals, hypodermis, periderm, secondary xylem.

Resumen:

Antecedentes: El género *Coryphantha* es el segundo con mayor número de especies de la tribu Cacteae-Cactaceae. Morfológicamente se ha descrito que el tallo presenta variaciones globosas, ovoides y cilíndricas principalmente. Sin embargo, a nivel anatómico las descripciones son escasas y enfocadas a un tejido en particular (epidermis o xilema). El objetivo este trabajo contribuir al conocimiento del género.

Preguntas y / o Hipótesis: ¿Cuáles son las características anatómicas que permiten diferenciar a una especie con respecto a otra? ¿La presencia de cristales permite la diferenciación entre las especies?

Especies de estudio: *Coryphantha clavata*, *Coryphantha radians*y *Coryphantha cornifera*

Sitio y años de estudio: San Luis Potosí y Querétaro, México, 2017, 2020.

Métodos: Se colectaron tres individuos por especie y se le aplicaron las técnicas histológicas convencionales. Las descripciones anatómicas se hicieron por tejidos y se midieron las características estructurales para las especies.

Resultados: Las especies exhibieron diferencias en la epidermis e hipodermis como la presencia de estomas subepidérmicos (*C. radians*), hipodermis de tres estratos (*C. clavata*) e hipodermis no colenquimatosa (*C. cornifera*). No se observaron cristales en la epidermis, solo en la hipodermis, drusas (*C. cornifera* y *C. radians*), prismas y cuerpos redondos (*C. clavata*). En el córtex *C. clavata* presentó abundantes células de mucilago. El xilema y floema exhibieron características similares a las de otras especies de *Coryphantha*.

Conclusiones: Las características anatómicas de la epidermis e hipodermis se consideran de alto valor sistemático y podrían utilizarse para separar otras especies del género.

Palabras clave: Cacteae, cristales, hipodermis, peridermis, xilema secundario.

Coryphantha is the genus with the second highest species richness (only below *Mammillaria*) in the Cacteae tribe (Vázquez-Benítez *et al*. 2016); it is distributed from the southern United States down to Oaxaca in southern Mexico (Dicht & Lüthy 2005). The species of *Coryphantha* have predominantly globose, ovoid, cylindrical-ovoid and depressed globose stems (Bravo-Hollis & Sánchez- Mejorada 1991, Vázquez-Sánchez *et al*. 2012, Vázquez-Benítez *et al*. 2016, Sánchez *et al*. 2022). The tubercles exhibit different shapes and vary according to their position on the stem (Dicht & Lüthy 2005, Hunt *et al*. 2006, Vázquez-Benítez *et al*. 2016). However, cylindrical growth form prevails; in the youngest and older tubercles, they are conical and medial conical-deltoid (Vázquez-Benítez *et al*. 2016). Recently, a phylogenetic analysis of the recognized species of *Coryphantha* revealed that the genus is monophyletic, including 43 species recovered in two clades (Sánchez *et al*. 2022). At the anatomical level, it has been reported that the wood of *Coryphantha* is similar to that of other species of the Cacteae tribe, with solitary vessels embedded in a matrix of wide-band tracheids with little paratracheal parenchyma (Gibson 1973, Mauseth *et al*. 1995, Vázquez-Sánchez & Terrazas 2011). However, in the Cactaceae family, anatomical descriptions of the stem are scarce since most studies focus on a particular tissue (Terrazas & Arias 2002). For example, the cited studies on the description of the secondary xylem of various species of *Coryphantha* by Gibson (1973), the variation in the tracheary elements in relation to their position in the stem and in the tubercle (Terrazas *et al*. 2016) and the dimorphism of the areoles (Boke 1961). Descriptive studies of the secondary phloem for Cactoideae species are scarce (Mauseth & Ross 1988, Mauseth *et al*. 1998, Loza-Cornejo & Terrazas 1996, Mauseth 1996, Herrera-Cárdenas *et al*. 2000) since this tissue has characteristics that vary little at the family level (Mauseth 2006). Recently, in Cactaceae, studies on the epidermis and the types of crystals have become relevant, since these attributes have been described as characteristics with value in systematic analyses (Grego-Valencia *et al*. 2014, De la Rosa-Tilapa *et al*. 2018). Therefore, the aim of this work was to describe the anatomy of *Coryphantha radians*, *Coryphantha cornifera* and *Coryphantha clavata*, with the purpose of contributing to the knowledge of the anatomy of the genus.

