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Investigations on *Ebenus cretica* L. (*Leguminosae*)

By

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Key words: *Ebenus cretica*, development, epidermal cells, trichomes, morphology, functions.

Summary

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In the present work the aerial surface and structural elements in the woody tissue of *Ebenus cretica* during its life cycle were investigated. The morphology and distribution of these features on the different organs were studied by scanning electron microscopy. One characteristic type of non-glandular trichomes (eglandular hairs) is derived from epidermal cells and covers most of the aerial surface of the plant. The development of trichomes before the development of ordinary epidermal cells and of stomata indicates the protecting nature of the trichomes. In cotyledon and in ephemeral flower organs trichomes are nearly absent. They are replaced by developing ordinary cells and transformed ordinary cells (papillae). The role of the papillae is postulated to be connected with the pollination ecology of the plant due to the optical properties of their cuticle ornamentation. The hypocotyledonary region of the stem is characterised by a woody cylinder predicting the woody nature of the plant. Xylem (libriform) fibres with thick gelatinous walls, integrated with the tracheary elements dominate the tissues of the woody root and stems. Their evident role as supporting elements for giving strength and flexibility to the wood is in agreement with the local names and uses of the plant. Storage (reserve) starch grains of characteristic spherical form are accumulated on the parenchymatic tissue of the stems confirming further more the plurality of names given to *Ebenus cretica*.

Introduction

Ebenus cretica L. belongs to the family *Fabaceae* (*Leguminosae*), subfamily *Papillionoideae*, tribe *Hedysareae* (HUBER-MORATH 1965, TUTIN & al. 1968,

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KYPRIOTAKIS 1998, PRENNER 2002). Plants of *Ebenus cretica* are unarmed woody perennial evergreen shrubs, up to 60 cm tall. *Ebenus cretica* is encountered exclusively in Crete, where it occurs on lime rocks (Fig. 1c), crevices, and on sandstone in phrygana from 0-700 (-1300) m, as a casual chasmophyte (POLUNIN 1987, TURLAND & al. 1993, JAHN & SCHÖNFELDER 1995, VLAHOS 1996, KYPRIOTAKIS 1998). The name probably derives from Hippocrates who first used the name *Εβενος*, or from *κντισου εβενος*, *εβενη* of Theophrastus. Linnaeus, in his Species Plantarum, referred to it as *Ebenus creticus* L., while its name was finally bestowed by Bentham-Hooker in Genera Plantarum. It was also referred by the name *Anthyllis cretica* Wild and *barba Jovis lagopoides cretica* (Zeus beard, in the form of a hare's leg of Crete) according to Tournefort (WILLSTEIN 1852 cit. in WILLSTEIN 1958, VLAHOS 1996).

In Crete it is known under many names such as: ploumi "plumule" (Fig. 1e), poupoulo "feather down", poulia "bird feather" (Fig. 1d), archontoxilo "Nobleman's wood", kouneloxorto or kounelophyton "rabbit weed, herb", lagoudokimithia "hare's hole", katsoula "cat", alimatsa "fibrous brush" and others depending on the region of the island and the usage of the plant (FRAGAKI 1969, HAVAKIS 1980, AUTHORS investigations). In English, it is known as "Cretan silver bush", in German "Kretischer Ebenholzstrauch" and in French "L' ebenier de Crete". Due to its name is often confused with *Diospyros ebenum* Koenig ex Retz., *Ebenaceae*, (*Ebenus* sp. Commers., *Lucumeeae*), the *Εβενος* of Theophrastus, the tree that produces the ebony (FRAAS 1845, WILLSTEIN 1958, VLAHOS 1996).

The plant has been known in Western Europe since 1737, and it was registered in all the European Botanical Gardens as a greenhouse or rock garden xerophyte. Today, several Botanical Gardens of the old and new world carry *Ebenus cretica* in their collections (CURTIS 1892, ANDRE 1902, authors observations). This Cretan endemic, with the plumose vivid pink to porphyry racemes dominates the spring landscape of the island of Crete. Among others its pictures have been used to decorate the Greek stamps (Fig. 1a) and the front covers of Botany books like *Βοτανική* (VLAHOS 1998, Fig. 1b) and *Exkursionsflora für Kreta* (JAHN & SCHÖNFELDER 1995).

