

A multivariate analysis of the trichomes of *Hedera* L.

C. LUM and J. MAZE

Department of Botany, University of British Columbia, Vancouver, B. C., V6T 2B1, Canada

ABSTRACT

Measurements were taken from scanning electron micrographs of representative trichome arms of selected taxa of *Hedera* L. (Araliaceae) and the data were subjected to principal components and cladistic analyses. This was done in order to contrast taxonomic opinions and determine evolutionary trends in trichome attributes. Based on these analyses, specimens from North Africa and the Azores, Madeiras and Canary Islands do not constitute a single species, as has been proposed, but instead consist of at least two species of rather distant relationship; there are perhaps more. *Hedera hibernica*, which has been segregated from *H. helix*, is not strongly differentiated from the latter and the two taxa form a monophyletic group; thus strong support for the recognition of *H. hibernica* as a species is not found in this study. The group of ivies characterized by having large white hairs is natural whereas that which has small red hairs appears to be paraphyletic, i.e. unnatural. The most rapid trichome evolution is seen in taxa of Europe, and more especially in those that occur in North Africa and the Azores, Madeiras, and Canary Islands.

INTRODUCTION

In a previous study on *Hedera* L., Lawrence & Schulze (1942) recognized five species, *H. canariensis* Willd., *H. colchica* K. Koch, *H. helix* L., *H. nepalensis* K. Koch and *H. rhombea* (Miq.) Bean, based on gross morphology, trichome type and geographic distribution. More recent studies on *Hedera* (McAllister & Rutherford 1983; Rutherford 1984; Rutherford & McAllister 1983) have indicated that these five species should be, at least in part, subdivided into more species. These authorities split *H. helix* of Lawrence & Schulze (1942) into *H. helix* and *H. hibernica* (Kirch.) Bean, which is found along the Atlantic Coast of Europe from Spain through France and England to Ireland and Scotland, and *H. canariensis* into *H. canariensis*, *H. algeriensis* Hibb., *H. azorica* Carr., *H. maderensis* K. Koch and *H. "Morocco"*, each of the segregate taxa occupying more restricted distributions at the western end of the Mediterranean or on islands in the eastern Atlantic. The last name was one used by McAllister & Rutherford (1983) to refer to a possible new species related to *H. canariensis*. These species have also been placed in two groups by McAllister & Rutherford (1983), those with large white trichomes (*H. azorica*, *H. helix* and *H. hibernica*) and those with small reddish ones (*H. canariensis*, *H. maderensis*, *H. nepalensis*, *H. rhombea* and *H. colchica*).

There were two purposes to this study. The first was to compare the contrasting taxonomic opinions of Lawrence & Schulze (1942) and McAllister & Rutherford (1983), Rutherford (1984) and Rutherford & McAllister (1983). The second was to evaluate the naturalness of groups based on gross trichome features, using data derived from scanning electron microscopy (SEM) of trichomes and analysed by multivariate methods. The trichomes of *Hedera*, which have yet to be studied under SEM, are well known for their richness of form and usefulness in the systematics of the genus (Dehgan 1981). The general usefulness of trichomes in systematic studies is also well known (e.g. Carolin 1971; Cowan 1950; Gornall 1986; Hardin & Bell 1986; Hunter & Austin 1967; Jones 1986; Tucker 1963). Multivariate analysis has the advantage of simultaneously evaluating both variable variances and covariances in order to describe the relationships within and amongst taxa. If the groups recognized by Lawrence & Schulze (1942) are natural, although more inclusive than those recognized by McAllister & Rutherford (1983), Rutherford (1984) and Rutherford & McAllister (1983), there are two predictions that would follow. First, the within species variation would approximate that of other species. Second, specimens of *H. helix* and *H. canariensis* sensu Lawrence & Schulze (1942) would occupy close positions in graphic displays of the results of multivariate analysis. If *H. helix* and *H. canariensis* as recognized by Lawrence & Schulze (1942) are not natural,

then the converse predictions would hold, i.e. the within species variation for their taxa would be high and the segregate taxa of McAllister & Rutherford (1983), Rutherford (1984) and Rutherford & McAllister (1983) would occupy disparate positions in the graphic displays derived from multivariate analysis. Furthermore, if the split into two groups based on hair size and colour (McAllister & Rutherford 1983) is appropriate, then such groups should also appear as distinct entities in the results of multivariate analysis.

