

THE BIODIVERSITY OF THE LEGUMINOSAE-GENISTEAE AND ITS GENESIS

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Abstract

The biological diversity of *Genisteae* is unevenly distributed within the Mediterranean region. About 100 out of 208 species recognised (48%) occur in the Iberian-NW African area, and 53 (26%) in the Balkan peninsula; in all other regions the species concentration is lower. If higher taxa are considered (i.e. genera, and sections of the two largest genera *Cytisus* and *Genista*), as many as 28 of the 36 taxa recognised (78%) occur in the Iberian-NW African range, and 20 (55%) in the Balkan peninsula. The diversity at the generic and sectional levels does not correspond to an obvious geographic pattern. A cladistic analysis of the relationships among genera and sections indicate that mutually related taxa are often distributed in widely disjunct areas. This is true not only for ancient, relict taxa (e.g. *Cytisophyllum-Hesperolabium*), but also for the most derived groups (e.g. *Cytisus* sections *Oncospartum* - *Tubocytisus*, and *Genista* sections *Phyllotrochys-Voglana-Genista*). Some hypothesis on time and mode in the genesis of the tribal diversity is discussed.

The present report deals with the biodiversity of *Leguminosae-Genisteae*, examined according the criteria of cladistic biogeography.

The Tribe *Genisteae* is intended here in the circumscription defined by POLHILL (1976) in his fundamental monograph. The genera recognised are as in CRISTOFOLINI & FEOLI CHIAPPELLA (1984), with the only exception of the genus *Cytisanthus*, that is treated here as *Genista* sect. *Spartocarpus*. At divergence with Polhill, the genera *Lupinus* and *Argyrolobium* are excluded from this study, since their geographic distribution is heterogeneous with respect to the rest of the tribe. Molecular data on *Lupinus* (BADRET al., 1994) and on *Argyrolobium* (CRISTOFOLINI & FEOLI CHIAPPELLA, 1984) also indicate these genera as outliers.

As a result, 17 genera with 208 species are treated in the present study. The genera *CYTISUS* and *GENISTA* are taken in their largest acception (BISBY, 1981; CRISTOFOLINI, 1991); however, due to their complexity, they are subdivided into Sections, that are morphologically consistent. The systematic treatment of *Genista* follows fundamentally GIBBS (1966), that of *Cytisus* follows FEOLI CHIAPPELLA & CRISTOFOLINI (1980). In conclusion, the operational taxonomic units are 15 genera, 8 sections of *Cytisus*, and 10 sections of *Genista* (Tab. 1).

The geographic subdivision of the Mediterranean area (Appendix 1) was derived from GREUTER & al. (1989), with some modifications. The geographic distribution of the species was largely deduced from TUNN & al. (1968), GREUTER & al. (1989), LOCK (1989), LOCK & SIMPSON (1991).

The tribe *Genisteae* is basically circum-mediterranean, with an important extension to the Canary Islands. The Mediterranean distribution is uneven. The lowest number of species is found in the South-east (Egypt, Israel); two maxima are located in the

<i>Adenocarpus</i> DC.	<i>Erinacoides</i> Spach
<i>Argyrocytisus</i> (Maire) Raynaud	<i>Scorpioides</i> Spach
<i>Calicotome</i> Link	<i>Phyllobotrys</i> Spach
<i>Cytisophyllum</i> Lang	<i>Voglera</i> Spach
<i>Cytisus</i> Desf.	<i>Spartocarpus</i> P. Gibbs
<i>Cytisus</i>	<i>Acanthospartum</i> Spach
<i>Emeroides</i> Ducommun	<i>Fasselospartum</i> P. Gibbs
<i>Tubocytisus</i> DC.	<i>Cephalospartum</i> Spach
<i>Alburnoides</i> DC.	<i>Pterospartum</i> Spach
<i>Corothismus</i> (Koch) Nyman	<i>Teline</i> (Medicus) Benth.
<i>Spartopsis</i> Dumort.	<i>Gonocytisus</i> Spach
<i>Oreosparton</i> (Webb) Frodim ex Polhill	<i>Hesperolaburnum</i> Maire
<i>Chronanthus</i> DC.	<i>Laburnum</i> Fabr.
<i>Echinospartum</i> (Spach) Rothm.	<i>Lembotropis</i> Griseb.
<i>Erinacea</i> Adanson	<i>Petteria</i> C. Presl
<i>Genista</i> L.	<i>Podocytisus</i> Boiss. & Heldr.
<i>Genista</i>	<i>Retama</i> Rafin.
<i>Genistella</i> (Tourn.) Spach	<i>Spartium</i> L.
<i>Spartioides</i> Spach	<i>Ulex</i> L.