This "historical" and characteristic xerophyte has been widely studied for its floricultural use (VLAHOS 1996). Subsequent studies have been focused on the methods and factors affecting the propagation of the plant (POLUNIN 1987, VLAHOS & DRAGASSAKI 2000, SYROS & al. 2000, 2004), the natural and artificial pollination (LYDAKI & VLAHOS 2000), the floral development (PRENNER 2002), the chemical composition (flavonoid) (MITROCOTSA & al. 1999) and the essential oil content (PFEIFHOFER & VRACHNAKIS unpubl. data). Information also exist on the floral, pollen and caryological morphology on the other *Ebenus* species or close related taxa (AYTAC & al. 2000, PINAR & al. 2000, PRENNER 2003, 2004); however informations concerning developmental morphology, anatomy and structure of this "well known" plant are scarce.

In the present study features the plant's surface and its structural elements from seed germination until seed formation have been investigated using Scanning Electron Microscopy (SEM) and Stereoscope.

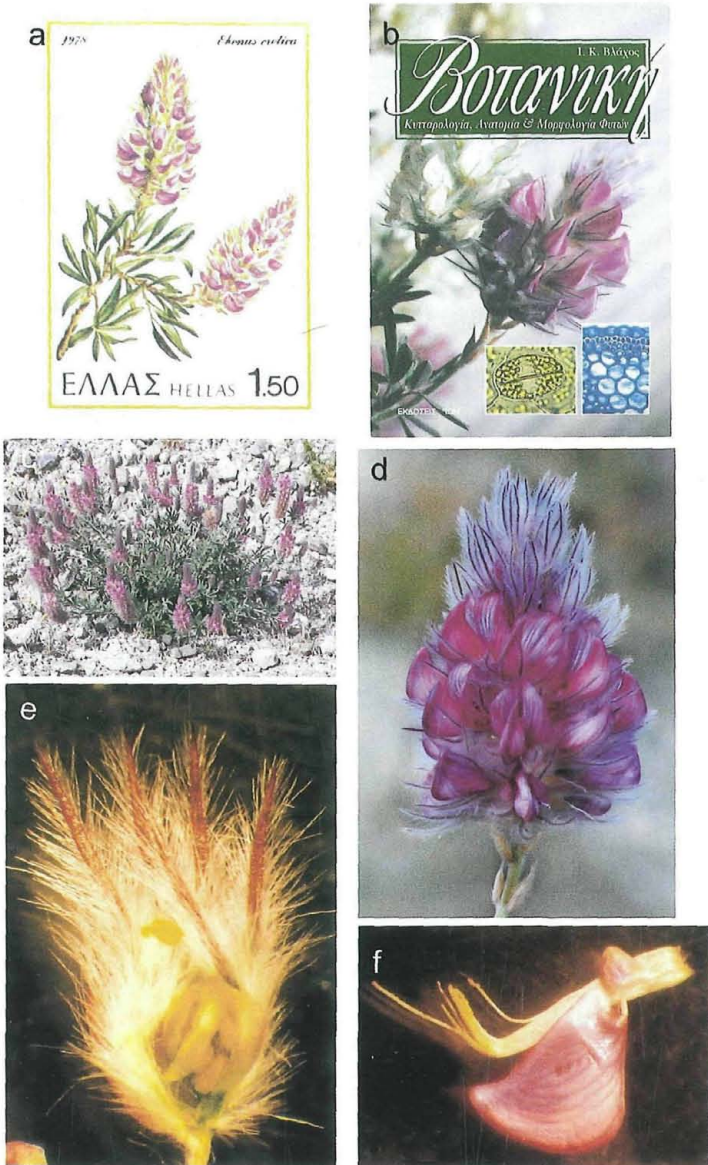


Fig. 1. *Ebeneus cretica*. a. Greek stamp of 1.5 drh.: 0.0043 Euro (Hellenic Postes 1978); b. front cover from a Greek Botany book (VLAHOS 1998); c. flowering on lime rocks, mount Psiloritis alt. 1000 m. in June (from PRENNER 2002); d. raceme of papilliomorphic flowers in full bloom (from Natural History Museum of Crete); e. pilose calyx with enclosed stamens and gynaecium (Stereomicroscope); f. wing and keel petals with exposed reproductive organs (Stereomicroscope).