Materials and methods

Three adult individuals per species were collected in different locations (Table 1). The *Coryphantha clavata* individuals were simple globose with 8-15 cm long and 10 cm in the wider diameter of the stem with a thick root; the *Coryphantha cornifera* individuals had stems that were up to 16 cm long and up to 8.6 cm in total diameter and the *Coryphantha radians* individuals had four branches with thick stems 5 to 8 cm in diameter and 8 cm long. The three species were in the same phenological stage (without flowering).

Sections with areas of 3 × 3 cm corresponding to the basal, middle and apical parts of the stem of each species were cut and fixed with FAA (formaldehyde, 37 % glacial acetic acid, 95 % ethanol 95 % and distilled water; Ruzin 1999) for 48 hours. Then, they were washed with running water, sectioned into smaller portions up to the vascular cylinder and dehydrated with alcohol (70 % for one month). The alcohol solution was replaced every two weeks to reduce the mucilage content. The samples were cut with a double-edged knife to obtain transverse planes of the tubercle and stem as well as tangential and radial planes for each section of the stem. Subsequently, they were dehydrated in 96 and 100 % xylene and included in Paraplast®. The anatomical sections were 14 and 16 µm thick and were obtained using a rotary microtome (Leica RM2125RT, Leica, Wetzlar, Germany). They were stained with safranin and fast green and mounted in synthetic resin according to methods previously reported by Loza-Cornejo & Terrazas (1996). Descriptions were made of the three regions (apical, middle, basal) of the epidermal, fundamental and vascular tissues. The terminology used for the description of the secondary xylem is in accordance with the International Association of Wood Anatomists (IAWA Committee 1989). For the epidermal characteristics, the terminology of Metcalfe & Chalk (1980, 1983) was used. The mean and standard error were obtained from 30 measurements per attribute per individual per species. Anatomical characters were quantified with a Zen Lite 3.0 image analyzer.

Table 1. Species of *Coryphantha* studied and collection locations.

Species	Collector number	Location
C. radians (DC) Britton & Rose	T. Terrazas 877	Out of Moctezuma a 5 km road to Morados, San Luis Potosí, Mexico
C. cornifera Briton	S. Arias 1700	Highway Peñamiller-Cadereyta, Queretaro, Mexico
C. clavata (Scheidw.) Backeb.	T. Terrazas 886	Road to Guadalcazar, road to mina from Gerardo, San Luis Potosí, Mexico
	T. Terrazas 963	Highway to Santa Maria del Río-Tierra Quemada, San Luis Potosí
	S. Arias 1672	Near Tula bridge, Tasquillo, Hidalgo, Mexico
	S. Arias 1705	Near the pantheon, Cadereyta, Queretaro

Results

Epidermis. In the transverse section, the cuticle was smooth for all three species, the thicknesses were as follows: 2.49 ± 0.30 µm for *C. clavata*, 2.75 ± 0.16 µm for *C. cornifera* and 3.0 ± 0.13 µm for *C. radians*. The epidermis was simple and rectangular, and the largest in *C. radians* (42. 05 ± 1.88 µm), followed by *C. cornifera* (35.24 ± 4.27 µm) and *C. clavata* (20.97 ± 2.2 µm), with the outer periclinal wall being more variable (Figure 1).