Tab. 1. Genera and Sections recognized.

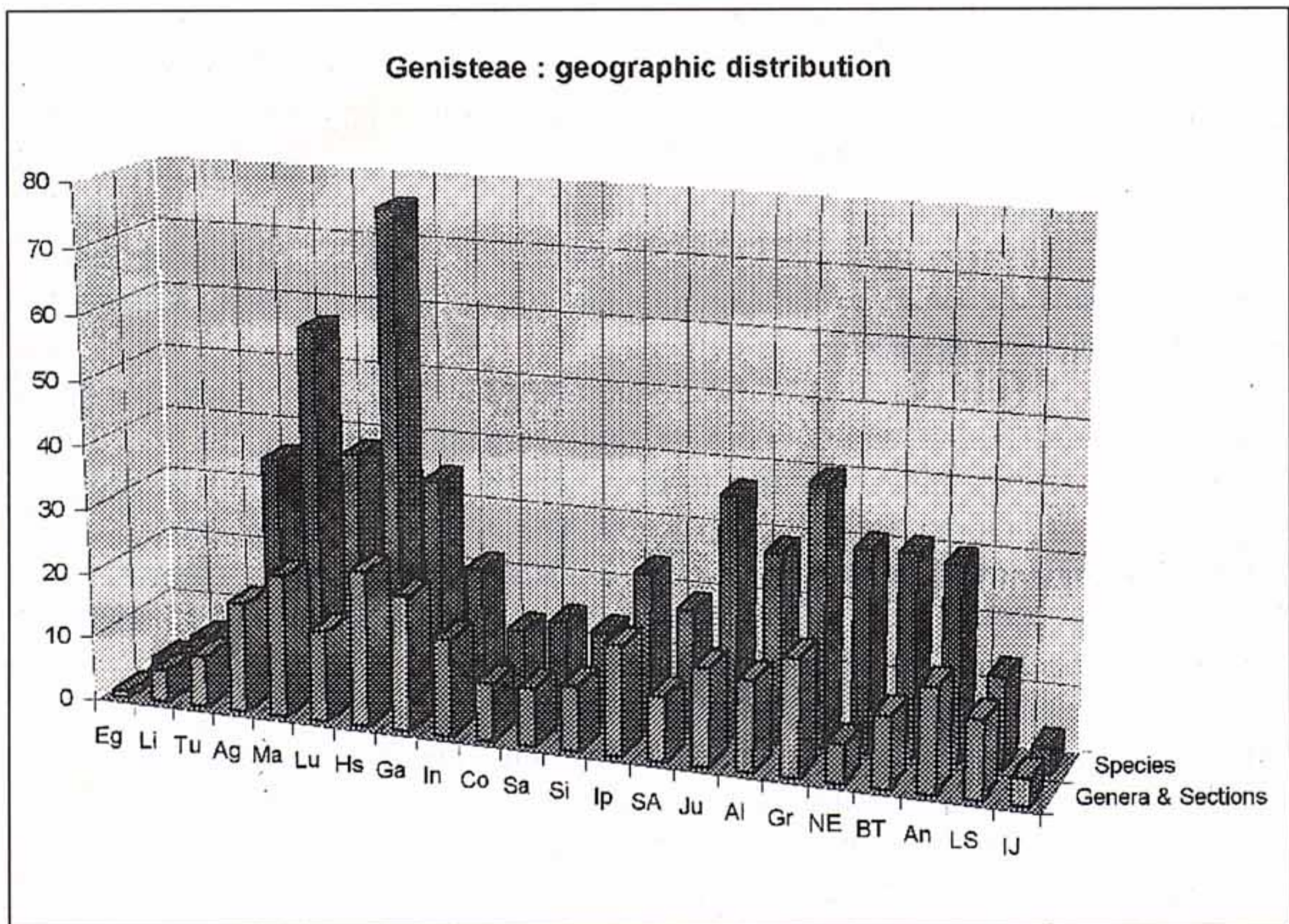


Fig. 1. Frequency distribution of Species and of Genera around the Mediterranean. Abbreviations of geographic areas as in Appendix 2.