It is acknowledged that we are comparing classifications of *Hedera* using only trichomes but one way to contrast different classifications is a detailed comparison of one part of the organisms under study, what Simpson (1961) has referred to as the criterion of "minuteness of resemblance", to arrive at conclusions about relationships *sensu lato*. The assumption in such an approach is that, known anomalies aside, if taxa and their relationships are real, they should be revealed in whatever feature is analysed.

MATERIALS AND METHODS

PLANT MATERIAL

The material used in the analysis was mainly living material obtained from the American Ivy Society, British Ivy Society and the Botanical Gardens of the University of British Columbia. Herbarium specimens were used when living material was not available. Certain species such as *H. pastuchovii* were not included due to the lack of specimens from which trichome data could be gathered. The taxa analysed and the source of the material is presented in Table 1. Geographic locations of the source material are shown in Fig. 1. Identifications were, for the most part, based on



FIGURE 1. Map showing location of samples used in this study. Taxa as recognized by McAllister & Rutherford (1983), Rutherford (1984) and Rutherford & McAllister (1983). 1, *H. nepalensis*; 2, *H. rhombea*; 3, *H. colchica*; 4, *H. maderensis* (*H. canariensis* of Lawrence & Schulze 1942); 5, *H. azorica* (*H. canariensis* of Lawrence & Schulze 1942); 6, *H. canariensis*; 7, *H. algeriensis* (*H. canariensis* of Lawrence & Schulze 1942); 8, *H. "Morocco"* (*H. canariensis* of Lawrence & Schulze 1942); 9, *H. helix*; 10, *H. hibernica* (*H. helix* of Lawrence & Schulze 1942).

TABLE 1. SOURCE OF MATERIAL ANALYSED. TAXA AS RECOGNIZED BY MCALLISTER & RUTHERFORD (1983), RUTHERFORD (1984) AND RUTHERFORD & MCALLISTER (1983)

Species	Origin of material
<i>H. algeriensis</i> (AIS 82-238) ¹	Montasterre, south of Sousse, Tunisia.
<i>H. azorica</i>	Sao Miguel, Azores, Portugal.
<i>H. canariensis</i>	La Mercedes, Tenerife, northeast end of Canary Islands, Spain.
<i>H. maderensis</i>	Miel Valley, Algeciras, Cadiz Prov., Spain.
<i>H. "Morocco"</i>	Between Ifrane and Ketama near Fes, Middle Atlas Mts., Morocco.
<i>H. colchica</i> (AIS 82-256)	Turkey.
(AIS 82-268)	Caucasus between Telavi and Zagodeki, USSR.
(AIS 81-149)	Hillside above Novy Afron, Black Sea, USSR.
(LG 305-10) ²	Batumi Botanical Garden, Georgia, USSR.
(LG 62-1125)	Cultivated from American Ivy Society.
<i>H. helix</i>	Dybeso, Rorvig, Denmark.
	On road to Zalamen, between Clanas and El Villar, Huelva Prov., Spain.
	Samaria Gorge, Crete.
<i>H. hibernica</i>	South of Balonnart Farm, Ayrshire, Scotland.
	Glen Mayo, Isle of Man.
<i>H. nepalensis</i> (LG 83-0227)	Mt. Omei, Sichuan Prov., China; Yunnan Prov., China.
(AIS 87-202)	Cultivated in Univ. British Columbia Botanical Garden.
	Shennongjia Forest, Hubei Prov., China.
	Cultivated by Calif. Acad. Sci.
<i>H. rhombea</i> (LG 85-0359)	Ryukyu Island, Japan.
	Honshu pref. Shizuoku, western slope of Mt. Monju-dake, Japan.
	Honshu; Shirahama in Awa Prov., Japan.
	Mt. Taiping, I-lan Hsien, Taiwan.
	Cultivated in Koishidawa Botanical Garden, University of Tokyo, Tokyo, Japan.

¹ American Ivy Society accession number; ² Longwood Gardens accession number.

comparisons with published descriptions and geographic distributions. Specimens of *H. hibernica* were those identified by H. McAllister.

In order to determine that part of the plant from which to obtain trichome data, preliminary observations were made under a dissecting microscope, on ab- and adaxial surfaces of both young and old leaves, petioles, stems, and inflorescences. Based on these preliminary observations, it was decided that the abaxial surfaces of juvenile leaves, usually the second or third leaf from a shoot tip, was the most appropriate for further study. It was these leaves that had the most trichomes. In some cases, juvenile leaves of *H. nepalensis* were absent and adult leaves had to be used. In choosing specimens for analysis, representation from as many geographical areas as possible was attempted.

