A morphometric analysis of *Hedera* L. (the ivy genus, Araliaceae) and its taxonomic implications

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ABSTRACT
This study examines patterns of morphological similarity within *Hedera* (the ivy genus, Araliaceae). Both cluster and principal components analyses reveal two major groupings corresponding to species of *Hedera* with stellate and scale-like trichomes. Characters traditionally used to delimit members of the genus were evaluated. Morphometric analyses found that the major delimiting characters for taxa with scale-like trichomes are: 1) number of leaf lobes, 2) length of the middle leaf lobe, 3) ratio of trichome center diameter to overall size, and 4) overall width of the leaf. The major delimiting characters for taxa with stellate trichomes are: 1) degree of leaf sinus shallowness, 2) length of leaf lobes, 3) width of the leaf middle lobe, 4) number of leaf lobes, and 5) trichome position. The newly described *Hedera maderensis* K. Koch ex Rutherford subsp. *iberica* McAllister is highly distinct morphologically from the typical subspecies, confirming evidence from chloroplast and nuclear ribosomal DNA data that suggest an independent origin of the two taxa. *Hedera iberica* (McAllister) Ackerfield & J. Wen is recognized at the species level. A key to the taxa of *Hedera* is provided to aid in the identification of this complex group.

KEY WORDS
Hedera,
Araliaceae,
morphometric analysis,
Hedera iberica,
taxonomy.

RÉSUMÉ
Analyse morphologique du genre Hedera L. (les Lierres, Araliaceae) et implications taxonomiques.
Cette étude évalue les schémas de ressemblance morphologique au sein du genre *Hedera* (les Lierres, Araliaceae). Des analyses de classification hiérarchique et en composantes principales révèlent l'existence de deux groupements qui correspondent aux espèces à trichomes stellés et à celles à trichomes

en forme d'écaille. Les caractères utilisés traditionnellement pour délimiter les taxons du genre *Hedera* sont évalués. Les analyses morphométriques montrent que les principaux caractères utilisés pour délimiter les taxons à trichomes en forme d'écaille sont : 1) nombre de lobes foliaires, 2) longueur du lobe médian, 3) rapport entre le diamètre de la partie centrale du trichome et son diamètre total, et 4) largeur totale de la feuille. Les principaux caractères utilisés pour délimiter les taxons à trichomes stellés sont : 1) profondeur du sinus foliaire, 2) longueur des lobes foliaires, 3) largeur du lobe médian, 4) nombre des lobes, et 5) emplacement des trichomes. *Hedera maderensis* K. Koch ex Rutherford subsp. *iberica* McAllister, récemment décrit, est morphologiquement très distinct de la sous-espèce typique, conformément aux données fournies par l'étude de l'ADN chloroplastique et de l'ADN ribosomal nucléaire indiquant l'origine indépendante des deux taxons. *Hedera iberica* (McAllister) Ackerfield & J. Wen est reconnu au niveau spécifique. Une clé des taxons de *Hedera* est fournie pour faciliter l'identification du matériel appartenant à ce complexe.

MOTS CLÉS
Hedera,
Araliaceae,
analyse morphométrique,
Hedera iberica,
taxonomie.

INTRODUCTION

Hedera L., the ivy genus, (Araliaceae) consists of approximately 15 species distributed throughout Europe (STACE 1997), North Africa (RUTHERFORD et al. 1993), Macaronesia (RUTHERFORD et al. 1993), and Asia (TOBLER 1912). *Hedera* is an important element in European and Asian woodlands, comprising a large portion of the forest understory, especially in the British Isles. Members of the genus are highly valued as ornamentals, and are commonly used in the landscape as well as indoors. In spite of its economic importance, however, the taxonomy and phylogenetic relationships of the species of *Hedera* are unclear.

LINNAEUS (1753) described the first species of *Hedera*, *H. helix*, in his *Species Plantarum*, and for many years, this was the only accepted species. WILLDENOW (1807) described *H. canariensis* based on specimens from the Canary Islands. Since then, 13 additional taxa of *Hedera* have been described and several treatments of the genus have been published (e.g., HIBBERD 1864, 1893; TOBLER 1912; BEAN 1915; LAWRENCE & SCHULZE 1942; POYARKOVA 1973; MCALLISTER 1981, 1990; RUTHERFORD et al. 1993). MCALLISTER (1981) and RUTHERFORD et al. (1993) recently examined species delimitations within *Hedera* and recognize 12 species, three subspecies, and one variety (Table 1).

Taxon delimitations for the Macaronesian and North African species of ivy are especially controversial. Several early treatments (TOBLER 1912; BEAN 1915; LAWRENCE & SCHULZE 1942) recognized only *H. canariensis* from the region. RUTHERFORD et al. (1993) treated *H. algeriensis*, *H. maderensis* subsp. *maderensis*, *H. maderensis* subsp. *iberica*, and *H. maroccana* as distinct from *H. canariensis* (Table 1) based on morphology, cytology, and distributions. ROSE (1996), however, treated *H. algeriensis* and *H. maderensis* as varieties under *H. canariensis*, but he corroborated the species status of *H. maroccana*, which differs from *H. canariensis* in the presence of reddish petioles and up to five juvenile leaf lobes. He further placed *H. cypria* as a variety under *H. pastuchovii*, disagreeing with RUTHERFORD et al. (1993) who regarded *H. cypria* as a distinct species based largely on the presence of distinct white markings over the veins in its young leaves as compared to less distinct white markings in young *H. pastuchovii* leaves, coupled with greater vigour in *H. cypria* plants. *Hedera cypria* is found on the island of Cypria and *H. pastuchovii* is distributed in close proximity in Iran and the Caucasus (Table 1).

TABLE 1. — Distribution, chromosome numbers and trichome types of ***Hedera***.

Taxon	Chromosome number	Distribution	Trichome Type
H. algeriensis Hibberd	2*n* = 96 (4*x*)	Mediterranean coast of Algeria and Tunisia	Scale
H. azorica Carr.	2*n* = 48 (2*x*)	Azores	Stellate
H. canariensis Willd.	2*n* = 48 (2*x*)	Canary Islands	Scale
H. colchica K. Koch	2*n* = 192 (8*x*)	Caucasus, Turkey	Scale
H. cypria McAllister	2*n* = 144 (6*x*)	Troodos Mountains in Cyprus	Scale
H. helix L. subsp. *helix*	2*n* = 48 (2*x*)	Europe (Scandinavia, Bulgaria, western Turkey, Cyprus, Greece, Crete) and the Ukraine	Stellate
H. helix L. f. *poetarum* (Nyman) McAllister & Rutherford		Italy and western Transcaucasia	Stellate
H. helix L. subsp. *rhizomatifera* McAllister	2*n* = 48 (2*x*)	Southern Spain	Stellate
H. hibernica Carr.	2*n* = 96 (4V)	Atlantic Coast of Europe from Ireland through the southwest of England and France to southwestern Spain	Stellate
H. maderensis K. Koch ex Rutherford subsp. *maderensis*	2*n* = 144 (6*x*)	Madeira	Scale
H. maderensis K. Koch ex Rutherford subsp. *iberica* McAllister	2*n* = 144 (6*x*)	Gibraltar-Algeciras and Lisbon areas of Portugal and Spain	Scale
H. maroccana McAllister	2*n* = 48 (2*x*)	Morocco	Scale
H. nepalensis K. Koch var. *nepalensis*	2*n* = 48 (2*x*)	Nepal, Kashmir	Scale
H. nepalensis var. sinensis Rehder	2*n* = 48 (2*x*)	Southwest China	Scale
H. pastuchovii G. Woronow	2*n* = 144 (6*x*)	Caucasus, Elburz Mts. in Iran	Scale
H. rhombea Miq.	2*n* = 48 (2*x*)	Taiwan, Japan, South Korea	Scale