West (Morocco-Spain and surrounding countries) and in the East (Balkan region) (Fig. 1). About 100 out of 208 species recognised (48%) occur in the Iberian-NW African area, and 53 (26%) in the Balkan peninsula. The frequency distribution of genera and sections follows the same pattern, with as many as 28 of the 36 taxa recognised (78%) occurring in the Iberian-NW African range, and 20 (55%) in the Balkan peninsula. The maximum in the Balkanic region is largely due to a high number of species belonging to one single Section (*Cytisus* sect. *Tubocytisus*). Consequently, the maximum of genera and sections in the Eastern region is much lower than the maximum in the West.

The rough data above should be interpreted as the result of the evolutionary process. Indeed, there is a basic difference between biological diversity, and the diversity of any set of non-living things. Namely, the biological diversity is but a stage in a dynamic forthcoming process; it makes sense if and only if it is considered in a dynamic context.

The phyletic relationships within the tribe and within the largest genera have been explored by means of a cladistic analysis of morphological characteristics. A set of 44 characters (Appendix 2) was selected. The evolutionary trend of each character (primitive state and derived state) was defined primarily by considering as primitive the state that is predominant in the ancestral group Thermopsidae (see POLHILL, 1976; CRISTOFOLINI & FEOLI CHIAPELLA, 1984; CRISTOFOLINI, 1989). The polarity of 35 characters was so defined; nine more characters remained with undefined polarity. The cladistic analysis was done using a mixture of Wagner parsimony method (for characters with defined polarity) and Camin-Sokal parsimony method (for characters with undefined polarity). The stability of the resulting phylogenies was explored by processing the same data with different procedures (Programs Penny and Mix from the package "Phil", FELSENSTEIN, 1990), and by varying the character set and the taxa set. Majority consensus trees were computed using Program Consense from the same package. Separate analyses were performed on *Cytisus*, *Genista*, and on the rest of the tribe.

The cladograms of *Cytisus* were stable in most of their topology (Fig. 2), independent on the algorithm used. Only two nodes must be considered as unresolved, as they were affected by changes in the computing procedure. The Sections were grouped in two terminal clades (*Tubocytisus* + *Oreosparton*, and *Corothismus* + *Spartopsis* + *Alburnoides*) and three outliers (*Cytisus*, *Emeroides*, *Chronanthus*).

The analysis of *Genista* (Fig. 3) also resulted in a stable cladogram, with only two unresolved nodes. The sections were clustered in three clades (*Cephalospartum* + *Spartocarpus* + *Acanthospartum* + *Fasselospartum*, *Spartioides* + *Erinacoides* + *Genistella* + *Genista*, *Voglera* + *Phyllobotris* + *Scorpioides*), while *Teline* and *Pterospartum* were isolated.

A cladistic interpretation of the tribe as a whole was most problematic. Varying the algorithm, as well as the set of characters, or the set of taxa, resulted in dramatic changes in the topology of the cladograms. Only few clades were recurrent, independent of the conditions of analysis, namely: *Spartium* + *Retama* + *Petteria* + *Gonocytisus*, *Erinacea* + *Echinopartum*, *Podocytisus* + *Ulex*, *Hesperolaburnum* + *Cytisophyllum*.

A common feature is shared by the cladograms of *Cytisus*, *Genista*, and the tribe as a whole, i.e. most of the clades comprise taxa having different geographic ranges (Fig. 4). "Eastern" and "Western" Genera (or Sections) coexist in most clades.