DATA ACQUISITION

Five samples from each species, as recognized by Lawrence & Schulze (1942), were chosen so that the species also recognized by McAllister & Rutherford (1983), Rutherford (1984) and Rutherford & McAllister (1983) were represented. The classification of Lawrence & Schulze (1942) was used as a starting point since it is the better known, being commonly referred to in general references (Rose 1980), and is the one whose naturalness we wanted to assess.

The leaves chosen for analysis were removed from the plant and air dried. Then, a small piece, approximately 5 mm × 5 mm was cut from each sample and mounted abaxial side up on an aluminium stub with silver paste. The stub and mounted leaf sample were air dried for another 24 hours to allow the fumes to dissipate from the paste and then coated in a gold sputter coater. The samples were observed and photographed in a Cambridge 250 ET SEM.

There are advantages and disadvantages to using SEM in such a study. The advantage is a clear display, which recaptures a certain three-dimensional component of the trichomes that facilitates

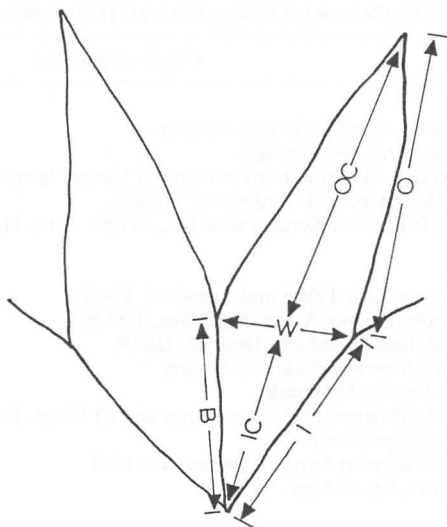


FIGURE 2. Variables measured shown on part of the trichome of *H. colchica*. O, length of arm along its edge from the point of fusion with other arms to its tip; I, length over which one side of trichome arm is fused; B, length over which other side of trichome arm is fused; W, width of arm along line connecting points of fusion on opposite side of trichome arm; OC, distance from line along which W was measured to tip of trichome; IC, distance from line along which W was measured to centre of trichome.

accurate measurement. The disadvantage is the time and cost of preparing material for, and producing pictures from SEM, which means that there will be a restriction on sample size.

From each specimen five trichomes were chosen for photographing and the data were gathered from these photographs. The variables measured were those shown in Fig. 2. In addition, the number of arms per stellate trichome was also noted. The measurements were designed to assess the length of the portion of the trichome arms that are free from each other (OC and O), the relative amount of trichome arm that is fused (I, B, and IC) and the width of the trichome arm (W). It is acknowledged that there is a certain amount of interdependency in the variables measured. That, however, is not wholly undesirable since the interdependency allows the assessment of attributes beyond those measured. For example, the relationship among B, I and W will reflect the angle formed at the junction of the arms of a trichome as will the relationship among O, OC and W capture the angle at the free tip of each arm. The relationship between IC and OC will reflect the relative size of the fused portion of the stellate trichome. These interrelationships are revealed by multivariate methods through the use of variable correlations.

DATA ANALYSIS

The main method of data analysis was principal components analysis (PCA) of a correlation matrix, a method which describes the relationships among objects analysed. These relationships are mathematically depicted as statistics, which summarize the relationships between the variables, and graphically by PCA axis scores, summary variables that display the relationships among the objects analysed. The PCA axis scores more accurately describe relationships than the original variables measured.

In this study, the objects subjected to PCA were individual trichome arms. The PCA axis scores were then displayed as means and standard deviations for taxa on the first two principal component axes. The taxa so presented were those recognized by Lawrence & Schulze (1942) and McAllister & Rutherford (1983), Rutherford (1984) and Rutherford & McAllister (1983). With such a display we could compare the treatment of *H. helix* and *H. canariensis* of Lawrence & Schulze (1942) with that of McAllister & Rutherford (1983), Rutherford (1984) and Rutherford & McAllister (1983). If the

taxa of Lawrence & Schulze (1942) are natural, then all trichomes from those taxa should have a comparable amount of within-species variation to other species and occupy a similar position on the first two principal axes. This would be revealed by those taxa having a standard deviation similar to other species and by the segregate taxa of McAllister & Rutherford (1983), Rutherford (1984) and Rutherford & McAllister (1983) existing as a tight cluster on the first two axes.

