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THE THORNY-CUSHIONS VEGETATION IN MEDITERRANEAN ITALY. PHYTOGEOGRAPHICAL PROBLEMS

by

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INTRODUCTION

True thorny-cushions formations include all the associations dominated by thorny — cushion plants with hollow inside (Radialhohlkugelpolster; RAUH, 1940). Such plants are characterized by the following morphological features: acrotonic ramification with hypotony of peripheral branches, presence of thorns derived either from leaves or from branches, early abortion of the main axis, allorhize roots, buds not covered by perulae; the general shape approaches more or less a half-sphere. In thorny-cushion plants, the characteristic growth-form seems to be a genetically fixed character, that appeared indipendently in taxonomically widely separated groups (PIGNATTI, AVANZINI & NIMIS, 1980).

Thorny-cushions stands are known to occur in the Irano-Turanian and Mediterranean regions, and in the South American Andes. The associations of the first two regions are, at least in part, historically and floristically related; the analogous formation in South America grows in comparable ecological conditions, being completely different from the floristical point of view (ELLENBERG, 1975). The mediterranean thorny-cushions vegetation has been the object of many phytosociological studies: thorny-cushions associations have been described for North Africa (QUÉZEL, 1957), Spain (QUÉZEL, 1953; GAUSSEN, 1953; BAUDIERE & *al.*, 1968), South France (MOLINIER, 1954), Corsica (LITARDIERE & MALCUIT, 1926; GAMISANS, 1977), Greece (QUÉZEL, 1964, LAURENTIADES, 1969) and the Etna Vulcano (POLI, 1965). With the exception of the latter work, the knowledge of thorny-cushions vegetation in mediterranean Italy was rather poor, in spite of their relative importance in the vegetational characterization o the region. A project for a comprehensive study of thorny-cushions vegetation in mediterranean Italy started at the Botanical Institute of the Trieste University in 1973, and was concluded in 1980 with the publication of a monographical paper (PIGNATTI, AVANZINI & NIMIS, 1980). In the present work the discussion will be centered

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above all on some phytogeographical problems that were only marginally treated in the latter monography, to which we refer for a discussion of morphological, ecological and syntaxonomical problems related to the thorny-cushions vegetation in mediterranean Italy.

THE THORNY-CUSHION PLANTS OF MEDITERRANEAN ITALY

Genus *Astragalus:*

Since the revision of the irano-turanian species by BOISSIER (1872), no comprehensive taxonomical study on thorny-cushion *Astragalus* species has been made. The thorny-cushion *Astragalus* species of the italian flora belong to three different subgenera: *Tragacantha, Cercidotrix* and *Calicophysa* sect. *Acidodes*. The differentiation center for the three subgenera is located in the Irano-Turanian region.

Subgen. *Tragacantha*

Astragalus calabrus (Ten.) Fiori	(Calabria: Sila and Aspromonte).
Astragalus nebrodensis (Guss.) Strobl	(Sicily: Madonie).
Astragalus siculus Biv.	(Sicily: Etna Vulcano).

The three species are morphologically very similar. They are related to *Astragalus rumelicus* and *A. parnassi,* of the Balkan Peninsula. *Astragalus rumelicus* Bunge is considered by SIRJAEV (1939, see also GILLI, 1943) as the probable ancestor of *A. siculus, A. nebrodensis* and *A. boissieri* Fischer (Spain). In Flora Europaea the three species are considered as subspecies under the name *A. granatensis* Lam., the subsp. *granatensis,* including *A. nebrodensis* and *A. boissieri,* whereas the *Astragalus* of the Etna Vulcano is treated a subsp. *siculus* (Biv.) Franco & P. Silva. *A. calabrus* is considered as a subspecies of *A. parnassi* Boiss. The latter species, according to SIRJAEY (1939), should be more recent than *A.rumelicus.*

An east-west oriented differentiation pathway for the italian species of the subgenus seems to be most probable: *A. calabrus* and *A. nebrodensis* derived from populations coming from the Balcan Peninsula. A central position is held by *A. nebrodensis,* that is most probably more ancient than *A. siculus* (because of the relatively young age of the Etna Vulcano) and *A. boissieri* (being *A. boissieri* the westernmost species of a group whose differentiation pathway is oriented in an east-west direction). The extremely localized and fragmented distribution of the various species of the subgenus could be interpreted as a consequence of an ancient differentiation, that took probably place in the late Tertiary period.