The outer periclinal wall was flat for all three species. The periclinal wall thickness was thicker for *C. radians* (11.84 ± 0.48 µm) than for *C. cornifera* (5.55 ± 0.21 µm) and *C. clavata* (4.68 ± 0.13 µm). For all three species, the stomata were superficial, while in *C. radians,* the stomata appeared to be sunken only at the base of the stem, and all three species had substomatal cavities throughout the hypodermis (Figure 1E).

Hypodermis. The number of hypodermal layers was variable from two layers in *C. cornifera* and *C. radians* to up to three layers in *C. clavata* (Figure 1B). The hypodermis of *C. cornifera* possessed parenchymatous cells (Figure 1D), while those of *C. radians* and *C. clavata* showed collenchymatous cells (Figure 1A-B). The hypodermal cells of *C. cornifera* and *C. radians* had crystal shapes of druses and druse clusters (Figure 1A, C), and only those of *C. clavata* had rounded and prismatic crystals (Figure 1B, C).

Cortex. All the taxa studied had palisade and storage parenchyma; in the storage parenchyma, collateral cortical bundles were found (Figure 2D). The cortical bundles may have secondary growth. In the xylem, we found few tracheary elements. The phloem was scarce and had sieve tube elements with a simple horizontal sieve plate and one companion cell per element. Mucilage cavities were observed for *C. clavata*, but they were absent for *C. cornifera* and *C. radians*.

Pith. The pith had only parenchyma cells and medullary bundles were present; druses occurred for all three species as in the cortex but were more abundant for *C. cornifera*.

Secondary tissues. Secondary xylem.- For all three species, vessels were embedded in a matrix of wide-band tracheids (Figure 2A-C). The vessels were mostly solitary and narrow, with radial and tangential diameters of 33.42 ± 1.14 µm and 31.68 ± 1.43 µm for *C. cornifera*, 31.73 ± 0.97 µm and 31.25 ± 0.89 µm for *C. clavata* and 27.88 ± 1.81