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Material and Methods

Plant material

Branches of wild *Ebenus cretica* were collected from the Knossos area, near Heraklion Crete, also from selected clones of phenotypically different plants (12 years old) cultivated in the farm of the TEI of Crete, during the summer 2004. Seeds were germinated in containers with a potting mix based on sand, under 12 h light/dark 20° C/15° C, 70% RH (VLAHOS 1996, VRACHNAKIS 2002).

Voucher specimens were deposited in the Department of Biology, University of Crete and Institute of Plant Sciences, University of Graz and living plants can be found in the farm of the TEI of Crete.

Scanning electron microscopy (SEM)

Free-hand sections of all plant's parts were cleaned of soil and other debris and were immersed in a 1% solution of Tween20[®] for 24 hours. Plant parts were fixed with 2% Glutaraldehyde and 2% Paraformaldehyde in 0,1 M sodium cacodylate buffer, pH 7.2 overnight at room temperature and dehydrated in a graded acetone series, critical point dried with CO₂ (BAL-TEC CPD 30) and coated in a BAL-TEC SCD 050 sputter-coater. Observations were carried out on a JEOL JSM-840 scanning electron microscope, operating at 20 KV (GALANOPOULOS & SIAKOULI-GALANOPOULOU 2004).

Parallel observations took place in vivo and under a Wild Heerbrugg Stereomicroscope.

Results and Discussion

The early vegetative stage

In the early stage of germination when the seedling emerges, the hypocotyl and cotyledons are looking glabrous (devoid trichomes). The epidermis of cotyledons consists of undeveloped ordinary cells. Although stomata are absent, at the tip of the cotyledons, modified stomata can be found (Fig. 2a). These openings are considered to be epithem-hydathodes (passive hydathodes), and they replace stomata in the very young tissues. Epithem-hydathodes are reported in cotyledons and other ephemeral tissues in other Cretan xerophytes: *Origanum calcaratum*, *O. dictamnus* (VRACHNAKIS 2002). The epidermal surface of hypocotyl like that of the cotyledons, with the ordinary cells more elongated due to the elongated form of the hypocotyl. The cross section of the hypocotyl presents a circular and complete woody cylinder (Fig. 2c). JEFFREY 1917, has reported same features in the hypocotyledonary region of the stem in bean and the lower region of the epicotyl in the pea (both of the *Fabaceae* family). In the surface of this cylinder, developing ordinary cells, stomata and fully developed trichomes are observed. The presence of developed trichomes on the woody cylinder (situated inside a glabrous sheath tissue, Fig. 2c), indicates the ephemeral of the outer (sheath) tissue and confirms the structural relationship between the hypocotyl and the woody stem so that "clearly points to the derivation of herbaceous forms from woody ones and not the arboreal perennials from annuals, logically following from the account of the origin of the structures of the stem in dicotyledons" (JEFFREY 1917), or "the beginning of shoot organization is found in the hypocotyl-cotyledon system in which the hypocotyl is the first stem" (ESAU 1965).