The status of *Hedera hibernica* has also been controversial (ROSE 1996). Several workers (e.g., LAWRENCE & SCHULZE 1942; POYARKOVA 1973; KENT 1991; STACE 1997) have treated this taxon as *H. helix* subsp. *hibernica*, whereas others recognize it as a distinct species (BEAN 1915; MCALLISTER 1990; ROSE 1996). MCALLISTER (1990) reported a difference in chromosome number between *H. helix* subsp. *helix* and *H. hibernica* (Table 1). He also found that the trichomes of *H. helix* subsp. *helix* are positioned at a right angle to the leaf surface giving a bristling appearance whereas those of *H. hibernica* lie flat on the leaf surface. In addition, the leaves of *H. helix* subsp. *helix* were described as being generally smaller at all phases compared to those of *H. hibernica*. It was also noted that *H. hibernica* and *H. helix* subsp. *helix* differ in geographic distribution, the former occurring along the Atlantic Coast of Europe and the latter widespread throughout Europe and the Ukraine (Table 1). Based on these differences, MCALLISTER (1990) argued for the recognition of *H. hibernica* as a distinct species.

The Asian species of *Hedera* have received comparatively little attention taxonomically (RUTHERFORD et al. 1993). Most workers have recognized four taxa from Asia: *H. nepalensis* var. *nepalensis*, *H. nepalensis* var. *sinensis*, *H. pastuchovii*, and *H. rhombea*. POYARKOVA (1973) also recognized *H. caucasigena* Pojark., and *H. taurica* Carr. from Asia as distinct from *H. helix* subsp. *helix*, and described *H. robusta* Pojark. as another species found in China that resembles *H. colchica*. *Hedera nepalensis* var. *nepalensis* and *H. nepalensis* var. *sinensis* are generally separated by two characters (MCALLISTER 1981). The juvenile leaves of var. *nepalensis* generally have five lobes whereas those of var. *sinensis* usually have only three lobes (POYARKOVA 1950; ROSE 1996). Also, the leaves of var. *nepalensis* are noted to have considerable lateral lobing giving them an oak-leaf appearance while those of var. *sinensis* have little or no lateral lobing. However, the variational pattern of these characters has not been examined in detail.

Trichome morphology has been widely used to delimit taxa in *Hedera* (SEEMANN 1868; HIBBERD 1893; TOBLER 1912; LAWRENCE & SCHULTZE 1942; MCALLISTER 1981; ROSE 1996). Species of *Hedera* fall into two groups: those with stellate trichomes and those with scale-like trichomes (MCALLISTER 1981; ACKERFIELD 2001). Taxa with stellate trichomes are: *H. azorica*, *H. helix* subsp. *helix*, *H. helix* f. *poetarum*, *H. helix* subsp. *rhizomatifera*, and *H. hibernica*; those with scale-like trichomes are: *H. algeriensis*, *H. canariensis*, *H. colchica, H. cypria*, *H. maderensis* subsp. *iberica*, *H. maderensis* subsp. *maderensis*, *H. maroccana*, *H. nepalensis* var. *nepalensis*, *H. nepalensis* var. *sinensis*, *H. pastuchovii*, and *H. rhombea* (Table 1). LUM & MAZE (1989) performed a multivariate analysis on the trichomes of *Hedera*. They found weak support for the recognition of *H. hibernica* as distinct from *H. helix* subsp. *helix*. Since then, however, new taxa such as *H. cypria*, *H. helix* subsp. *rhizomatifera,* and *H. maderensis* subsp. *iberica* have been described (RUTHERFORD et al. 1993). Moreover, LUM & MAZE (1989) were unable to examine the trichomes of *H. pastuchovii*, which suggests that a new analysis of this feature may be desirable.

The phylogenetic relationships of *Hedera* have recently been evaluated using sequences of the internal transcribed spacer (ITS) regions of nuclear ribosomal (nr) DNA (VARGAS et al. 1999) and chloroplast (cp) DNA (ACKERFIELD & WEN, in press). The cpDNA and nrITS data were highly incongruent (cf. VARGAS et al. 1999; ACKERFIELD & WEN, in press) and the comparison of the two datasets strongly support the idea that allopolyploidy has been important in speciation within *Hedera* as suggested by VARGAS et al. (1999). ACKERFIELD & WEN (in press) hypothesized the maternal parents for several allopolyploid taxa based on cpDNA evidence. The ITS phylogeny (VARGAS et al. 1999) suggests that the hexaploid *H. maderensis* subsp. *iberica* (2*n*=144) originated as the result of hybridization between a diploid taxon with reddish-scale hairs (probably *H. canariensis* as the maternal ancestor) and the tetraploid *H. hibernica* (2*n*=96). The chloroplast DNA evidence strongly supports an independent evolution of *H. maderensis* subsp. *iberica* from *H. maderensis* subsp. *maderensis*, thus rendering the species polyphyletic as currently circumscribed and suggesting the need to re-evaluate its status.

This study examines the patterns of morphological variation among *Hedera* taxa by emphasizing juvenile phase plant morphology and trichome characters. A morphometric analysis using cluster and principal components analyses is employed to analyze variation and evaluate taxon delimitations. In addition, a key to the members of *Hedera* is presented based on characters that differentiate the taxa in the morphometric analysis.

MATERIALS AND METHODS

Specimens examined

A total of 105 specimens were analyzed (Table 2), with each specimen representing an Operational Taxonomic Unit (OTU). The number of specimens for each taxon examined ranged from 2 to 22, depending upon availability.

The number of specimens available for analysis was limited by two factors: 1) a lack of juvenile phase collections as most specimens have been made from adult plants, which are similar throughout the genus; and 2) a paucity of collections of newly described species such as *H. algeriensis*, *H. cypria*, *H. helix* subsp. *rhizomatifera*, *H. maderensis*, and *H. maroccana*, although in each case at least a type specimen was examined.

Data compilation

Size and width were measured to the nearest millimeter from three leaves from each OTU (Table 2) and averaged together. Leaves approximately six to eight nodes down on the juvenile shoot were measured, to ensure that they were at

TABLE 2. — Specimens of ***Hedera*** examined for morphometric analysis.

