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Adaptive Anatomical and Histological Characters of the Leaf and Stem of Three Desert Species of *Capparis*

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ABSTRACT. The anatomy of the leaf and stem of *Capparis spinosa* L., *C. cartilaginea* Decne. and *C. decidua* (Forssk.) Edgew. have been studied and shown to be distinctive in these three species. Photosynthetic tissue is present in the leaf midrib region in all three species but differs as to the cell type (palisade *vs.* spongy) and distribution. Collenchymatous tissue is present in *C. spinosa* and *C. cartilaginea* but not in *C. decidua*. Ground parenchymatous tissue is conspicuous in *C. cartilaginea*, less developed in *C. decidua* and is not observed in *C. spinosa*. Differences occur in the stem cortex of these species as to photosynthetic tissue cell type and distribution; *C. cartilaginea* and *C. decidua* have lignified primary phloem fibres, while *C. spinosa* has unlignified primary phloem fibres. This study elucidates the presence of extensive water-storing parenchymatous tissue and the considerable thickness of the outer epidermal cell walls especially in the leaves as the adaptive structural mechanism of *C. cartilaginea* that underlies its ability to grow and survive in dry rocky habitats.

The genus *Capparis* L. (Capparaceae) is represented in the flora of Saudi Arabia by five species which are widely distributed in various habitats and climatic conditions. Three species: *C. spinosa* L., *C. cartilaginea* Decne. and *C. decidua* (Forssk.) Edgew. growing in the Riyadh region were examined in this study. The anatomy of the genus, *Capparis* was reviewed by Metcalfe and Chalk (1950) but none of the species investigated was studied in detail. Sabnis (1919) however, studied the internal structure of *C. decidua* whereas Jorgensen (1981) has investigated the presence of myrosin cells in *C. spinosa*. Rao (1978) studied the idioblast typology of *C. spinosa* and *C. cartilaginea*, while Bokhari and Hedge (1975) studied the anatomical characters of *C. spinosa* and *C. cartilaginea*. Rao and Das (1971) investigated the anatomy of *C. cartilaginea*. This present study compares the anatomical and histological features with respect to the habitat of the three species.

Materials and Methods

Stems and leaves were collected from flowering specimens of *C. spinosa, C. cartilaginea* and *C. decidua* growing in their natural habitats in the Riyadh region and were immediately preserved in 70% v/v ethanol or examined directly. Epidermal strips were prepared from preserved or fresh materials and mounted in 50% v/v glycerol solution for microscopic examination of epidermal characters. Sections were prepared from material embedded in paraffin; these were cut at 10 to 30 μm (thickness), stained with safranin and light green and then mounted in Canada balsam. Some sections were mounted in iodine solution when testing for the presence of starch; in phloroglucinol solution and hydrochloric acid when examined for lignified elements, or in Sudan IV for cutin. Millon's test was used to determine the presence and location of myrosin cells. Drawings were prepared with the aid of a Reichert screen microprojector. Stomatal frequency on leaves and stems of the three species represent the average of 25 readings taken on 5 epidermal strips. Cell wall thickness was determined as an average of 50 readings of 10 sections of each stem and leaf of each species. This was scored as: very thick $>$ 12 μm; thick, 6-12 μm; slightly thick, 2.5-6 and thin $<$ 2.5 μm. Samples: Five samples of each species were taken. Three leaves (upper, middle, lower) of each sample were choosen to make 10 epidermal strips and sections of each leaf part (base, middle). Three epidermal strips and sections of each stem part (upper, middle, lower) were taken.

Results

Gross morphology of the plants

C. spinosa is a shrubby or rocky desert type plant up to 1.5 m high. Its leaves are simple, ovate or suborbicular, 2-4 cm long. It occurs on rocky ground and steep cliffs (Migahid 1978). *C. cartilaginea* is shrubby with erect branches, up to 1.5 m high, having simple, fleshy, ovate to elliptical leaves 2-5 cm long. It occurs in rocky habitats (Magahid 1978). *C. decidua* is a yellow-green shrub up to 4-5 m tall with long virgate, naked branches. Its leaves are simple, small and linear, 1-1.5 cm long (Migahid 1978).

Anatomical characters

Anatomical features of the leaves and stems of *Capparis spinosa, C. cartilaginea* and *C. decidua* are illustrated in Figures 1-5 and summarized in Tables 1-6.

Characters common to the three species

The three species have the following epidermal features in common: (1) epidermal cells of leaves and stems with thin, straight, anticlinal walls, (2) stomata

frequent, ovate, commonly anisocytic, occasionally anomocytic, (3) absence of glandular trichomes on the leaf and stem epidermis and (4) stem epidermal cells covered with thick, smooth cuticle. In addition, they have certain common internal features in their leaves and stems. Thus, in the leaves, reservoir-tracheids are present near the vascular bundles in the intercostal region (Fig. 2). There is a single vascular bundle in the midrib region (Fig. 2). In the stem the outer cortex is composed in all three species of several layers of photosynthetic cells. The phloem and xylem tissues form a continuous cylinder in the lower part of the stems (Fig. 4). The pith consists of parenchymatous cells with conspicuous intercellular spaces and thin cellulosic walls (Fig. 5).