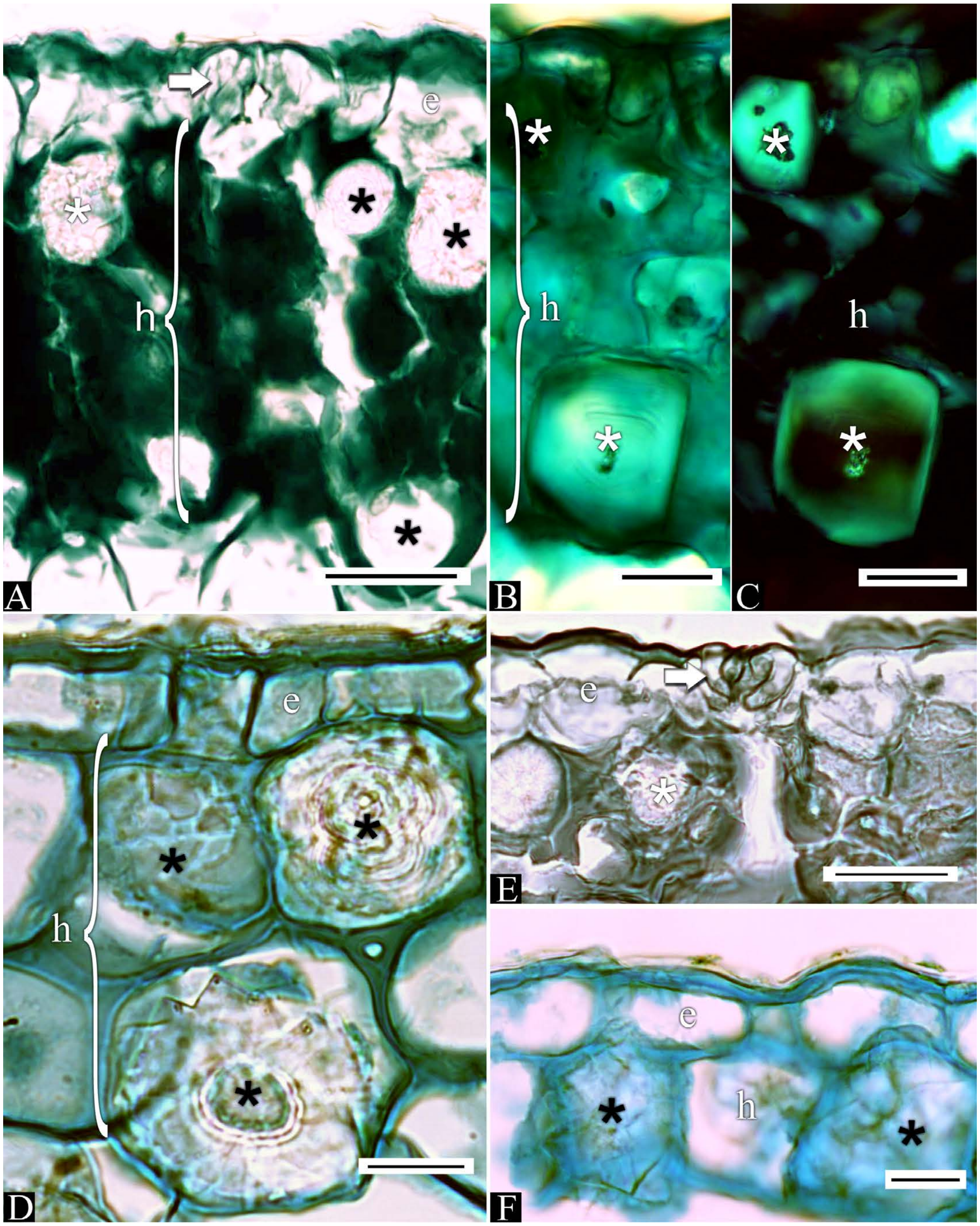

Figure 1. Epidermis and hypodermis of three species of *Coryphantha*, transverse sections. A, *C. radians*, B, C, E. *C. clavata*, D, F. *C. cornifera*, e = epidermis, h = hypodermis (square bracket), stoma, (white arrow), crystals = *. Bar: B-D, F = 20 µm, A, E = 50 µm.

µm and 29.26 ± 3.22 µm for *C. radians*, respectively. Vessel elements had simple perforation plates and helical or annular secondary wall thickenings (Figure 2D). The wide-band tracheids had the same type of secondary walls as the vessel elements with radial and tangential diameters of 40.35 ± 0.96 µm and 38.41 ± 1.23 µm for *C. cornifera*, 24.34 ± 0.72 µm and 23.42 ± 0.49 µm for *C. clavata* and 27.65 ± 0.86 µm and 26.06 ± 0.85 µm for *C. radians*. For *C. radians,* the primary and secondary rays are distinctive (Figure 2A). The rays were unlignified (2-4-seriate for

