ANATOMICAL CHARACTERS IN CAPPARIS SPINOSA AND ITS ALLIES

M. H. BOKHARI* & I. C. HEDGE

ABSTRACT. Four SW Asiatic taxa of the *Capparis spinosa* L. complex (Capparaceae) were investigated anatomically to determine whether additional taxonomic characters could be found. This showed that features of leaf, petiole and stem did provide useful characters. In particular, it suggested that *C. spinosa* var. *mucronifolia* (Boiss.) Hedge & Lamond merited independent specific status.

INTRODUCTION

The high degree of polymorphism in the *Capparis spinosa* complex is reflected both by the large number of taxa of varying rank that have been described in it and by the varying treatments that have been accorded to it in past and recent Floras. The complex as a whole occurs in the Mediterranean region, N Africa, SW and C Asia and the Himalayas. It is also known from Malesia, islands in the western Pacific, Australia, Madagascar and SW Africa but may not be native in all these regions. Not surprisingly in the case of such a species-complex, local revisions have tended to recognise numerous taxa, and broader-based accounts few taxa. Zohary (1960) dealing with the situation in the Mediterranean region recognised five species and fifteen varieties. In contrast, Jacobs (1965) in his monographic revision of the mainly eastern asiatic species of *Capparis* recognised only one species, *C. spinosa*, and five varieties. In the Flora Iranica region where the complex is well-represented, Hedge & Lamond (1970) recognised the following taxa: *C. spinosa* L. with three varieties, var. *spinosa*, var. *mucronifolia* (Boiss.) Hedge & Lamond, var. *parviflora* (Boiss.) Boiss.; *C. cartilaginea* Dcne. It is with these four taxa that this note is concerned.

Because of the baffling range of morphological variation in the generally used characters of leaf shape, texture, petiole length, depth of posterior sepal and fruit size, and the difficulties of correlating them to form a satisfactory working classification, it seemed that an investigation of the anatomical situation might be a profitable new line of approach. Accordingly, one of us (M.H.B.), using both fresh and herbarium material (mainly the latter) listed in the appendix, undertook an anatomical study of leaf lamina, petiole and stem.

Herbarium specimens were selected from the collections at Edinburgh (E), Tehran (IRAN) and the Pahlavi University, Shiraz where the slide preparations are all deposited.

METHODS

As indicated above, both fresh and herbarium material was used in this study. Most of it was from Iran, particularly the west and south, but some Iraqi, Pakistan and Afghan material was also examined. The fresh material

* Biology Department, Pahlavi University, Shiraz, Iran.

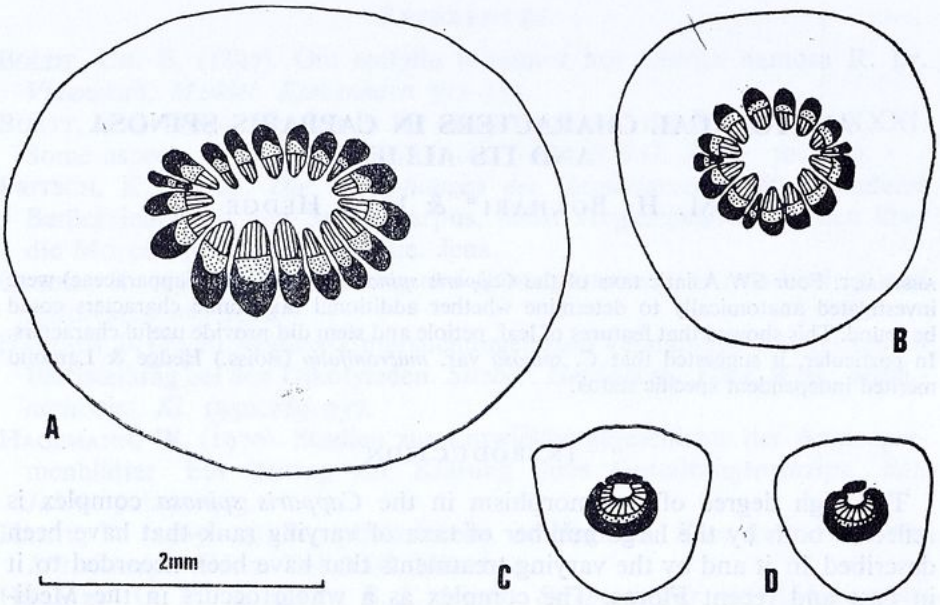

FIG. 1. A–D. Diagrammatic transverse sections of petioles. A, *C. cartilaginea*; B, *C. spinosa* var. *spinosa*; C, *C. spinosa* var. *mucronifolia*; D, *C. spinosa* var. *parviflora*.

was preserved in F.A.A. before sectioning; the techniques used for leaf clearing and preparing herbarium material for section cutting were the same as those described for *Limonium* (Bokhari, 1970).

