

Homenaje al Prof. Dr.
**WOLFREDO WILDPRET
DE LA TORRE**

Smilax canariensis, *S. azorica* (Smilacaceae) and the genus *Smilax*
in Europe

HANNO SCHAEFER & PETER SCHOENFELDER



INSTITUTO DE ESTUDIOS CANARIOS

LA LAGUNA - TENERIFE

2009

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**Esperanza Beltrán Tejera, Julio Afonso-Carrillo,
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(Editores)**



INSTITUTO DE ESTUDIOS CANARIOS

LA LAGUNA - TENERIFE

2009

Serie
MONOGRAFÍA LXXVIII

Esta edición ha contado con el patrocinio de
la Consejería de Educación, Universidades, Cultura y Deportes del Gobierno de Canarias,
el Área de Sanidad y Relaciones con la ULL del Cabildo de Tenerife,
la Fundación Canaria Salud y Sanidad,
el Excmo. Ayuntamiento de San Cristóbal de La Laguna,
la Facultad de Biología de la Universidad de La Laguna,
la Obra Social y Cultural de CajaCanarias,
el Colegio Oficial de Farmacéuticos de la Provincia de Tenerife,
la Cooperativa Farmacéutica de Tenerife (COFARTE)
y el Colegio Oficial de Biólogos de Canarias.

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© De esta edición: 2009, Instituto de Estudios Canarios
c/ Bencomo, 32, Apartado de correos 498
38201 La Laguna (Santa Cruz de Tenerife)

Imprime: Gráficas Sabater
Maquetación: Cande da Silva
Diseño de la cubierta del libro: Víctor M. Gómez Reneses
Elaboración, diseño y desarrollo multimedia: Ahora, S.L., Omar Quino Zoncu, Ruymán Gil García & Guillermo
Pozo Cabeza
ISBN: 978-84-88366-82-5
Depósito Legal:

Ilustración de la cubierta y DVD: W. Wildpret de la Torre (archivo de O. Rodríguez Delgado)
Ilustración de la contracubierta: El Drago de Icod de los Vinos a comienzos del siglo XX (foto tomada por Burchard,
1911)

Modo de citación:

Libro completo:
Beltrán Tejera, E., J. Afonso-Carrillo, A. García Gallo & O. Rodríguez Delgado (Eds.), 2009. *Homenaje al Profesor Dr. Wolfredo Wildpret de la Torre*. Instituto de Estudios Canarios. La Laguna (Tenerife. Islas Canarias). Monografía LXXVIII. 872 pp.
ISBN: 978-84-88366-82-5

Un capítulo:
Nezadal, W. & W. Welss, 2009. Aportaciones al conocimiento del bosque termófilo en el noroeste de Tenerife (Islas Canarias). In Beltrán Tejera, E., J. Afonso-Carrillo, A. García Gallo & O. Rodríguez Delgado (Eds.): *Homenaje al Profesor Dr. Wolfredo Wildpret de la Torre*. Instituto de Estudios Canarios. La Laguna (Tenerife. Islas Canarias). Monografía LXXVIII. pp.229-244.
ISBN: 978-84-88366-82-5

El DVD:
Beltrán Tejera, E., 2009. Semblanza de un botánico comprometido con su tiempo. Profesor Wolfredo Wildpret de la Torre. Documentación anexa. DVD. In Beltrán Tejera, E., J. Afonso-Carrillo, A. García Gallo & O. Rodríguez Delgado (Eds.): *Homenaje al Profesor Wolfredo Wildpret de la Torre*. Instituto de Estudios Canarios. La Laguna (Tenerife. Islas Canarias). Monografía LXXVIII.
ISBN: 978-84-88366-82-5

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Smilax canariensis, *S. azorica* (Smilacaceae) and the genus *Smilax* in Europe

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Resumen: Un análisis morfológico y de sistemática molecular de las especies Europeas de *Smilax* dio como resultado el reconocimiento de una especie endémica de las Azores, *Smilax azorica* H. Schaefer & P. Schoenfelder, nom. nov. (= *S. divaricata* Sol. ex H. C. Wats., nom. illegit.). Su pariente más cercano es *S. canariensis* Brouss. ex Willd. de Canarias y Madeira. Junto con la especie del este de Europa *S. excelsa* L., todas ellas forman un grupo dentro del clado de las especies norteamericanas, las cuales parecen pertenecer a un linaje asiático.

Palabras claves: Azores, biogeografía, Islas Canarias, refugio glacial, *Smilax azorica*, *Smilax canariensis*, *Smilax divaricata*.

Abstract: A morphological and molecular systematic analysis of the European species of *Smilax* results in the recognition of a species endemic to the Azores, *Smilax azorica* H. Schaefer & P. Schoenfelder, nom. nov. (= *S. divaricata* Sol. ex H. C. Wats., nom. illegit.). Its closest relative is *S. canariensis* Brouss. ex Willd. from the Canary Islands and Madeira. Together with the Eastern European *S. excelsa* L. they are nested in a clade of North American species, which seem to belong to an Asian lineage.

Key words: Azores, biogeography, Canary Islands, glacial refugia, *Smilax azorica*, *Smilax canariensis*, *Smilax divaricata*.

INTRODUCTION

The genus *Smilax* comprises about 200 species distributed mainly in the Northern hemisphere from the temperate regions to the Subtropics (CAMERON & FU, 2006). Diversity centres of the genus are located in Northern and Central America and East Asia, while the European region harbours only four species and Africa and Australia only two each (CAMERON & FU, 2006). The comparatively reduced diversity in European *Smilax* is presumably a result of the ice ages and is well known from other genera like *Quercus*, *Acer*, and *Cornus* (e.g. SVENNING *et al.*, 2008; XIANG *et al.*, 2006).