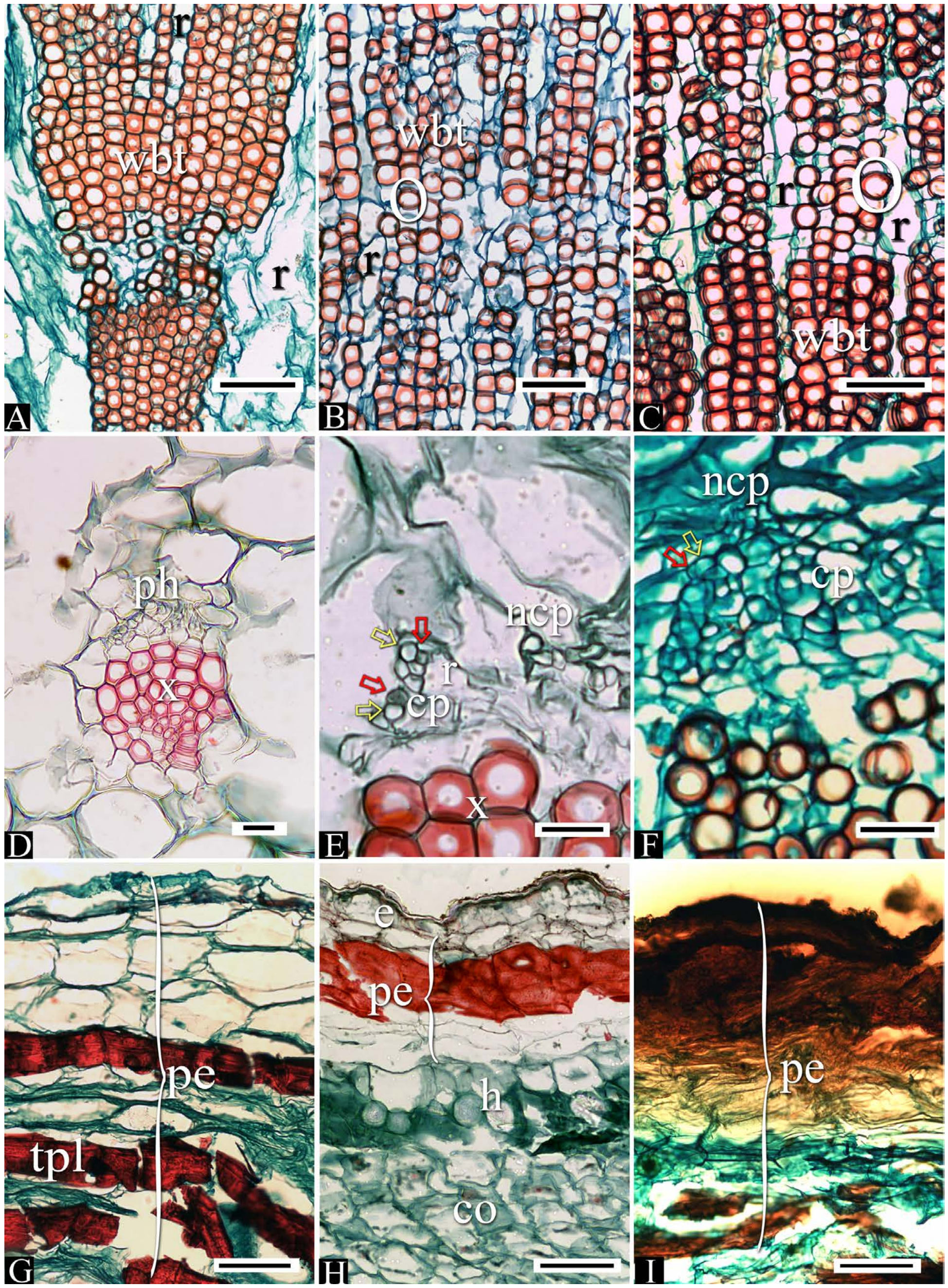

Figure 2. Secondary xylem, secondary phloem and periderm in three species of *Coryphantha*, transverse and tangential sections. A-C. secondary xylem; D. cortical bundle; E, F. secondary phloem; G-I. Periderm. A, E, H. *C. radians*; B, D, I. *C. cornifera*; C, F, G. *C. clavata*. co = cortex, cp = conductive phloem, e = epidermis, h = hypodermis, ncp = nonconductive phloem, pe = periderm, ph = phloem, tpl = thick phellem cells, r = ray, white circle = vessel, wbt = wide band tracheids, x = xylem, yellow arrows = sieve tube element, red arrows = companion cell. Bar: A-C, G-I = 100 µm, F = 50 µm, D, E=20 µm.

C. radians, 2-6-seriate for *C. clavata* and 2-3- seriate for *C. cornifera*) and composed almost entirely of erect cells. Druses were observed in some ray cells for all three species.