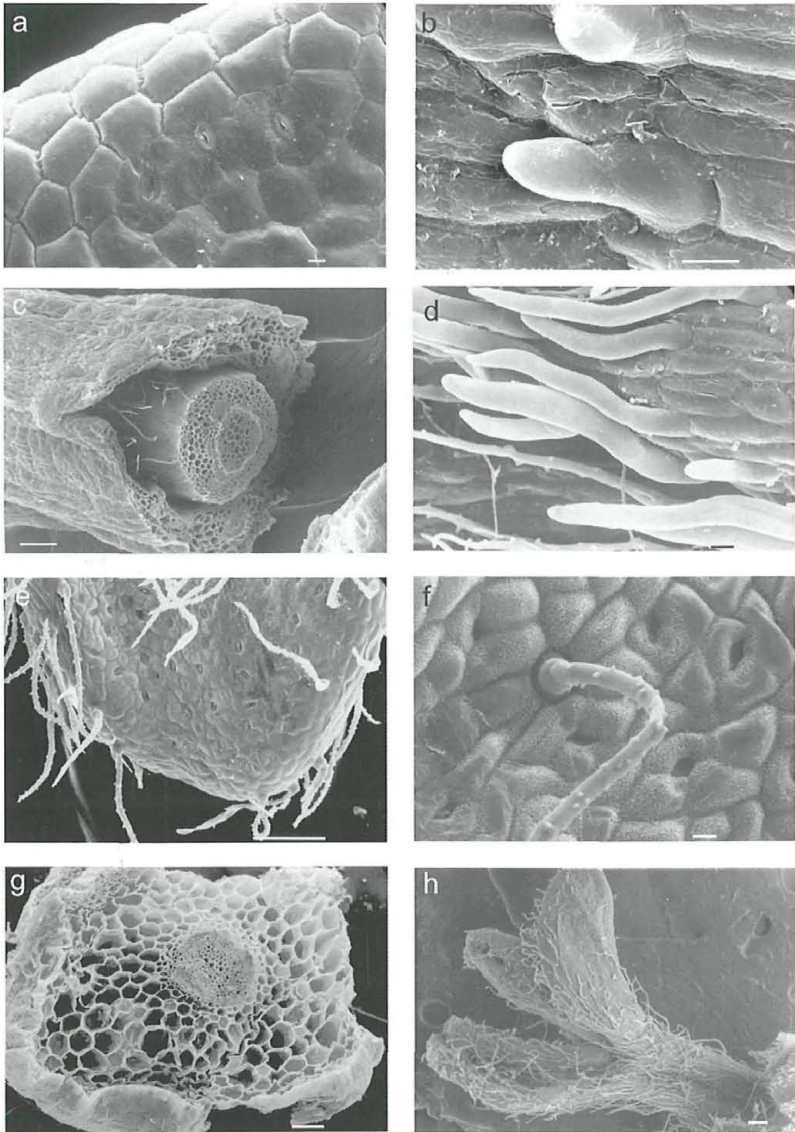


Fig. 2. The early vegetative stage (SEM micrographs). a. passive hydathodes (modified stomata) in cotyledonary margin (adaxial side), bar: 10 μ m; b. trichomes in very early stage, bar: 10 μ m; c. the woody cylinder in the hypocotyledonary region of the stem, bar: 10 μ m; d. elongated trichomes in early stage, bar: 10 μ m; e. trichomes and stomata in the upper part of the first leaf (adaxial side), bar: 10 μ m; f. waxy cells and sunken stomata, surrounding the base of a trichome, bar: 10 μ m; g. root of a young seedling (cross section), bar: 10 μ m; h. fully developmental trichomes in expanding leaf, bar: 10 μ m.