Subgen. *Cercidothrix*

Astragalus sirinicus Ten.	(Southern Appennines)
Astragalus genargenteus Arcang.	(Sardinia: Gennargentu, M. Albo)
Astragalus massiliensis Lam.	(Sardinia)

Also for the species belonging to the subgen. *Cercidothrix*, an east-west oriented differentiation pathway from populations in the Balkans is most probable. They are closely related to *A. angustifolius* Lam., a thorny-cushion species occurring in the Balkan Peninsula and Crete.

The areal of *A. sirinicus* extends from the Balkans to the Appennines. *A. genargenteus* is endemic in Sardinia and Corsica. The two species are very similar, and by some authors they are not separated at specific level (CHATER, 1968). *A. massiliensis* is the only thorny *Astragalus* species of the italian flora that is bound to littoral stations: outside Sardinia, it occurs with scattered populations in Corsica and South France, always in wind-exposed stations near the coast. Its fragmented areal, the fact that the species is limited to rocky coasts and the affinities with *Astragalus sirinicus* and *A.genargenteus*, suggest a differentiation of a primitive species of eastern origin into two populations, in stations characterized by the prevalence of strong and continous humid winds, i.e. mountain ridges and rocky coasts, where they evolved independently as a consequence of geographic isolation («double insularity» for the populations in the mountains). These stations most probably represent small enclaves of a strongly xeric climate that acted as refuge areas for plants not adapted to subsequent climatic changes. The period could be located at the end of the Tertiary, when a climatic shift took place, characterized by a progressive increase in precipitation. The present fragmented areal of *A. massiliensis* is probably formed by all the refuge stations on rocky coasts that were not completely submerged by sea during the interglacial periods. This seems to be the case for the satations in Sardinia, Corsica and South France (FURON, 1947).

The same considerations could be made as far as *A. balearicus* Chater is concerned, a species that is very near to *A. massiliensis*, endemic of the Baleares. The differentiation process took probably place as a consequence of the separation of the Baleares from Sardinia-Corsica at the end of the Oligocene. The distribution of these two littoral thorny — *Astragalus* species is quite remarkable from the biogeographic point of view: Sardinia-Corsica and the Baleares broke away from the Southern French coast by rotation in the Oligo-Miocene, so that the two *Astragalus* are presently distributed at the margins of a once continuous area.

Subgen. *Calicophysa*

Astragalus sempervirens Lam. (Western Alps, Appennines up to M. Papa)

A. sempervirens is a polimorph species occurring in Italy from the western Alps to the M. Papa, on the Appennines, being among thorny-*Astragalus* species the one whose areal extends more to the north. Its areal extends from Spain (subsp. *navadensis* (Boiss.) P. Monts.) on the Sierra Nevada, Central Spain (subsp. *muticus* (Pau) Rivas Goday & Borja), Pyrenees (subsp. *catalaunicus*), to South Italy (different subpecies, see PIGNATTI, 1973). A taxon known as subsp. *cephalonicus* (C. Presl.) Asch. & Graebn. occurs on the mountains of Greece. To the same subgenus belong other species as *A. giennensis*, *A. clusii* (Spain), and *A. armatus*, *A. fontanesii* (North Africa).

The occurence of *Astragalus sempervirens* s.l. in the Balkan peninsula (that is anyway doubtful for the subsp. *sempervirens*), could suggest that for this species too the migration pathway started from the Balkans westwards, like for the other thorny-cushion *Astragalus* species of the italian Flora. However, there are some aspects of the chorology, sociology and morphological variation of *A. sempervirens* s.l., that could suggest a different hypohesis.