Of the four European species, one, *Smilax aspera* L., is widespread and often common throughout the Mediterranean region (Fig. 1). The three remaining species are restricted to glacial refugia: (i) *Smilax canariensis* Brouss. ex Willd. is endemic to the Canary Islands and Madeira (SCHOENFELDER & SCHOENFELDER, 2005), (ii) *Smilax azorica* H. Schaefer & Schoenfelder, nom. nov. (= *S. divaricata* Sol. ex H. C. Wats., nom. illegit., see DISCUSSION)

is known only from the Azores, and (iii) *Smilax excelsa* L. is found mainly in the Black Sea and Caspian Sea region from Greece and Bulgaria to Iran (BROWICZ, 1988).

MATERIAL AND METHODS

Morphology

The authors studied herbarium material at AZU, BM, K, LISU, M, and REG. Both authors spent many months of fieldwork in the Mediterranean region and the middle-Atlantic Islands and studied morphology and ecology of *Smilax* in many different countries and habitats.

Sampling and DNA extraction

Total genomic DNA was isolated from herbarium specimens or, more rarely, silica-dried material following the standard CTAB method of DOYLE & DOYLE (1987). We amplified the *rbcL* and *matK* genes, the *trnL* intron and the *trnL-F* intergenic spacer. Polymerase chain reactions (PCR) were performed with the standard protocol and primers described in SCHAEFER *et al.* (2008), and products were purified with the Wizard SV PCR clean-up kit (PROMEGA GmbH, Mannheim, Germany). Cycle sequencing was performed with BigDye Terminator cycle sequencing kits on an ABI Prism 3100 Avant automated sequencer (Applied Biosystems, Foster City, California, USA).

In addition to these plastid regions, we sequenced the nuclear internal transcribed spacer region using the ITS primers of CAMERON & FU (2006). Direct PCR amplification of ITS yielded single bands and unambiguous base calls. Twenty-seven sequences were generated for this study. Table 1 lists the relevant taxonomic names with authors and plant sources. All new sequences have been deposited in GenBank (<http://www.ncbi.nlm.nih.gov/>). Additional sequences for Asian and American species (mostly generated by CAMERON & FU, 2006) were downloaded from GenBank.

Sequence alignment and phylogenetic analyses

Sequences were edited with Sequencher (4.6; Gene Codes, Ann Arbor, Michigan, USA) and aligned by eye, using MacClade 4.06 (MADDISON & MADDISON, 2003). The aligned plastid matrix comprised 3517 nucleotides. The aligned ITS matrix comprised 867 nucleotides. Maximum likelihood (ML) tree searches and ML bootstrap searches were performed using RAXML 7.0.3 (STAMATAKIS *et al.* 2008, available at <http://phylobench.vital-it.ch/raxml-bb/>). RAXML searches relied on the GTR + G + I model (six general time-reversible substitution rates, assuming gamma rate heterogeneity and a proportion of invariable sites), with model parameters estimated over the duration of specified runs. Analyses in RAXML were run both with the combined un-partitioned data and with a model that partitioned the plastid regions from the ITS region. Trees were rooted on *Philesia magellanica* (sequences from GenBank). The data matrix and trees have been deposited in TreeBASE (<http://www.treebase.org/>).

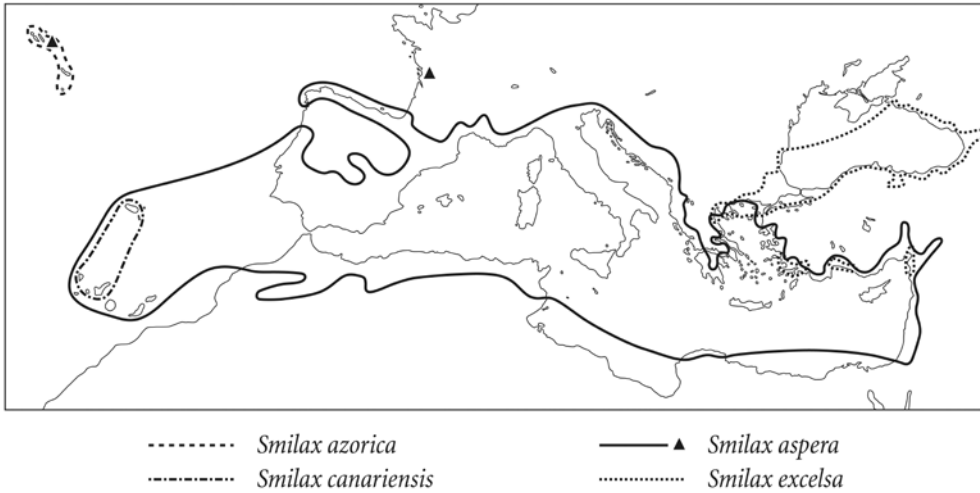


Figure 1. European distribution of *Smilax* species (modified after BOLÓS & VIGO, 2001; BROWICZ, 1988).

Table 1. Species sampled and their origin.

