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LEAF ANATOMY OF A *QUERCUS COCCIFERA* L. FORM FROM THE EAST ADRIATIC COAST

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Two related *Quercus* species grow near the coast of the Mediterranean: *Quercus coccifera* L. and *Q. calliprinos* Webb. The centres of spreading of *Q. coccifera* are Spain and France, and of *Q. calliprinos* is Israel. In the central parts of the Mediterranean, between Israel and France, various new forms have developed which are more or less distant from the two starting species. One of these new forms, found in Yugoslavia in South Croatia on the East Adriatic coast, was determined as *Q. coccifera,* and is a representative of a plant association *Orno-Cocciferetum* H-ć (Horvatić 1963a, b; Horvat et al. 1974).

In order to obtain more information about *Q. coccifera* form which grows on the east coast of the Adriatic, we performed anatomical and some morphological investigations of the leaf. Some similarities have been found between this form and *Q. calliprinos;* they both have thorny-serrate leaf margins. However, the characteristics of the type form of *Q. coccifera* prevailed, such as a relatively thin leaf blade, poorly developed hypoderm, early loss of trichomes and obvious intercellulars in the mesophyll.

Introduction

Recently, *Quercus coccifera* L. s. l. has been thoroughly investigated especially by Gentile and Gastaldo (1976), who established that in the Mediterranean countries in fact two related *Quercus* species could be differentiated: *Q. coccifera* L. and *Q. calliprinos* Webb. The species *Q. coccifera* has the centre of spreading in the West Mediterranean (Spain, France) and *Q. calliprinos* in the East Mediterranean (Israel). Some morphological and anatomical characteristics of the leaf of both species are given in Table 1, which originates from Gentile and Gastaldo

(1976). The two species in their typical form are spread near the centres of their areas. However, transitive forms grow in central parts of the Mediterranean: in Sicilia, Apulia, Greece and Yugoslavia.

Table 1. Properties of type forms of the species *Quercus coccifera* L. and *Q. calliprinos* Webb. according to Gentile and Gastaldo (1975)*

Characteristics		Leaves of plants from Pamplona (Spain)	Leaves of plants from Hebron (Israel)
Petiole	Surface	Partially pilose	Completely pilose
Blade	Margin	Cartilaginous Thorny-dentate	Cartilaginous Thorny-serrate
	Middle thickness	287 μm	324 μm
	Leaf blade	Partially hairy	Completely hairy
	Starry hairs	Small number of hairs	Abundant number of hairs
	Mesophyll	With large intercellulars	Without large intercellulars
	Upper hypoderm	Poor, not continuous	Abundant, discontinuous
	Lower hypoderm	Only in region of vascular bundles	Only in direction of vascular bundles, poorly

* The Table contains only part of plant properties presented in the table published by Gentile and Gastaldo. For complete instructions the readers are directed to use these authors' paper.

In this paper the leaf anatomy of a form of *Quercus* determined by Horvatić (1963a, b) as *Q. coccifera*, which is spread on the east coast of the Adriatic Sea on the island of Korčula and the peninsula of Pelješac, is presented.

Material and Methods

The leaf material of *Q. coccifera* spread on the East Adriatic coast was collected on the island of Korčula, in Korčula and the surroundings of this town, in the association *Orno-Cocciferetum* H-ć (Horvatić 1963a, b; see also Šilić 1973). For limited comparative purpose the leaves collected from a plant of *Q. coccifera* originating from Macedonia and grown for many years in Zagreb Botanical Gardens were used.

Some investigations of leaf surface and cross sections were made with a scanning electron microscope. During these investigations the leaves were exposed to carbon and gold in a vacuum evaporator and then micrographed with a JSM-U$_3$.

Results

Leaf morphology and falling off of the leaves

The leaves of *Quercus coccifera* are very hardy, similar to those of evergreen oak (*Q. ilex* L.).

The leaves of *Q. coccifera* from Korčula differ considerably from those of *Q. coccifera* plant from Macedonia. The leaf margin of the former was of cartilaginous character and thorny-serrate from with 3—7 dents on each part of the lamina (Fig. 1A). The whole leaf was 3.5 to 5 cm long. In contrast, the leaves from the plant origination from Macedonia had widely dentate leaf margins with long and sharp thorns (Fig. 2). The whole leaf was about 3 to 4.5 cm long.

Like the leaves of *Q. ilex*, the leaves of *Q. coccifera* remain on the tree for several years. According to the data of Giperborejski and Marković (1952), they remain on the trees for two years on the average. We note that the leaves of *Q. ilex* also remain on the trees for two years (cf. Bačić and Miličić 1985; Jovanović and Ilić-Vukićević 1959).

The leaf epidermis

The upper and the lower epidermis of *Q. coccifera* leaves from Korčula had a very thick outer wall, whose thickness was about 10 μm on the average and larger than the lumen of the epidermal cells (Fig. 1F). After staining with Sudan III, the whole outer wall became red, which suggested that the xeromorphic conditions were strongly expressed (Braune et al., 1967). Many lateral walls of the epidermal cells were also stained red with Sudan III, which also shows that the xeromorphy of this plant is very significant. By way of comparison we can mention that the thickness of cutin containing outer walls of *Q. ilex* is about 5 μm. Consequently, the grade of xeromorphy of *Q. coccifera* is certainly higher than that of *Q. ilex*.