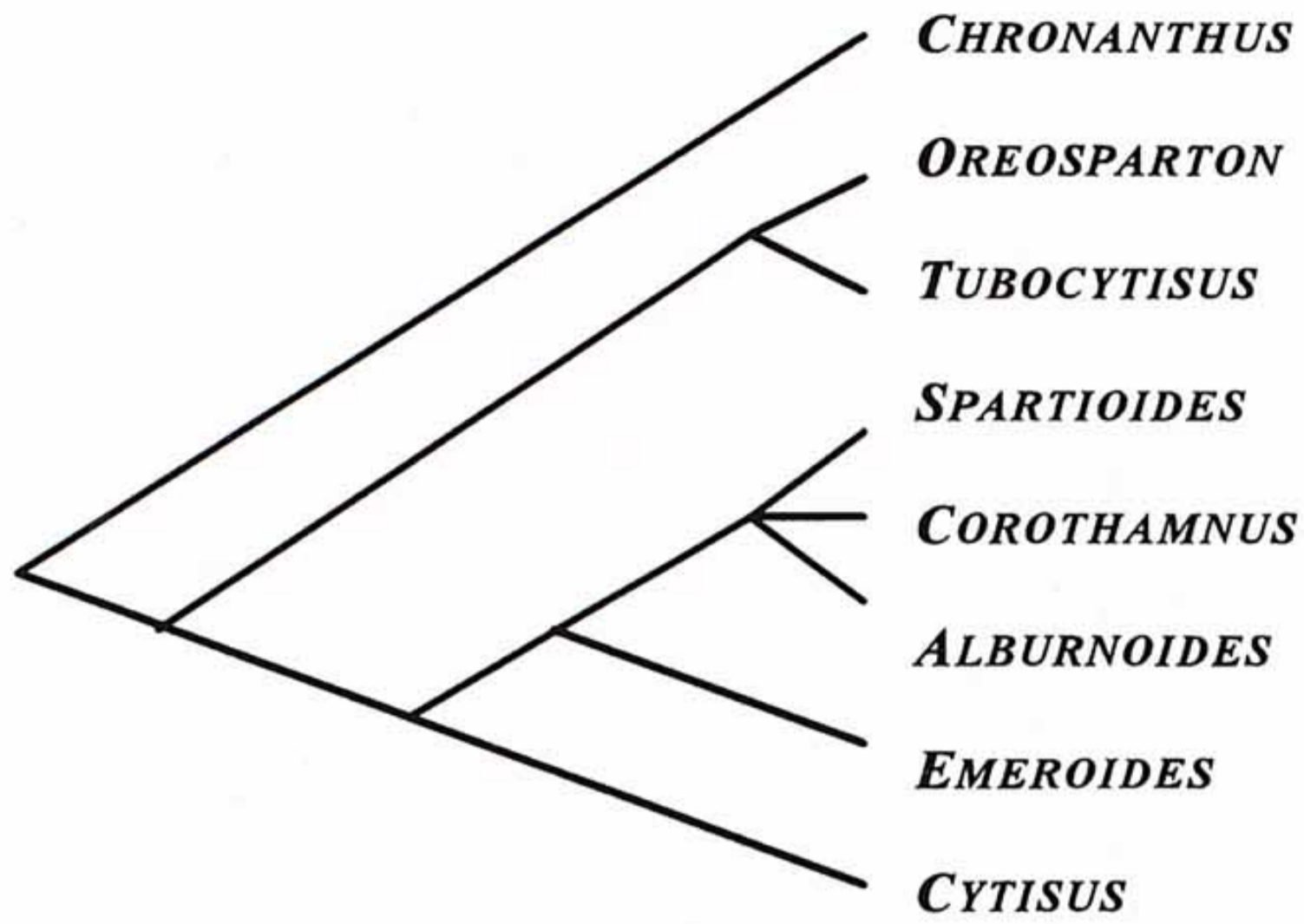


Fig. 2. Majority consensus tree of the Genus *Cytisus*.