The morphological variability of *A. sempervirens* s.l. led to the subdivision of the species in several subspecies or varieties (BAUDIERE & KÜPFER, 1968; CHATER, 1968; PIGNATTI, 1973). According to PIGNATTI (1973), at least 6 subspecies can be distinguished, some of which could be ranked at specific level, the whole group being clearly centered in the West-Mediterranean region. A parallel variation cline can be observed from the subsp. *nevadensis* (South Spain) to the subsp. *gussonei* Pign. (South Italy), concerning the shape and nervature of the bracts (see also MONTSERRAT-RECORDER, 1959). The growth-form of *A. sempervirens s.l.* undergoes a more or less continuous change from South Spain to South Italy, with a progressive loss of the typical hemispherical thorny-cushion shape (QUÉZEL, 1953; BAUDIERE & KÜPFER, 1968; PIGNATTI, NIMIS & AVANZINI, 1980). This is linked with a progressive loss of the phytosociological indicator value of the species: *A. sempervirens* subsp. *nevadensis* is characteristic of the *Xero-Acanthion* alliance *(Erinacetalia)* in the Sierra Nevada (QUÉZEL, 1953), where it enters as a dominant species in many thorny-cushions associations; the stands of the Pyrenees could be considered as the northernmost outpost of the Order. In Italy, *A. sempervirens s.l.* is present within different syntaxa from the Alps to the Appennines, never giving way to true thorny-cushions formations.

According to MEUSEL & *al.* (1965), the areal of *A. sempervirens* s. l. is very similar to the one of *Astragalus purpureus* Lam., *Anthyllis montana L. s.l.* and *Ononis rotundifolia* L.; the three species have a clearly west-mediterranean differentiation center, and could be considered as representatives of west-mediterranean montane stepps. The last point concerns the affinities of *A. sempervirens:* the taxonomically nearest species within the subgenus are either endemic of the Iberian Peninsula, or of the North African mountains (Atlas).

All these facts seem to suggest a west-east oriented migration pathway of the *Astragalus sempervirens* group in Europe, from South Spain to South Italy through the Pyrenees and the Western Alps. The stations of *A. sempervirens* subsp. *gussonei* on the Apennines would be located at the extreme of the species areal, a fact that could explain the rather anomalous behaviour of *A. sempervirens* in Italy, in comparison with the other thorny-cushion *Astragalus* of the italian flora. *Astragalus sempervirens* probably evolved from ancestors coming from the Irano-Turanian region to South Spain along the southern edge of the Egäis, and extended its areal northwards up to the Alps, and southwards along the Appennines, giving way to the differentiation of several subspecies and varieties that originated as a consequenc of later geographical isolation. The generally weak differentiation of the subspecific taxa could suggest a more recent origin of the group, during a xeric interglacial stage.

In the region corresponding to their differentiation center (i.e. the Irano-Turanian region), thorny cushion *Astragalus* species are bound to a strongly xeric climate (300-400 mm pecipitation/year), with constant and strong winds, and normally occur on primitive gravelly soils, derived either from siliceous or calcareous parent material (HANDEL-MAZZETTI, 1913; KRIVONOGOVA, 1965; BRECKLE, 1971; FREITAG, 1971). The migration into the mediterranean basin must have taken place in a period characterized by an extension of a strongly xeric climate in the mediteraenan area. Xeric interglacial stages should be excluded since the distribution pattern of the various species suggests a more ancient differentiation process. This could be most probably located in the Tertiary, when the climate of the mediterranean area was marked by an increasing aridity that reached its maximum in late Miocene (BENDA, 1973). In this period a flora of steppic character extended through the region (BERGER, 1953, 1958), and some authors, on the basis of recent geological data, support the hypothesis of a partial dessiccation of the old Mediterranean basin during the Messinian period, 5,5 to 4,5 Mio. years ago. (OGNIBEN, 1957; PERRODON, 1957; NESTEROFF, 1971; BOCQUET & *al., 1978)*. During this period the thorny-cushion formations probably covered extensive areas. As a consequence of the subsequent climatic changes towards more oceanic conditions at the beginnings of the Quaternary period, the thorny-cushion *Astragalus* species retreated in refuge stations characterized by a xeric local microclimate due to the physiological effect of wind, i.e. rocky coasts and tops of the high mountains, where they evolved indipendently for geographic isolation. The present stands of thorny-*Astragalus* species in the Mediterranean region are to be considered as the only remnants of a very ancient, once much more widespread vegetation.