Another fact is the presence of lignin in the epidermal cell walls. Treated with phloroglucin and HCl the epidermal cell walls became intensively red. According to investigations of Bačić and Miličić (1985), the cell walls of the leaf epidermis of *Q. ilex* also give a positive reaction with phloroglucin and HCl. On the basis of data by Esau (1965, p. 116) and Linsbauer (1930) lignin is very rare in the cell walls of leaf epidermis of dicotyledons, but it appears in some plants, such as *Quercus, Nerium oleander* and *Laurus nobilis*.

Stomata

On the lower epidermis there is a large number of stomata (Fig. 1E), on average 270 to 490 stomata per 1 sq mm. That is much more than with *Q. ilex* (Bačić et Miličić 1985).

As can be seen in Fig. 1D, the central parts of guard cells of a stoma have very thick cell walls which cannot be widened, but the opening of the stomata is made possible by the lateral parts of these stomata, which have thin cell walls and therefore can be enlarged when the turgor in the guard cells increases. At this moment the porus becomes open. This type of stomata was described by Aneli (1975) as »gantele-gubovidnyj (Russ.) = (Engl. dumbell-lip like) type.

On the same stoma in Fig. 1D a cuticular lamella is visible on the left guard cell. This lamella can diminish transpiration. Above this, in the places where the outer walls meet the ventral walls of the guard cells, there are well developed cuticular horns (h in Figs. 1C, D). The cuticular horns can also diminish transpiration to a certain extent and can be treated as xerophytic adaptation. The parallelly arranged cuticular pleats can be observed in Fig. 1C.

It should be mentioned that the stomata of *Q. coccifera*, just as the stomata of *Q. ilex* (Bačić and Miličić 1985), have no thickennings on the exterior guard cell walls. The thickenings are characteristic of some oaks with decidous leaves such as *Q. robur, Q. cerris* and *Q frainetto*, but not of the two evergreen oaks (cf. Bačić 1981).

The arrangement of epidermal cells of *Q. coccifera* around the stomata shows no peculiarities. It is possible to establish that the guard cells are surrounded with varying numbers (5 to 10) but most frequently with 7 neighbouring epidermal cells. Thereafter the most frequent numbers are 8, 6, 9, 5 and 10 neighbouring cells. This type of arrangement of neighbouring epidermal cells in the region of stomata is named anomocytic type (Metcalfe and Chalk 1950).

Trichomes

In the young leaves of *Q. coccifera* hairs were present on both epidermes (Fig. 3A). A large number of hairs, however, soon fall off so that on full-grown leaves the hairs are present only on the lower epidermis near the central leaf vein (Fig. 3C). As in *Q. ilex*, in *Q. coccifera* (cf. Fig. 3A) the hairs belong to the type of tufted hairs (Esau 1965; see also Bačić and Milićić 1985; Martinis et al. 1986).

The cells of tufted hairs present on the upper epidermis of *Q. coccifera* grow parallelly with the epidermis forming a star-like hair at the end (cf. Fig. 3A). These star-like trichomes of a tufted hair structure were very frequent.

On the other hand, the hairs on the lower epidermis (Fig. 3A, B, C) had the characteristics of »true« tufted hairs which are very common, for instance, in *Q. ilex*. They grow obliquely from the leaf epidermis and have a more constant and durable function. By their appearance they laso resemble the tufted hairs of *Q. ilex*.

The »true« tufted hairs of the lower epidermis were strengthened in the epidermis by a group of cells arranged around the hair basis which, by their appearance, could be considered as pedestal. However, the cells of a pedestal always have cutin in its walls, and in the investigated *Q. coccifera* form, cutin could be established in cell groups around some hair bases, but not in the others.

In the basal region of *Q. coccifera* leaves between 25 and 98 hairs per 1 sq mm were counted. This number is two times as low as that in *Q. ilex*.

Glandular hairs

These hairs are also situated on both epidermes, but only in the young leaves. In fully developed leaves they were not observed. It is certain that glandular hairs live shorter than common hairs.

Glandular hairs are multicellular. According to the division by Aneli (1975) they belong to the »capitate« type. They contain a head and a filamentous basal part (Fig. 4). The head consists of 2 to 8 cells and can be round, elliptic or elongated. The filamentous basal part consists of 2 to 5 cells. In shape and structure the glandular hairs of *Q. coccifera* are similar to the glandular hairs of *Q. ilex*.

Mesophyll

The leaf parenchyma is firmly, built almost exclusively of palisade parenchyma cells (Table 2).

Typical palisade parenchima is situated in the upper part of the mesophyll. It includes two thirds of the total palisade parenchyma, more precisely 62%. Under this first very important layer, follows a second

very thin layer of spongy (round) parenchyma which is made of short cells. The spongy parenchyma includes a small part of mesophyll, only 7% of the leaf mesophyll. The third layer is again made of palisade parenchyma cells. This last parenchymatic tissue has elongated, but somewhat shorter cells than the typical palisade parenchyma below the upper epidermis and makes about 31% of the total quantitiy of mesophyll.

Table 2. Data on the mesophyll structure of *Q. coccifera* from Korčula

Tissue	Parts of mesophyll	Length	Percentage
Mesophyll (Height of the mesophyll 245 μm)	Palisade parenchyma	152 μm	62%
	Spongy parenchyma	17 μm	7%
	Short palisade parenchyma	76 μm	31%

Supporting walls

The midrib and lateral veins are composed of various hardy cell elements which are continuous from the upper to the lower epidermis making the leaf very firm. Figs 5A and 6B show supporting walls which are connected with firm parts of upper and lower epidermis. Similar supporting walls are developed in the leaves of the xerophyte plant *Q. ilex*. (Bačić and Miličić 1985, p. 27).