In the petiole, the shape of the vascular cylinder varies at different levels and it is essential that sections of strictly comparable portions of the petiole should be taken. Petioles of fully developed leaves were sectioned from the middle region and the lamina through the midrib.

ANATOMICAL CHARACTERS

PETIOLE. In this complex the petiole presents some diversity in anatomical features and this, when taken in conjunction with other endomorphic characters, may characterise some species. Petioles in transverse section show the following two types of vascular structure: 1, a number of vascular bundles forming a closed cylinder (fig. 1 A, B)—found in *C. cartilaginea* and *C. spinosa* var. *spinosa*; 2, a small crescent of very closely placed vascular bundles with incurved ends (fig. 1C, D)—found in *C. spinosa* var. *mucronifolia* and *C. spinosa* var. *parviflora*. When the vascular bundles are in a crescent, the phloem is always on the abaxial side, but when vascular bundles are in a ring phloem is oriented towards the periphery of this petiole.

HISTOLOGY OF LAMINA. A few characters of diagnostic value are to be found in the leaf blade, the most important concerning the types of mesophyll, fibres, sclereids and the presence or absence of collenchyma.

Epidermis. In transverse section, the epidermal cells have a broad lumen and are provided with a cuticle of varying thickness. The cells of the upper epidermis are similar to those of the lower epidermis. The cell walls as examined from the epidermal peels are smooth. Anomocytic stomata are