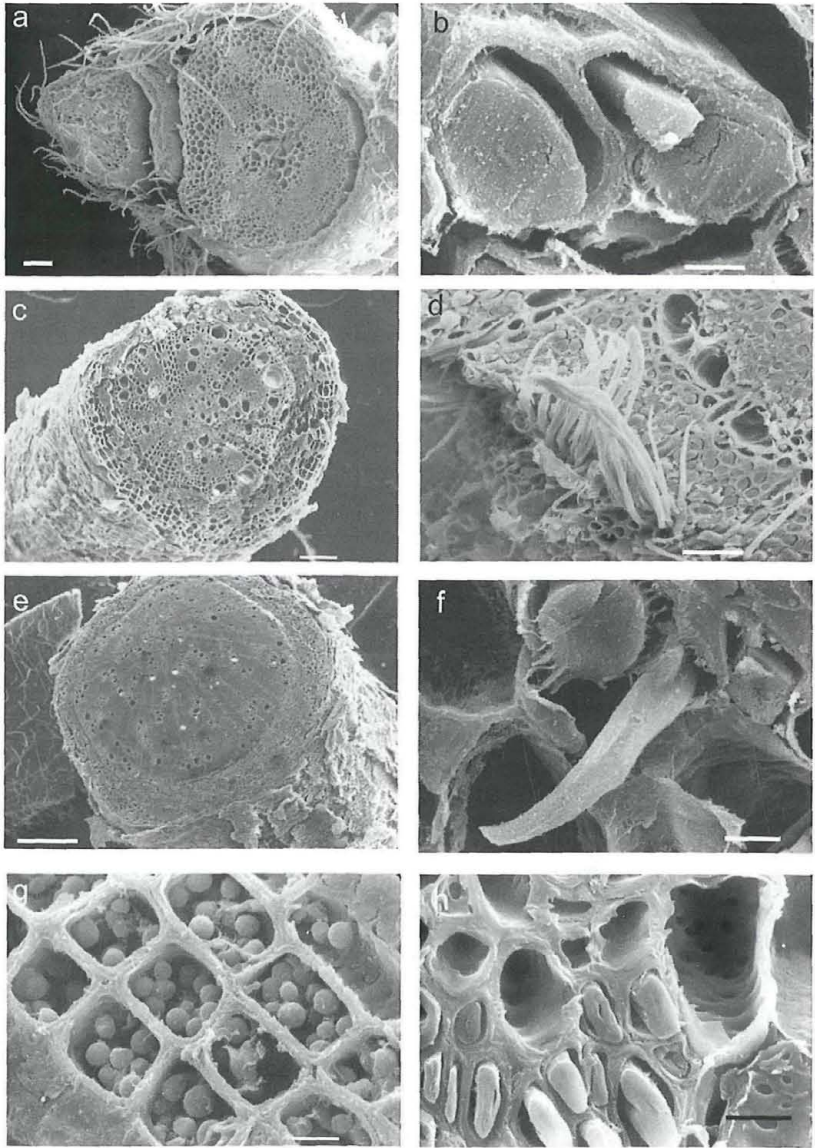


Fig. 3. The "woody" vegetative stage (SEM micrographs). a. vegetative bud from half-hardy stem (cross section), bar: 10 μm ; b. fibres in woody stem, bar: 1 μm ; c. main root (cross section), bar: 100 μm ; d. fibres in the tap root (uncompleted cross section), bar: 10 μm ; e. woody stem (cross section), bar: 50 μm ; f. fibres (gelatinous?) from woody stem, bar: 2 μm ; g. storage (reserve) starch grains in the ray parenchyma of woody stem, bar: 10 μm ; h. integrate tracheary elements in woody stem, bar: 10 μm .

As the apical meristem is differentiated to leaf primordial; trichomes, developing stomata and developing ordinary cells constitute the young leaf epidermis. The non glandular trichomes (eglandular hairs) of *Ebenus cretica* are considered of one type. They are unbranched, uniseriate with a short basal cell, accompanied by an elongated terminal cell. This type is particularly prevalent, according to SOLEREDER, in the tribe *Hedysareae* and others tribes in *Fabaceae* (METCALFE & CHALK 1979). In early ontogenetic stage (first leaf) one-celled hairs appear as a conical papillae with a smooth surface (Fig. 2b). With leaf expansion the elongated smooth trichomes (Fig. 2d) dominate the leaf blade and gradually their surfaces are covered with cuticular ornamentation (Fig. 2e,f). Trichomes in mature tissues are heavily ornamented with a coarsely striate cuticle or with a knobby cuticle (Fig. 2f and Fig. 4g), resulting in hair appearance uncommon for the tribe *Hedysareae* and the *Fabaceae* family. They resemble the unbranched trichomes of *Carpodetus major* (CUTTLER & GREGORY 1998), or the dendritic (branched) trichomes of *Dipteryx rosea* (METCALFE & CHALK 1979), *Alternanthera stellata* (METCALFE & CHALK 1979); plants unrelated to *Ebenus cretica*. A feature associated with mature tissues is the presence of epicuticular wax on the plant epidermis and sunken stomata (Fig. 2f); that is a common feature for plants in arid habitats (HABERLANDT 1914, ESAU 1965, METCALFE & CHALK 1979, EHLERINGER 1984, FAHN & CUTLER 1992, VRACHNAKIS 2003).