SPECIES	ORIGIN
<i>Smilax aspera</i> L. subsp. <i>aspera</i>	France, Camargue
<i>Smilax aspera</i> L. subsp. <i>balearica</i> (Willk.) Romo	Spain, Balearic Islands, Mallorca
<i>Smilax aspera</i> L. subsp. <i>mauritanica</i> (Desf.) Malag.	Spain, Canary Islands, Tenerife
<i>Smilax canariensis</i> Brouss. ex Willd.	Portugal, Madeira
<i>Smilax canariensis</i> Brouss. ex Willd.	Spain, Canary Islands, Tenerife
<i>Smilax azorica</i> H. Schaeff. & P. Schoenfelder	Portugal, Azores, São Miguel
<i>Smilax excelsa</i> L.	Georgian Republic
<i>Smilax hispida</i> Muhl. ex Torr.	United States, seeds bought from "BT World Seeds"
<i>Smilax lasioneura</i> Hook.	United States, seeds bought from "BT World Seeds"

RESULTS

Morphology

The mediterranean *Smilax aspera* differs from the remaining European species above all in its inflorescences, which are composed of several umbel-like sub-inflorescences and often more than 20 cm long (fig. 2a). All other European taxa have their flowers in simple umbels (SCHOENFELDER & SCHOENFELDER, 2005; our Fig. 2 c-d, Fig. 3).

The leaves of *S. aspera* are coriaceous and very variable, usually with 7-9 main nerves and a \pm cordate base. The leaves of the remaining species are laurophyllous (*S. canariensis*, *S. azorica*) or deciduous (*S. excelsa*) with usually 3-5 main nerves and a cuneate to rounded or shallowly cordate base (BROWICZ, 1988; S. Arndt, Jena Botanical Gardens, pers. comm.). Leaf shape is variable, especially on young shoots. Leaves on second-year or older shoots are more uniform in shape and in general broadly ovate in *S. azorica* and more narrowly ovate in *S. canariensis*. The older stems of *S. excelsa* carry considerable thorns (Fig. 2d), while thorns on stems of *S. canariensis* and *S. azorica* are small or absent.

A taxon with extremely narrow leaves that has been described as *S. aspera* subsp. *balearica* (Willk.) Romo is apparently restricted to the Balearic Islands and accepted as an endemic variety in BOLÒS & VIGO (2001), but not accepted as a separate taxon by AEDO (2005). Forms with broadly cordate leaves that lack thorns almost completely are known as *S. aspera* subsp. *mauritanica* (Desf.) Malag. (= *S. altissima* Roxb.). They are found in the Western Mediterranean region and in the Canary Island's laurel forest but also in dry lowland areas and cliffs on Madeira (PRESS & SHORT, 1994), and the Azores (Terceira Island). The Madeiran plants have been described as endemic species *S. pendulina* Lowe but they do not differ considerably from *S. aspera* subsp. *mauritanica*.

Phylogenetic analyses

The topologies of the best likelihood tree for the plastid and ITS datasets (not shown) were not contradicting in any well-supported node. We therefore combined the data and in the following focus on the result of the combined data (Fig. 4). Resolution and bootstrap support was in general low, a problem already reported in previous studies (CAMERON & FU, 2006). However, the placement of *S. aspera* as sister to all other analysed ingroup taxa is moderately supported. Furthermore, we found support for a clade consisting of the North American *S. herbacea* and other American species, a clade of Asian species, and a clade consisting of *S. china*, two North American species, *S. excelsa*, and the middle-Atlantic island species. The Azorean plants are clearly different from *S. canariensis*, while the sample from Madeira seems to be genetically very close to the Canary Island plants.