Secondary phloem.- The phloem of all three studied species had sieve tube elements with companion cells (STE-CCs) and axial and radial parenchyma. In the conductive phloem, the STE-CCs were arranged in groups among the diffuse axial parenchyma cells; the CC occurred on one side of the STE (Figure 2E, F). The STEs had simple sieve plates, with small sieve areas on the sidewalls. In the nonconductive phloem, the STE-CCs collapsed and formed a furrow region between the dilate rays (Figure 2E, F).

Periderm.- For all three species, the periderm was unidirectional. The phellogen was epidermal in origin. The phellem showed thin-walled suberized cells alternating with one to two strata of very thick-walled lignified cells for *C. clavata* and *C. radians* (Figure 2G, H), while for *C. cornifera,* the lignified and suberized cells maintained thin walls, and the outer cells collapsed (Figure 2I).

Discussion

The cuticle thicknesses showed a variation of less than one µm among the three species studied here, and this variation was similar to that exhibited by *Coryphantha pallida* and *Coryphantha retusa* (Loza-Cornejo & Terrazas 2003). However, this cuticle thickness was greater (2.49 - 3.00 µm) than the cuticle thickness of 1.8 µm for *Coryphantha elephantidens* (Gasson 1981). Variations in cuticle thicknesses do not determine survival in arid and semiarid species (Gibson & Horak 1978). The cuticle was smooth for all three species, as for *C. elephantidens* (Gasson 1981), and did not present ornamentations, as for other Cactaceae species (Loza-Cornejo & Terrazas 2003). The presence or absence of cuticle ornamentations and papillose epidermis may allow recognition between genera. Such is the case for *Peniocereus*, genus where its seven species have a papillose epidermis and smooth cuticle (Loza-Cornejo & Terrazas 2003, Franco-Estrada *et al*. 2021). Whereas the former subgenus *Pseudocanthocereus* (now in *Acanthocereus*, Arias *et al*. 2005) has two species that have cuticles with micropapillae (Sánchez-Mejorada 1974), one of them *Peniocereus fosterianus* (=*Acanthocereus*) (Loza-Cornejo & Terrazas 2003). *Acanthocereu*s needs further studies since *A. chiapensis*, *A. horridus* and *A*. *tetragonus* have a smooth cuticle (Loza-Cornejo & Terrazas 2003, Martínez-Quezada *et al*. 2020). The simple epidermises of the three species had greater sizes (height 20.97 µm, 42.05 µm width) than those reported for other species of *Coryphantha* (Gasson 1981, Loza-Cornejo & Terrazas 2003). The outer periclinal wall exhibited greater thickening than the rest of the walls that made up the epidermal cells. This thickening is common for various species of the Cactaceae family and requires future studies to determine the nature of the primary wall thickening and confirm whether it is collenchymatous with the ability to provide flexibility and storage of water (Leroux 2012). The superficial positions of the stomata are maintained along the stem for *C. cornifera* and *C. clavata*, which is similar to that recorded by Eggli (1984), while *C*. *radians* exhibited sunken stomata similar to *Coryphantha elephantidens* (Gasson 1981). If the stomata are sunken throughout the stem and this is a characteristic of the species, it should be studied in a greater number of species of the same genus to evaluate whether the sunken stomata are associated with species from drier habitats and could be an adaptation to reduce water loss through transpiration (Gibson 1983, Garcia *et al*. 2012).