Differences between the three species

These three species show distinct anatomical characteristics. Non-glandular unicellular trichomes are present only on the lower epidermis of the leaves of *C. spinosa* (Fig. 1D), while they are present on the lower epidermis of the leaves and the stem epidermis of *C. cartilaginea* (Figs. 1E, 1H). They are absent from the epidermis of the leaf and stem of *C. decidua*. In the leaf midrib region, photosynthetic tissue is present in all three species but differs as to cell type and distribution. In *C. spinosa* it comprises 3 or 4 layers of palisade-type cells extending half-way around the midrib flanks where it meets the collenchyma on the abaxial side (Figs. 2A, 3A). In contrast, 3 to 5 layers of palisade-type cells occur only below the upper epidermis in *C. decidua,* (Figs. 2C, 3C) whereas in *C. cartilaginea* there are 4 or 5 layers of chlorenchymatous cells only below the upper epidermis (Figs. 2B, 3B; Table 2). Collenchyma is absent from the leaf midrib of *C. decidua* (Table 2; Fig. 3C). Ground parenchymatous tissue is obvious in *C. cartilaginea* (Fig. 3B) reduced in *C. decidua* and almost not distinguishable in *C. spinosa* (Fig. 3A). The midrib vascular bundle is large and arc-shaped containing vessels in rows and with wide rays in *C. spinosa* (Figs. 2A, 3A), small round-shaped with vessels in rows and with narrow rays in *C. cartilaginea* (Figs. 2B, 3B) and small, ovate with vessels arranged irregularly in *C. decidua* (Figs. 2C, 3C). The outer epidermal cell walls are thick (7.3-11 μm) in *C. spinosa,* very thick (13-33.5 μm) in *C. cartilaginea* and slightly thick (3.6-4.8 μm) in *C. decidua.*

Obvious differences in the internal structure of stems in these species have been observed: Outer epidermal cell walls are thick (6-9.5 μm) in *C. spinosa* (Fig. 5A) and *C. cartilaginea* (Fig. 5B), whereas they are slightly thick (3.6-4.8 μm) in *C. decidua* (Fig. 5C). Cortical parenchyma comprises several layers of chlorenchymatous cells with conspicuous intercellular spaces in *C. spinosa* (Fig. 5A) and *C. cartilaginea* (Fig. 5B) while it consists of 4 to 6 layers of palisade-type cells containing chloroplasts and several layers of polygonal chlorenchymatous cells in *C. desidua* (Fig. 5C). Primary phloem fibres have slightly thickened walls in *C. spinosa* (Fig. 5A) but in contrast, primary phloem fibres have thick lignified walls in *C. cartilaginea* (Fig. 5B) and *C. decidua* (Fig. 5C). Vascular tissue forms a continuous cylinder in *C. cartilaginea* (Fig. 4B) and an almost continuous cylinder

in *C. decidua* (Fig. 4C) while in *C. spinosa* (Fig. 4A) it is a discontinuous cylinder. Pith parenchymatous cells have thin, cellulosic walls with conspicuous intercellular spaces in all species (Fig. 5).