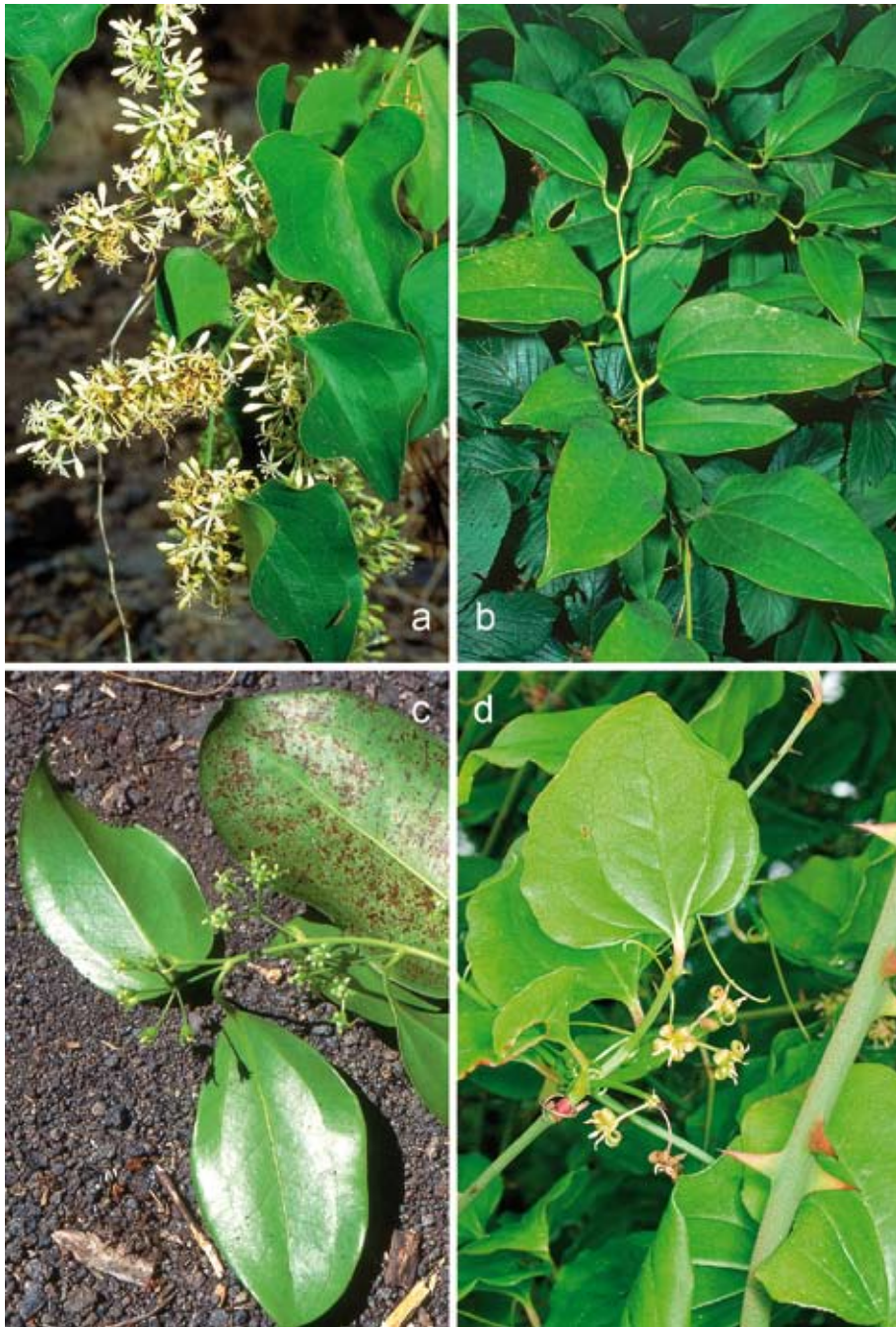


Figure 2. Inflorescences and leaves of European *Smilax*: a) *S. aspera* subsp. *mauritanica* (La Palma, Canary Islands, 10-10-1993); b) *S. canariensis* (La Palma, Canary Islands, 7-10-1993); c) female inflorescence of *S. azorica* (Faial Island, Azores, 17-7-1999); d) male inflorescence of *S. excelsa* (Botanical Garden, Jena, 31-5-2003).

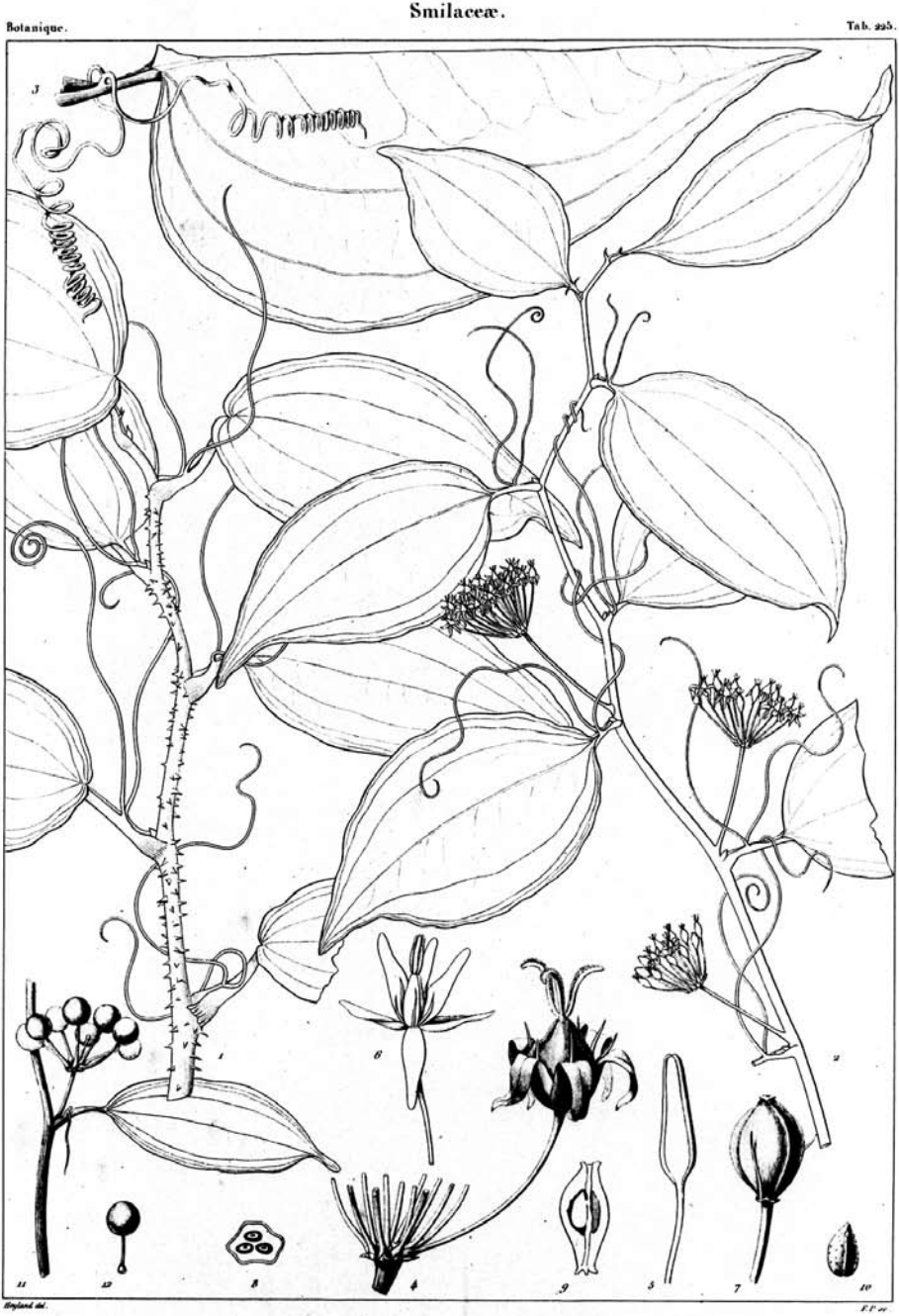


Figure 3. Illustration of *S. canariensis* reproduced from WEBB & BERTHELOT (1847).