The number of strata in the hypodermis was variable for *C. clavata* (three strata) with respect to the other two species; this variation was recorded for *C. elephantidens* with one stratum and two strata for *C. pallida* and *C. retusa* (Boke 1952, Gasson 1981, Loza-Cornejo & Terrazas 2003). The variations in the number of strata and thicknesses of the hypodermis are induced by the environment (Nyffeler & Eggli 1997). In addition, the hypodermis acts as a protective, supportive tissue that provides elasticity (Mauseth 1989, Vázquez-Sánchez *et al*. 2005) and is another defense mechanism against herbivory attack and excessive radiation, especially when associated with the accumulation of crystals in hypodermal cells (Pierantoni *et al*. 2017, De la Rosa-Tilapa *et al*. 2020). Loza-Cornejo & Terrazas (2003) recorded druses in the hypodermis of *C. radians* and *C. retusa*, which was also confirmed for *C. radians* in this work and for *C. cornifera*. In *C. clavata* prisms and rounded crystals were detected. Crystals in the hypodermis are of high diagnostic value (Terrazas & Arias 2002, De la Rosa-Tilapa *et al*.2020), so the study of the other species of *Coryphantha* will contribute to support the subclades within the genus according to the recent phylogeny proposed (Sánchez *et al*. 2022).

It is worth mentioning that *C. clavata* possessed abundant mucilage cells in the cortex, in agreement with the clade named mucilaginous by Sánchez *et al*. (2022). *Coryphantha cornifera* belongs to a species with a characteristic watery cortex. Our observations confirmed this: the cortices of the *C. cornifera* and *C. radians* individuals in this study lacked mucilage cells.

The tracheary elements of the three species showed the same anatomical characteristics already described for other *Coryphantha* species: for example, the vessel elements have simple perforation plates and helical thickening (Terrazas *et al*. 2016); the vessels were narrow and solitary, characteristic of species with small growth forms (Gibson 1973); the diameter of the vessels (27.88-33.42 µm radial, 29.26-31.68 µm tangential) in *C. clavata* was consistent with that reported by other authors (Gibson 1973, Terrazas *et al*. 2016). Wide-band tracheids showed wall thickening similar to that of the vessel elements. However, the diameter was greater than the diameter of the vessel elements, as was also reported for six species of *Coryphantha* by Terrazas *et al*. (2016). The authors mentioned that wide-band tracheids have the ability to contract and expand depending on the availability of water (Gibson 1973, Mauseth 2004) and the vessel elements will have the same ability since both have the same characteristics in the primary and secondary walls. The rays were not lignified and were arranged in series of 3 to 7, similar to the results of Terrazas *et al*. (2016), where they observed rays in series of 2 to 5 for the six species of *Coryphantha* studied; the rays were mainly composed of erect cells.

The divisions of the epidermis originate the periderm; this had already been reported for other cacti species (Gibson & Nobel 1986, Terrazas *et al*. 2005, Evans & Dombrovskiy 2020) and seems to be a conserved characteristic throughout the family relating to late development in the stems, especially of the Cactoideae subfamily (Terrazas & Arias 2002). Evans *et al*. (1994, 2001) suggested that early development of the periderm is associated with the accumulation of epicuticular waxes in the epidermis, which stimulates cell division and in turn the production of phellogen. It is interesting that, of the three species studied here, only one of them does not have thick-walled lignified cells, *C. cornifera*, which could be a diagnostic characteristic. To support this assertion, further studies should analyze the periderm of a greater number of species of *Coryphantha*.

In conclusion, we recognized only a few unique characteristics in each analyzed species to discriminate species. The differences found here between *C. cornifera* and *C. radians* may contribute to recognize them as distinct entities. For *C. cornifera,* the hypodermis is parenchymatous and no thick-walled phellem cells occur in the periderm, whereas *C. radians* has collenchymatous hypodermis and *C. clavata* possesses distinctive prisms and rounded crystals in the collenchymatous hypodermis and abundant mucilage cells in the cortex. The epidermis and hypodermis were the tissues that presented the greatest variation between species. The type of crystals and their location could be of value and may contribute to the systematics of the genus. The xylem and phloem seem to be highly conserved since the three species showed the same characteristics already described for other members of *Coryphantha*, but this is not so for the periderm, considering that the phellem cells can have very thick and lignified walls.

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