Species*	Specimens measured	Locality	Obs.
alg	*J. Owens Eu10* (CS)	Ness Botanic Gardens, England	1
alg	*J. Owens 221* (CS)	American Ivy Society #93-130, grown at *Hedera* etc. garden center, Lionville, Pennsylvania, U.S.A.	2
azo	*P. Dansereau et al. 316* (NY)	Pico Alto, Santa Maria, Azores	1
azo	*C.S. Brown 106* (A)	Pico, Azores	2
azo	*P. Dansereau et. al.* 197 (NY)	Serra de Santa Barbara below Lagoa do Madruga, Terceira, Azores	3
azo	*J. Botello Goncalves 1241* (DPPF)	Flores, Azores	4
azo	*I. Botello Foucal Vs 4593* (DPPF)	Caldenia, Azores	5
azo	*I. Botello Foucal Vs 4318* (DPPF)	Velus, Island of Säo Jorge, Azores	6
azo	*L. Botella Goncalves1573* (DPPF)	Corvo, Azores	7
can	*E. Asplund 765* (B)	Valle de Orotava, Barranco de la Calera, Tenerife, Canary Islands	1
can	*J. Dixon et al.* (E)	La Mercedes, NE Tenerife, Canary Islands	2
can	*M. Muike 2625* (B)	Agna Garria, Tenerife, Canary Islands	3
can	*A.C. Cook 1095* (US)	Las Mercedes, Tenerife, Canary Islands	4
can	*A. Stork & Wanntorp 1977* (NY)	Cruz del Carmen, Las Mercedes, Canary Islands	5
col	*J. Owens Eu11* (CS)	Ness Botanic Gardens, England	1
col	*H.U.E. Walter 4849* (B)	Anadolu, Turkey	3
col	*G.H.M. Lawrence 2885* (NY)	*Hedera* collection of the Dept. of Floriculture, Cornell University, Ithaca, New York, U.S.A.	4
col	*N. Taylor* (NY)	NY Botanical Garden, cultivated plant	5
col	*Leg. Davis & Coode D. 39097* (E)	Karasu to Sogutlu, Prov. Adapazari, Turkey	6
col	*Davis, Coode, & Yaltirik 37820* (E)	Cimsirdere, above Yenice, Prov. Zonguldak, Turkey	7
col	*G. Wagenitz & H.-J. Beug* (B)	Prov. Bolu, NW-Anatolien, Turkey	8
cyp	*Della* (E)	River terraces, Kakopetria, Cyprus, isotype	2
cyp	*Della* (E)	River terraces, Kakopetria, Cyprus, isotype	4
cyp	*H. McAllister* (E)	Troodos Mts., Cyprus, cultivated at Ness Botanic Gardens	5
hib	*J. Owens Eu5* (CS)	Betwys-y-Coed, Wales	1
hib	*J. Owens Eu7* (CS)	Betwys-y-Coed, Wales	2
hib	*J. Owens Eu8* (CS)	Betwys-y-Coed: by Snowdonia information station, further down trail, on rock wall, Wales	3
hib	*J. Owens Eu2* (CS)	Penmon Pt., Wales	4
hib	*J. Owens 229* (CS)	Lewis Ginter Botanic Garden, Richmond, Virginia, U.S.A.	5
hib	*G.H.M. Lawrence 1588* (LH)	So. Sudbury, Mass. *Hedera* collection of Dept. of Floriculture, Cornell University, Ithaca, New York, U.S.A.	6
hib	*C. Baenitz* (US)	Ireland	7
hib	*J. Owens Eu1* (CS)	Penmon priory, Wales	8
hib	*J. Owens Eu3* (CS)	Penmon Pt., Wales	9
hib	*J. Owens 418* (CS)	Llangollen, Wales	10
hib	*J. Owens 406* (CS)	Avebury, England	11
hib	*J. Owens414* (CS)	Llangollen, Wales	12
hib	*J. Owens 419* (CS)	Llangollen, Wales	13
hib	*M. Lousa et al. 489* (DPPF)	Alcaria, Lisbon, Portugal	14
hel	(HU)	Hungary	1

*Species abbreviations are as follows: **alg** = *H. algeriensis*, **azo** = *H. azorica*, **can** = *H. canariensis*, **col** = *H. colchica*, **cyp** = *H. cypria*, **hib** = *H. hibernica*, **hel** = *H. helix subsp. helix*, **poet** = *H. helix f. poetarum*, **rhiz** = *H. helix subsp. rhizomatifera*, **mad** = *H. maderensis subsp. maderensis*, **madib** = *H. maderensis subsp. iberica*, **maro** = *H. maroccana*, **nep** = *H. nepalensis var. nepalensis*, **nepsin** = *H. nepalensis var. sinensis*, **past** = *H. pastuchovii*, and **rhom** = *H. rhombea*.

Species*	Specimens measured	Locality	Obs.
hel	*J. Lunell* (A)	Ruins of Bergholm Castle, Switzerland	3
hel	*G.A. Ringselle* (A)	Falhenberg, Holland	4
hel	*C. Baenitz 1525* (A)	Waldern, Germany	5
hel	*D. Suhur* (US)	Bulgaria	6
hel	*E. Anderson 36* (A)	Rila Monastery, Bulgaria	7
hel	*Dr. N. Uyladilin 749* (A)	Pei, Slovenia	8
hel	*E. Anderson 43* (A)	Vitosha, above Boyana, Sofia, Bulgaria.	9
hel	*H. & E. Walter 42* (B)	Dramalj, Croatia	10
hel (t)	*T.S. Elias et. al. 5225* (NY)	Yaila, Yaltinskii Mt. Forest Nature reserve, c. 36 km SW of Yalta, Crimea, Ukraine	11
hel (t)	*T.S. Elias et al. 5490* (NY)	Yaila, Shtangeyevskaya Path, 10 km W of Yalta, Crimea, Ukraine	12
hel (t)	*T.S. Elias 3214* (NY)	Near Gagra, Caucasus Mts., Georgia	13
hel (c)	*J. Cuba 1990* (NY)	Krasnodar, former USSR	14
hel	*G. Stohr* (B)	Sotchi, former USSR	15
hel	*A. Buia et al. s.n.* (B)	Severin, Romania	16
hel	*E. Yephbkobckar* (A)	Shores of Black Sea, Czerniakowska, Russia	17
hel	*H. Balslev* (NY)	Risskov at Aarhus, Jutland, Denmark	18
hel	*J. Owens 416* (CS)	Llangollen, Wales	19
hel	*J. Owens 415* (CS)	Llangollen, Wales	20
hel	*J. Owens 405* (CS)	Oxfordshire, England	21
hel	*J. Owens 403* (CS)	Oxfordshire, England	22
poet	*J. Dorfler 1243* (B)	Attica, Greece	1
poet	*L.G. Gellanda* (B)	Campania, Italy	2
rhiz	*J. & H. Rutherford 16* (E)	Aracena, Huelva Prov., Spain, isotype	1
rhiz	*S.L. Jury & L.C. Jury 13127* (E)	NW of Algeciras, Prov. Cadiz, Spain	2
rhiz	*J. Owens 231* (CS)	American Ivy Society #88-372, grown at *Hedera* etc. garden center, Lionville, Pennsylvania, U.S.A.	3
mad	*D. McClintock 18* (E)	Madeira, isotype	1
mad	*J. Owens 225* (CS)	American Ivy Society #91-097, *Hedera* etc. garden center, Lionville, Pennsylvania, U.S.A.	2
madib	*A. McG. Stirling 15* (E)	Los Barrios Rd., Alcala, Spain, isotype	1
madib	*M. Lousa & Y. Monjardino* (DPPF)	Ana-de Avis, between Chinjelos & Moinlios, Figuero-dos-vinhos, Portugal	2
madib	*M. Lousa & M.D. Espirito Santo* (DPPF)	S. Bento, between Azelhas & Casal dos Correias, Portes de Mos, Portugal	3
madib	*M. Pinheiro de Mello* (DPPF)	Santa Cristina de Aroes, Fafe, Portugal	4
madib	*M. Pinheiro de Mello* (DPPF)	S. Paio de Figueiredo, Guimaraes, Portugal	5
maro	*International Dendrological Society Expedition 86* (E)	35 km from Ketama, Middle Atlas, Morocco, isotype	1
maro	*S.L. Jury 13099* (E)	N from Algeciras, Prov. Cadiz, Spain	2
maro	*J. Owens Eu12* (CS)	Ness Botanic Gardens, England	3
maro	*J. Owens Eu13* (CS)	Ness Botanic Gardens, England	4
maro	*Clayton & Brinklow 107* (E)	Imlil Djebel Toubkal Massif, 2100 m, High Atlas, Morocco	5
maro	*J. Owens 234* (CS)	American Ivy Society #88-008, *Hedera* etc. garden center, Lionville, Pennsylvania, U.S.A.	6
nep	*M. Nath* (US)	Murree, Pakistan	1
nep	*A.E. Schulz 1058* (LH)	Coolidge Rare Plant Gardens, E. Pasadena, California, U.S.A.	2
nep	*H. Smith* (LH)	Swathmore, Pennsylvania, U.S.A.	3
nep	*W.J. Dress BH 64-418* (LH)	Grown at Cornell, New York, U.S.A, originally collected in Nepal	4