KEY TO THE EUROPEAN SPECIES OF *SMILAX*

- 1 Leaves usually with 7-9 main nerves. Male and female inflorescences compound of several umbel-like sub-inflorescences. Flowering time VIII-XI. Fruit ripening blackish-red..... *S. aspera*
- 1* Leaves usually with 3-5 main nerves. Male and female inflorescence a simple umbel..... 2
- 2 Plant deciduous, older stems with strong thorns. Flowering time V-VI. Black sea and Eastern Mediterranean region*S. excelsa*
- 2* Leaves wintergreen, thorns on older stems weak or absent. Flowering time V-VIII. Middle-Atlantic Islands 3
- 3 Leaf blades on older branches broadly cordate-ovate, almost as broad as long (relation length:width c. 1:0.9). Fruit ripening red. Endemic to the Azores..... *S. azorica*
- 3* Leaf blades on older branches narrower (relation c. 1: 0.6). Fruit ripening black (fide WEBB & BERTHELOT, 1847). Endemic to the Canary Islands and Madeira*S. canariensis*

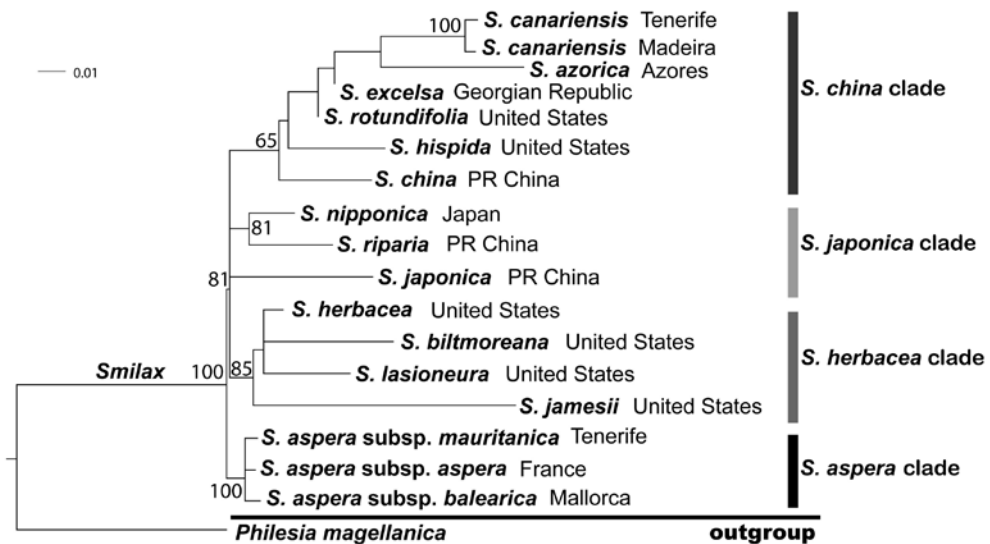


Figure 4. Maximum likelihood phylogram of *Smilax* plastid and ITS sequences produced with RAxML 7.0.3 (STAMATAKIS *et al.* 2008). Likelihood bootstrap support values > 60% are given at the nodes.

DISCUSSION

Taxonomy

Our results support the separation of a species endemic to the Azores from *S. canariensis*, endemic to the Canaries and probably Madeira. The species from the Azores was first collected by Francis Masson in 1777 on São Miguel (specimens in BM) and later described as *Smilax divaricata* Sol. ex H. C. Watson (WATSON, 1844), a name that had already been

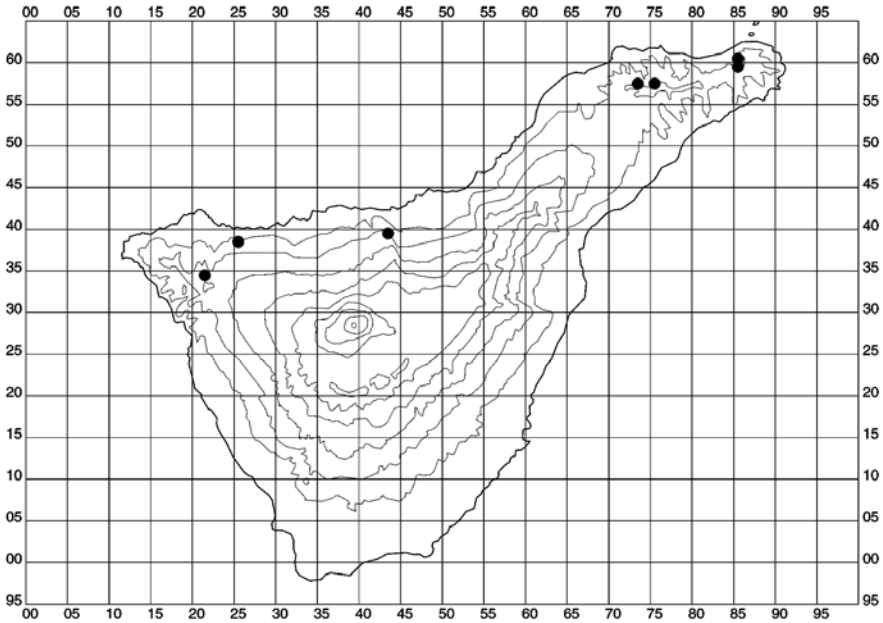


Figure 5. Distribution of *S. canariensis* on Tenerife, Canary Islands.