Consequently, the supporting walls of *Q. coccifera* (Fig. 5A) first include both epidermes followed by sclerotic parenchyma tissue joining both epidermes. In the middle part of the supporting walls single small fibrovascular bundles are situated. The vascular bundles are protected on both sides by mechanical fibres which join the sclerotic parenchyma tissue

In the region of supporting walls the lateral and the internal walls of both epidermes give a strong positive reaction with phloroglucine and HCl, while the outer walls give a weak reaction with this reagent. The sclerotic parenchyma tissue situated below the upper and the lower epidermis has thick lignified walls, especially the sclerotic parenchyma cells which are under the upper epidermis. This parenchyma cells usually contain a large calcium oxalate crystal. Equal crystals were also present in sclerotic parenchyma of *Q. ilex* (see Bačić and Miličić 1985, Fig. 6A, B). Tracheidal elements of the xylem with helical thickenings gave a clear reaction with phloroglucine.

Sclerotic palisade cells

In the leaves of *Q. coccifera* from Korčula we sometimes observed groups of sclerotic palisade cells under the upper leaf epidermis. These cells were of the same form as the adjacent parenchyma cells but with thick cell walls and many pits in the walls (Figs 5B, 6A).

First we found sclerotic palisade cells in a young leaf which had no hypoderm. Very similar single sclerotic palisade cells were found subsequently in a *Q. coccifera* leaf with well developed hypoderm. In this case sclerotic palisade cells were also situated directly below the epidermis.

Hypoderm

The hypoderm is a peripheral tissue which often appears below the upper and more rarely above the lower epidermis of *Q. coccifera* leaves (cf. Table 1). Fig. 6 presents well developed hypoderm which was formed under the upper epidermis of *Q. coccifera* plant originating from Macedonia, and has three layers of lignified cells. It seems that

Fig. 1.* **A** Leaves of *Quercus coccifera* L. from the island of Korčula (Croatia) with serrate leaf margins. **B** Lower epidermis with a stoma; z central part of stoma where the cell wall is thick, t marginal part of stoma where the cell wall is thin. **C** Stoma micrographed from above in a scanning electron microscope (SEM); h cuticular horn, l cuticular lamella. **D** Cross section of a xeromorphic stoma; h cuticular horn, l cultricular lamella. Lumen of the stoma is very narrow in the central part. **E** Lower epidermis with stomata in SEM. **F** Cross section of the outer leaf epidermis.

Fig. 2. Leaves of *Q. coccifera* plant from Macedonia with wide dentate margins. Bar represents 1 cm.

Fig. 3. **A** Cross section of a young leaf treated with sodium hypochlorite. Two types of tufted hairs are visible: the true tufted hairs on the lower epidermis, the cells of which are oriented in various directions, and the tufted hairs as star-like trichomes, the cell of which after leaving the epidermis stretch parallelly with the leaf surface. **B** A true tufted hair on the lower epidepmis micrographed in a SEM. **C** A large number of tufted hairs along a leaf midrib micrographed in SEM.

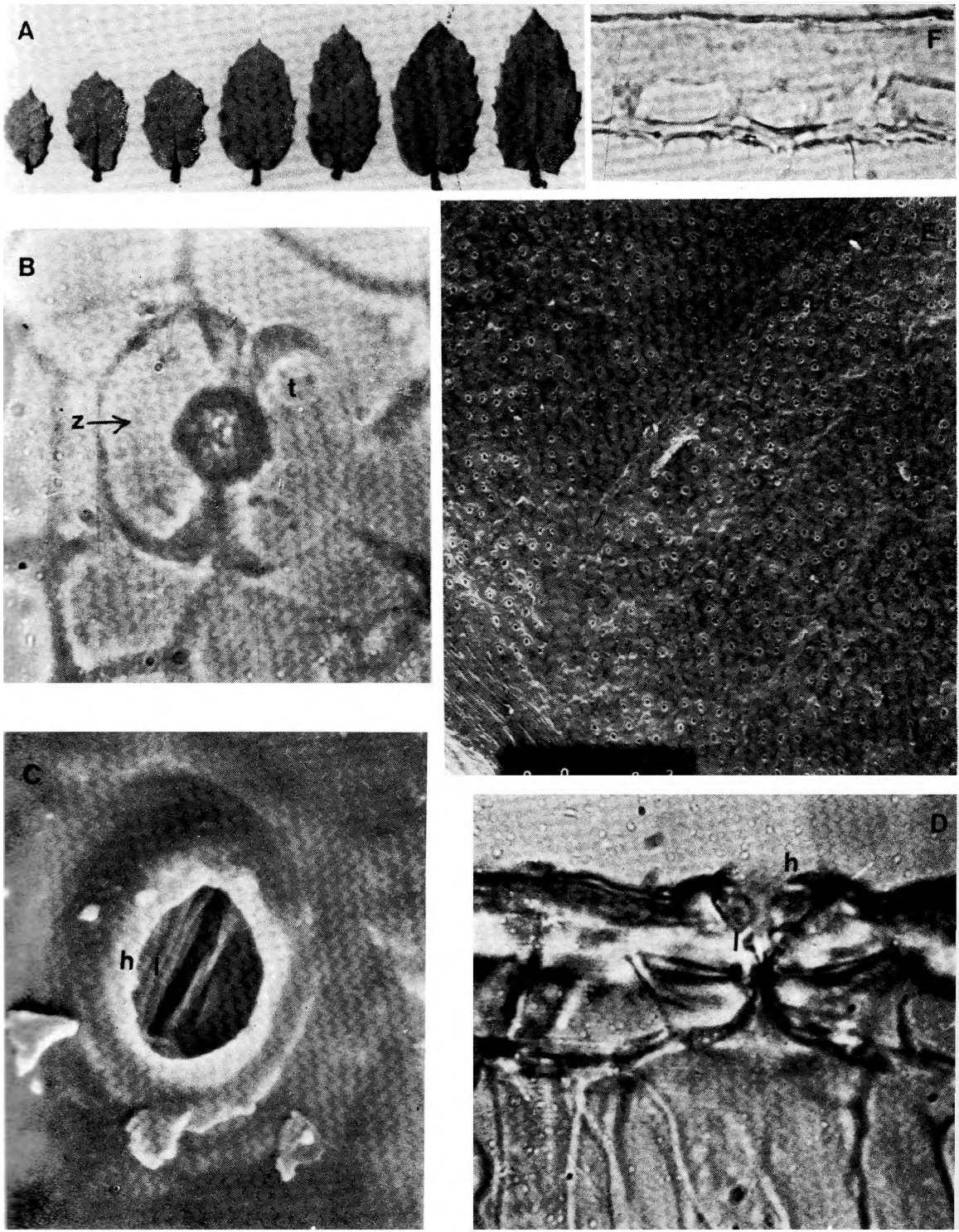
Fig. 4. Various forms of glandular hairs of *Q. coccifera*.