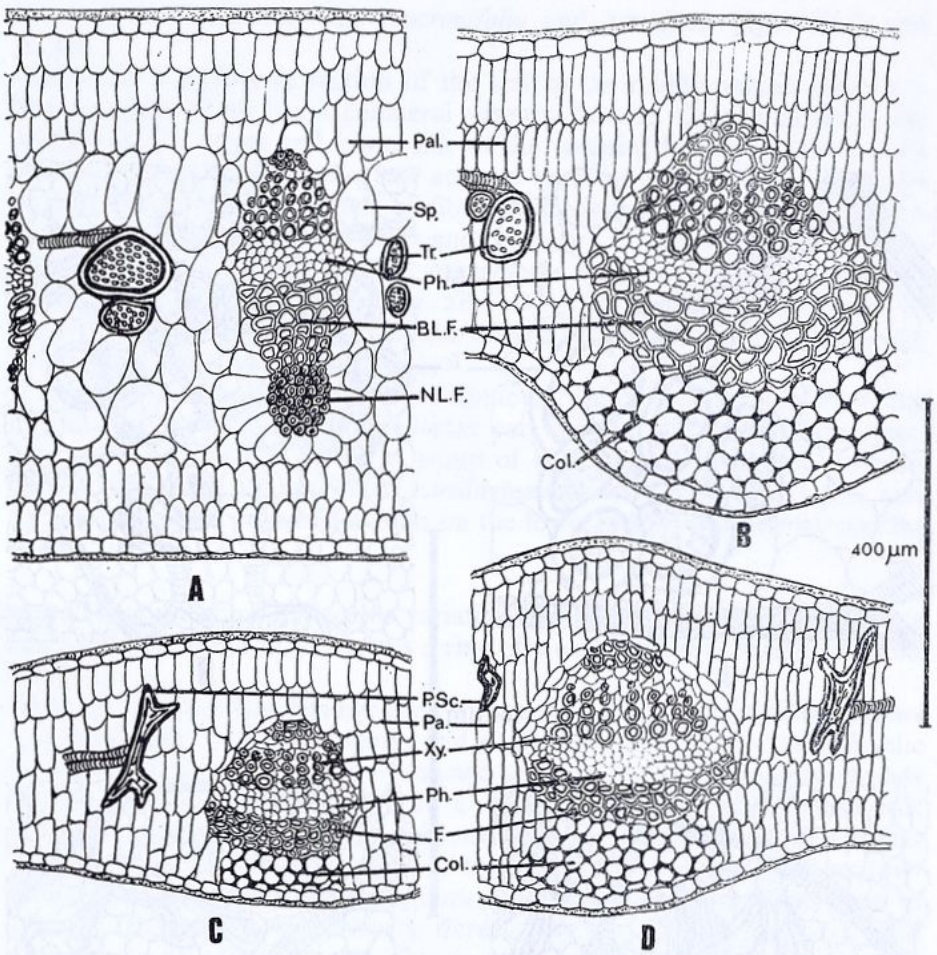

FIG. 2. A–D. Transverse sections of the lamina. A, *C. cartilaginea*; B, *C. spinosa* var. *spinosa*; C, *C. spinosa* var. *mucronifolia*; D, *C. spinosa* var. *parviflora*. B.L.F., broad-lumened fibres; Col., collenchyma; F, fibres; N.L.F., narrow-lumened fibres; Pal., Pa., palisade; Ph., phloem; Xy., xylem; P.Sc., polymorphic sclereids; Sp., spongy mesophyll; Tr., tracheoids.

present on both surfaces in approximately equal numbers and are sunk below the epidermis.

Mesophyll. In *C. cartilaginea*, mesophyll is clearly differentiated: there are 2–4 layers of short palisade cells on the upper and lower side of the lamina. In between the upper and lower palisade is a spongy mesophyll which has large cells (fig. 2A). These cells have a few chloroplasts, a thin layer of cytoplasm and a large central vacuole. Probably these are water storage cells in this species. In *C. spinosa* var. *spinosa* and the vars *mucronifolia* and *parviflora*, mesophyll is undifferentiated, consisting entirely of palisade-like cells (fig. 2B,C,D).

Sclereids. Smaller veinlets are nearly always embedded in the mesophyll and are accompanied by terminal sclereids. Sclereids are of two types. Firstly, tracheoids (pitted storage tracheids); previously only reported for *C. cartilaginea* (Metcalf & Chalk, 1950) but found here in *C. spinosa* var. *spinosa* (figs. 2A,B and 3A,B). Secondly, polymorphic sclereids which were