The early presence of trichomes on young expanding leaves (Fig. 4h) has been reported for other Cretan xerophytes (VRACHNAKIS 2002), and it seems to be the rule for hairy plants (UPHOF 1962, HEINRICH 1973, WERKER 2000). Besides the evident function of the trichomes protecting the leaf from the environment (LEVIN 1973, EHLERINGER 1984, FAHN & CUTLER 1992), their role as receptors of environmental signals is postulated (VRACHNAKIS 2003) and can be attributed to the cuticle, since the cuticle is an essential barrier in epidermal cell functions (JOHNSON 1975, GLOVER 2000).

The woody stage

Within the vegetative stage a simultaneous growth of the main stem and the lateral branches builds the bulk of the plant vegetation. This stage is characterised by the high proportion of woods with storied parenchyma and sclerenchyma tissue, which are important components of the skeletal system of the plant. Roots and stems exhibit a typical tissue organisation for a slow-growing xerophyte like *Ebenus cretica*. Cross section in the root of a young seedling (Fig. 2g) showed a central woody cylinder surrounded by loose cortex (parenchyma cells). This central cylinder is the lower part of the woody cylinder in the hypocotyledonary region of the stem (Fig. 2c), indicating the ontogenetic relation between the stem and root (initiated during the development of the embryo), that is the hypocotyl-root axis according to ESAU 1965.

Cross section on a vegetative bud on half-hardy stem (Fig. 3a) showed the nearly cylindrical woody stem and the triangular petiole surrounded by a sheath of the expanding compound leaf. The structure and shape of petiole in *Fabaceae* are very variable, correlated to some extent to the leaf morphology and habit of the

plant. Unusual triangular petioles with a single bundle in each of three angles were reported for the leguminous *Desmodium gyrans* DC. (METCALFE & CHALK 1950). Cross sections in an old (woody) stem (Fig. 3e) and in a tap root (Fig. 3c) showed that the sclerenchyma tissue of *Ebenus cretica* consist of xylary fibres, [*ξύλων* or *xylos* (JACKSON 1927 cit. in ESAU 1965) meaning wood], integrated with other tracheary elements (Fig. 3b,d,f,h). Tracheids and fibres are very important constituents of all woody organisations and present a wide range of structure from lower forms to higher; but their separation, terminology, phylogenesis, function and classification are unclear and rather controversial (HABERLANDT 1914, JEFFREY 1917, ESAU 1965, GREULACH 1973, METCALFE & CHALK 1979, BUTTERFIELD & MAYLAN 1980, BAREFOOT & HANKINS 1982, MARTIN 1987, CUTTLER & al.1987, ROMBERGER & al.1993, STERN 1994, BOWES 1996).