Genus *Genista:*

Several species of *Genista* and related genera behave as thorny-cushion plants, giving way to extensive formations, above all in the West-mediterranean region. In Italy 5 species of thorny-cushion *Genista* may be recognized *(Genista morisii* Colla, and *Genista anglica* L. cannot be considered as true thorny-cushion plants):

Subgen. *Genista*
- Sect. *Erinacoides*
  - *Genista lobelii* DC. var. *salzmannii* (DC.) Spach (Sardinia, Corsica)
  - *Genista lobelii* DC. var. *lobelioides* Gamisans (Corsica)
- Sect. *Scorpioides*
  - *Genista corsica* (Lois.) DC. (Sardinia, Corsica)

Subgen. *Phyllobotrys*
Sect. *Voglera*
Genista cupanii Guss. (Sicily, Madonie)
Genista michelii Spach (Gargano peninsula)
Sect. *Acanthospartum*
Genista acanthoclada DC. subsp. *sardoa* (Beg. et Landi) Valsecchi (Sardinia)

The chorology of the genus *Genista* as a whole is quite different to the one of the genus *Astragalus:* the latter is a clearly eastern group, whereas the differentiation center for the genus *Genista* is located in the west-mediterranean region.

Genista lobelii var. *salzmannii* belongs to the Sect. *Erinacoides,* into which at least 6 thorny-cushion species are included, whose distribution is centered around the Iberian Peninsula and Northwest Africa. Only one species, *Genista parnassica* Halacsy, is present in Greece, and according to GIBBS (1966), it is not specifically distinct from *G. lobelii* var *salzmannii* (by this author considered as a distinct species as *G. salzmannii* DC., see also GAMISANS (1973).

An analogous distribution pattern characterizes the Sect. *Scorpioides,* into which *Genista corsica* is included. The species forms a clearly related group with *G. scorpius* (L.) DC. (Spain) and *G. myriantha* Ball. (Atlas).

Genista cupanii Guss. and *G. michelii* Spach belong to the Sect. *Voglera* of the subgenus *Phyllobotrys.* Most of the species of this Sectio are concentrated in the southwestern portion of the Iberian Peninsula and North Africa, but some isolated species occur in Mallorca, Sicily, Italy, Yugoslavia and Turkey.

The italian *Genista* species of the above mentioned groups are to be considered as eastern differentiations from west-mediterranean ancestors; for them a migration pathway can be traced, that is opposite to the one discussed for most of the *Astragalus* species. The differentiation process took place as a consequence of geographic isolation after the migration of ancestor species from the Iberian Peninsula and perhaps (for *Genista cupanii)* North Africa.

An exception is the case of *Genista acanthoclada* subsp. *sardoa:* the species is the only representative of the sectio *Acanthospartum,* and it was only recently recognized for the flora of Italy (VALSECCHI, 1975). It occurs in a very narrow area on the northwestern coast of Sardinia, between M. Capparone and Capo Caccia. The species has a secundary differentiation center in Greece and Turkey, so that the areal is centered in the east-mediterranean region, with two subspecies: subsp. *acanthoclada* (Greece, Crete, Lybia) and subsp. *Echinus* (Spach) Vierh. (Turkey, Syria). A subsp. *balearica* (P.R.) Will. has been described for Maiorca. The subsp. *sardoa,* together with the latter subspecies, rapresents the westernmost outpost of the species. Its distribution recalls the analogous disjoinct areals of a group of species as *Satureja thymbra* L., *Astragalus suberosus* Banks, et Sol. *Sarcopoterium spinosum* (L.) Spach, *Laserpitium siler*

L. subsp. *garganicus* (Ten.) Arcang.,, *Hypericum aegyptiacum* L. and *Anthyllis hermanniae* L., that are considered as old eastern elements that migrated westwards during a period characterized by a particularly xeric climate (VALSECCHI, 1975, see also SCHMID, 1933).