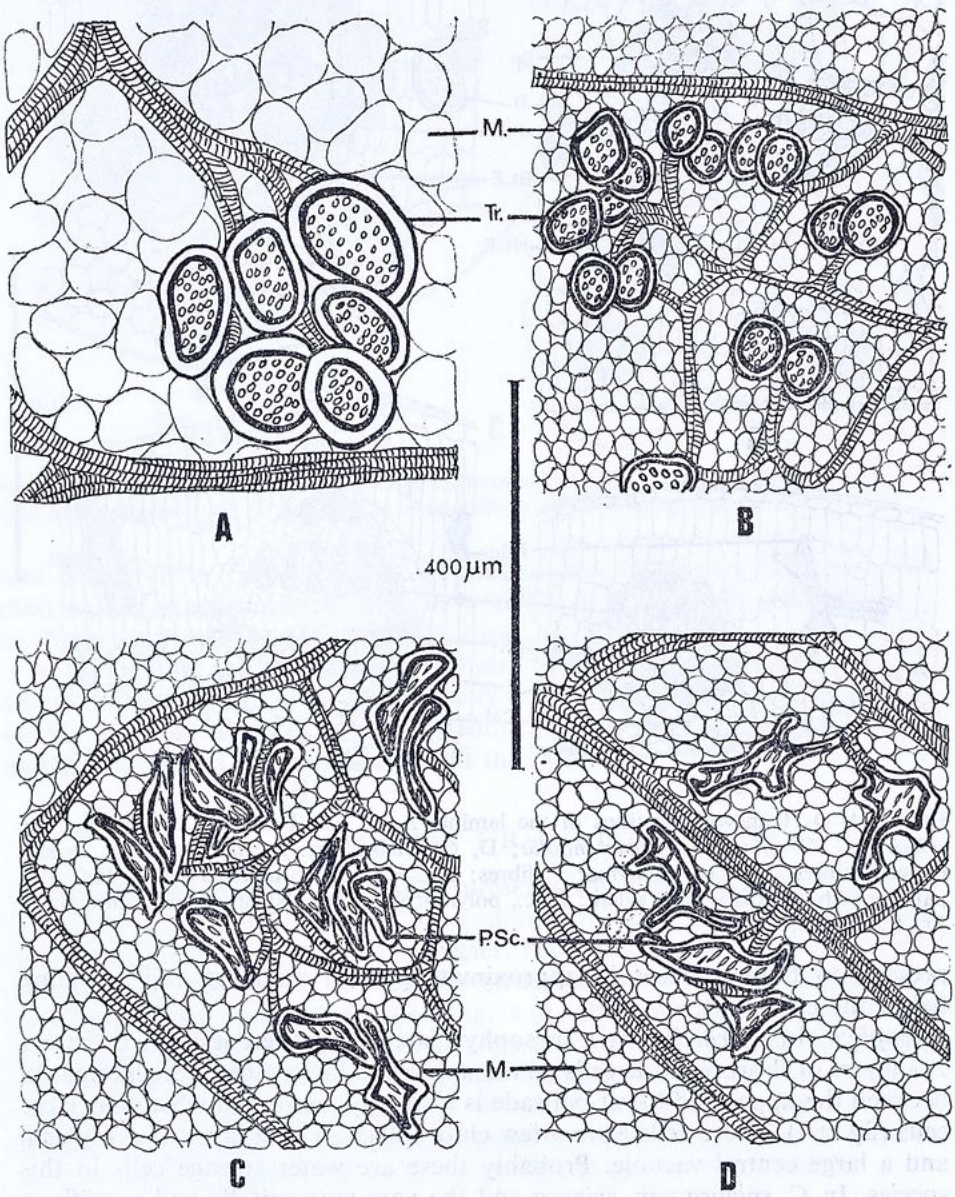

FIG. 3. A–D. Parts of cleared leaves showing terminal sclereids. A, *C. cartilaginea* showing tracheoids; B, *C. spinosa* var. *spinosa* showing tracheoids; C, *C. spinosa* var. *mucronifolia* showing polymorphic sclereids; D, *C. spinosa* var. *parviflora* showing polymorphic sclereids; P.Sc., polymorphic sclereids; M, mesophyll; Tr., tracheoids.

observed in *C. spinosa* vars *mucronifolia* and *parviflora* (figs. 2C,D and 3C,D).

Midrib. In a transverse section of the leaf in the middle region there is a single midrib which has a collateral vascular bundle. Groups of fibres are present on the upper and lower side of the vascular bundle in all the taxa examined. Only in *C. cartilaginea* are two types of groups of fibres present on the abaxial side. A patch of fibres immediately below the phloem is composed of broad-lumened fibres and below it is always a group of narrow-lumened fibres (fig. 2A). In the other three taxa, abaxial fibres are not found in two distinct patches (fig. 2B,C,D). The presence of two types of fibres on the abaxial side of a vascular bundle is thus apparently a diagnostic feature of *C. cartilaginea*.

In all the taxa, palisade is continuous over the upper side of the midrib vascular bundle. In *C. spinosa* var. *spinosa*, var. *mucronifolia*, and var. *parviflora* there is always a group of collenchyma below the vascular bundle (fig. 2B,C,D) but in *C. cartilaginea* there is no collenchyma and instead palisade is continuous even on the lower side of the midrib vascular bundle (fig. 2A).

STEM. There are some noticeable variations in the stem anatomy of the taxa examined (fig. 4) but in all there is a ring of closely placed collateral vascular bundles.

Pericyclic Fibres. The arrangement and nature of pericyclic fibres shows some variation. In *C. cartilaginea* and *C. spinosa* var. *spinosa* the pericyclic fibres are thick-walled, narrow-lumened and are found in separate strands outside the phloem (fig. 4A,B). In *C. spinosa* var. *mucronifolia* and var. *parviflora*, pericyclic fibres are in the form of a closed ring outside the vascular bundles (fig. 4C). The fibres are of two types: thick-walled and narrow-lumened; thin-walled and broad-lumened. They are found intermixed in this ring. In addition to pericyclic fibres, there are also scattered sclerified parenchyma cells immediately outside the fibrous ring in *C. spinosa* var. *mucronifolia* and *C. spinosa* var. *parviflora* (fig. 4C,Cc).