given to a species from the Philippines seven years earlier (BLANCO, 1837). Therefore the Solander name is a later homonym and illegitimate. A new epithet is required, which we propose as follows:

Smilax azorica H. Schaef. & P. Schoenfelder, nom. nov.

replaced synonym: *Smilax divaricata* Sol. ex H. C. Wats. in London J. Bot. 3: 608. 1844. – Type: F. Masson s.n. (holo BM!), Portugal, Azores, Sao Miguel 1777. – (non *Smilax divaricata* Blanco, Fl. Filip. 795. 1837).

HANSEN & SUNDING (1993) listed both species *Smilax canariensis* and *S. divaricata* (= *S. azorica* H. Schaef. & P. Schoenfelder, nom. nov.) in their Azores checklist and also added the East European *S. excelsa*, certainly a mistake. SCHAEFER (2003, 2005) based on morphology only, treated *S. divaricata* as a synonym of *S. canariensis* but with our new genetic data, this view is no longer supported. SEUBERT (1844) lists *S. tetragona* L.f. in his “Flora Azorica”, a synonym for *S. aspera* subsp. *mauritanica*, but his description of plants from Pico Island (Azores) matches *S. azorica*. The specimen C. Hochstetter 121, cited by Seubert, was studied at BM and identified as *S. azorica*.

Biogeography

The European *Smilax* species clearly belong to two long separated lineages: the widespread *S. aspera* is sister to all other *Smilax* species (see also CAMERON & FU, 2006),

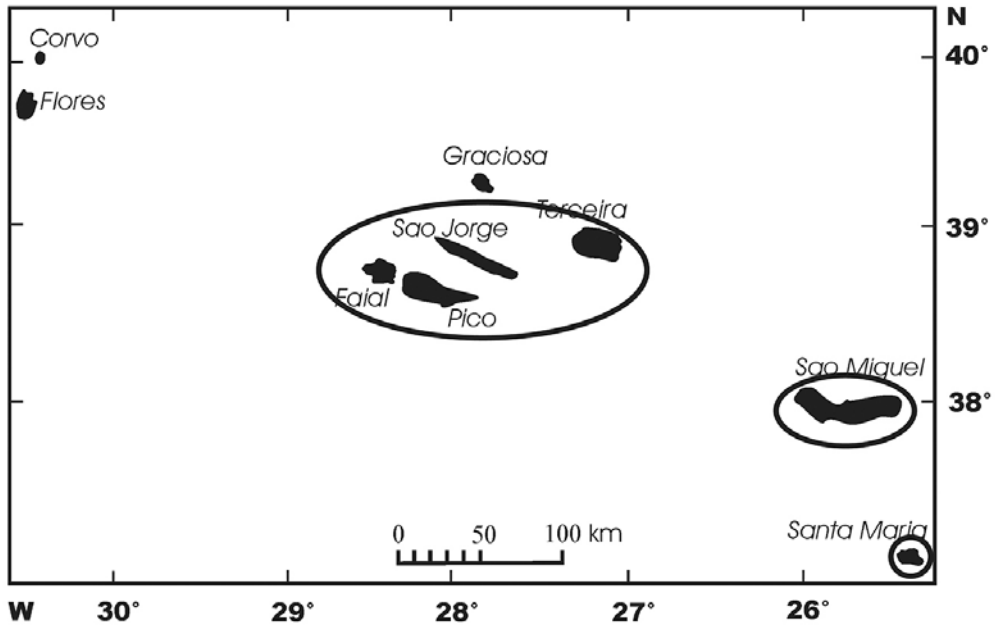


Figure 6. Distribution of *S. azorica* in the Azores archipelago.

while the remaining species *S. excelsa*, *S. canariensis*, and *S. azorica* form a monophyletic group. Their closest relatives seem to be North American species but these belong to an Asian lineage. All possible biogeographic scenarios locate the ancestors of the *S. canariensis* group in Asia. From there, in the most parsimonious scenario, the lineage spread via Beringia into North America and from there across the then narrow North Atlantic back into the European continent. During the glacial periods, this ancestral lineage was split into an eastern population in the Black sea region and a western population in the middle-Atlantic Islands. The lack of genetic exchange between the Azores and the Madeira/Canary islands population finally resulted in the evolution of two endemic species. An alternative, less parsimonious scenario would require at least two independent dispersal events from Asia into North America and one dispersal/range expansion of the *S. canariensis* lineage from Asia directly into the Mediterranean and the middle-Atlantic islands. A broader genetic analysis of *Smilax* samples from the islands, from North America, Asia, and especially from Africa (one or two endemic species) combined with molecular clock dating techniques will be required to confirm one of these scenarios.

Conservation

Today, *S. canariensis* is very rare in the Canaries and restricted to the central laurel forest regions on Tenerife (Fig. 5), La Palma, and La Gomera. On Madeira, it is a poorly known species that was collected only a few times (PRESS & SHORT, 1994). At least in the Canary Islands, it seems to be highly threatened. Despite years of search, the senior author could find

only one fruiting individual on La Palma and was unable to find a single flowering specimen in the archipelago. Notably, there is not a single picture of *S. canariensis* inflorescences in the contemporary literature on the Canary island flora and the flora of Madeira. An excellent description and a plate with flowers in all details, however, can be found in WEBB & BERTHELOT (1847) (our Fig. 3). Apparently, the species was reproducing more frequently in those days. Maybe the more intense use of the laurel forest in the 19th century produced more open spaces and clearings and favoured less competitive species like *S. canariensis*.