The different classificatory opinions were also compared by subjecting the PCA axis scores to analysis of variance (ANOVA). Two separate ANOVAs were performed. In one, the groups of trichomes compared were based on the taxa recognized by Lawrence & Schulze (1942) and in the other, the groups compared were defined by the taxa perceived by McAllister & Rutherford (1983), Rutherford (1984) and Rutherford & McAllister (1983). The ANOVAs were used as a description device, i.e. in the context of exploratory data analysis (Hoaglin *et al.* 1983, 1985). The interest was not in testing specific hypotheses but in terms of how well the different classifications agree with the data. The amount of agreement between the data and the different classifications is revealed in the amount of variation accounted for by each group (i.e. taxa) in an ANOVA. The assumption is that the classification which best agrees with the data, i.e. is the most natural, would be that in which the groups (taxa) account for more variation in the data. The amount of variation in the ANOVAs was determined as a ratio of sums of squares (η^2).

The data were also subjected to cladistic analysis using PHYSYS (Farris & Mickevich 1983). The cladistic analysis was applied in order to establish which trichome features are most plesiomorphic as well as the evolutionary trends seen in the trichome characters. Since an appropriate outgroup for cladistic analysis was not available, each taxon, in turn, was treated as the outgroup and the cladistic analysis chosen for inclusion in this paper was that one which gave the most parsimonious results.

The cladistic analysis was conducted on the taxa recognized by McAllister & Rutherford (1983), Rutherford (1984) and Rutherford & McAllister (1983) and the character values used for each taxon were the average of the variable values for all individuals in that taxon. Before the data were subjected to cladistic analysis, they were transformed from real to ranked numbers in order to facilitate presentation and interpretation of results. By analysing the taxa recognized by McAllister & Rutherford (1983), Rutherford (1984) and Rutherford & McAllister (1983), the naturalness of *H. helix* and *H. canariensis* as recognized by Lawrence & Schulze (1942) can be tested; if they are natural, then the taxa segregated out by McAllister & Rutherford (1983), Rutherford (1984) and Rutherford & McAllister (1983) will form monophyletic groups.

RESULTS AND DISCUSSION

The measurements were converted to means and standard deviations and are presented in Tables 2 and 3. Table 2 has statistics for the taxa recognized by Lawrence & Schulz (1942) and Table 3 for the

TABLE 2. MEANS AND STANDARD DEVIATIONS (IN PARENTHESES) OF TRICHOME CHARACTERS OF *HEDERA* TAXA RECOGNIZED BY LAWRENCE & SCHULZE (1942)

All measurements are in μm .

Taxa	Characters						No. of arms
	O	I	W	OC	IC	B	
<i>H. nepalensis</i>	56.5 (43.3)	54.6 (18.7)	25.1 (8.4)	52.0 (38.9)	56.6 (17.0)	62.0 (18.9)	13.0 (2.2)
<i>H. rhombea</i>	45.3 (29.7)	56.8 (19.9)	28.4 (14.5)	42.3 (30.4)	56.6 (18.1)	59.3 (15.2)	13.0 (2.7)
<i>H. colchica</i>	78.6 (29.4)	63.9 (20.0)	30.4 (7.8)	75.3 (28.3)	64.7 (19.8)	69.4 (20.5)	13.0 (2.4)
<i>H. canariensis</i>	162.8 (146.1)	45.8 (18.5)	30.7 (11.4)	141.3 (134.7)	49.0 (18.3)	57.9 (32.6)	11.0 (3.2)
<i>H. helix</i>	241.1 (92.2)	26.9 (12.8)	29.2 (10.8)	224.7 (94.5)	25.9 (13.5)	31.9 (16.3)	6.0 (1.6)

TABLE 3. MEANS AND STANDARD DEVIATIONS (IN PARENTHESES) OF TRICHOME CHARACTERS OF *HEDERA* TAXA RECOGNIZED BY MCALLISTER & RUTHERFORD (1983), RUTHERFORD (1984) AND RUTHERFORD & MCALLISTER (1983)

All measurements are in μm .