Other thorny-cushion species:

— *Centaurea horrida* Badaro: is endemic of Sardinia, with a narrow areal limited to some stations on the northwestern coast, at Punta Falcone (near the stations of *Astragalus massiliensis* and *Genista acanthoclada* subsp. *sardoa*). It is very similar to *Centaurea balearica* Rodr. (Baleares), with which it is included in the sect. *Horridae* Dostàl. *Centaurea spinosa* L., of the Cyclad islands, is similar in the general shape and lives in comparable ecological conditions, but is taxonomically rather isolated, belonging to the Sect. *Dumulosae* (Hayek) Dostàl. The vicarism *C. horrida* — *C. balearica* recalls the analogous vicarism *Astragalus massiliensis*— *Astragalus balearicus*. The history of the two couples of species is probably very similar.

— *Sarcopoterium spinosum* (L.) Spach: it is a clearly east-mediterranean element with some relict outposts in Italy (Puglia, Sicily, Sardinia) (LORENZONI, 1977). In the Aegean isles it enters as a dominant species in many thorny-cushions associations near the coast, often together with *Anthyllis hermanniae*.

— *Anthyllis hermanniae* L.: another east-mediterranean element with areal extended from Turkey to Greece, with a great disjunction in Sardinia (where it is rare and localized) and Corsica. In the latter isle it is particularly frequent, giving way to extensive thorny-cushions formations (GAMISANS, 1977).

— *Stachys glutinosa* L.: two taxonomically strongly related species, *Stachys glutinosa* L., endemic of Sardinia and Corsica, and *Stachys spinosa* L., endemic of the southern Balkan Peninsula, enter as occasional elements in thorny-cushions associations (PIGNATTI, NIMIS & AVANZINI, 1980). The two species belong to a sectio including several species with an eastern differentiation center: among them *Stachys fruticulosa,* of the Caucasus and Iran.

Conclusions:

With the relevant exception of the *Genista* species, for all the thorny-cushion plants of mediterranean Italy an ancient eastern origin may be supposed. *Genista acanthoclada* and *Astragalus sempervirens* are peculiar cases in the respective genera, the former being an east-mediterranean species with relict outposts in the west, the latter having probably developed from ancestors that entered in Europe through the southern margin of the Egäis. The chorology of the various groups is characterized by great disjunctions, narrow geographic distribution of the various populations in localized stations, and the presence of imposing phenomena of geographical vicarism among the different regions. All these facts support the hypothesis of a very ancient origin for this group of plants: they should have been much more widespread in the past. The period for their optimal development should have been the late Miocene. The hypothesis of a large-scale dessication of the Mediterranean basin during the Messinian could be a useful working hypothesis for an interpretation of their present disjunct distributions. They survived the Quaternary climatic changes in relict stations with a particularly xeric (windy) microclimate. Geological, tectonical and climatical events in the late Tertiary are the basis for an interpretation of their differentiation pattern.

THE THORNY-CUSHIONS VEGETATION

As it is to be expected from the very localized distribution of thorny-cushion species in mediterranean Italy, the occurrence of a thorny-cushions vegetation is restricted to narrow areas, mainly on the principal mountain groups of southern and insular Italy. Nevertheless, the thorny-cushions stands are to be considered as one of the most peculiar elements for the phytogeographical characterization of mediterranean Italy. At least 11 principal associations have been described (PIGNATTI, NIMIS & AVANZINI, 1980; NIMIS & DE FAVERI, 1980), they may be included into three separate groups, according to their altitudinal distribution. Within each group, the associations are characterized by floristical, historical, ecological and structural convergencies.

1. Cacuminal associations (*Sensu* PIGNATTI, 1979), with primary stations above or near timberline.

Astragaletum calabri Giacom. & Gentile (Sila Massive, Calabria).
Astragaletum genargentei Pign. & Nimis (Gennargentu, Sardinia).
Astragaletum nebrodensis Pign. & Nimis (Madonie Chain, Sicily).
Astragaletum siculi Poli (Etna vulcano, Sicily).