The fibres in *Ebenus cretica* were investigated as massive blocks in the mature (woody) roots (Fig 3c,d) and in the tension wood of branches (Fig. 3b,e, f). They are integrated with tracheids, vessels and other parenchymatic elements (Fig. 3d,f,h). Fibres, as far as we have investigated, were absent in the young roots (Fig. 2g), in the hypocotyledonary woody cylinder (Fig. 2c) or in other immature tissues (Fig. 3a). It should be noted that in cross section cuts, the form and size of these features were not possible to detect. (Fig. 3b,f,h). However, due to the razor blade's uncompleted (not acute) cutting, in another observation, their form was clearly revealed (Fig. 3d). Their appearance having an elongated form and a smooth surface may be easily confused with that of immature trichomes (Fig. 2d & Fig.3d). The transverse face of the fibres show that they are entirely filled with "gelatinous" material (Fig. 3b,f), or that they are "cellulosic" thick walled with small lumina in the centre (Fig. 3h).The fibres show considerable variation in diameter for the reason that some have been cut almost in half at their widest point, while others have been cut near their tips where their transverse dimensions are small and their lumina is constricted. Sclerenchymatic fibres in *Ebenus cretica* have been mentioned (SYROS & al. 2004). Various named fibres as: xylary, gelatinous, libriform, tracheary, thick walled, fiber-tracheids, multilayered cellulosic, substitute, mucilaginous, extraxylary, septate or bast fibres, have been reported in the woody and the parenchymatic tissue of other leguminous plants. The "traditional" function of these fibres is to give strength and flexibility to the tissue. But they are also involved in hygrochastic movement in xerophytes; and it has been suggested that gelatinous fibres may function in water storage (METCALFE & CHALK 1979, COTE 1967, BUTTERFIELD & MAYLAN 1980, CUTTLER & al.1987, FAHN & CUTLER 1992, MAUSETH 1995, BOWES 1996). In the ray parenchyma of woody stems in *Ebenus cretica*, characteristic spherical bodies filling the cells were investigated (Fig. 3g). These features are considered to be storage (reserve) starch grains. VLAHOS 1996 has reported that young stems of *Ebenus cretica* contain much starch and thus explaining why they are used by local farmers as food for goats and rabbits. Starch is an important metabolic product that occurs widely in leguminous plants and particularly accumulates in seeds, the parenchyma of stems, roots and storage organs (METCALFE & CHALK 1950, ESAU 1965, SHIGO 1994). Similar spherical starch