Taxa	Characters						No. of arms
	O	I	W	OC	IC	B	
<i>H. nepalensis</i>	56.5 (43.3)	54.6 (18.7)	25.1 (8.4)	52.0 (38.9)	56.6 (17.0)	62.0 (18.9)	13.0 (2.2)
<i>H. rhombea</i>	45.3 (29.7)	56.8 (19.9)	28.4 (14.5)	42.3 (30.4)	56.6 (18.1)	59.3 (15.2)	13.0 (2.7)
<i>H. colchica</i>	78.6 (29.4)	63.9 (20.0)	30.4 (7.8)	75.3 (28.3)	64.7 (19.8)	69.4 (20.5)	13.0 (2.4)
<i>H. maderensis</i>	171.0 (65.3)	45.4 (12.5)	32.4 (9.4)	165.3 (62.0)	49.1 (14.5)	73.1 (60.8)	9.0 (1.3)
<i>H. azorica</i>	426.7 (42.0)	31.1 (9.3)	28.9 (6.1)	343.3 (168.9)	153.3 (280.8)	40.0 (14.9)	7.0 (0.5)
<i>H. canariensis</i>	54.7 (13.2)	41.8 (15.0)	24.8 (10.1)	56.2 (16.3)	39.0 (11.6)	36.6 (11.3)	12.0 (4.3)
<i>H. algeriensis</i>	58.8 (24.9)	52.3 (11.7)	29.7 (12.9)	48.7 (15.4)	59.1 (12.0)	67.6 (19.0)	14.0 (2.6)
<i>H. "Morocco"</i>	102.8 (39.3)	58.8 (29.2)	37.9 (16.5)	93.0 (39.2)	62.4 (22.0)	72.0 (18.7)	11.0 (0.7)
<i>H. helix</i>	282.1 (73.5)	30.0 (13.2)	32.1 (11.0)	253.9 (94.8)	29.6 (14.0)	33.8 (18.1)	5.4 (1.6)
<i>H. hibernica</i>	179.5 (85.2)	22.3 (11.1)	24.9 (9.2)	180.8 (79.3)	20.4 (10.9)	29.1 (13.5)	6.3 (1.6)

the taxa recognized after McAllister & Rutherford (1983), Rutherford (1984) and Rutherford & McAllister (1983). The main point of comparison between Tables 2 and 3 is *H. canariensis* where in some variables measured, O and OC, the standard deviations greatly exceed the standard deviations for the same variables in the other taxa. When *H. canariensis* is split into the species recognized by McAllister & Rutherford (1983), Rutherford (1984) and Rutherford & McAllister (1983), the standard deviations for the above mentioned variables are greatly reduced.

The results of the PCA are presented in Table 4. Only the first two axes are presented since only these have eigenvalues >1.0 , the average eigenvalue for the PCA of a correlation matrix. We followed the convention of using only those axes with eigenvalues greater than the average (Legendre & Legendre 1983). All variables have a rather high value on the first axis with the exception of W. This indicates a strong relationship between most variables and the overall correlation structure for the trichome data. As well, the presence of both positive and negative values on the first PCA axis, that which reflects most of the variation in trichome data, indicates that the features measured do not all show the same trends in variation; as certain values decrease (O and OC), others will increase. This indicates that the trichomes of *Hedera* differ not only in size but also in shape.

Graphic results of PCA are presented in Figs. 3 and 4. Fig. 3 shows the means and standard deviations on the first two axes for the taxa recognized by Lawrence & Schulze (1942) and Fig. 4 the taxa recognized by McAllister & Rutherford (1983), Rutherford (1984) and Rutherford & McAllister (1983). In Fig. 3, *H. nepalensis* and *H. rhombea* are very close to each other and to *H. colchica*. *Hedera helix* is the most distantly removed from the above group of species and *H. canariensis* occupies an intermediate position in the ordination. Even more interestingly, in Fig. 3 the variation in *H. canariensis* is greater than that seen in the other species, as indicated by the larger standard deviations on the first PCA axis; *H. helix* shows the same on the second axis. The same basic pattern is seen in Fig. 4 with respect to *H. nepalensis*, *H. rhombea*, *H. colchica* and *H. helix*. However, at least some of the taxa split out of *H. canariensis* by McAllister & Rutherford (1983), Rutherford (1984) and Rutherford & McAllister (1983) occupy extreme positions in the scatterplot,

with *H. algeriensis* being to one side and close to *H. nepalensis* and *H. rhombea*, and *H. azorica* being on the opposite side and close to *H. helix*. *Hedera helix* and *H. hibernica* are close to each other on the first PCA axis but are separated on the second. *Hedera maderensis* and *H. canariensis* are in the middle portion of the ordination and *H. "Morocco"* is close to *H. nepalensis*, *H. rhombea*, *H. algeriensis*, and *H. colchica*. Fig. 4 also reflects the split in ivies based on trichome size and colour (McAllister & Rutherford 1983) with *H. hedera*, *H. hibernica* and *H. azorica*, the taxa with large white trichomes, being separated from the rest on the first PCA axis.