Cortex. In *C. cartilaginea* there are two distinct zones of cortex: an outer zone of smaller cells and an inner zone of larger ones. In both zones there are groups of cells containing whitish yellow refractive bodies (fig. 4A,Aa). Tracheoids are always present in the cortex. Crystals are also present in the cortical cells of this species. These are secreted either as solitary, rhomboidal or rectangular crystals or in clusters, druses (fig. 4A,Aa).

In *C. spinosa* var. *spinosa* and vars *mucronifolia* and *parviflora* the cortex is uniform and is composed of one type of cell. Tracheoids and groups of cells with refractive bodies and crystals are entirely absent in the cortex (fig. 4B,Bb,C,Cc).

Wood. Tangential and radial sections of wood were studied and their structure does offer some useful characters of diagnostic value (fig. 5). Vessels always have simple, oblique or horizontal perforations at the end walls with alternate intervascular pittings. Rays are 1–4 cells wide, mostly homocellular, that is made up of entirely procumbent cells. Some heterocellular rays were also observed. These are made up of procumbent and upright cells. The percentage of different types of rays and the height of the highest ray are of diagnostic value as shown in the table.

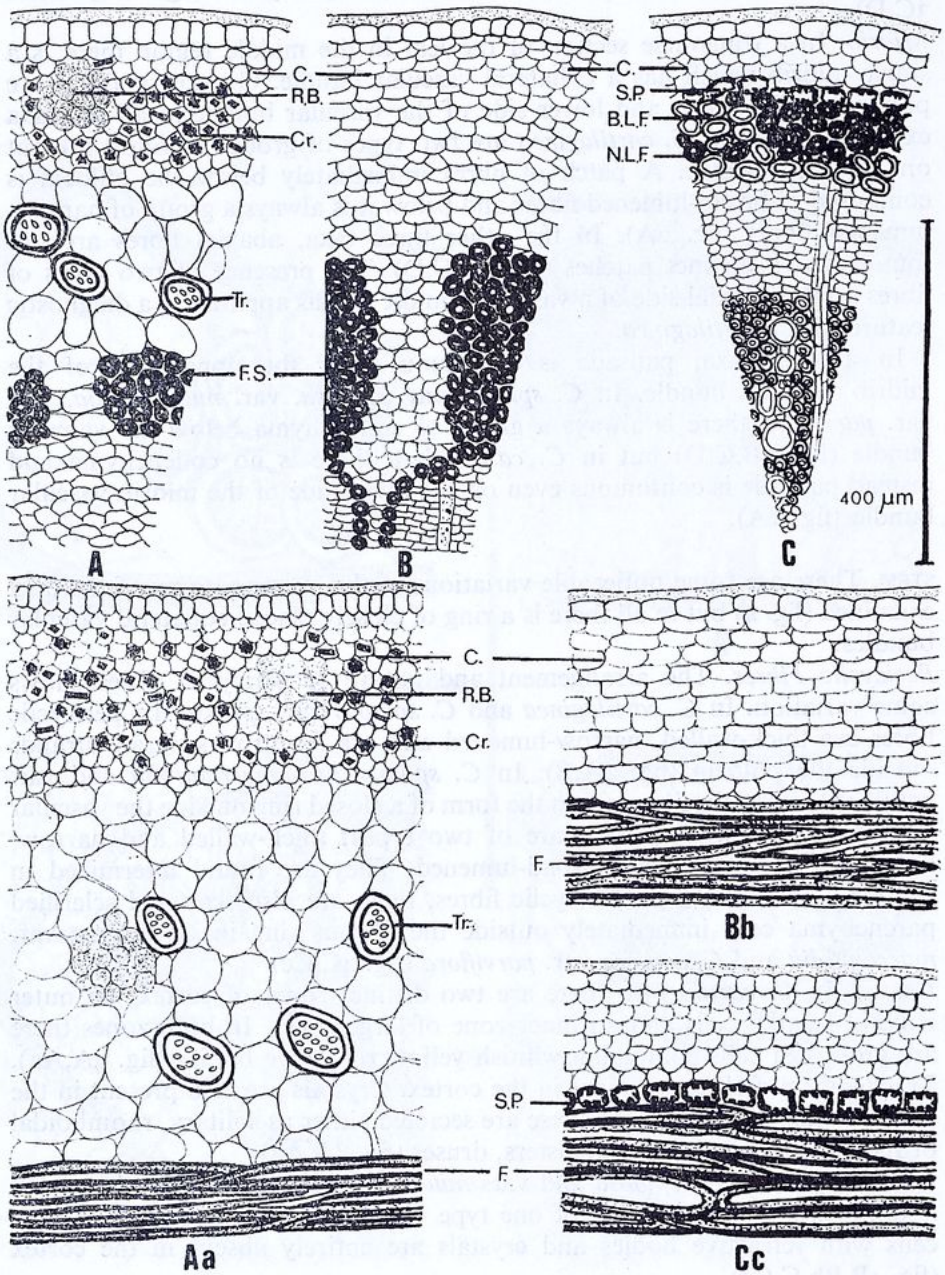

FIG. 4. Transverse and longitudinal sections of stems. A, transverse section of the stem of *C. cartilaginea*; Aa, longitudinal section of the stem of *C. cartilaginea* showing cortex and pericyclic fibres; B, transverse section of the stem of *C. spinosa* var. *spinosa*; Bb, longitudinal section of the stem of *C. spinosa* var. *spinosa* showing cortex and pericyclic fibres; C, transverse section of the stem of *C. spinosa* var. *mucronifolia*; Cc, longitudinal section of the stem of *C. spinosa* var. *mucronifolia* showing cortex and pericyclic fibres. B.L.F., broad-lumened fibres; C, cortex; Cr., crystals; F, fibres; F.S., fibrous strand; N.L.F., narrow-lumened fibres; R.B., group of cells with refractive bodies; S.P., sclerified parenchyma; Tr., tracheoids.

	% of uni- and biseriate rays	% of multiseriate rays (3- & 4-celled)	height of highest ray
C. cartilaginea	47	63	500 μm
C. spinosa			
var. *spinosa*	85	15	860 μm
var. *mucronifolia*	95	5	645 μm