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Species*	Specimens measured	Locality	Obs.
nep	*W.T. Stearn* (LH)	Himalayan foothills and Mussoorie, United Provinces, India	5
nep	*J.J.* (A)	N.W. Himalaya, Nepal	6
nep	*R.N. Parker* (A)	Kalatop Reserve, Perganna Bathri, Charuba Srale, Nepal	7
nep	*R.R. Stewart* (A)	Jhelum Valley, Kashmir, India	8
nep	*K.H. Rechinger 30595* (B)	Inter Khawazakhiela and Shangla, Swat, NW Pakistan	9
nepsin	*Sino-American Guizhou Botanical Expedition 1480* (A)	Yinjiang Xian, Hugnoshi, Guizhou, China	1
nepsin	*F.A. McClure 14169* (A)	Yam Na Mt., Kwangtung, China	2
nepsin	*W. Purdom 1011* (A)	Tai-pei-shan, Shaanxi, China	3
nepsin	*C. Schneider 320* (A)	Yunnan, China	4
nepsin	*F. G. Dickason 7562* (A)	Haka, Myanmar	5a
nepsin	*F. P. Metcalf 17627* (A)	Loh-Fau-Shan, Kwangtung, China	5
nepsin	*L.H. Bailey* (LH)	Kuling, Jiangxi, China	6
nepsin	*B. Harkness* (LH)	Kuan Hsien, Sichuan, China	7
nepsin	*H. Smith 4858* (A)	Sichuan, China	8
nepsin	*C. Schneider 409* (A)	Yunnan, China	9
past	*J. Owens 222* (CS)	American Ivy Society #82-118, *Hedera* etc. garden center, Lionville, Pennsylvania, U.S.A.	1
past	*J. Owens Eu14* (CS)	Ness Botanic Gardens, England	2
past	*J. Freyn 1399* (A)	Bender Ges, Prov. Asterabad, Persia borealis, Iran	3
rhom	*E.H. Wilson 8571* (A)	Oo-ryong-too (Dagelet Island), Korea	1
rhom	*J. Owens 230* (CS)	American Ivy Society #88-260, *Hedera* etc. garden center, Lionville, Pennsylvania, U.S.A.	2
rhom	*J. Owens 230a* (CS)	Lewis Ginter Botanic Garden, Richmond, Virginia, U.S.A.	3
rhom	*J. Owens 220* (CS)	Grown at Chicago Botanic Garden., originally from Ulluny-do island, Korea	4

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the same stage of development. Twenty-four quantitave characters were measured to the nearest millimeter and nine qualitative features were recorded (Table 3). Leaf lobes were numbered clockwise for the juvenile leaf measurements, with lobe three always assigned to the middle lobe (Fig. 1).

Trichome characters measured include length of rays, center diameter, overall length, width of rays, length of ray fusion, base length, and ratio of center diameter to overall length (see ACKERFIELD 2001 for detailed discussions of these characters). Leaf glossiness was not included in the morphometric analysis because it was not possible to evaluate this character reliably from herbarium specimens.

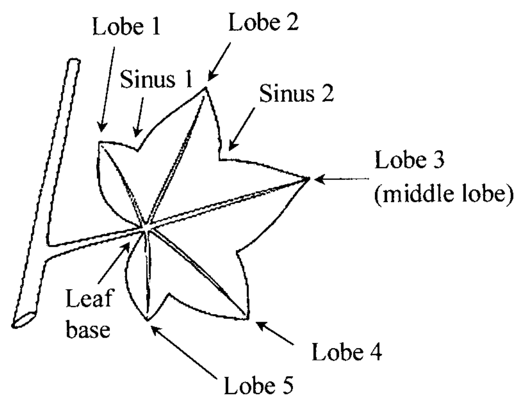

Fig. 1. — A juvenile ***Hedera*** leaf.

Table 3. — Characters and character states for morphometric analyses of ***Hedera***.

Number of lobes
Length of lobe one
Length of lobe two
Length of lobe three
Length of lobe four
Length of lobe five
Presence of lateral lobes (0 = none, 1 = few, 2 = many)
Fruit color (0 = black, 1 = orange/yellow)
Width of lobe one
Width of lobe two
Width of lobe three
Width of lobe four
Width of lobe five
Overall width (from point to point)
Length from base to sinus one
Length from base to sinus two
Petiole length
Leaf veins (0 = green, 1 = silver)
Leaf base (0 = cordate, 1 = truncate)
Rhizomes (0 = absent, 1 = present)
Trichome type (0 = scale, 1 = stellate)
Trichome position (0 = adpressed to leaf surface, 1 = at a right angle to leaf surface)
Trichome location (0 = both adaxial and abaxial leaf surfaces, 1 = abaxial leaf surface only)
Trichome center raised (0 = absent, 1 = raised, 2 = present but not raised)
Trichome center diameter (average from trichome measurements)
Trichome overall length (average from trichome measurements)
Ray length (average from trichome measurements)
Ratio of length of lobe two to length of lobe three
Ratio of width of lobe three to overall width
Ratio of trichome center diameter to overall size (average from trichome measurements)

Data analysis

One-way analysis of variance (ANOVA) was used to analyze each character for its mean, range, and standard deviation ($P = 0.00$) with species as the grouping criterion using Minitab version 12.23 (MINITAB™ INC. 1997). Dendrograms based on all specimens were produced by NTSYS-pc® version 1.70 (ROHLF 1992). Averages for each character were standardized to eliminate the effects of different scales of measurement. Similarity matrices were prepared using the simple matching coefficient. A single link cluster analysis was used for clustering, utilizing the unweighted pair-group arithmetic average clustering (UPGMA) method.

Principal components analysis was used to detect morphological variation among OTUs and to analyze relationships between characters. PCA can be used to uncover unexpected relationships among a large number of variables by reexpressing original variables into two or three new uncorrelated variables such that they retain most of the original variation (information) (TUKEY 1997). PCA makes no assumptions about group membership of OTUs, and maximizes the variation. PCAs were performed using NTSYS-pc® version 2.02 (ROHLF 1992). First, measurements for each character were standardized to eliminate the effects of different scales of measurement. Similarity matrices using product-moment correlation were then generated, and eigenvalue and eigenvector matrices were calculated from the correlation matrix. The standardized data were projected onto the eigenvectors of the correlation matrix and represented in a two-dimensional scatter plot.