Fig. 5. **A** Cross section of the leaf treated with sodium hypochlorite. Two supporting walls which strengthen the leaf stretching continuously from the upper to the lower epidermis. Between supporting walls there is soft tissue which consists mostly of palisade parenchyma cells. **B** Cross section of the leaf. Dark and round bodies are druses of calcium oxalate; some sclerotic palisade cells (s) are present below the upper epidermis.

Fig. 6. **A** Cross section of the leaf of *Q. coccifera* in the region of the main vascular bundle; x xylem, ph phloem, f fibres, s sclerotic palisade cells, h hypoderm. **B** Cross section of a part of *Q. coccifera* leaf from Macedonia with developed hypoderm (h).

Fig. 7. **A** Cross section of the main vascular bundle of the leaf; f fibres, ph phloem, x xylem, o sclerotic parenchyma. **B** and **C** Strengthening structures of leaf margin; e epidermis, h hypoderm, f fibres.

* All figures except Fig. 2 and Fig 6B to *Q. coccifera* from the East Adriatic Adriatic coast.



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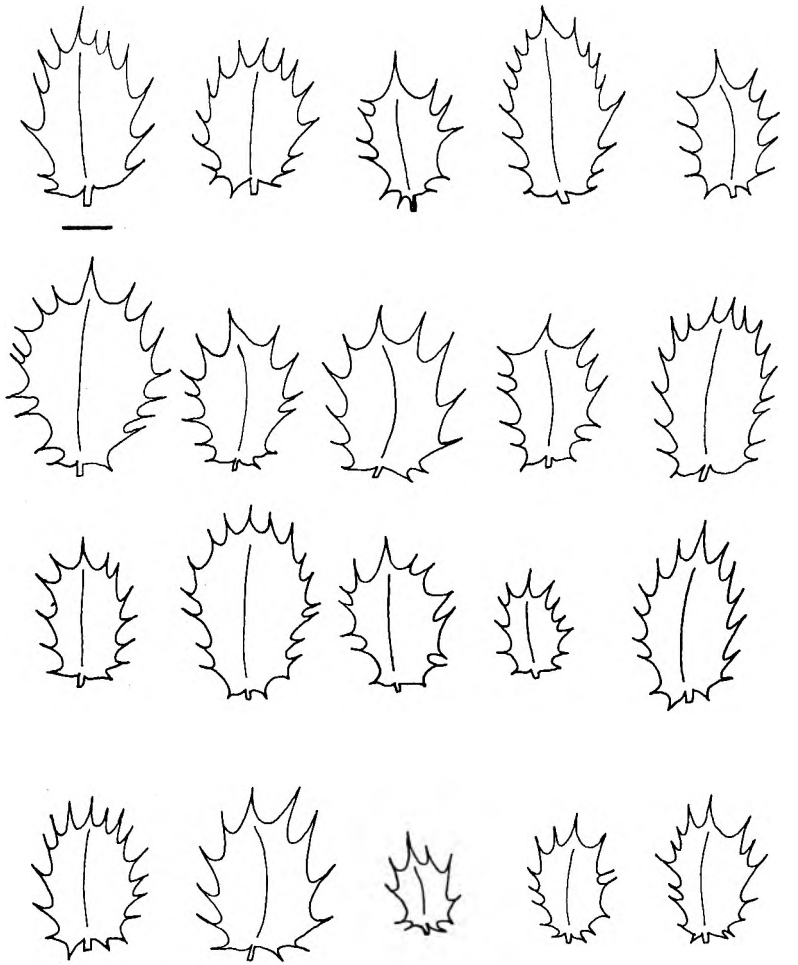

