CHARACTERIZATION OF THE DOMATIA OF *APOLLONIAS* (LAURACEAE) ON THE ATLANTIC ISLANDS

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With 2 figures and 1 table

ABSTRACT. Apollonias canariensis, a tree of the laurel forests on the Canary Islands and Madeira, was investigated in field and laboratory work. Its domatia appear as revolute basal leaf margins and are shown by almost every adult leaf. Even juvenile shoots with their much larger foliage develop these structures. The domatia are formed independently of arthropods, but are usually occupied by mites in the laurel forests. Hair crevices are a striking feature within the revolute margins, which give additional shelter to the mites.

INTRODUCTION

Domatia occur more frequently in the laurel forests of the Atlantic Islands (NICKOL 1994, 1995) than previously suggested. These structures were often overlooked or mistaken for extrafloral nectaries or oil glands (see BORNMÜLLER 1903, BRAMWELL & BRAMWELL 1990, HOHENESTER & WELSS 1993), but field studies reveal that they possess a distinct morphology, are regularly inhabited by mites of several species and usually do not have any secretory function.

LUNDSTRÖM (1887) gave the first systematic treatment of domatia. In Lauraceae he mentioned the domatia of *Laurus azorica*, and stated that they were inhabited by mites ("Die von mir untersuchten Domatien waren besonders reich an kleinen, länglichen oder gerundeten Excrementen, sowie an Milben-Häuten." p. 49). Since then a rediscovery of these taxonomically useful and ecologically important structures has begun (STACE 1965, JACOBS 1966, SCHNELL et al. 1968). Recently there has been some experimental work dealing with the ecological implications of domatia (O'DOWD & WILLSON 1989, 1991; DICKE & SABELIS 1988, 1989, PEMBERTON & TURNER 1989, TURNER & PEMBERTON 1989, WALTER &

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DENMARK 1991, WALTER & O'DOWD 1992b, GROSTAL & O'DOWD 1994).

Acarodomatia on the north Atlantic Islands are as far as known always specialized structures in the vein axils or the basal margins of the lower leaf surface. They have been almost completely neglected from an ecological viewpoint in the past, but have been used, under different terms, by some authors as taxonomic characters. Our knowledge of them is nevertheless very limited.

The opinion that European or African forests would lack domatia in comparison to the tropics of Australasia, North Asia and the forests of North America (ROZARIO 1995) does not reflect reality. On the contrary, European forests as well as the subtropical vegetation types on the Atlantic Islands discussed here have a high percentage of domatia bearing species.

Apollonias canariensis (WILLD.) NEES (syn. *Apollonias barbujana* (CAV.) BORNM.) is one of the main trees in the laurel forests (SUÁREZ RODRÍGUEZ 1991). It reaches 25 m in height, with laurophyllous leaves on adult trees sized up to 4-10 x 1,5-4 cm. The domatia at the basal leaf margins are mainly ignored in descriptions (BRAMWELL & BRAMWELL 1990, LUCIA SANQUILLO et al. 1990, HOHENESTER & WELSS 1993), and often domatia are distorted in herbarium specimens.

MATERIAL AND METHODS

Living specimens were observed during field studies in the laurel forests of La Gomera (1988), Tenerife (1988, 1990, 1993), La Palma (1992) and Madeira (1994). Some additional observations were made on Gran Canaria (1996). Photographs, notes and drawings documented the results. Herbarium specimens were seen in the collections K and W. Voucher specimens have been deposited in the herbarium of the author.

Some alcohol material (CN 9465) could be used for a SEM-study. The fixed material was prepared in alcohol, chemically dehydrated in Formaldehyddimethylacetal, dried following the critical point method and sputter coated with gold. A Cambridge Stereoscan 250 Mk 2 was used for observations, which were recorded with Ilford FP4 as film material.

RESULTS

Apollonias canariensis is a rather rare species of the Pruno-Lauretea in all forests studied and shows an affinity for thermophilous habitats within the remains of the laurel forests. There is a significant juvenile syndrome: leaves of the young shoots are four to seven times larger than those of adult trees and can reach a length of about 35 cm. Functionally this might be due to the lower light level on the forest floor, where the young individuals grow. They were found mainly along walkways, which often have more light and free space. Nevertheless the leaves of those shoots have domatia. They are also larger than those on

adult leaves, reflecting the same proportion of domatia to leaf-length.