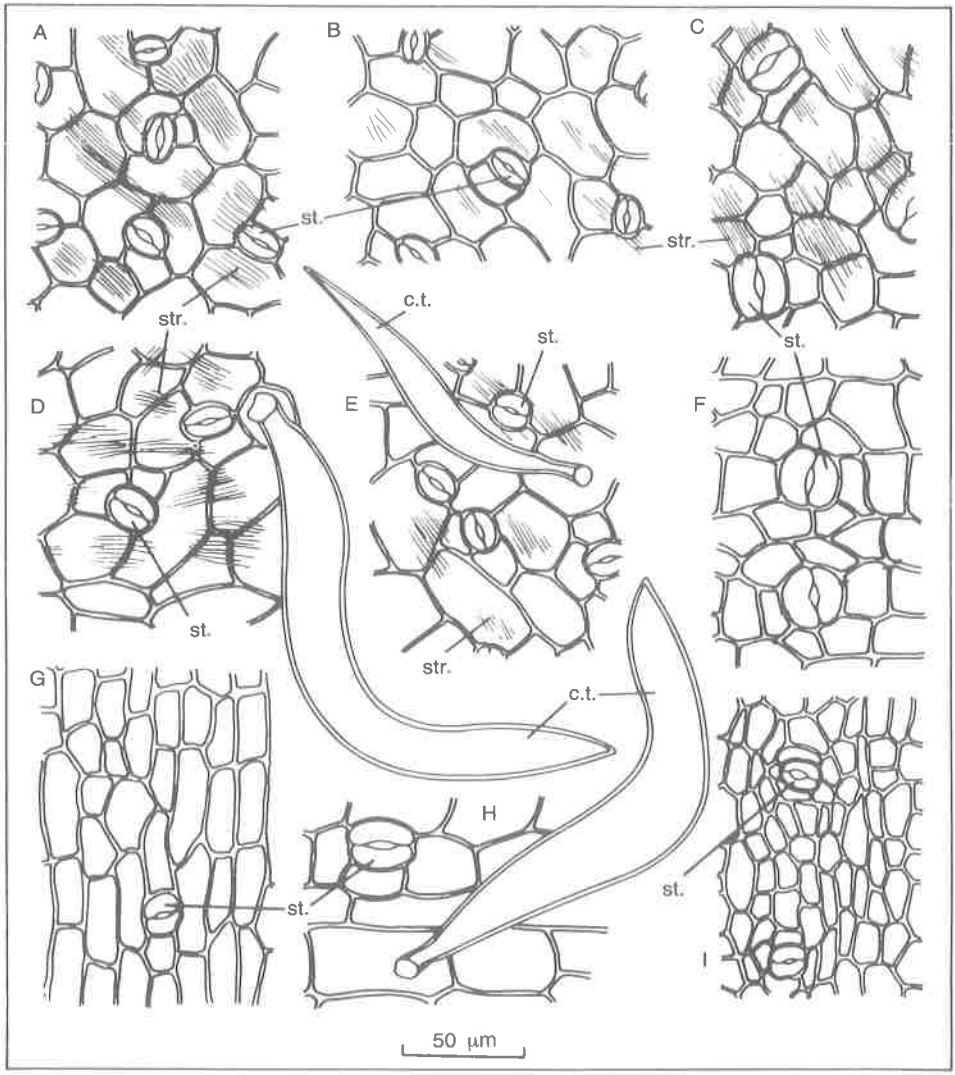

Fig. 1. Surface view of leaf and stem epidermis. Leaf upper epidermis (A), leaf lower epidermis (D) and stem epidermis (G) of *C. spinosa*. Leaf upper epidermis (B), leaf lower epidermis (E) and stem epidermis (H) of *C. cartilaginea*. Leaf upper epidermis (C), leaf lower epidermis (F) and stem epidermis (I) of *C. decidua*.

Myrosin cells in leaves and stems of all three species differ as to location and frequency. They occur more frequently in the leaf midrib of *C. cartilaginea* and *C. decidua* than in *C. spinosa*. Myrosin cells are frequent in the stem cortex of *C. spinosa*, more frequent in *C. cartilaginea* and less frequent in *C. decidua*. They occur rarely in the pith of the stems of all three species (Fig. 5, Table 5).