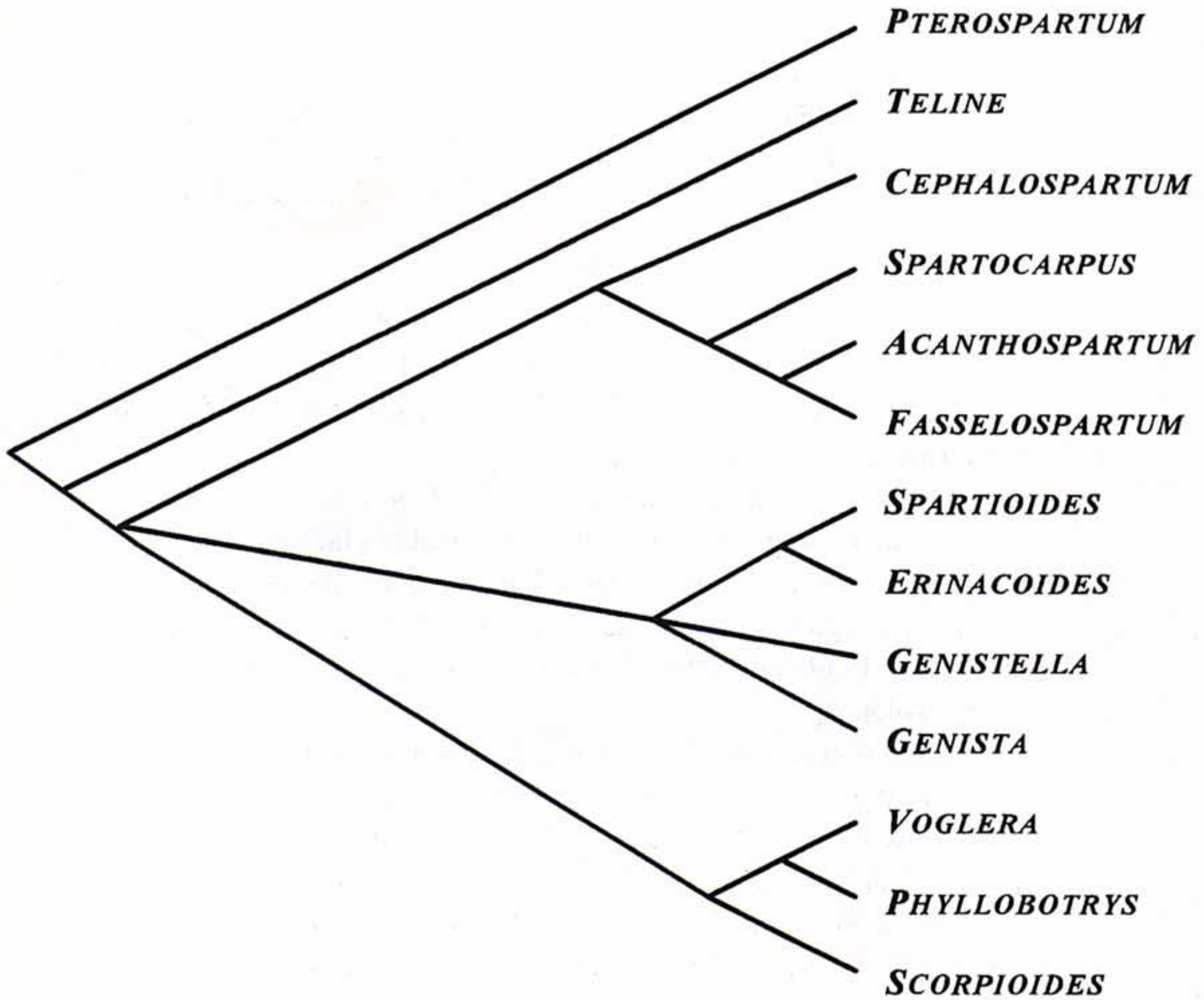


Fig. 3. Majority consensus tree of the Genus *Genista*.