Domatia can be seen on every mature leaf of *A. canariensis*, where the basal margins are revolute (fig. 1). The domatia of *A. canariensis* as well as of the other species investigated are formed in the absence of mites or other animals. They are, in contrast to galls, genetically fixed. A so far undescribed feature are the hair crevices between the revolute margin and the adjacent vein (fig. 2), which form a very peculiar pattern. Other plants of the Atlantic Islands with domatia of the same type lack such trichomes (tab. 1). These crevices are used by mites in the laurel forest, which deposit their debris in them (fig. 2c). The trichomes are up to 400 µm long and are either pressed flat on the surface, pointing towards the base of the leaf, or are slightly hooked, when sitting on the revolute margin (figs. 2a, b, d). In the same area many stomata (up to 128 per mm^2) are located (fig. 2d). In the material studied by SEM and LM most of them remained open (fig. 2d).

TABLE 1 - Domatia types found on the Canary Islands with representatives

Type of domatia	species	family
I. Revolute basal margin	*Apollonias canariensis*	Lauraceae
	Gesnouinia arborea	Urticaceae
	Hypericum canariense	Hypericaceae
II. Tufts of hairs	*Gesnouinia arborea*	Urticaceae
	Hydrangea spp.	Hydrangeaceae
	Viburnum rigidum	Caprifoliaceae
III. Pockets covered with hairs	*Laurus azorica*	Lauraceae
	Ocotea foetens	Lauraceae
	Rhamnus glandulosa	Rhamnaceae

DISCUSSION

Apollonias canariensis is the only lauraceous species of the Macaronesian islands with revolute basal margins functioning as domatia (tab. 1). Such domatia are not accepted

by some authors (e.g. BROUWER 1985), because there seemed to be no evidence for their use by mites. The SEM study, however, revealed the hair crevices at the underside of the leaf of *A. canariensis* and their use by mites in natural habitats (fig. 2d), which was confirmed by field observations in the laurel forests. Therefore, following the definitions of LUNDSTRÖM (1887), DELPINO (1901), JACOBS (1966), HICKEY (1973) and others, these revolute basal margins have to be regarded as true domatia. Domatia are not always associated with the mid vein of a leaf, as is shown by many other species, e.g. in the families Moraceae or Rubiaceae.

Domatia of *Apollonias* should not be confused with galls, described by RÜBSAAMEN (1902), and they cannot be regarded merely as meaningless recurvations of the leaf margin.

The many stomata situated along those margins which are inhabited by mites may be an indication of the hypotheses of LUNDSTRÖM (1887), that the by-products of the mites may be used by the plants in addition to the other benevolent effects mentioned below. This has been prooved for many ant domatia (e.g. RICKSON 1984, FIALA 1988, RICO-GRAY et al. 1989, TRESEDER et al. 1995). In Melastomataceae even open stomata inside the domatia were recognized (NICKOL 1993).

Domatia appear to have evolved many times in parallel among angiosperms and even in related taxa they are often new adaptations in the sense of an autapomorphy (e.g. *Hypericum*). Within the Lauraceae of the Macaronesian islands two different types of domatia can be recognized (tab. 1). *Apollonias canariensis* shows revolute basal margins whereas *Ocotea foetens* and *Laurus azorica* develop pockets of different size in the vein axils, which are covered with hairs.

There are some fossils from the Tertiary of continental Europe, which show that domatia evolved in several lauraceous genera of the ancient sclerophyllous forests. It has been suggested that some of the fossil leaves belong to *Ocotea* and *Laurus* (BRAMWELL & BRAMWELL 1990). Therefore the domatia in the laurel forests of the Atlantic Islands can be traced back through millions of years. The interaction of arthropods and domatia on angiosperms is at least as old as the early Tertiary (PEOLA 1904, O'DOWD et al. 1991).

Because of the stable climatic conditions in the laurel forests, which were not disturbed during the ice ages, and the common possession of domatia by fossils and living taxa on the one hand and of extant sister species inhabiting the mediterranean sclerophyllous plant communities and the laurel forests of the northern Atlantic Islands on the other hand, it seems obvious that domatia are also an ancient feature in this habitat.