RESULTS

The dendrogram of the entire data set, based on results from the PCA, separates all taxa with no overlap (Fig. 2). The taxa with scale trichomes and those with stellate trichomes form two major groups, and the former is divided into two subgroups. The first of which consists of *H. nepalensis* var. *sinensis* and *H. nepalensis* var. *nepalensis*, and the second includes *Hedera algeriensis*, *H. canariensis, H. colchica*, *H. cypria*, *H. maderensis* subsp. *iberica*, *H. maderensis* subsp. *maderensis*, *H. maroccana*, *H. pastuchovii*, and *H. rhombea*. Three subgroups are recognizable within the stellate trichome group: *Hedera helix* and *H. helix* f. *poetarum*, *H. hibernica*, and *H. azorica.*

A plot of the entire data set for principal components one and two is shown in Fig. 3. Principal component 1 accounts for 37.1% of the variation, principal component 2 accounts for 26% of the variation, and principal component 3 (not shown) accounts for 8% of the variation for a total of 71.1%. All three dimensions had observed proportions greater than those of the broken stick model (JOLIFFE 1986) and thus explain more of the variance than expected due to chance alone.

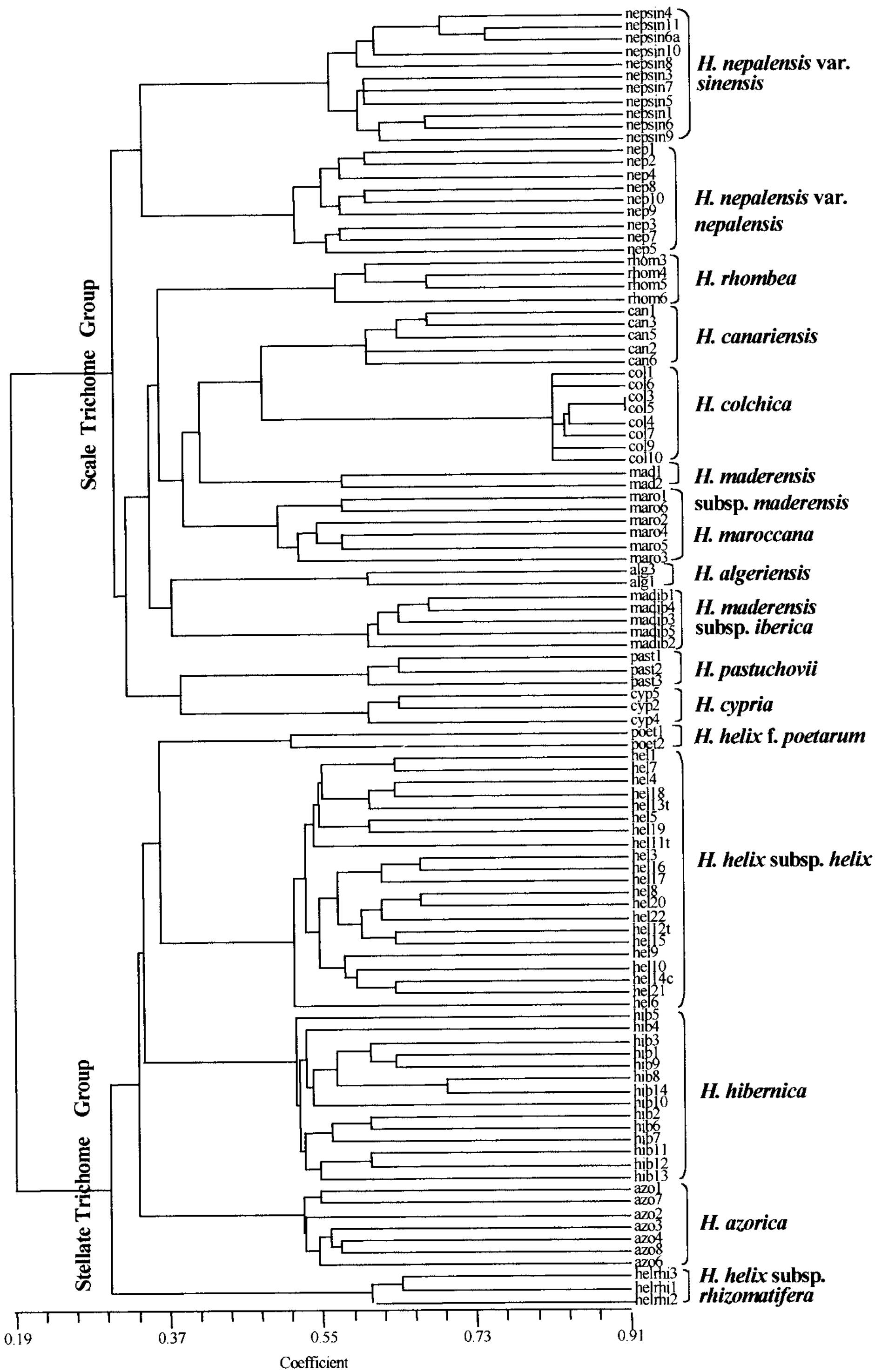

Fig. 2. — UPGMA cluster dendrogram of ***Hedera*** based on 30 morphological characters.