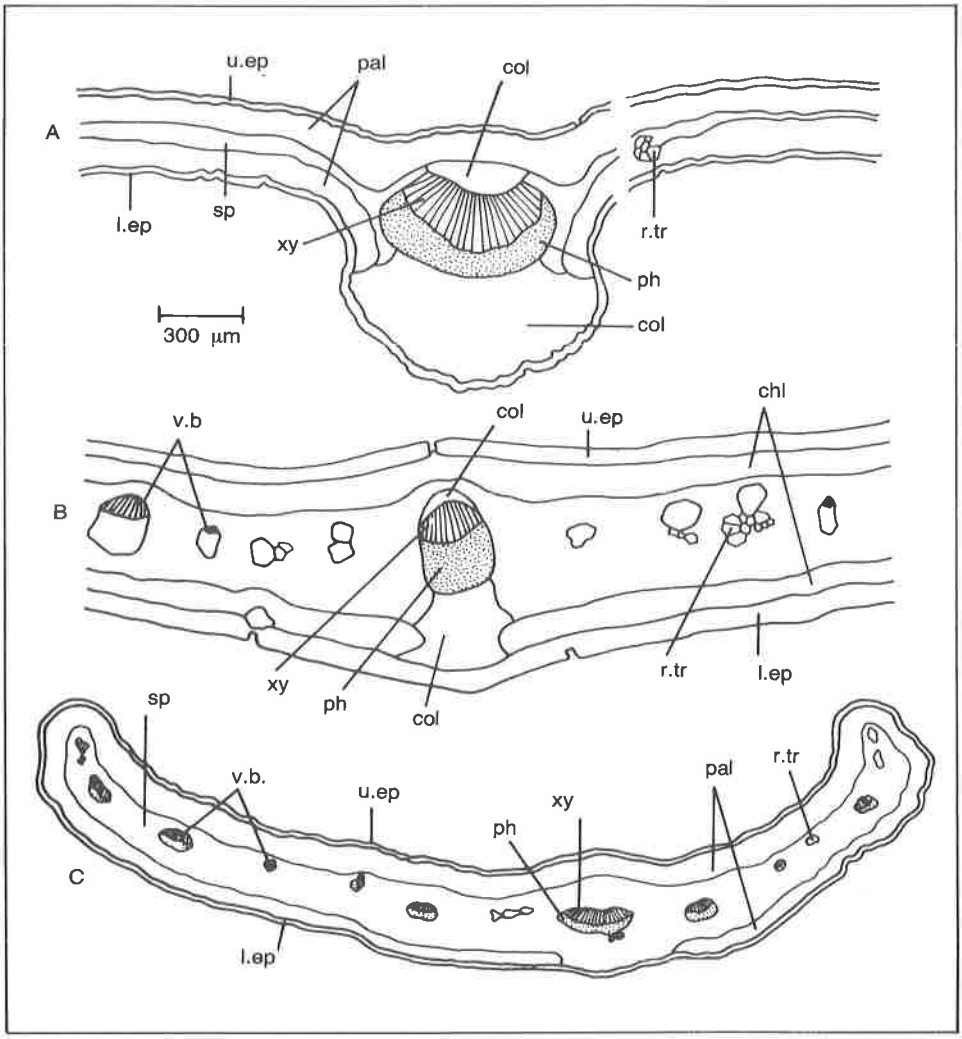

Fig. 2. Transverse sections of leaves. The midrib region of *C. spinosa* (A), the midrib region of *C. cartilaginea* (B) and the midrib region of *C. decidua* (C).

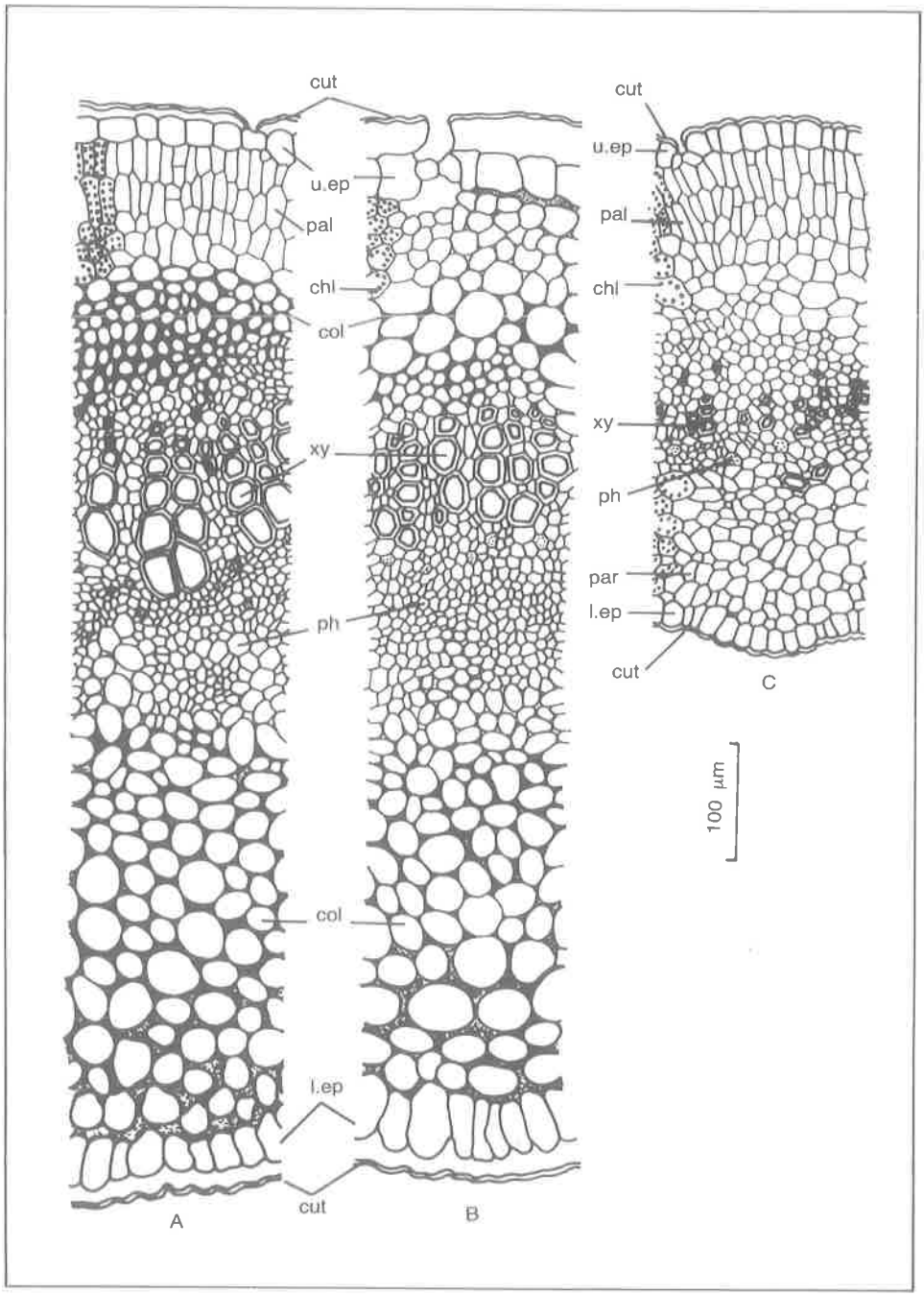

Fig. 3. Transverse sections of leaves. The midrib region of *C. spinosa* (A), the midrib region of *C. cartilaginea* (B) and the midrib region of *C. decidua* (C).