Because these structures are genetically fixed and develop even in the complete absence of arthropods, they are a resource for mites in search of dwellings (see WALTER & O'DOWD 1992a). There are no experiments which demonstrate clearly the symbiotic value of this community, but several observations indicate that mites belonging to Phytoseidae and Oribatidae may collect particles from the leaves, e.g. eggs and adults from herbivores

or spores of fungi. As such they may increase photosynthetic activity by decreasing leaf-damage.

It can be assumed that *A. canariensis* takes part in such a system by providing dwellings for mites in the revolute basal margins of the leaves.

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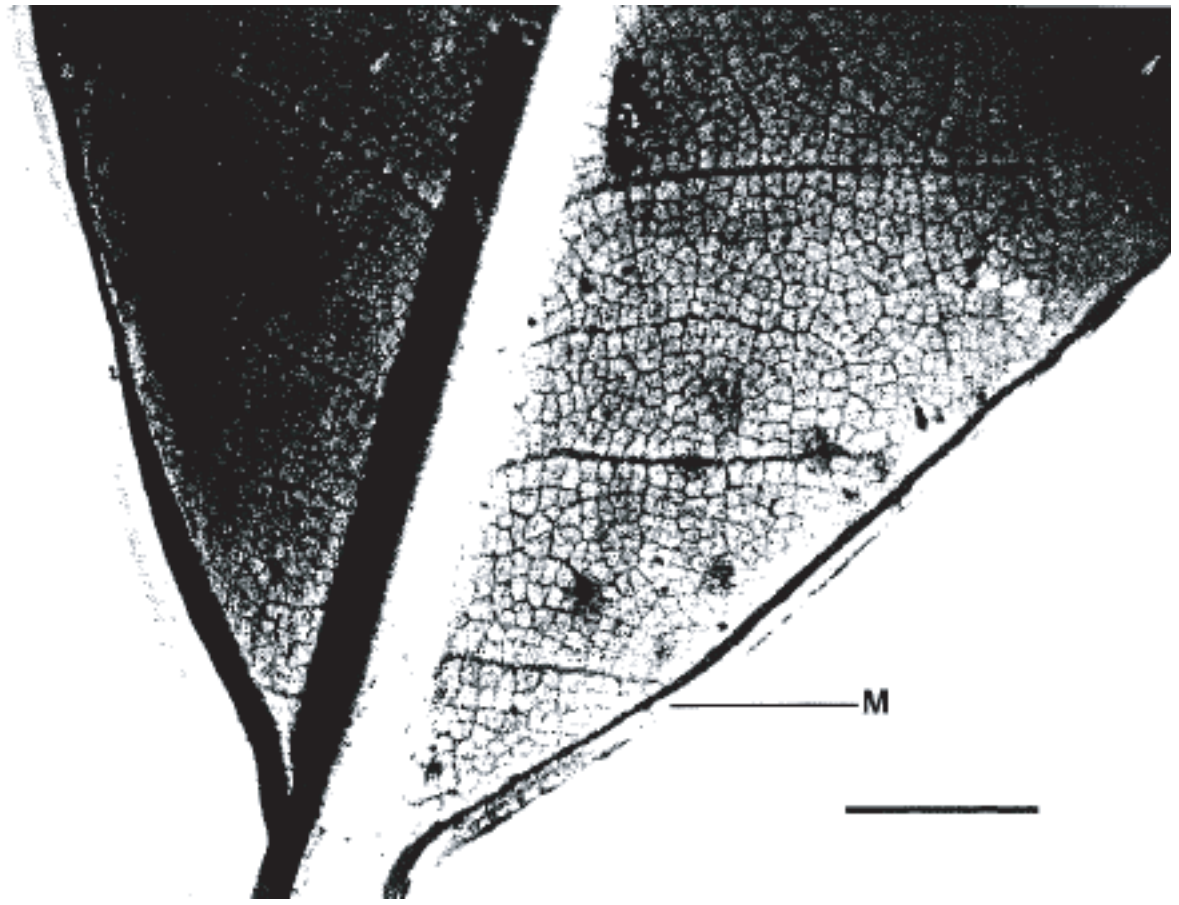

Fig. 1 - Lower surface of a leaf of *Apollonias canariensis* with the domatia as revolute basal margins (M). Bar = 0,5 cm