Smilax azorica, is known from six islands of the Azores archipelago (Fig. 6). While absent in the western group and rare in the central group, it is locally common on São Miguel and Santa Maria in the eastern group. Flowers and fruits are regularly found and the species seems to be not threatened. It is protected by the Berne convention on the conservation of European wildlife and natural habitats.

ACKNOWLEDGEMENTS

The authors are grateful to C. Heibl (Munich), H. J. Esser (M), M. Carine (BM), S. Arndt (Jena), R. Jahn (Großschirma) and K. Tan (Copenhagen) for material and information, to W. Lang for drawing figure 1 after the authors' draft, and to O. Fiz-Palacios (London) for the Spanish abstract. HS is grateful to the Azorean Direcção Regional do Ambiente for a permit to collect DNA samples in the islands.

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ÍNDICE

<i>TABVLA GRATVLATORIA</i>	13
Presentación	
Milagros Luis Brito	21
Antonio Alarcó Hernández.....	23
Eduardo Doménech Martínez.....	25
Esperanza Beltrán Tejera: Semblanza de un botánico comprometido con su tiempo. Profesor Wolfredo Wildpret de la Torre	27
Esperanza Beltrán Tejera: Producción bibliográfica de la Unidad de Botánica de la Universidad de La Laguna. Etapa wildpretiana (1969-2008). I	71
Jorge Alfredo Reyes-Betancort & María Catalina León Arencibia: <i>Helichrysum x wildpretii nothosp. nov.</i>, un nuevo híbrido natural de las Islas Canarias	159
Marcelino José del Arco Aguilar, Octavio Rodríguez Delgado, Juan Ramón Acebes Ginovés, Marcos Salas Pascual & Víctor Garzón Machado: Los retamares de <i>Retama rhodorrhizoides</i> Webb & Berth. en las Islas Canarias: <i>Retamation rhodorhizoidis all. nov.</i>	163
Arnoldo Santos Guerra & Jorge Alfredo Reyes-Betancort: Contribución al conocimiento de las comunidades comofíticas de la Clase <i>Greenovio-Aeonietea</i> Santos 1976. <i>Aichryso laxi-Monanthetalia laxiflorae</i> ord. nov.	173
Octavio Rodríguez Delgado: El Barranco del Agua de Güímar, un espacio natural de gran interés botánico, turístico y etnográfico	181
Pedro L. Pérez de Paz, Vicente L. Lucía Sauquillo & Ricardo González González: Las Charcas de Erjos: enclave antrópico de singular naturaleza	213
Werner Nezadal & Walter Welss: Aportaciones al conocimiento del bosque termófilo en el noroeste de Tenerife (Islas Canarias)	229

Marcos Salas Pascual, Emilio Fernández Negrín & Gregorio Quintana Vega: <i>Salvia canariensis-Pterocphaletum dumetori</i> ass. nov. (<i>Artemisio thusculae-Rumicion lunariae</i> ; <i>Forsskaoleo angustifoliae-Rumicetalia lunariae</i> ; <i>Pegano-Salsoletea</i>) nueva asociación para la Isla de Gran Canaria (Islas Canarias-España)	245
Salvador Rivas-Martínez: Ensayo geobotánico global sobre la Macaronesia	255
Hanno Schaefer & Peter Schoenfelder: <i>Smilax canariensis</i> , <i>S. azorica</i> (Smilacaceae) and the genus <i>Smilax</i> in Europe.....	297
Julia Pérez de Paz, Olga Fernández-Palacios & Rosa Febles: Polimorfismos y series polínicas en el género canario <i>Parolinia</i> y parientes continentales <i>Diceratella</i> y <i>Morettia</i> (Matthioleae-Brassicaceae). Significado biológico y filogenético	309
Irene E. La Serna Ramos: <i>Parkinsonia aculeata</i> L.: un ejemplo del interés de la flora ornamental en la caracterización geográfica de las mieles canarias.....	329
Victoria Eugenia Martín Osorio: Jardines Sostenibles	345
Beatriz Hernández Bolaños & Victoria Eugenia Martín Osorio: El Jardín Botánico del Parque Nacional del Teide (Tenerife, Islas Canarias), a través de un Sistema de Información Geobotánica	371
Antonio García Gallo, Israel Pérez Vargas & Francesco Salomone Suárez: Los olmos de La Laguna	383
Richard Pott & Joachim Hüppe: Canary Islands: A Botanical Paradise in the Atlantic Ocean	395
María Candelaria Gil-Rodríguez, Myrian Rodríguez García del Castillo, Óscar Monterroso Hoyos & Rodrigo Riera Elena: Perturbaciones en ecosistemas marinos canarios. Un modelo: Guayonje-Tacoronte, Islas Canarias	421
Julio Afonso-Carrillo & Marta Sansón: Aún lejos de un completo conocimiento de la biota canaria: el ejemplo de la flora de algas rojas gelatinosas efímeras del sublitoral	433
Esperanza Beltrán Tejera, J. Laura Rodríguez-Armas, Luis Quijada, Janira Gutiérrez Peraza, Jonathan Díaz & Ángel Bañares: Contribución al estudio de la microbiota de los castaños del Norte de Tenerife (Islas Canarias. España). II..	453
María Carmen Jaizme-Vega: Las micorrizas, una simbiosis de interés en agricultura	479