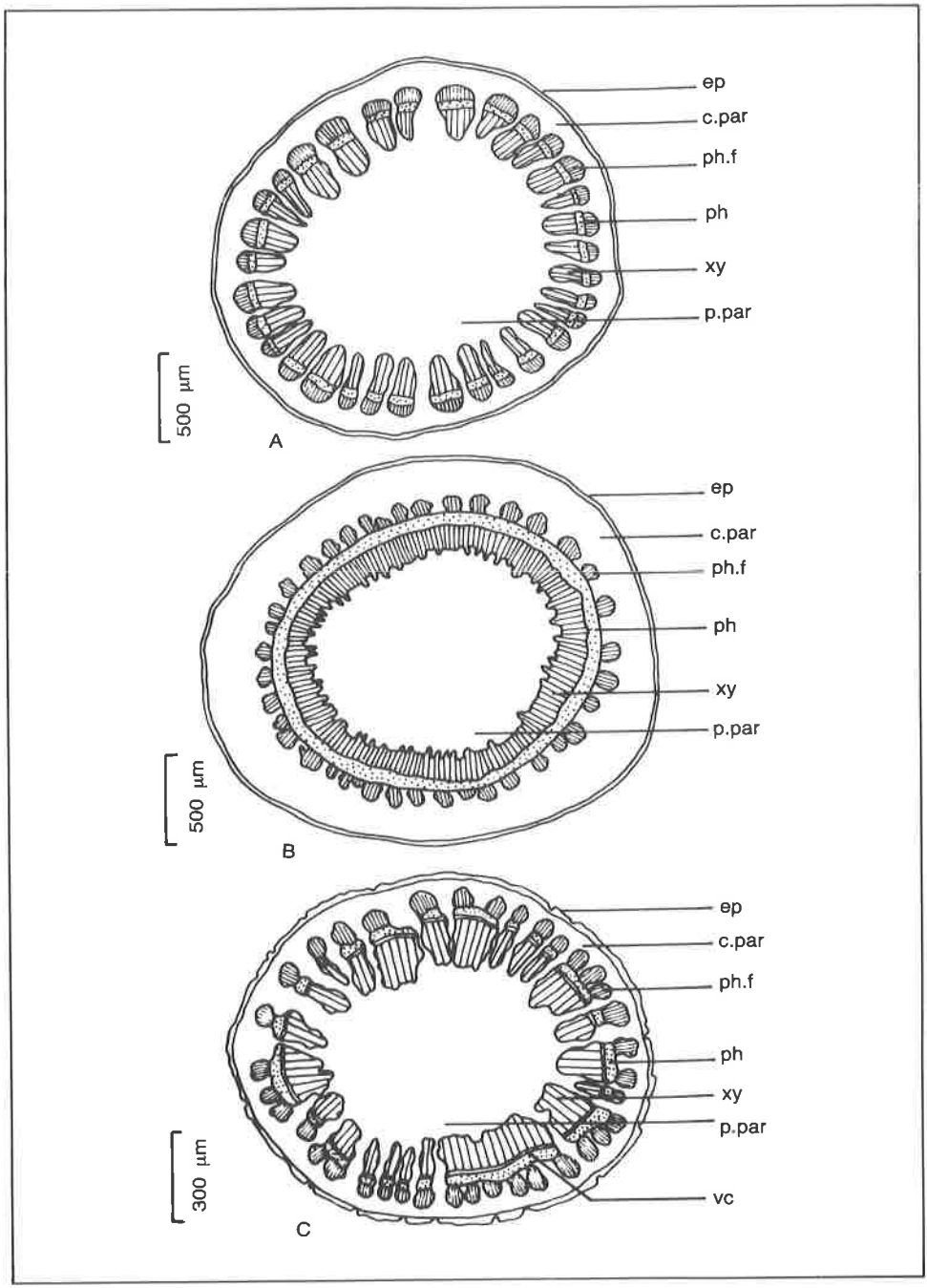

Fig. 4. Transverse sections of stems. Stem of *C. spinosa* (A), stem of *C. cartilaginea* (B) and stem of *C. decidua* (C).