To the list some relict thorny-cushions stands on the southern Appennines may be added, dominated by *Astragalus sirinicus* (CAPUTO, 1970; BONIN, 1978). *Astragalus sempervirens* in Italy never gives way to true thorny-cushions formations.

The associations included into this group are characterized by the absolute dominance of thorny-*Astragalus* species, whose primary stations of relict character have been localized on rocky ridges or other «Baumfeindliche Standorte» above or near timberline. In many cases a downslope extension of secundary stations has been observed, as a consequence of deforestation or cattle grazing by man. This has led to a secundary contact with associations of group 2. From the structural point of view, they recall the analogous thorny-cushions formation of North Africa and Southern Spain (QUÉZEL, 1953, 1957), with the exception of the *Astragaletum calabri*, where *Astragalus calabrus* never covers more than 50 % of the surface, the whole formation recalling the «Pelouses écorchées» of the Balkan Peninsula (QUÉZEL, 1964). The high incidence of endemics (from 37 % in the *Astragaletum nebrodensis* to 51.0 % in the *Astragaletum genargentei*) is a further indication of the ancient origin of these vegetation types. Among the different associations, imposing phenomena of geographical vicarism can be described. An example is the case of the *Viola* subgen. *Melanium,* that behave as cushions-hosts (Polstergaeste) in Sardinia *(Viola corsica* Nyman), on the Etna Vulcano *(Viola aethnensis* Parl.) and on the Madonie (*Viola nebrodensis* Presl). Other phenomena of vicarism and structural convergence affect the contact communities in the more wind-swept stations, with which the thorny-cushions associations often form mosaics: these are associations dominated by a *Plantago* (*Plantago subulata* Vill. var. *sarda* Presl, in Sardinia; *Plantago subulata* Vill. var. *humilis* (Jan) Guss., on the Madonie, and *Plantago serpentina* All. on the Sila Massive), and *Armeria (Armeria sardoa* Sprengel in Sardinia; *Armeria multiceps* Wallr. in the vicariant association in Corsica; *Armeria nebrodensis* (Guss.) Boiss. in the Madonie, and *Armeria canescens* (Host) Boiss., on the Sila Massive).

Only the Etna Vulcano is sufficiently high to allow an optimal development of the thorny —*Astragalus* belt, in the other mountain groups the *Astragalus*-associations are rather localizaed near the top of the mountains. These associations may be considered as the mediterranean counterparts of the *Rhododendron*— formations in the Alps. According to PIGNATTI (1979) they define the «Irano-Nevadian Vegetation Belt», whose areal extends from the Irano-Turanian region to the Sierra Nevada. From the syntaxonomical point of view, the associations of this group are so rich in endemics that they have to be included in different syntaxa, in spite of ther evident phytogeographical and historical affinities (PIGNATTI, AVANZINI & NIMIS, 1976; PIGNATTI, NIMIS & AVANZINI, 1980).

2. Montane associations

Chamaecytiso-Genistetum michelii Nimis & De Faveri (Gargano Peninsula).

Genistetum cupanii Pign. & Nimis (Madonie, Sicily).

Helychryso-Genistetum salzmannii Gamisans (Sardinia, Corsica).

Triseto-Genistetum corsicae Gamisans (Gennargentu, Sardinia).

To the list a *Genista salzmannii*-community may be added, ocurring in the isle of Elba (PIGNATTI, NIMIS, AVANZINI, 1980).

All of these associations are characterized by the absolute dominance of thorny-*Genista* species. They occur under timberline, and should be considered as secundary stages of different vegetational series.