These results indicate that *H. canariensis* of Lawrence & Schulze (1942) is a highly heterogeneous taxon most likely consisting of more than one species. Our data and analyses will not allow us to say how many taxa should be recognized but those that stand out are *H. azorica*, *H. canariensis* and, perhaps, *H. maderensis*. *Hedera "Morocco"* and *H. algeriensis* are fairly close, a point of interest since McAllister & Rutherford (1983) hypothesized a relationship between *H. "Morocco"* and *H. canariensis*, which are not close in Fig. 4. Any difference between *H. helix* and *H. hibernica* is not clear-cut.

The comparison of the classifications of Lawrence & Schulze (1942) and McAllister & Rutherford (1983), Rutherford (1984) and Rutherford & McAllister (1983), as they are depicted by the results of the PCA (Figs. 3 & 4), indicate that the latter classification is likely to be superior, at least in its general structure. The same is indicated by the ANOVAs. Eta² for the ANOVA based on taxa recognized by Lawrence & Schulze (1942) (59.76 and 10.04 for the first and second axes respectively) is lower than that for the taxa recognized by McAllister & Rutherford (1983), Rutherford (1984) and Rutherford & McAllister (1983) (72.29 and 30.25 respectively).

The most parsimonious result of the cladistic analysis was that using *H. rhombea* as the outgroup and this is illustrated in Fig. 5. The first aspect to be commented on is the two groups of ivies recognized by McAllister & Rutherford (1983) based on trichome type. The taxa with large, white trichomes form a monophyletic group; those with small red trichomes a paraphyletic group, i.e. an unnatural one.

With respect to relationships depicted by the cladogram, the first striking aspect is that *H. canariensis* of Lawrence & Schulz (1942) is not natural, its segregates occurring in different monophyletic lines, ranging from one of the most plesio- to the most apomorphic. The situation is different with *H. helix* and *H. hibernica*. These two taxa form a monophyletic group thus indicating that *H. helix* of Lawrence & Schulze (1942) is a natural taxon. Thus the trichome data presented here will not allow a definitive statement on the appropriateness of recognizing *H. hibernica*. However, the indication that *H. helix* and *H. hibernica* are monophyletic and that they are separated only on the second PCA axis means that support for the recognition of the two species may well have to be found elsewhere. Also, *H. canariensis* and *H. "Morocco"* are not monophyletic indicating, like the results of PCA, that these two taxa are not close. We realize that our sampling is not extensive and therefore our conclusions must be tentative.

With respect to evolution of trichome attributes, generally speaking, with the exception of *H. canariensis* sensu McAllister & Rutherford (1983), Rutherford (1984) and Rutherford & McAllister

TABLE 4. PCA OF TRICHOME CHARACTERS RECORDED FOR *HEDERA* TAXA

Principal component	1	2
Eigenvalue	3.8	1.6
Percentage of total variance accounted for	54.7	23.2
Trichome characters	Eigenvectors	
O	-0.366	0.465
I	0.436	0.255
W	0.003	0.516
OC	-0.357	0.468
IC	0.456	0.288
B	0.392	0.369
No. of arms	0.432	0.120

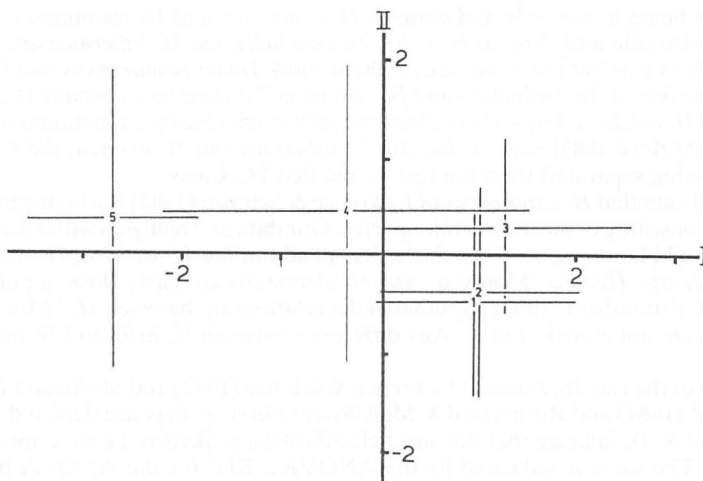


FIGURE 3. Ordination of PCA axis scores based on classification of Lawrence & Schulze (1942). Numbers identify taxa, their positions denote average values, horizontal and vertical lines indicate one standard deviation on the first (I) and second (II) PCA axes respectively. 1, *H. nepalensis*; 2, *H. rhombea*; 3, *H. colchica*; 4, *H. canariensis*; 5, *H. helix*.