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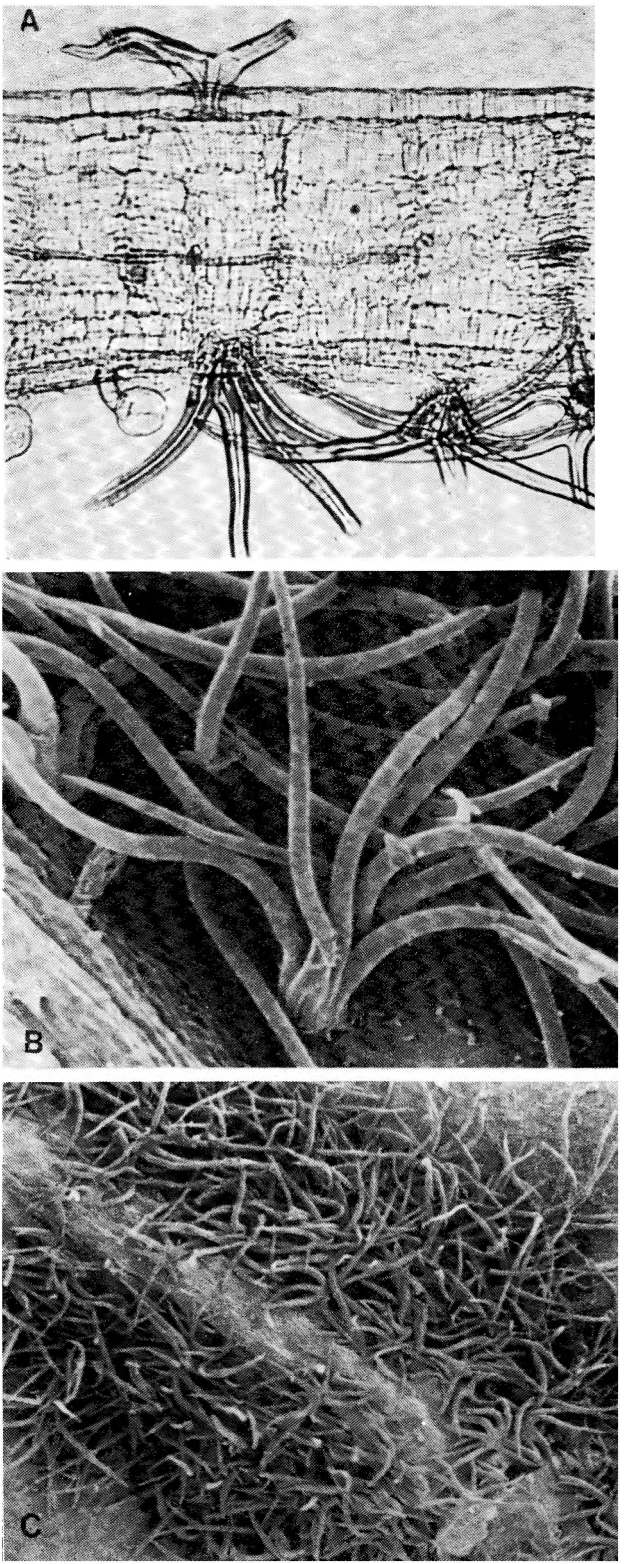

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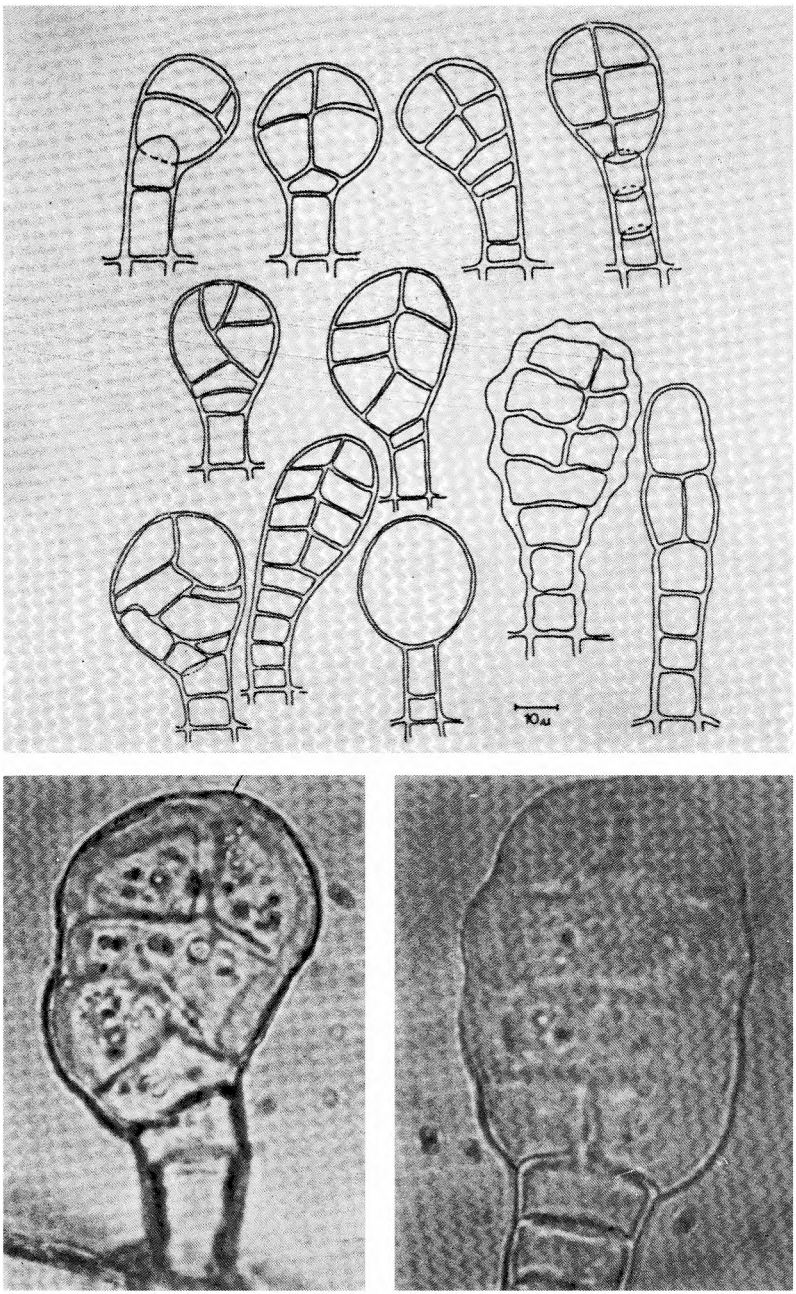