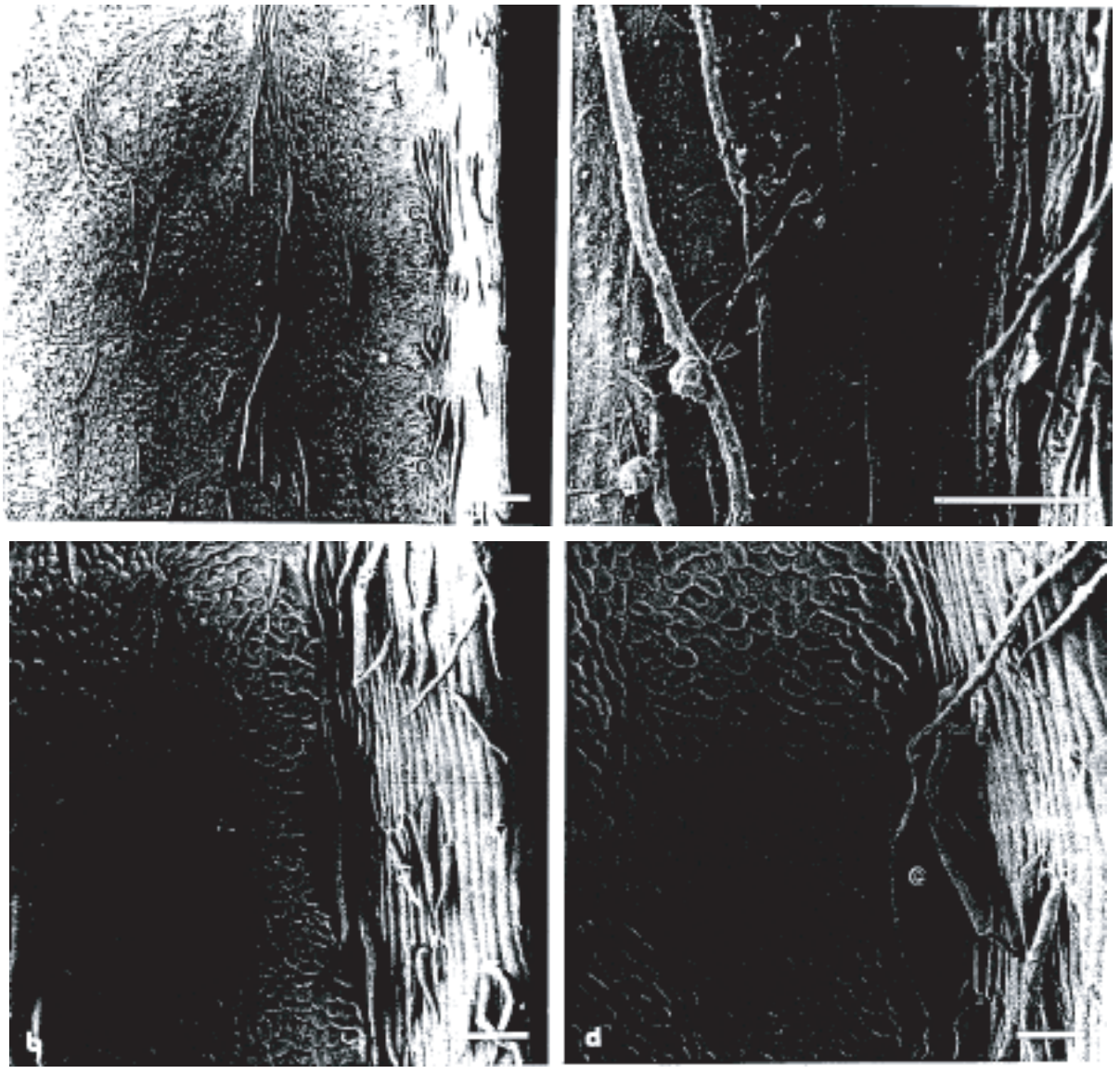

Fig. 2 - SEM photographs of the lower leaf surface of *Apollonias canariensis*. a. Thick laurophyllous margin, on the left the adjacent vein. b. Domatium with hair crevices. c. Uncleaned surface, showing detritus stored by mites within the domatium (arrows). d. Hair crevice, open stomata.
(C) = hair crevices. Bar = 100 μm

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