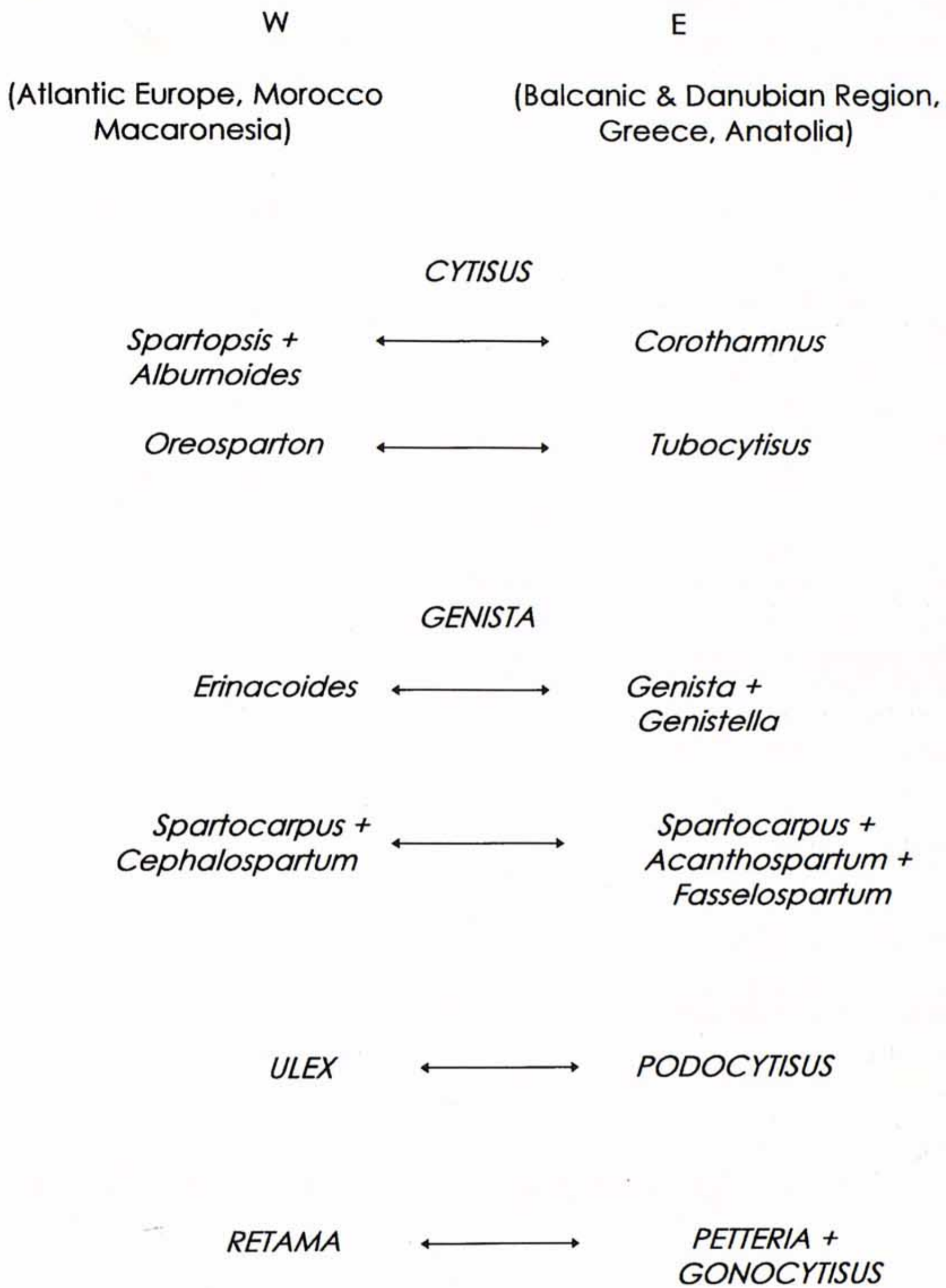


Fig. 4. East-west disjunction in some clades of *Genisteeae*.

Correspondingly, the sets of Genera and Sections of the Western and the Eastern Region do not seem phyletically consistent. This is true not only for ancient, relict taxa (e.g. *Cytisophyllum-Hesperolaburnum*), but also for the most derived groups (e.g. *Cytisus* sections *Oreosparton - Tubocytisus*, and *Genista* sections *Phyllobotrys-Voglera-Genista*). In some case a single Section (e.g. *Genista* Sect. *Spartocarpus*) is split between the two regions.

The phylogeographic and cladistic relationships described above can be explained in several ways. A parallel migration of so many plant groups in either direction seems hardly sustainable, in the absence of a continuous gradient of species diversity through the range. Following the criteria suggested by HUMPHREYS & PARENTI (1986) and HUMPHREYS (1992), it seems more appropriate to suppose a phyletic relation between the two regions.

The area surrounding Thetis was climatically uniform, without geographic barriers, during the Palaeogene. A sharp climatic and geomorphological isolation did not fragment the Mediterranean range until the Early Miocene.

The present distribution of biodiversity could be explained by assuming that the cladogenesis down to the level of genera and sections was achieved before the end of Palaeogene.

Most genera and sections, on the contrary, are restricted within conterminous areas (with some exceptions, especially in *Genista*). The biodiversity within the Genera and Sections, therefore, should be largely due to later evolution, after the arid crisis during the Miocene, and the cold crisis during the Pliocene-Pleistocene, fragmented the distribution range of many taxa.

Appendix 1. Basic (operational) geographic areas, and abbreviations used.

Lu - Portugal, Hs - Spain, Ga - France, In - Italy (north), Co - Corse, Sa - Sardegna, Si - Sicilia, Ip - Italy (peninsular), SA - Slovenia+Austria, NE - Eastern and North-eastern Europe (CS, Hu, Po, Rm, Uk, Ru), Ju - former Yugoslavia excl. Slovenia, Al - Albania, Gr - Greece, BT - Bulgaria + European part of Turkey, An - Turkey (excl. European part), LS - Lebanon+Syria, IJ - Israel + Jordan, Eg - Egypt, Li - Libya, Tu - Tunisia, Ag - Algeria, Ma - Morocco, CI - Islas Canarias.