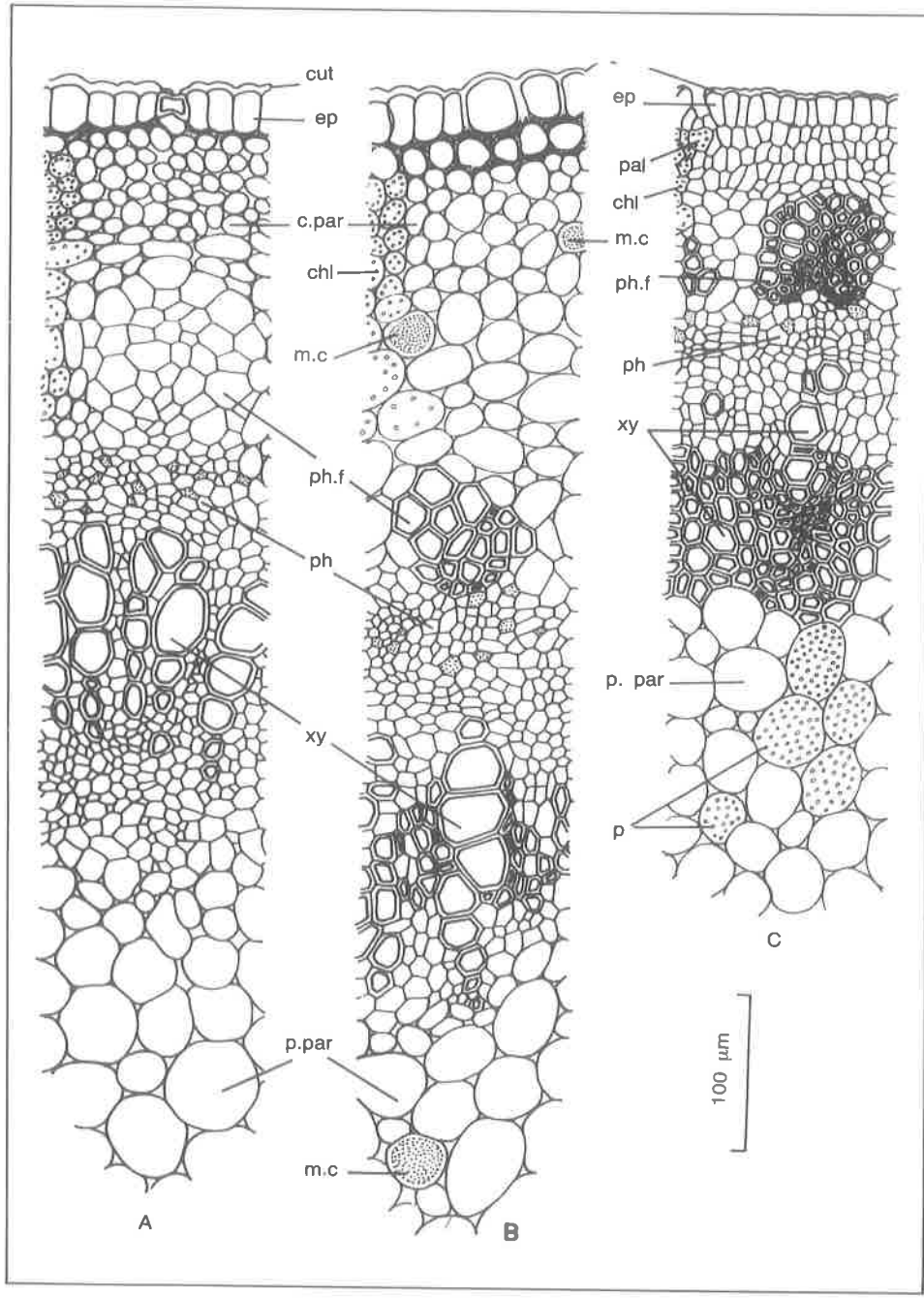

Fig. 5. Transverse sections of stems. Stem of *C. spinosa* (A), stem of *C. cartilaginea* (B) and stem of *C. decidua* (C).

Discussion

Our observations concerning *C. decidua* agree with those of Sabnis (1919). Metcalfe and Chalk (1950) reported the presence of thin walled, ascus-shaped, non-glandular, pointed trichomes with wide luminae. This study confirms their findings. They reported also the presence of myrosin cells in the seedlings of *C. spinosa*. Jorgensen (1981) reported the presence of myrosin cells in the stem cortex of *C. spinosa*. This work confirms their observations.

While this study indicates the adaptive features of the species to aridity it shows also the presence of some variations in this regard between *C. spinosa* and *C. cartilaginea* on the one hand and *C. decidua* on the other.

It is interesting to note that *C. decidua* possesses certain xeromorphic characters which make this species better adapted to aridity than *C. spinosa* and *C. cartilaginea*. The leaves of *C. decidua* have a much reduced surface area, small cells, well-developed palisade tissues and lower stomatal frequencies. Lekhak *et al.* (1983) working with *C. decidua* (Forssk.) Edgew. reported that it belongs to the leaflets division of xerophytes since the plant produces minute short-lived leaves during low soil moisture content in the Indian desert. Only newly developed branches produce leaves while older branches are leafless. He thus considered this feature a means of water conservation by minimizing the transpiring surface.