In comparison with the associations of group 1, the thorny-cushion *Genista* associations are characterized by a relatively low percentage of endemics, and higher incidence of mediterranean species and therophytes. For most of the *Genista* species the primary stations were probably located within the old mediterranean woods, where they behaved as understory or mantle species. From these facts it could be inferred that the

Genista species occupied the new niches after destruction of the woods, probably in historical times, and that the *Genista*-associations should have a more recent origin than the *Astragalus*-associations. However, an interesting fact is that the *Genista*-associations occur in areas characterized by the presence of relict fragments of the old sclerophyll montane forests with *Ilex* and *Taxus* (Colchical Vegetation Belt, PIGNATTI, 1979): so on the Gennargentu Massive, in Corsica, on the Madonie and in the Gargano Peninsula. The fragments are mostly reduced to the presence of isolated trees, so that it is difficult to find more evidence for an hypothesis that would consider these associations as degradation stages of the Colchical Belt.

3. Littoral associations

Centaureetum horridae, Molinier (Northwestern Sardinian Coast).
Genista acanthoclada-community, Valsecchi (Northwestern Sardinian Coast).
Sarcopoterium spinosum-community, Lorenzoni (Southern Sardinian Coast).

The first two associations occur on the northwestern coast of Sardinia: they are respectively dominated by *Centaurea horrida* and *Astragalus massiliensis*, and *Genista acanthoclada* (MOLINIER & MOLINIER, 1955; VALSECCHI, 1976; PIGNATTI, NIMIS & AVANZINI, 1980). The *Sarcopoterium spinosum*-community has been described by LORENZONI (1977) for a narrow area at Capo St. Elia, on the southern sardinian coast. They rapresent the only fragmentary remnants within the italian territory of the Phrygana-formation type, a thorny-cushions littoral formation much more widespread in the isles of the Aegean Basis (LAURENTIADES, 1969). Other Phrygana fragments are known to occur in Southern France (MOLINIER, 1954), in Corsica (MOLINIER & MOLINIER, 1955; GAMISANS, 1977), and the Baleares, with *Astragalus balearicus* and *Centaurea balearica*. The dominant species have all an ancient eastern origin, *Genista acanthoclada* being the only clearly east-mediterranean thorny-cushion *Genista* species of the italian flora. From the syntaxonomical point of view, the associations included into this group are characterized by a great incidence of species both of the *Chrithmo-Staticetalia* and the *Oleo-Ceratonion*, a fact that reflects their particular ecological requirements: strongly wind-swept stations on rocky coasts. The lack of other well-developed Phrygana fragments in mediterranean Italy is most probably due to their disappearance as a consequnce of sea-level raising during the Pliocene, when most of the present coasts of Sicily and Calabria were submerged by sea. The sardinian thorny-cushions stations are characterized by a very steep coast, rapidly raising to more than 100 metres, a fact that could have allowed the survival of the thorny-cushions stands. This could explain the presence of the only remanants of a clearly east-mediterranean vegetation at the westernmost corner of mediterranean Italy.

CONCLUSIONS

The thorny-cushions associations of mediterranean Italy do not represent an homogeneous group from the historical-genetical point of view; they may be divided into three groups: cacuminal and littoral formations are of clearly eastern origin, the montane formation is dominated by rapresentatives of a west-mediterranean genus. The first two include stable communities in «Baumfeindliche Standorte», the associations belonging to the latter, are secundary degradation stages of woody stands. The origin of the cacuminal and littoral formations could be located in late Miocene, under a warm-arid climate, when an east-west migration of thorny-cushion plants took place from the Irano-Turanian region. The subsequent climatic changes reduced the thorny-cushions stands to a few relict stations characterized by the permanence of a particularly dry microclimate due to the physiological effect of wind, i. e. mountain tops and rocky coasts. Geographic separation favoured the differentiation (double insularity of the alpine stands) with the consequent formation of new species, most of which are schizoendemics. Consequently, their present distribution is rapresented by a series of relict stations of very ancient origin. The only exception is given by the Etna Vulcano, the origin of which is more recent, and whose flora is characterized by a great richness in neoendemics, mostly derived from species present in the Madonie and Nebrodes Chains.

The montane thorny-cushions associations dominated by *Genista*-species are still of unclear origin: they could have originated in the Quaternary, as a consequence of the destruction of the old mediterranean woods for cattle-grazing by man. The hypothesis of their relation with the Colchical belt, as a degradation stage of the latter, needs to be supported by more phytogeographical data.

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