Appendix 2. List of characters used for the cladistic analysis.

(*) Characters whose polarity has not been defined. (°) Characters used only for *Cytisus* and for the whole tribe (excl. *Genista*). (°°) Characters used only for *Genista*.

1° - *Habitus*: 0 - Tree, 1 - Shrub or Herb woody at the base; 2 - *Ramification*: 0 - Alternate, 1 - Opposite; 3*° - *Twigs (surface)*: 0 - Terete, 1 - Angled in transverse section; 4 - *Twigs (metamorphosis)*: 0 - Unarmed, 1 - Spiny; 5°° - *Twigs (metamorphosis)*: 0 - Not winged, 1 - Winged; 6°° - *Leaves (development)*: 0 - Normally developed, 1 - Absent; 7 - *Leaves (structure)*: 0 - Trifoliolate, 1 - Unifoliolate; 8 - *Leaves (persistence)*: 0 - Persistent, 1 - Early caducous; 9 - *Leaves (petiole)*: 0 - Petiolate, 1 - Sessile; 10 - *Leaves (metamorph.)*: 0 - Normally developed, 1 - Reduced to phyllodes; 11° - *Leaves (dimorphism)*: 0 - Monomorphic, 1 - Dimorphic; 12°° - *Pulvines*: 0 - Not prominent, 1 - Prominent; 13 - *Vascular traces*: 0 - Three per leaf, 1 - One per leaf; 14°° - *Axillary spines*: 0 - Absent, 1 - Present; 15° - *Stipules*: 0 - Present, 1 - Absent; 16°° - *Stipules spinescent*: 0 - Absent, 1 - Present; 17 - *Flowers (position)*: 0 - Terminal, 1 - At the axil of leaves; 18° - *Inflorescence (structure)*: 0 - Raceme, 1 - Fascicle; 19°° - *Inflorescence (structure)*: 0 - Raceme, 1 - Head; 20° - *Infloresc. (if terminal)*: 0 - On normoblasts, 1 - On brachyblasts; 21*°° - *Inflorescence (if axillary)*: 0 - Many-flowered fascicle, 1 - Few-flowered

fascicle; 22° - *Calix (shape)*: 0 - Bilabiate, 1 - Spataceous; 23° - *Calix (if bilabiate)*: 0 - Divided to less than a half, 1 - Divided to more than a half; 24° - *Calix (rescission)*: 0 - Not breaking away, 1 - Breaking away at anthesis; 25*° - *Calix (shape)*: 0 - Campanulate, 1 - Tubular; 26*° - *Calix upper lip*: 0 - Almost undivided, 1 - Deeply bifid; 27*° - *Calix lower lip*: 0 - Almost undivided, 1 - Deeply trifid; 28*°° - *Calix (hairs)*: 0 - hairy, 1 - glabrous; 29° - *Corolla (if white)*: 0 - No, 1 - Yes; 30° - *Corolla (if yellow)*: 0 - No, 1 - Yes; 31° - *Corolla (if purple)*: 0 - No, 1 - Yes; 32° - *Corolla (if pink)*: 0 - No, 1 - Yes; 33*°° - *Corolla (hairs)*: 0 - hairy, 1 - glabrous; 34*°° - *Standard*: 0 - Ovate, 1 - Triangular; 35°° - *Standard (length)*: 0 - as long as wings, 1 - shorter than wings; 36°° - *Standard (length)*: 0 - as long as keel, 1 - longer than keel; 37° - *Style*: 0 - Straight, 1 - Curved; 38° - *Stigma*: 0 - Terminal, 1 - Introrse; 39° - *Stigma*: 0 - Terminal, 1 - Extrorse; 40° - *Legume*: 0 - Dehiscent, 1 - Not dehiscent; 41° - *Legume (shape)*: 0 - Flat, 1 - Torulose or articulate; 42° - *Legume (surface)*: 0 - Smooth, 1 - Tuberculate; 43 - *Seeds (number)*: 0 - Three or more, 1 - one or two; 44* - *Seeds (if strophiolate)*: 0 - Strophiolate, 1 - Estrophiolate.

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