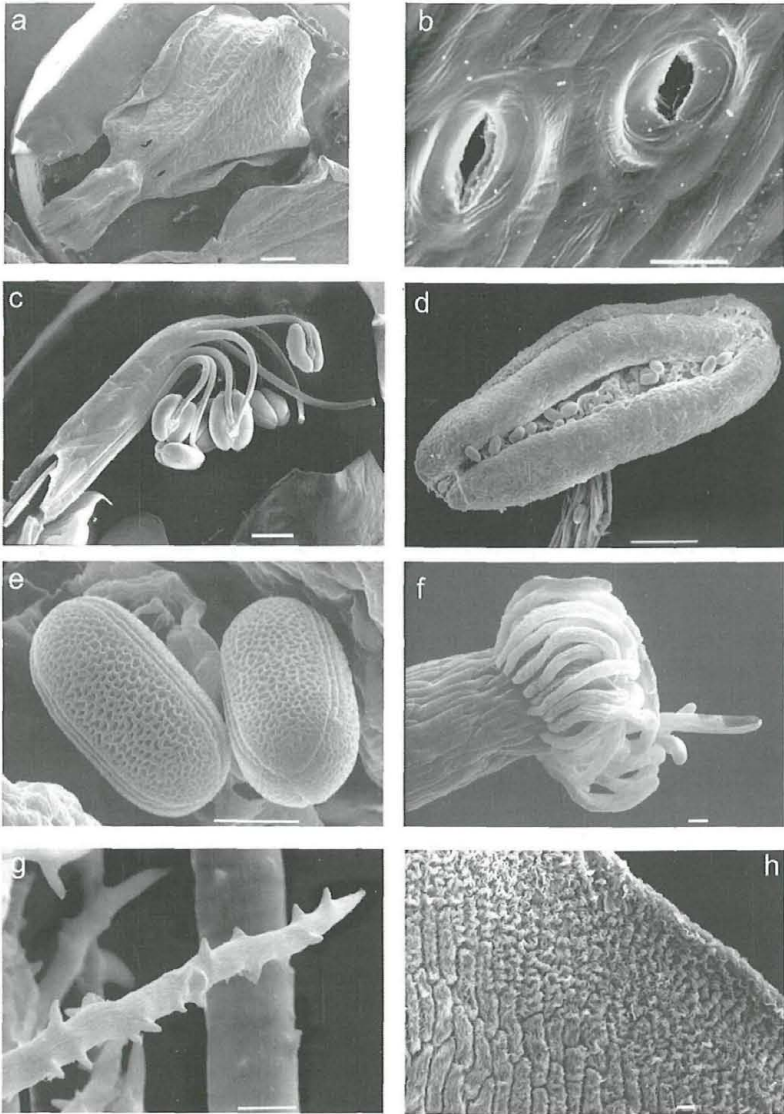


Fig. 4. The reproductive stage (SEM micrographs). a. the standard (petal) with peculiar openings (abaxial side), bar: 1mm; b. bract with stomata like openings (abaxial side), bar: 10 μ m; c. the diadelphous stamens with the protruded style, bar: 1mm; d. papillose anther with pollen grains in the opened loculus, bar: 100 μ m; e. tricolpate pollen grains with reticulate tectum, bar: 10 μ m; f. stigma with unicellular curved and exposed hairs along its rim, bar: 5 μ m; g. eglanular trichomes with the characteristic knobby cuticle on calyx, bar: 10 μ m; h. papillate-cells and papillae in the abaxial side of the keel petal, bar: 10 μ m.

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grains were observed (in SEM micrographs) in septate fibres of *Fuchsia excortiana* (*Onagraceae*) and in parenchyma cells of *Myoporum laetum* (*Myoporaceae*) (BUTTERFIELD & MAYLAN 1980).

The reproductive stage

Ebenus cretica plants in Crete flower from April to June, depending on altitude and area (Fig. 1c). The papilliomorphic flowers are pink to porphyry (Fig. 1a,b,c,d,f); however in specific locations plants with white flowers (Fig. 1b), were also found (VLAHOS 1996, authors observations). The flowers are arranged in dense racemes (Fig. 1d) that develop from axillary buds. Flowers become a yellow-brown towards the end of the flowering period or they keep the bright colour when treated properly. The flower morphology, development and pollination of *Ebenus cretica* are well documented (VLAHOS 1996, LYDAKI & VLAHOS 2000, PRENNER 2002). Parallel observations, microscopic and in vivo, confirm their findings and enrich the information concerning these temporally, shining tissues. SEM observations on mature and dried standard (petal) showed two distinct openings above the clawed part of this petal (Fig. 4a). However, stereoscopic observations on fresh standard (petal) showed that these openings (tiny membranous marks in vivo) are the endings of red coloured lines parallel to the main nerves of the standard blade. Considering the vertical (up right) orientation of the standard petal during anthesis and the pollination mechanism by bumblebees (LYDAKI & VLAHOS 2000), it is suggested that these marks (openings in maturity) serve as visual signals to the bumblebees and other pollinators. Peculiar, stomata like, openings were observed in the abaxial side of the bract (Fig. 4b), with a suggested tactile or visual role. Examination of the stamens and style system showed that the nine staminate filaments form a sheath with the adaxial stamen free at the base (diadelphica) and apically this stamen is connate secondarily forming the closed filament tube (Fig. 4c). The long glabrous style is curved in the filament sheath and is ascending apically, overarching the level of the phaneranthrous stamens (Fig. 1f, Fig. 4c). The anther lobes, joined by the connective tissue on the dorsal surface of the filaments (Fig. 4c) present a papillosus epidermis, and in the opened loculus the pollen grains are situated (Fig. 4c,d). The pollen grains are radially symmetrical, isopolar, tricolpate with reticulate ornamentation (Fig. 4e). The stigma is characterised by unicellular curved and exposed hairs along its rim (Fig. 4f). The most characteristic peculiarity in the "flowering" stage of *Ebenus cretica* is the smooth papillosus epidermis of the five petals: standard (Fig. 4a), wings and keel (Fig. 1f, Fig. 4h) in contrast the heavily-pubescent epidermis of the five sepals (calyx) and the leguminous fruit (pod) (Fig. 1e, Fig. 4g). The suggested explanation resides on the advertising (alluring) role for the former and the protecting role and zoochory (animal dispersal of the seeds) for the later. Our observations in the reproductive stage are in agreement with other researchers (PRENNER 2002 studying the *Ebenus* floral development; LUNAU 2000 studying floral visual and tactile signals and VRACHNAKIS 2002 studying other hairy Cretan endemic) and confirm furthermore the plurality of the names of *Ebenus cretica*.

A c k n o w l e d g e m e n t s

In memory of V. GALANOPOULOS (1953 -2005) Professor in Biological Sciences.

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