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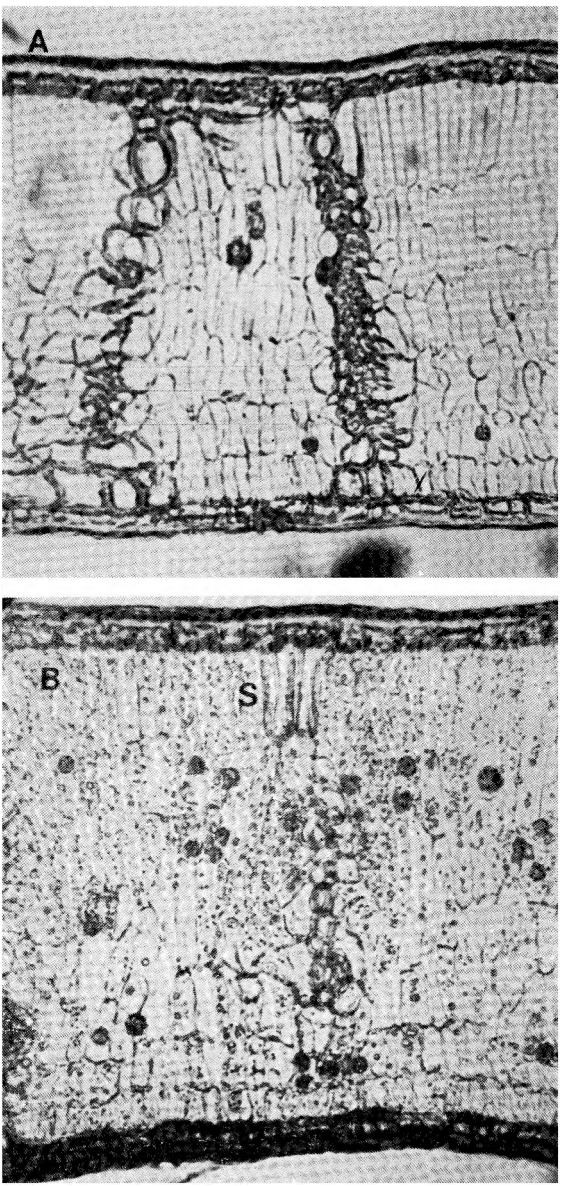
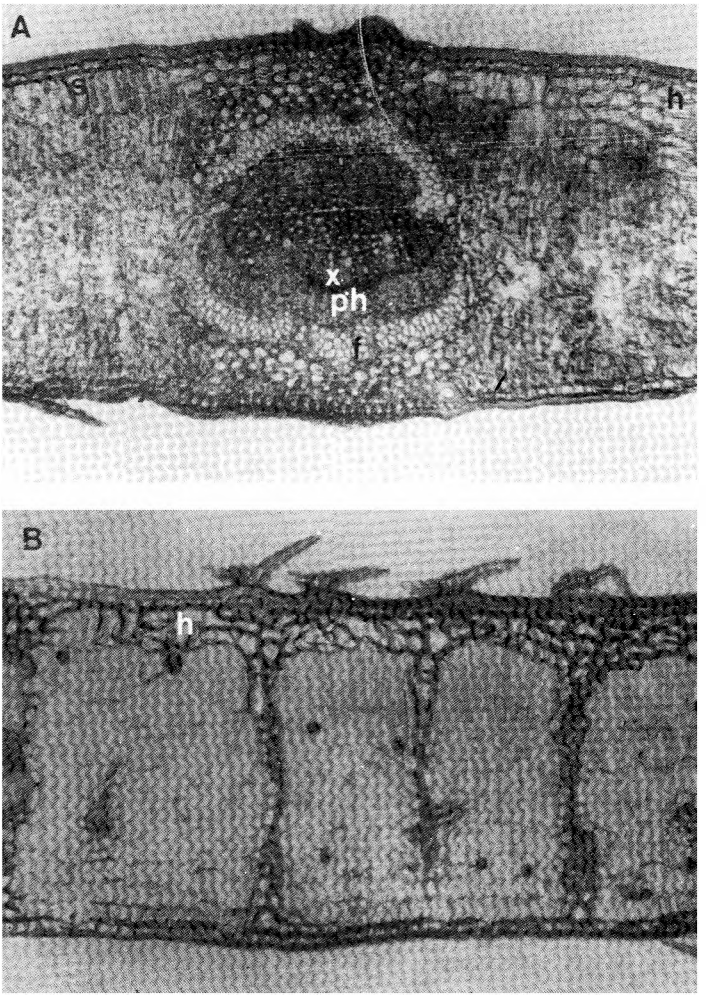


Fig. 5.