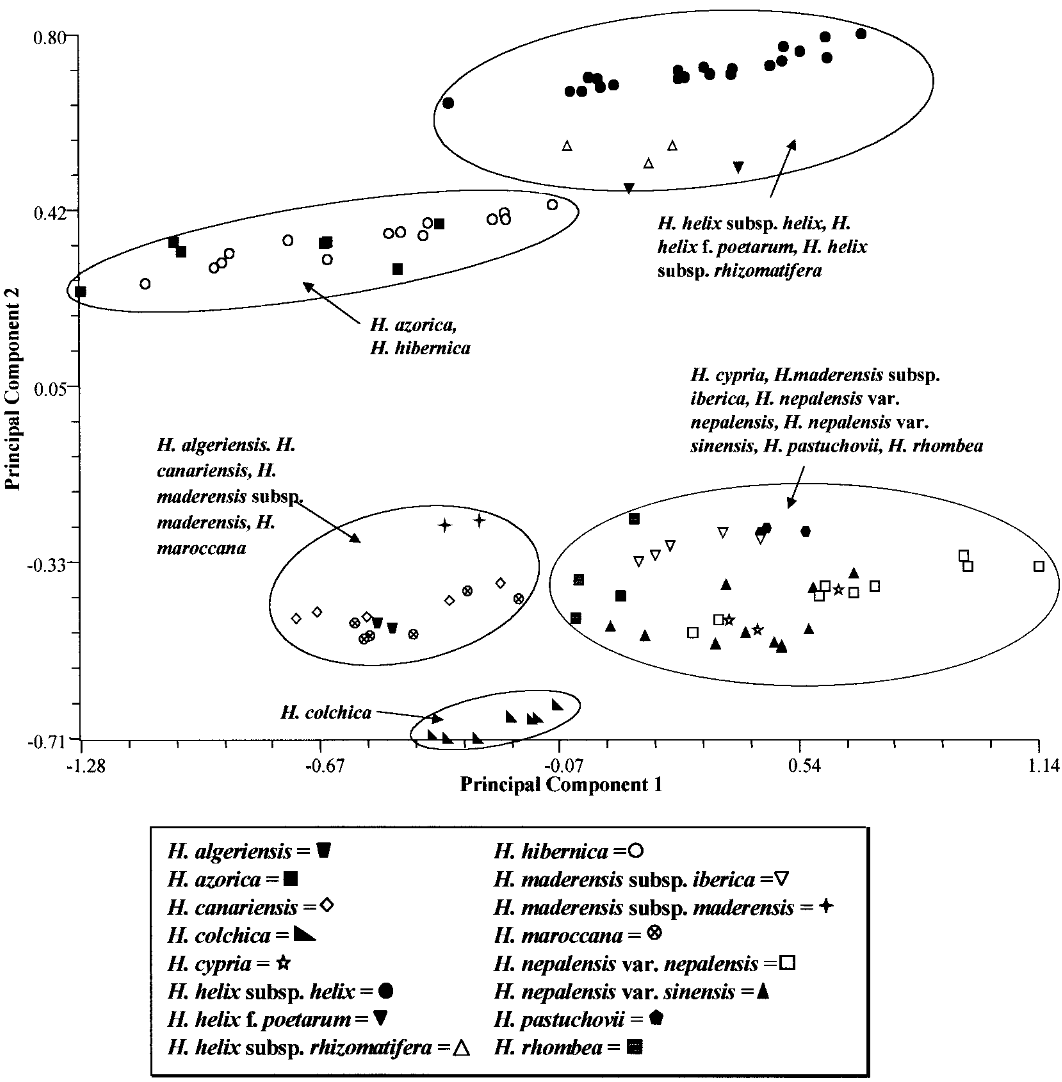

Fig. 3. — Plot of principal components one and two for all ***Hedera*** species.

Four variables load heavily on the first component (presented in decreasing order of loadings): 1) fruit color, 2) presence of lateral lobes, 3) ratio of trichome center diameter to overall length, and 4) trichome center length. The following characters load heavily on the second component but little on the first: 1) trichome ray length, 2) center length, type, 3) width of rays, and 4) trichome position, as well as 5) leaf veins, and 6) number of leaf lobes. PCA axis 3 is most influenced by: 1) number of leaf lobes, 2) presence of lateral lobes, and 3) fruit color, which also load some on the first and second components.

PCAs were performed on the groups comprising taxa with separate scale trichomes and stellate trichomes to enhance the resolution. A PCA of the data set for taxa with stellate trichomes is shown in Fig. 4. Principal component 1 accounts for 56.3% of the variation, component 2 for 11.9%, and component 3 for 10.8% for a total of

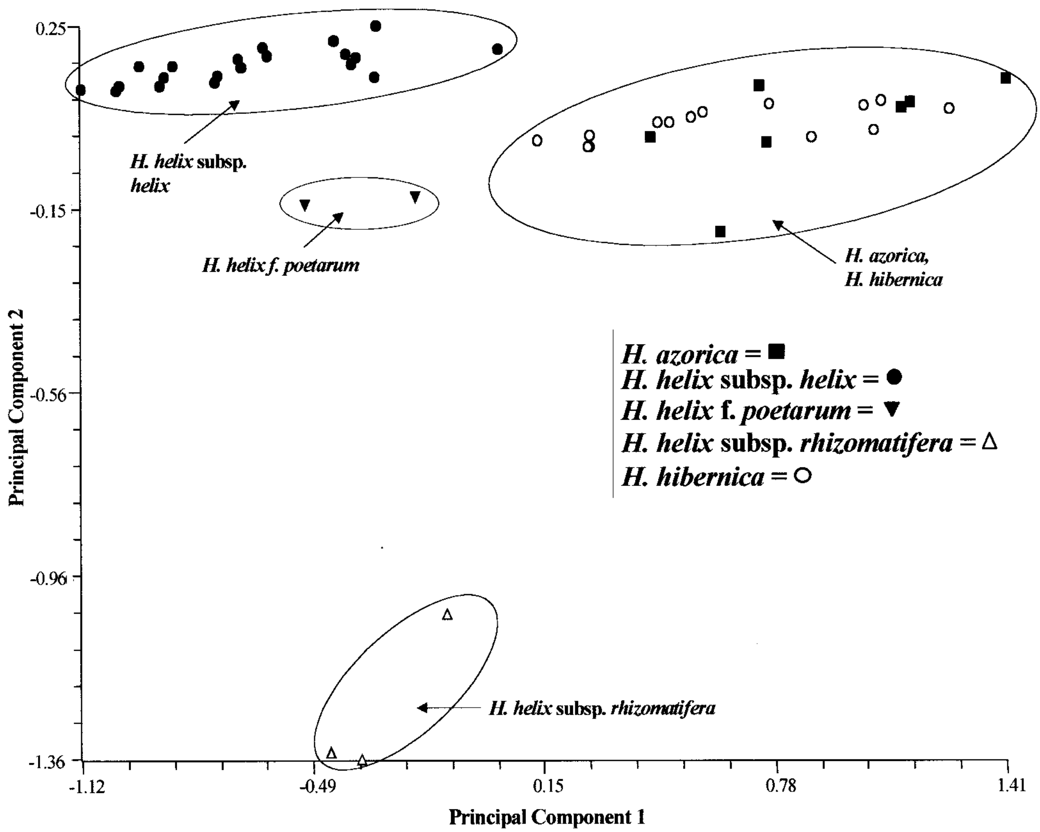

Fig. 4. — Plot of principal components one and two for ***Hedera*** species with stellate trichomes.

79%. The following variables load heavily on the first component variables (presented in decreasing order of loadings): length from base to sinus 1, length of middle lobe, length from base to sinus 2, length 2, length 1, and width 3. The number of lobes, width of trichome rays, and trichome position load heavily on the second component but little on the first. PCA axis 3 is most influenced by width of trichome rays, coloration of leaf veins, petiole length, trichome fusion length, and length of middle leaf lobe, which also load some on the first and second components.

A PCA of the data set for taxa with scale trichomes is shown in Fig. 5. Principal component 1 accounts for 46.3% of the variation, component 2 for 15.3%, and component 3 for 10.2%, for a total of 71.8%. The following variables load heavily on the first component (presented in decreasing order of loadings): fruit color, presence of lateral lobes, and the ratio of trichome center diameter to overall size. The number of leaf lobes, length of middle leaf lobe, presence of lateral lobes, and fruit color load heavily on the second component and on the first. PCA axis 3 is most influenced by: trichome overall length, number of leaf lobes, trichome fusion length, and if the trichome center is raised, which also load some on the second component.

DISCUSSION

Taxa with scale trichomes

The projection of principal components one and two from the analysis using all taxa shows two major groupings within *Hedera*, one comprising the taxa with scale trichomes and the other including those with stellate trichomes (Fig. 3). The major delimiting characters for taxa within the scale trichomes cluster are: 1) number of leaf lobes, 2) length of the middle lobe, 3) ratio of trichome center diameter to overall size, and 4) overall width of the leaf. Within the scale trichome cluster, there are three subgroupings. The most clearly distinguishable one consists of only *H. colchica*, and is separable from the others primarily by the presence of unlobed leaves. The Macaronesian and North African species with larger leaves and a low ratio of trichome center diameter to overall size (*H. canariensis*, *H. algeriensis*, *H. maderensis* subsp. *maderensis*, and *H. maroccana*) form the second subgrouping. The taxa with smaller leaves and an extended middle lobe (*H. cypria*, *H. pastuchovii*, *H. nepalensis* var. *nepalensis*, *H. nepalensis* var. *sinensis*, *H. maderensis* subsp. *iberica*, and *H. rhombea*) form the third subgrouping. All of these taxa are from Asia or Cyprus, except *H. maderensis* subsp. *iberica*, which occurs in Spain and Portugal.