Índice

Consuelo Hernández, Israel Pérez-Vargas, Dessire Sicilia & Pedro L. Pérez de Paz: Los líquenes de la alta montaña canaria	489
Ana Losada-Lima, Sofia Rodríguez-Núñez & Arnoldo Santos Guerra: Referencias a briófitos de las Islas Canarias anteriores al siglo XIX: Dillenius y <i>Leucodon canariensis</i>	501
Mari Carmen Alfayate, Eugenia Ron, Agustín Fernández, Belén Estébanez, David Gómez, Miguel Ángel Pérez-Batista & Benjamín Fernández: Biontes entrometidos en cápsulas de musgos Canarias	509
Juana María González-Mancebo, Jairo Patiño, Julio Leal Pérez, Stephan Scholz & Ángel Fernández-López: Amenazas sobre la flora briofítica de la Isla de Fuerteventura. SOS para los últimos supervivientes del extinto bosque de Jandía	517
Marie-Luise Schnetter, Andreas Opitz & Reinhard Schnetter: Estructura y función de las glándulas submarginales del mangle <i>Laguncularia racemosa</i> (Combretaceae)	539
Domingo Morales & M ^a Soledad Jiménez: Ecofisiología de algunos tipos de vegetación de las Islas Canarias	555
Juan Felipe Pérez Francés, Isabel Santana López, Emma Suárez Toste, Raquel Martín Pérez, Miguel Cabrera Pérez, Juan Cristo Luis Jorge & Francisco Valdés: Aplicaciones del cultivo <i>in vitro</i> a la conservación de plantas canarias en peligro	567
Germán Santana Henríquez: Una farmacopea un tanto singular. Sobre los remedios para el dolor de cabeza en Galeno	581
José N. Boada, Eduardo Navarro & C. Marina Álvarez: Nuestras aportaciones al conocimiento de las propiedades farmacológicas de productos obtenidos de plantas de Canarias	591
José Juan Jiménez González: Etnohistoria y arqueología de las plantas entre los antiguos canarios	603
Fernando Lozano Soldevilla, Ignacio J. Lozano, José M ^a . Landeira & Fátima Hernández: Antecedentes históricos de la taxonomía zooplanctónica en aguas de la región Canaria	613
Lázaro Sánchez-Pinto, Francisco García-Talavera, José López Rondón & Mercedes Martín Oval: Sobre la presencia del icnofósil <i>Dactyloidites otto</i> (Geinitz, 1849) en sedimentos neógenos de la costa occidental de Fuerteventura (Islas Canarias)	625

Juan José Bacallado, José Espinosa, Jesús Ortea, Lázaro Márquez, Leopoldo Moro, Osmani Borrego & Manuel Caballero: La península de Guanahacabibes y su Parque Nacional (Cuba): biodiversidad marina y terrestre	633
Marisa Tejedor, Jonay Neris, María Ascención Dorta & Concepción Jiménez: Evaluación del recurso suelo con alta potencialidad agrológica en la isla de Tenerife. 1981-2008	651
Juan Luis Mora Hernández, Carmen Dolores Arbelo Rodríguez & Antonio Rodríguez Rodríguez: Características de los suelos de las Islas Canarias en relación a la vegetación natural	665
Constantino Criado, Carmen Machado & José Afonso: Geomorfología eólica en el Parque Nacional del Teide (Tenerife)	685
Sara del Río, Luis Herrero & Ángel Penas: Tendencias recientes en la precipitación de las Islas Canarias occidentales y su relación con la oscilación del Atlántico Norte (NAO)	705
Sebastián Delgado Díaz: Las nuevas aguas en Canarias	723
Gonzalo Lozano Soldevilla: Miscelánea académica del quinquenio 1983-1988 en la Facultad de Biología de la Universidad de La Laguna	731
Nácere Hayek: Un ensayo histórico sobre la aportación matemática a la Biología durante períodos anteriores a su creación	739
Andrés Sánchez Robayna: Viene del mar la integridad de más allá del mar	753
Juan Hernández Bravo de Laguna: La Teoría del Estado fallido: Estados débiles, Estados aparentales y otras formas fallidas de Estado	755
Matilde Arnay de la Rosa & Emilio González Reimers: La ocupación humana de Las Cañadas del Teide a partir del siglo XV	767
Conrado Rodríguez Martín, Rafael González Antón & María del Carmen del Arco Aguilar: La colonización humana de islas en la prehistoria. Un modelo teórico para el estudio de poblamientos insulares	785
Cristóbal Corrales Zumbado & Dolores Corbella Díaz: Creación y adaptación del término <i>malpaís</i>	797
Josefa Dorta Luis & María del Carmen Muñiz Cachón: La entonación de las interrogativas en el español de Canarias y en asturiano	809

Índice

Juan Antonio Frago Gracia: El español de Canarias en la historia de la lengua española	823
Javier Medina López: La gramática olvidada de D. Ireneo González y Hernández: el <i>Compendio de gramática castellana</i> (1895)	837
Francisco Salas Salgado: Influencia clásica en los poemas a Filis de Juan Bautista Poggio Monteverde	849
Teodoro Ravelo Mesa, María Carmen Moreno Perdigón & Moulaye Ahmed Ould Ahmed Deoula: Un análisis multicriterio de la capacidad de atracción de los destinos turísticos en la Isla de Tenerife	861