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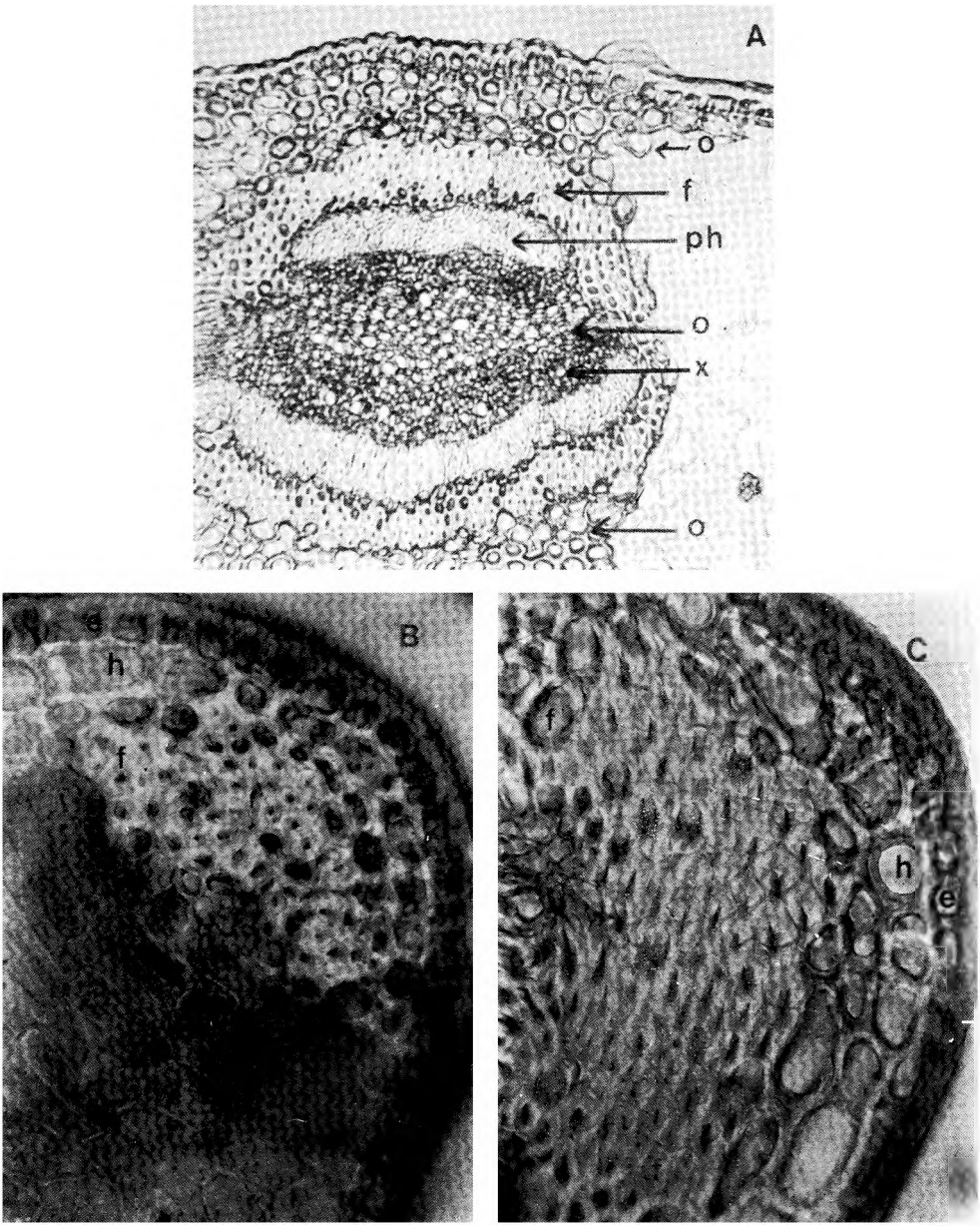

Fig 7

this hypoderm also has a mechanical function. It is obvious that this hypoderm is connected with the supporting walls, where it acts on behalf of the sclerotic parenchyma tissue. This last tissue disappears and is replaced by the hypoderm. Such abundant hypoderm could not be found in the leaves of *Q. coccifera* form from Korčula.

The hypoderm can also appear below the upper epidermis in places without veins, but this hypoderm is short and interrupted or discontinous.

Structure of the leaf margin

All leaves investigated had a layer of hypoderm cells on the upper part of the leaf margin. The hypoderm layer consisted of round or quadrangular cells which were lignified and had a large lumen. The walls of hypoderm cells contained a large number of pits.

On the leaf margin below the hypoderm there was a large number of fibres with very thick lignified cell walls. Fig. 7B, C shows, the structure of the leaf margin which is very firmly built.

The large central vein

The anatomy of the midrib of *Q. coccifera* leaf is similar to that of *Q. ilex* leaf midrib (Bačić and Milićić 1985). Therefore we shall note only the basic data about this leaf vein. The midrib of *Q. coccifera* also has an almost concentric structure (Figs 6A, 7A). As it is visible from the Figs, in the middle part of the vein of *Q. coccifera* is the sclerotic parenchyma tissue. Above and below this tissue is the xylem with protoxylem which is in direct contact with the central sclerotic parenchyma tissue. The xylem is followed by phloem which is better developed on the lower part of the vein.