Early workers (e.g., TOBLER 1912; BEAN 1915; LAWRENCE & SCHULZE 1942) recognized only a single species of *Hedera* in the Macaronesian islands, North Africa, and the Iberian peninsula, *H. canariensis*. RUTHERFORD et al. (1993) suggested that *H. algeriensis*, *H. maderensis* subsp. *maderensis*, *H. maderensis* subsp. *iberica*, and *H. maroccana* are distinct from *H. canariensis* based on cytological and morphological examinations. Results from our morphometric analyses show that *H. canariensis*, *H. algeriensis*, *H. maroccana*, and *H. maderensis* subsp. *maderensis* are not strongly separated in either the PCA of all taxa or of just those with scale trichomes. Characters used by RUTHERFORD et al. (1993) to distinguish *H. algeriensis* (truncate leaf base), *H. maroccana* (five lobes and trichome center not raised), and *H. maderensis* (five lobes) as distinct from *H. canariensis* are not well supported by the PCA. Additional sampling of these taxa will be needed to resolve this taxonomic controversy.

Hedera maderensis subsp. *iberica* is separable from the *H. canariensis* complex including *H. maderensis* subsp. *maderensis* in the morphometric analyses (Figs. 2, 3, 5). By several characters, including a smaller leaf width and length, an elongated middle lobe, a smaller number of lobes (usually three), and a truncate leaf base. This finding supports the idea that *H. maderensis* subsp. *iberica* should be recognized as a distinct species. The two recent molecular phylogenetic analyses of *Hedera* (VARGAS et al. 1999; ACKERFIELD & WEN, in press) strongly support an independent evolution of *H. maderensis* subsp. *iberica* from *H. maderensis* subsp. *maderensis*. Biogeographically, the typical subspecies is endemic to the island of Madeira whereas *H. maderensis* subsp. *iberica* is restricted to the Gibraltar-Algeciras and Lisbon areas of Portugal and Spain (MCALLISTER 1981; RUTHERFORD et al. 1993). Thus, using the phylogenetic species concept sensu NIXON & WHEELER (1990), we hereby recognize *Hedera iberica* at the species level and make the following nomenclatural change:

Hedera iberica (McAllister) Ackerfield & J. Wen, **comb. et stat. nov.**

Hedera maderensis K. Koch ex Rutherford subsp. *iberica* McAllister, Plantsman 15: 124 (1993). — Type: *McAllister 15*, specimen of cultivated material at University of Liverpool Botanic Gardens, England, source material originally from Spain, prov. Málaga, between Alcala and Los Barrios, roadside bank, 25-200 m, 17 Apr. 1974, *A.M. Stirling s.n.* (holo-, LIV; iso-, E!, 2 sheets).

The taxa of *Hedera* from Asia and Cyprus are not clearly defined. *Hedera rhombea*, *H. pastuchovii*, *H. cypria*, *H. nepalensis* var. *nepalensis*, and *H. nepalensis* var. *sinensis* group together in the principal component analysis. In the PCA of only those taxa with scale trichomes, the two varieties of *H. nepalensis* are separated from the others by having orange/yellow instead of black fruit. Traditionally, *H. nepalensis* var. *nepalensis* and var. *sinensis* are separated based on two characters, the number of lobes (5 in var. *nepalensis* and 3 in var. *sinensis*) and amount of lateral lobing (considerable in var. *nepalensis* and little to none in var. *sinensis*). However, some specimens of *H. nepalensis* var. *sinensis* show variability in the number of leaf lobes, with values ranging from three to five. Moreover, some specimens of *H. nepalensis* var. *sinensis* having considerable lateral lobing

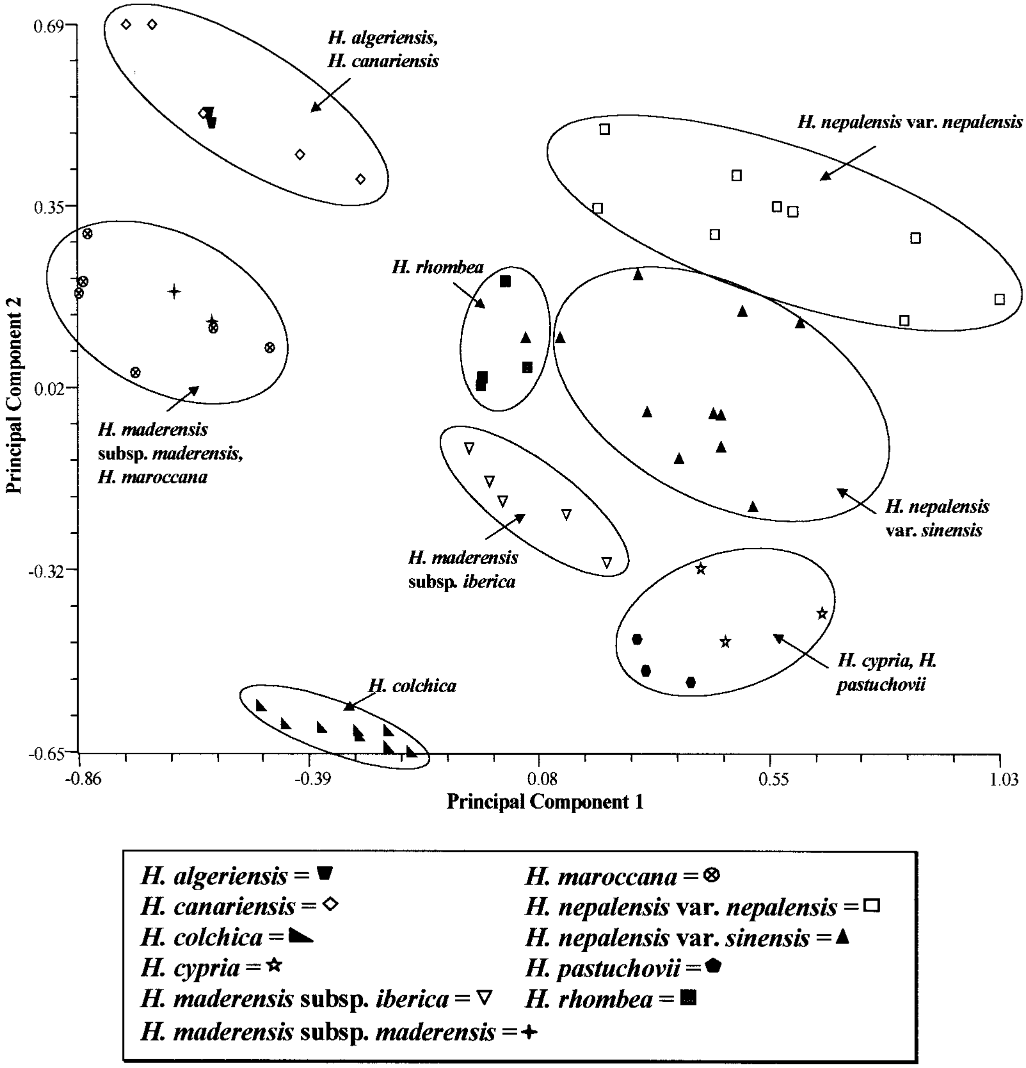

Fig. 5. — Plot of principal components one and two for ***Hedera*** species with scale trichomes.

present. In the PCA of all taxa, overlap occurs between *H. nepalensis* var. *nepalensis* and var. *sinensis* because the characters used to distinguish between them are inconsistent. However, in the analysis of just those taxa with scale trichomes, the two varieties do separate. The fact that these two taxa are differentiated by so few characters supports retaining *H. nepalensis* var. *sinensis* as distinct only at the variety level.