In addition to the small size of the leaf in *C. decidua*, the blade exhibits an upward folding of the margins. This morphological character makes the plant more adapted to the desert climate due to its reduction of the effective leaf area and the solar energy load on the plant (Begg 1980). Furthoremore, the upward folding of leaf margins also minimizes the water loss in transpiration from the upper epidermis which contains a significant number of stomata (Lekhak *et al.* 1983). This reduced water loss from leaf rolling is considered a common response to stress and in some plants (for example grass), can reduce transpiration to 50-70% (Oppenheimer, 1960) as well as increasing water use efficiency (Johns 1978). The leaf-blade rolling is a response which results from a loss of water from the bulliform cells in the upper epidermis of the leaf (Esau 1977) and it appears to be very sensitive to diurnal changes in leaf water deficits. Thus, it enables the plant to respond rapidly to periods of high evaporative demand, to avoid some of the radiation load when the water use efficiency is higher (Bigg 1980). Weaver and Clements (1938) summarized the anatomical features that characterize true xerophytes. These features are: a decrease in cell sizes including guard cells, a distinct thickening of cell walls, a strongly developed palisade in the mesophyll, and a dense network of veins. These features are consistent with the present data for the three species of *Capparis*. However, *C. decidua* has a higher degree of adaptability as far as these xeric features are concerned. On the other hand, *C. cartilaginea* may be classified as second to *C. decidua* in enduring a desert climate,

due to its considerable thickness of the outer epidermal cell walls and the possession of extensive water-storing parenchymatous tissue in its leaves. Both of these features are associated with water conservation (Begg 1980, Bokhari and Hedge 1977, Nobel 1980, Shield 1950 and Weaver and Clements 1938). Therefore, *C. cartilaginea* may be considered able to grow and survive in dry, rocky habitats because of these xeric features.

In view of the aforementioned discussion, it may be concluded that these *Capparis* species possess morphological and anatomical characters that enable them to endure and resist drought conditions of the desert. Furthermore, *C. decidua* seems to be more adapted than the other two *Capparis* species due to the more xeric features possessed by it. Moreover, *C. cartilaginea* appears more adapted than *C. spinosa* due to its thick outer epidermal cell walls and the relatively more extensive water-storing tissues in the leaves.

Table 1. Leaf: Epidermal characters

Characters	Upper (U) Lower (L) Epidermis	Species		
		C. spinosa	*C. cartilaginea*	*C. decidua*
Cuticle	U	thin, irregularly striated	thin, occasionally, irregularly striated	thin, irregularly striated
	L	similar	similar	thin, smooth
Epidermal cells	U	thin, straight anticlinal walls	as for *C. spinosa*	as for *C. spinosa*
	L	similar	similar	similar
Stomata	U	frequent, anisocytic or anomocytic, ovate	as for *C. spinosa*	as for *C. spinosa*
	L	similar	similar	similar
Nonglandular trichomes	U	absent	absent	absent
	L	frequent, unicellular, thick, smooth walls, wide lumen	as for *C. spinosa*	absent

Table 2. Leaf: internal anatomy

Region	Character	Species		
		C. spinosa	*C. cartilaginea*	*C. decidua*
Intercostal	Mesophyll	2 to 4 layers of palisade-type cells below upper and lower epidermises, 3 or 4 layers of spongy-type cells between, near the midrib region, not observed near the leaf margin. Myrosin cells frequent, individual.	4 to 6 layers of chlorenchymatous cells below upper and lower epidermises; several layers of polygonal parenchymatous cells devoid of chloroplasts surrounding the vascular bundles. Myrosin cells frequent, in groups.	1 to 5 layers of palisade-type cells below upper and lower epidermises, 6 to 8 layers of spongy tissue surrounding the vascular bundles. Myrosin cells very frequent, in groups.
	Reservoir-tracheids	present	present	present
	Chlorenchyma	3 or 4 layers of palisade-type cells extend on the half length of the flanks reaching the collenchyma on the lower side.	4 or 5 layers of chlorenchymatous cells only below the upper epidermis followed by several layers of polygonal parenchymatous cells on both sides of vascular bundle.	3 to 5 layers of palisade-type cells containing chloroplasts only below the upper epidermis followed by several layers of isodiametric chlorenchymatous cells surrounding the vascular bundle.
Midrib	Collenchyma	angular-type cells, several layers, on the upper and lower sides of vascular bundle reaching the lower epidermis.	as for *C. spinosa*	absent
	Myrosin cells	frequent individual	very frequent, in groups	very frequent, in groups
	Vascular bundle	arched, large; vessels in rows commonly with wide lumina and wide rays	rounded, small; vessels in row with wide lumina and with narrow rays	ovate, small; vessels with narrow lumina and arranged irregularly
	Epidermal cells walls	outer walls thick (7.25-11 μm)	outer walls very thick (26-33 μm)	outer walls slightly thick (3.6-4.8 μm)

Table 3. Stem: Epidermal characters

Character	Species		
	C. spinosa	*C. cartilaginea*	*C. decidua*
Cuticle	thin, smooth	as for *C. spinosa*	as for *C. spinosa*
Epidermal cells	polygonal, elongated with thick, straight anticlinal walls	as for *C. spinosa*	as for *C. spinosa*
Stomata	ovate or circular, anomocytic	ovate, anomocytic	as for *C. spinosa*
Nonglandular trichomes	absent	unicellular, thin cellulosic walls, wide lumen	absent