The midrib was surrounded by a ring of fibres. Between the fibres and the upper and the lower epidermis there were sclerotic parenchyma cells (Fig. 7A).

Discussion

Taking into consideration the results of Baranov (1925), xerophytes always have a cuticle with cuticular layers which are at least 5 μm thick. As these layers are much thicker in *Q. coccifera,* i. e. about 10 μm, this species is a true xerophyte.

The exemplars of the type form of *Q. coccifera* from Spain and France are uniform and always have leaf margins of a thorny-dentate type with large incisions between the long thorns and the adjacent leaf margin (similar to Fig. 2). In the eastern part of the Mediterranean, in Israel, typical representatives of *Q. calliprinos* have thorny-serrate leaf margins like the exemplars presented in Fig. 1A. However, while the populations of *Q. coccifera* in Spain and France and of *Q. calliprinos* in Israel are uniform and regular, in central parts of the Mediterranean the populations are mixed and changeable, and in this area properties of both species are expressed. Gentile and Gistaldo (1976) state that it would be necessary to investigate not only the anatomical properties of these genetically mixed plants but also the morphological characteristics, i. e. the habitus of plants, the morphology of cupula and acorn.

On the basis of the data in Table 1, we shall try to establish to which Mediterranean Quercus species our transitive form from the association *Orno-Cocciferetum* H-ć on the East Adriatic coast, is more closely related.

With regard to the quality of the leaf margin, both *Q. coccifera* forms have cartilaginous margins; however, the forms of their margins are different. *Q. coccifera* from the East Adriatic coast has thorny-serrate leaf margins (Fig. 1A) and the type form of *Q. coccifera* has very wide thorny-dentate leaf margins (Fig. 2). Therefore, the form of the margin indicates a connection with *Q. calliprinos.*

The second characteristic is the thickness of the leaf blade. The measurement of the East Adriatic *Q. coccifera* leaves showed that the blade was 280 μm thick. The result shows that this form belongs to *Q. coccifera* since the blade thickness of *Q. calliprinos* is over 320 μm (cf. Table 1).

The third characteristic concerns the hypoderm. In plants from the East Adriatic coast the hypoderm was poorly present. According to Gentile and Gastaldo (1976) the hypoderm in *Q. calliprinos* is very frequent and abundant, and poorly developed in *Q. coccifera.* Consequently, the poor presence of the hypoderm makes it similar to *Q. coccifera.* On the other hand, better developed hypoderm, which we found in *Q. coccifera* plant originating from Macedonia, shows a certain similarity with *Q. calliprinos.*

The fourth characteristic is related to the hairiness. With regard to the hairiness, it can be mentioned that the Adriatic forms of *Q. coccifera* lose many trichomes relatively early so that the leaves are not too hairy at the developed stage. On the contrary, the leaves of *Q. calliprinos* are completely covered with hairs. (cf. the data about Trichomes in the text and Table 1). Consequently, this property also suggests the relatedness of the East Adriatic oak with *Q. coccifera* rather than with *Q. calliprinos.*

The fifth characteristic is related to the mesophyll. The differences between the East Adriatic form of *Q. coccifera* and *Q. calliprinos* are present also in the structure of mesophyll. The East Adriatic form and the common form of *Q. coccifera* have obvious intercellulars in the central part of the mesophyll, which are not present in *Q. calliprinos* (Table 2, and Gentile and Gastaldo 1976). Thus, the presence of large intercellulars in the mesophyll shows that the East Adriatic oak belongs to *Q. coccifera.*

Having examined five various leaf anatomy characteristics of the East Adriatic *Q. coccifera* L. form, we can conclude that this form should undoubtedly retain its original taxonomic name.

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SAŽETAK

ANATOMIJA LISTA JEDNOG OBLIKA VRSTE *QUERCUS COCCIFERA* L. S ISTOČNOJADRANSKOG PRIMORJA

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Dvije srodne vrste hrasta rastu na suprotnim obalama Sredozemnog mora: *Quercus coccifera* L. i Q. calliprinos Webb. Središte rasprostranjenosti vrste Q. coccifera nalazi se u Španjolskoj i Francuskoj, a vrste *Q. calliprinos* u Izraelu. U središnjem dijelu Mediterana, između Izraela i Francuske, raširen su prijelazni oblici između tih dviju vrsta.

Jedan od tih prijelaznih oblika s istočnojadranskog primorja i pripadnik vrste *Q. coccifera* element je asocijacije *Orno-Cocciferetum* H-ć (Horvatić 1963, a, b). Taj oblik u ovom je radu podrobno anatomski analiziran.

Rub lista je pilast. To je prilično važan kriterij koji je svojstven vrsti *Q. calliprinos*. Međutim, svi drugi kriteriji kao srednja debljina plojke od 280 μm, slaba dlakavost plojke, prisutnost intercelulara u srednjem dijelu mezofila i slaba razvijenost hipoderme upozoravaju na to da se ne radi o vrsti *Q. calliprinos*. Prema tome opravdano je oblik s Pelješca i Korčule i dalje nazivati *Q. coccifera* L.

Čini se da je ovo prva podrobna analiza jedne forme vrste *Q. coccifera* koja ima primjesa vrste *Q. calliprinos*. Budući da prevladavaju morfološko-anatomske karakteristike vrste *Q. coccifera*, moramo za našu jadransku vrstu zadržati taj naziv.

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