Hedera cypria and *H. pastuchovii* are not strongly separated in the PCA of all species and that involving just those with scale trichomes. The main character that distinguishes these taxa is the presence of trichomes on both abaxial and adaxial sides in *H. pastuchovii* juvenile leaves, those of *H. cypria* have trichomes only on the abaxial side. While *H. cypria* groups within the *H. nepalensis* complex in the PCA for all species, it is distinct from *H. nepalensis* by several characters such as trichome location, absence of lateral lobing, and fruit color (black in *H. cypria*, orange/yellow in *H. nepalensis* var. *nepalensis* and var. *sinensis*). In the analysis of species with scale trichomes (Fig. 5), *H. cypria* groups with *H. pastuchovii* apart from the *H. nepalensis* complex.

Hedera rhombea is separated from the *H. nepalensis* complex and all other taxa, supporting its long-held recognition as a distinct species. *Hedera pastuchovii*, *H. cypria*, and *H. nepalensis* share one easy-to-recognize character, i.e., the middle lobe is generally twice as long as the surrounding lobes. By contrast, *H. rhombea* does not have the elongated middle lobe, making it distinctly different from the other Asian taxa. *Hedera rhombea* is further separated by having smaller leaves (generally < 4 cm in length and < 3.5 cm in width), and shallow leaf sinuses (> 2 cm from the base to the first sinus).

Taxa with stellate trichomes

The projection of principal components one and two for all taxa shows two distinct subgroups within the stellate trichome cluster (Fig. 3). The major delimiting characters for taxa with stellate trichomes are: 1) degree of sinus shallowness, 2) length of leaf lobes, 3) width of middle lobe, 4) number of lobes, and 5) trichome position. Taxa in the first grouping have smaller leaves and deeper leaf sinuses; the include *H. helix* subsp. *helix*, *H. helix* subsp. *rhizomatifera*, and *H. helix* f. *poetarum*. Although these three taxa group together, they remain distinct in the projection of principal components one and two for taxa with stellate trichomes (Fig. 4). *Hedera helix* subsp. *rhizomatifera* differs from the other two by the presence of rhizomes, trichomes that lie parallel to the leaf surface, and generally three leaf lobes instead of five. *Hedera helix* f. *poetarum* is separable from by its yellow fruits (vs. black in *H. helix* subsp. *helix* and *H. helix* subsp. *rhizomatifera*).

The second grouping consists of *H. hibernica* and *H. azorica*, which overlap considerably in morphology, with both species having large leaves and relatively shallow sinuses. *Hedera hibernica* differs by having trichomes that lie parallel to the leaf surface, and the geographic distribution of the two taxa do not overlap, with *H. azorica* endemic to the Azores archipelago and *H. hibernica* found in Europe alont the Atlantic Coast from Spain north to the British Isles.

Hedera helix subsp. *helix* and *H. hibernica* are strongly separated in the PCA by several characters: overall juvenile leaf size, petiole length, depth of sinuses, and trichome position. *Hedera helix* subsp. *helix* has smaller leaves, deeper sinuses, and shorter petioles. In addition, the trichomes of *H. hibernica* lie parallel to the leaf surface while those of *H. helix* subsp. *helix* are set at a right angle, giving it a more bristly appearance.

Specimens of *H. caucasigena* and *H. taurica* do not group together in either the dendrogram or PCA and are intermixed with specimens of *H. helix* subsp. *helix*. There is no support for the recognition of *H. caucasigena* and *H. taurica* as distinct from one another or from *H. helix* subsp. *helix*. Material originally assigned to *H. caucasigena* and *H. taurica* is listed in Table 2 under *H. helix* subsp. *helix* followed by the designation (c) and (t) respectively.

Based on the characters notably differentiating taxa in the morphometric analysis, we provide the following key to the taxa of *Hedera* to aid in identification of this complex group.

Key to Taxa of *Hedera*

1. Trichomes stellate, large (0.5-1 mm), with fewer than 10 rays, white in color 2
1'. Trichomes scale-like, small (0.1-0.4 mm), generally with more than 10 rays, reddish brown or white in color 6
2. Trichomes parallel to leaf surface 3
2'. Trichomes at a right angle to leaf surface 4
3. Length from leaf base to first sinus 2.5-4 cm, juvenile leaves located 6-8 nodes below the apex large (6-9 cm across), 5-lobed, petioles long (5-12 cm), rhizomes absent .... **H. hibernica**

3'. Length from leaf base to first sinus 1.5-2 cm, juvenile leaves located 6-8 nodes below the apex smaller (3.5-6.5 cm across), 3-5-lobed, petioles short (3.5-5.5 cm), rhizomes present ...... **H. helix** subsp. **rhizomatifera**
4. Mature fruits orange/yellow, found only in Italy and western Transcaucasia .... **H. helix** f. **poetarum**
4'. Mature fruits black, found throughout Europe or the Azores 5
5. Juvenile leaves located 6-8 nodes below the apex large (5-8 cm across), 3-5/-7-lobed, with few to no white markings on the veins, length from leaf base to first sinus 2-4 cm .... **H. azorica**
5'. Juvenile leaves located 6-8 nodes below the apex smaller (3-6 cm across) and usually 5-lobed, with white markings on the veins, length from leaf base to first sinus 1-2 cm .... **H. helix** subsp. **helix**
6. Juvenile leaves always unlobed and very coriaceous, fresh leaves strong-scented when crushed .. **H. colchica**
6'. Juvenile leaves lobed, fresh leaves not strong-scented when crushed 7
7. Juvenile leaves located 6-8 nodes below the apex large (5-8 cm across), lateral lobes generally longer than or as long as the middle lobe 8
7'. Juvenile leaves located 6-8 nodes below the apex small (2-4.5 cm, rarely 6 cm across), lateral lobes only about half as long as the middle lobe (except for *H. rhombea*) 11
8. Base of juvenile leaves truncate or only slightly cordate, leaves glossy on adaxial surface .... **H. algeriensis**
8'. Base of juvenile leaves cordate or slightly truncate, leaves matte or glossy on adaxial surface 9
9. Center of trichomes not raised, juvenile leaves located 6-8 nodes below the apex 5 -lobed .... **H. maroccana**
9'. Center of trichomes raised, juvenile leaves with 3-5-lobed 10
10. Junvenile leaves generally 5-lobed .... **H. maderensis**
10'. Juvenile leaves unlobed or 3-lobed .... **H. canariensis**
11. Mature fruits orange/yellow, found in Nepal or southwestern China 12
11'. Mature fruits black, found elsewhere 13
12. Juvenile leaves generally with much lateral lobing, usually 5-lobed (rarely 3- lobed) .... **H. nepalensis** var. **nepalensis**
12'. Juvenile leaves generally with little or no lateral lobing, usually 3-lobed .... **H. nepalensis** var. **sinensis**
13. Juvenile leaves with distinct white markings on the veins 14
13'. Juvenile leaves without distinct white markings on the veins, or only very slight white markings present 15
14. Trichomes present only on abaxial juvenile leaf surface .... **H. cypria**
14'. Trichomes present on both abaxial and adaxial juvenile leaf surface .... **H. pastuchovii**
15. Leaf base truncate or only slightly cordate, leaves 3-lobed .... **H. iberica**
15'. Leaf base cordate, leaves 3-5-lobed .... **H. rhombea**

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