var. *parviflora*	95	5	642 μm

Conclusions

In the material examined, certain anatomical characters appear to be quite constant and characteristic for some taxa. For example, *C. cartilaginea*, regarded by Jacobs (1965) as a variety of *C. spinosa* but given specific status in *Flora Iranica* and other recent Floras, is anatomically distinct on the following characters: differentiated mesophyll; absence of collenchyma and presence of palisade tissue below the vascular bundles of the midrib; two types of fibre below the vascular bundle of the midrib; stem cortex with two distinct zones; crystals and groups of cells with refractive bodies in cortex; high percentage of multiseriate rays.

Likewise, *C. spinosa* var. *spinosa* can be separated from vars *mucronifolia* and *parviflora* on the following anatomical features: a closed ring of vascular bundles in the petiole; the presence of tracheoids in the leaf; the presence of pericyclic fibres in strands; the higher percentage of multiseriate rays and the presence of the highest rays.

Although var. *spinosa* can be distinguished from vars *mucronifolia* and *parviflora*, it seems impossible anatomically to separate the latter varieties from each other. They have the following characters in common: crescent-shaped vascular tissue in the petiole; polymorphic sclereids; pericyclic fibres of two types in a closed ring; sclerified parenchyma outside the ring of fibres; the highest percentage of uni-biseriate rays.

On anatomical grounds alone, there are therefore good reasons for regarding var. *mucronifolia*, with var. *parviflora* as a synonym of it, as an independent species.

How then does the anatomical evidence agree or conflict with that of general morphology? Firstly, it confirms *C. cartilaginea* as an independent species. This already seemed clear on the morphological characters of thick cartilaginous leaves with distinct petioles and the prominently galeate posterior sepals, both of which clearly separate it from the other Iranian taxa. In Iran, it is restricted to the south of the country where it usually is found as a sprawling shrub on hot dry cliff ledges. Although it was suggested in *Flora Iranica* that *C. cartilaginea* had red fruits and *C. spinosa* green, this is not so, both having red fruits at maturity.