Table 5. Stomatal number/mm^2 in the leaf and stem

Species	Stomatal number/mm^2		
	Leaf		Stem epidermis
	Upper epidermis	Lower epidermis	
C. spinosa	560	590	90
C. cartilaginea	425	515	95
C. decidua	230	285	75

Table 6. Occurrence of myrosin cells in the leaf and stem

Organ	Tissue or region	*C. cartilaginea*	*C. spinosa*	*C. deciuda*
STEM	Epidermis	–	–	–
	Cortex	a	b	c
	Pith	c	b	c
LEAF	Epidermis	–	–	–
	Midrib	a	b	a
	Intercostal	b	b	a

a = very frequent, b = frequent, c = rare, – = absent

Table 4. Stem: Internal anatomy

Character	Species		
	C. spinosa	*C. cartilaginea*	*C. decidua*
Epidermal cell walls	outer walls thick (6-8 μm), radial walls thin.	outer walls thick (7.25-9.5 μm) radial walls commonly thick.	outer walls less thick than *C. spinosa* (3.6-4.8 μm) radial walls thin.
Cortex	one layer hypodermis, cells with thick walls. Several layers, rounded, chlorenchymatous cells with conspicuous intercellular spaces. Myrosin cells occur individually, frequent.	as for *C. spinosa* but myrosin cells occur in groups and very frequent.	4 to 6 layers, palisade-type cells containing chloroplasts followed by several layers of polygonal chlorenchymatous cells. Myrosin cells occur individually and rare.
Vascular tissues	primary phloem fibres with thin, unlighnified walls. Phloem and xylem tissues form a discontinuous cylinder in the upper part of the stem, and a continuous cylinder in the lower part.	primary phloem fibres with thick, lignified walls. Wide lumina. Phloem and xylem tissues form a continuous cylinder in the upper and lower parts of the stem.	primary phloem fibres with thick lignified walls, commonly narrow lumina. Phloem and xylem tissues form a discontinuous cylinder in the upper part of the stem and a continuous cylinder in the lower part.
Medulla	Parenchymatous cells with conspicuous intercellular spaces; cells with thin cellulosic walls. Myrosin cells occur individually and rare.	as for *C. spinosa*	as for *C. spinosa*

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Abbreviations

chl, chlorenchyma; col, collenchyma; c. par, cortical parenchyma; c.t, covering trichomes; cut, cuticle; ep, epidermis; l.ep, lower epidermis; m.c, myrosin cell; pal, palisade tissue; par, parenchyma; ph, phloem; ph.f, primary phloem fibres; p, pith; p. par, pith parenchyma; r.tr, reservoir-tracheids; sp, spongy tissue; st, stomata; str, striations; u. ep, upper epidermis; v.b, vascular bundle; v.c, vascular cambium; xy, xylem.

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الصفات التشريحية والهستولوجية للورقة والساق المؤقلمة لثلاثة أنواع صحراوية من الكاباريس *Capparis*

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و محمد جلال محمد عبدالفتاح

قسم النبات ـ كلية العلوم ـ جامعة الملك سعود ـ ص. ب ٢٤٥٥ الرياض ١١٤٥١ ـ المملكة العربية السعودية

تمت دراسة صفات البشرة والصفات التشريحية للورقة والساق في كل من *Capparis decidua, Capparis cartilaginea, Capparis spinosa* وتظهر هذه الأنواع النباتية الثلاثة تمايزا في صفاتها التشريحية، ففي منطقة العرق الوسطى: يوجد نسيج البناء الضوئي في هذه الأنواع الثلاثة مع وجود اختلافات في نوع الخلايا المكونة له (عمادى مقابل اسفنجي) وفي توزيع الخلايا (عند كل من السطح العلوي والسطح السفلي) ويوجد نسيج كولنشيمي في كل من *C. cartilaginea, C. spinosa* مع عدم وجوده في *C. decidua* أما النسيج الأساسي البارنشيمي فقد لوحظ وجوده بوضوح في *C. cartilaginea* ومختزلا لدرجة كبيرة في *C. decidua* ولم يمكن ملاحظته في *C. spinosa*. وبالمثل لوحظت اختلافات واضحة في الأنسجة المكونة لقشرة ساق كل من هذه الأنواع الثلاثة من حيث نوع خلايا نسيج البناء الضوئي وتوزيعها. كما تميز كل من *C. decidua, C. cartilaginea* بوجود ألياف لحاء ابتدائي ملجننة. بينما في *C. spinosa* لوحظ أن ألياف اللحاء الابتدائي غير ملجننة.

تشير هذه الدراسة إلى آلية الأقلمة البنائية لنبات *C. cartilaginea* والممثلة في وجود نسيج بارنشيمي مختزن للماء وسماكة واضحة في الجدار الخارجي لخلايا البشرة خاصة في الورقة، والذي يوضح مقدرته على النمو والمعيشة في المناطق الصخرية.