(1983), the most plesiomorphic taxa are those of Asia, *H. nepalensis* and *H. rhombea*, with the taxa of Europe being the more apomorphic.

The most rapid evolution of trichome features, as indicated by the number of character state changes, occurs in the taxa of North Africa and the islands offshore from there, with the exception of *H. algeriensis*. These data suggest an Asiatic origin followed by the evolution of taxa in the western Mediterranean and then by those in Europe.

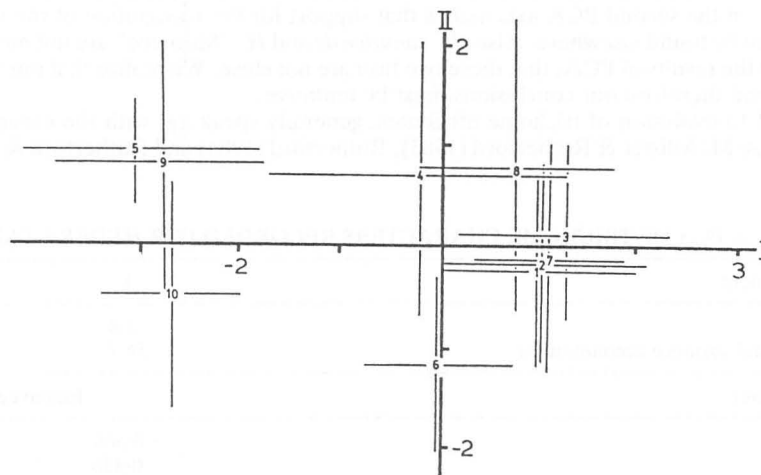


FIGURE 4. Ordination of PCA axis scores based on classification of McAllister & Rutherford (1983), Rutherford (1984) and Rutherford & McAllister (1983). Numbers identify taxa, their positions denote average values, horizontal and vertical lines indicate one standard deviation on the first (I) and second (II) PCA axes respectively. 1, *H. nepalensis*; 2, *H. rhombea*; 3, *H. colchica*; 4, *H. maderensis*; 5, *H. azorica*; 6, *H. canariensis*; 7, *H. algeriensis*; 8, *H. "Morocco"*; 9, *H. helix*; 10, *H. hibernica*.