The second investigation, that of *C. spinosa* and its varieties, is of greater interest in that the anatomical evidence conflicts with the existing taxonomy. The essential differences between the three varieties recognised in the *Flora Iranica* account were that: var. *spinosa* had large leaves, c. 1–2 × longer than broad and large flowers; var. *mucronifolia* much smaller leaves with an acute apex, c. 2–3·5 × longer than broad and small flowers; var. *parviflora*, small leaves c. 1–1·5 × longer than broad, with an obtuse apex and small flowers. The characteristic form of the type variety is most unlikely to be confused

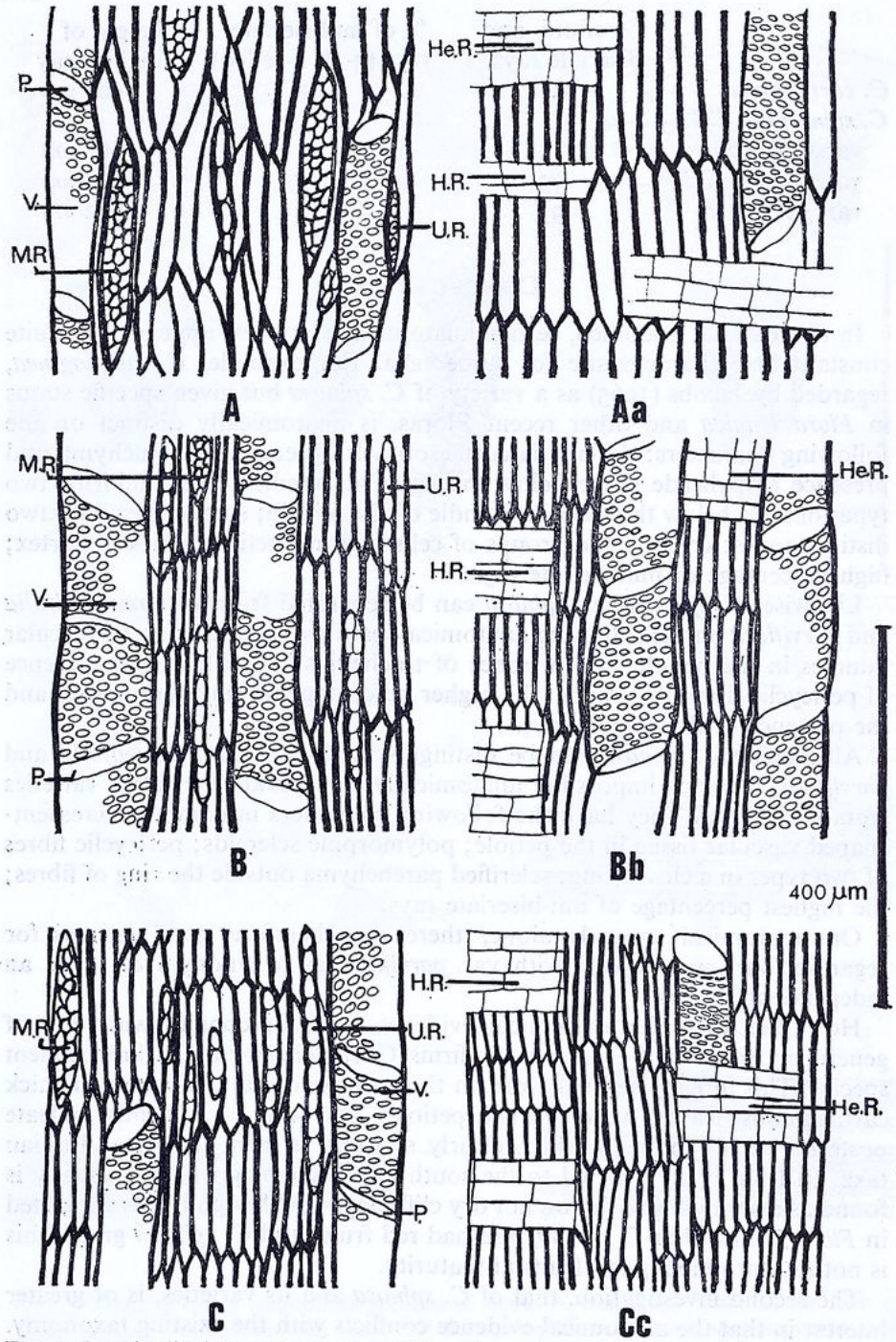

FIG. 5. Longitudinal tangential and radial sections of wood. A, tangential section of the wood of *C. cartilaginea*; Aa, radial section of the wood of *C. cartilaginea*; B, tangential section of the wood of *C. spinosa* var. *spinosa*; Bb, radial section of the wood of *C. spinosa* var. *spinosa*; C, tangential section of the wood of *C. spinosa* var. *mucronifolia*; Cc, radial section of the wood of *C. spinosa* var. *mucronifolia*; HeR., heterocellular rays; HR., homocellular rays; M.R., multiseriate rays; P., perforation; U.R., uniseriate rays; V., vessel.

with the other two. The latter are not, in contrast, so readily separated from each other on external morphology. Both, unlike the type variety—the progenitor of the cultivated caper, are found in habitats away from cultivated areas such as cliffs or stony slopes, often in sub-desertic conditions. The main problem for the taxonomist in this complex is how to classify the numerous intermediates between these three varieties. Although it was not possible to examine anatomically anything like the quantity of material that was at hand when the *Flora Iranica* account was prepared, a few specimens that morphologically appeared intermediate were examined and they clearly fell into one group or the other. Truly intermediate anatomical forms were rare.

Although the new evidence points strongly towards resuscitating *C. mucronifolia* Boiss. as a separate species we have delayed doing so formally. Including var. *parviflora*, and several other apparent synonyms, the taxon appears to extend from NW Africa through Egypt, Israel, Iraq and Arabia to Afghanistan and C Asia. The material examined in this study covers only a small section of this vast area and it seems wiser not to change the existing, admittedly unsatisfactory, classification until a wider range of material has been studied. It is quite clear, however, that anatomical investigations do have much to offer in this difficult complex and are potentially a source of important taxonomic facts.

Acknowledgment

We are greatly indebted to Mr Afzal, Instructor, Biology Department, Pahlavi University, Shiraz, for cutting the sections of all the available material, making permanent slides and reconfirming the anatomical characters.

References

Bokhari, M. H. (1970). Morphology and taxonomic significance of foliar sclereids in Limonium. *Notes R.B.G. Edinb.* 30:43–53.

Jacobs, M. (1965). The genus Capparis from the Indus to the Pacific. *Blumea* 12:385–541.

Hedge, I. C. & Lamond, J. (1970). Capparidaceae in Rech. fil., ed., *Flora Iranica*, 68. Graz, Austria.

Metcalf, C. R. & Chalk, L. (1950). *Anatomy of the Dicotyledons*. 2 vols. Oxford.

Zohary, M. (1960). The species of Capparis in the Mediterranean and the near eastern countries. *Bull. Res. Counc. Israel* 8D:49–64.

Appendix

Specimens examined of the *Capparis* taxa investigated.

C. cartilaginea Decne.

Iran: Makran, *Behboudi* 506; Baluchistan, *Sharif* 768; Gavbandi, *Davis & Bokhari, D.* 56071.

C. spinosa L. var. *spinosa*
Iran: Khorasan, *Walton* 200; Azerbaijan, *Lamond* 3097, *Aellen & Behboudi* s.n.; Gorgan, *Sharif* 315, *Dan. Bot. Trans. As. Exped.* 244; Khuzestan, *Grant* 15908; Sistan, *Ayazi* 5824; Yazd, *Archibald* 2782; Shiraz, *Bokhari* 1245; Ghassre Shirin, *Behboudi* 1538.
Iraq: Dohuk, *Wheeler Haines* s.n.; Babylon, *Grant* 15667; Baghdad, *Barkley & Jumaa* 1689.
Afghanistan: Nangarhar, *Hedge & Wendelbo, W.* 7468; Bamian, *Hedge & Wendelbo, W.* 3423.
Pakistan: Chitral, *Stainton* 2780; Kohat, *Burtt* 1086.

C. spinosa var. *mucronifolia* (Boiss.) Hedge & Lamond
Iran: Bandar Lengeh, *Davis & Bokhari, D.* 56176; Baluchistan, *Sharif* 973; Bandar Khamir, *Soltani* s.n.
Pakistan: Makran, *Lamond* 409; Sind, *Lamond* 866a; Quetta, *Lace* 3938.

C. spinosa var. *parviflora* (Boiss.) Boiss.
Iran: Shiraz, *Bokhari* 1245; *Sharafeh* 13404, *Archibald* 2940, *Grant* 15107, 15574; Sistan, *Sharif* 1536.
Afghanistan: Girishk, *Dan. Bot. Trans. As. Exped.* 452; Fariah, *Hedge & Wendelbo, W.* 7674.
Pakistan: Baluchistan, *Lamond* 733.

In addition to the herbarium material listed, a quantity of fresh or preserved material of *C. spinosa* vars *spinosa* and *parviflora* was examined. These two varieties are both quite common in the province of Fars, Iran.