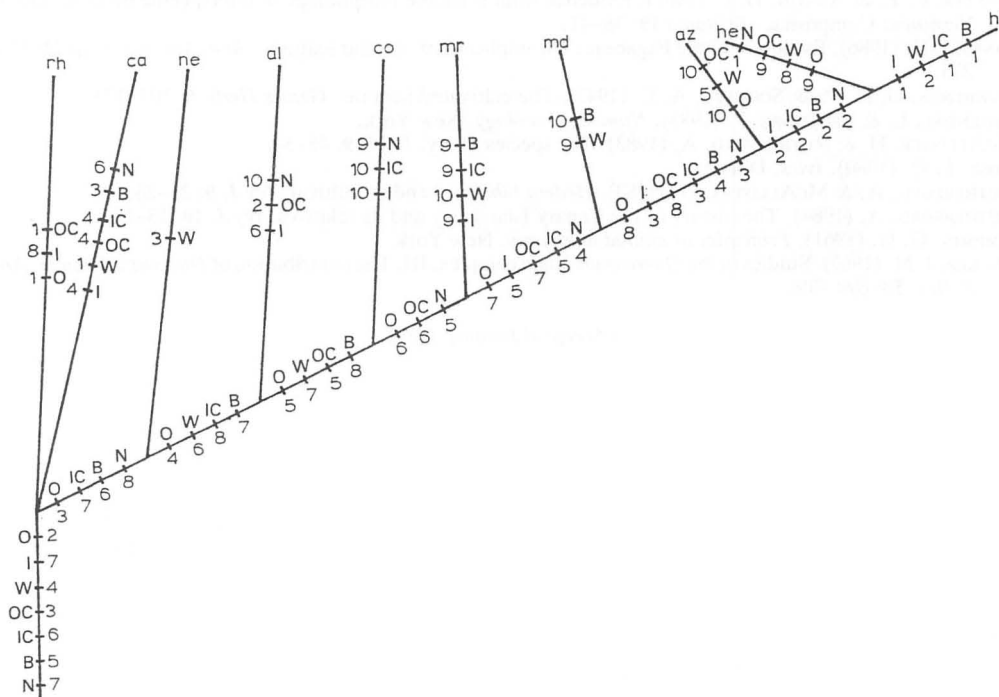


FIGURE 5. Cladistic analysis of trichome characters of taxa of *Hedera*. Characters are designated O, I, W, OC, IC, B (see Fig. 2) and N = number of arms. Character states represent ranked variables and are numbered. Taxa are abbreviated as follows: ne, *H. nepalensis*; rh, *H. rhombea*; co, *H. colchica*; md, *H. maderensis*; az, *H. azorica*; ca, *H. canariensis*; al, *H. algeriensis*; mr, *H. "Morocco"*; he, *H. helix*; hi, *H. hibernica*.

ACKNOWLEDGMENTS

We wish to thank M. Weis for help with the SEM and P. Wharton, S. Sulgrove, A. Rutherford, J. McNeill, D. Boufford, R. Lancaster, P. Hammer, C. Boody and H. van de Laar for helpful advice and suggestions. Both the British and American Ivy Societies generously gave plant materials and the curators of CAS, A, DAV, NA, US and DWC (abbreviations follow Holmgren & Keuken 1974) provided loans.

REFERENCES

- CAROLIN, R. D. (1971). The trichomes of the Goodeniaceae. *Proc. Linn. Soc. N.S.W.* **96**: 8–22.
 COWAN, J. M. (1950). *The Rhododendron leaf*. London.
 DEHGAN, B. (1981). Comparative morphology of *Fatsia japonica*, *Hedera helix*, and their hybrid, $\times$ *Fatshedera lizei*. *J. Am. Soc. hort. Sci.* **112**: 1053–1060.
 FARRIS, J. S. & MICKEVICH, M. E. (1983). *PHYSYS*. New York.
 GORNALL, R. J. (1986). Trichome anatomy and taxonomy of *Saxifraga* (Saxifragaceae). *Nord. J. Bot.* **6**: 257–275.
 HARDIN, J. W. & BELL, J. M. (1986). Atlas of foliar surface features in woody plants. IX: Betulaceae of eastern United States. *Brittonia* **38**: 133–144.
 HOAGLIN, D. C., MOSTELLER, I. & TUKEY, J. W. (1983). *Understanding robust and exploratory data analysis*. New York.
 HOAGLIN, D. C., MOSTELLER, I. & TUKEY, J. W. (1985). *Exploring data tables, trends and shapes*. New York.
 HOLMGREN, P. & KEUKEN, W. (1974). *Index herbariorum*. Utrecht.

- HUNTER, C. E. & AUSTIN, D. F. (1967). Evidence from trichome morphology of interspecific hybridization in *Vernonia*: Compositae. *Brittonia* **19**: 38–41.
- JONES, J. H. (1986). Evolution of the Fagaceae: The implications of foliar features. *Ann. Mo. bot. Gdn* **73**: 228–275.
- LAWRENCE, G. H. M. & SCHULZE, A. E. (1942). The cultivated hederas. *Gentes Herb.* **6**: 107–173.
- LEGENDRE, L. & LEGENDRE, P. (1983). *Numerical ecology*. New York.
- MCALLISTER, H. & RUTHERFORD, A. (1983). The species of ivy. *Ivy J.* **9**: 45–54.
- ROSE, P. Q. (1980). *Ivies*. Dorset.
- RUTHERFORD, A. & MCALLISTER, H. (1983). *Hedera hibernica* and its cultivar. *Ivy J.* **9**: 23–28.
- RUTHERFORD, A. (1984). The history of the Canary Islands ivy and its relatives. *Ivy J.* **10**: 13–18.
- SIMPSON, G. G. (1961). *Principles of animal taxonomy*. New York.
- TUCKER, J. M. (1963). Studies in the *Quercus undulata* complex. III. The contribution of *Quercus arizonica*. *Am. J. Bot.* **50**: 699–708.

(Accepted January 1989)