The Messinian Model – A new outlook for the floristics and systematics of the Mediterranean area

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Résumé

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Un nouveau modèle floristique est proposé pour la région méditerranéenne, le modèle messinien, qui s'inspire des théories géologiques de la dessiccation de la Méditerranée au Messinien (Miocène supérieur). Un premier essai d'application à quelques exemples floristiques et systématiques est ici présenté. Les origines de la flore corse sont plus particulièrement considérées.

Abstract

BOCQUET, G., B. WIDLER & H. KIEFER (1978). The Messinian Model – A new outlook for the floristics and systematics of the Mediterranean area. *Candollea* 33: 269-287. In English, French abstract.

A new floristic model for the Mediterranean area, the Messinian Model, based on the geological theories about the desiccation of the Mediterranean during the Messinian (Late Miocene), is proposed. In a first evaluation, some systematic and floristic examples are discussed, in particular the question concerning the origin of the flora of Corsica.

Introduction

Compared to the Oceanic Islands, the islands of the Mediterranean are very special: we do not find the typical pattern of adaptive radiation due to haphazard inoculation by long-distance dispersal but entire floristic elements from the Alps, South-Spain, North-Africa, etc. This fact has been an enigma to botanists for a very long time. All sorts of hypotheses have been set up and rejected, to no reveal.

Geologists have now supplied a new theory about the Mediterranean: desiccation during the Messinian (late Miocene, approximately –5 Mio years). We have applied this theory to our work, floristic studies on Corsica, which is particularly suited as a test-case because of its position in the Mediterranean, and systematic studies on *Silene* L. and *Digitalis* L.

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The first results, presented here as a general discussion, are very promising. We are therefore proposing a new floristic model, the Messinian Model based on the theory of a late Miocene salinity crisis, as a working-hypothesis for botanical research on the Mediterranean and its manifold connections. A fairly comprehensive bibliography for further information is given.

Floristic models

The question about the origin of the flora of Corsica, particularly its alpine elements, is basically the one of how isolation could have been temporarily overcome. Many authors have put forth hypotheses to this reveal. We shall briefly consider the most important ones.

The hypothesis of long-distance dispersal (ENGLER, 1879) suggests the gradual introduction of alpine species by animals and wind. We will discuss this possibility further on.

The hypotheses about land-connections follow the well-established biogeographical examples of the Bering- and Panama-straits, relying on various continental bridges for the explanation of floristic affinities:

Solely based on biogeographical data was FORSYTH-MAYOR'S view (1883), that the connection to Africa survived that to the Continent, breaking only by the end of the Quaternary. Its supposedly vast extensions, with the testimonial remains of the Mediterranean islands, are to this day designated by the name "Tyrrhenis".

BRIQUET (1901) believed that the system of terrestrial connections in the Mediterranean broke down at the latest during the Pliocene. The subtropical climate of the coastal areas at this time, however, would have prevented boreal and alpine plants from invading the island. Consequently he inferred a parallel evolution of the Continental and Corsican alpines from common, widely distributed precursors of the lower vegetational zones. This theory has been extensively discussed and rejected by CONTANDRIOPOULOS (1962) and FAVARGER & KÜPFER (1969). However, though polytopism cannot explain the origin of a whole flora, it is none the less worthwile remembering that, given similar conditions, convergent evolution from a common ancestral stock is feasible.

BRAUN-BLANQUET (1926) maintained that the flora of Corsica had basically developed "in situ" during the Oligo-Miocene period from Mediterranean ancestors. In order to explain the composition of the flora, he suggests a connection between the various regions of the Mediterranean basins by means of a continent which has now disappeared, thus giving a palaeogeographical dimension to the floristic relationships. Because many of the Continental species are missing on the Tyrrhenian islands, a pre-Quaternary separation must be assumed.

CONTANDRIOPOULOS (1962) followed up this hypothesis by conceiving a whole geological "happening" with various bridges and continents appearing and disappearing through the eras. Distinguishing five main phases of migration, she listed actual floristic examples for each of the bridges.

GAMISANS (1975) adapted Braun-Blanquet's idea, updating it according to more recent geological data. In his view the isolation of Corsica dates from the

Oligo-Miocene when, by rotation, the Sardo-Corsican complex broke away from the French coast. The flora had basically been established then, later introductions being negligible in number. Thus he categorically rejects any suggestion of continental bridges, ascertaining the independent status of the Corsican alpines from the lower Oligo-Miocene onwards.

However, none of these models stands up to close geological and palaeobotanical scrutiny. The results from studies on the formation of the Mediterranean basins do not allow for repeated mutiple connections by the way of continental bridges. Therefore the models of BRIQUET (1901) and particularly CONTANDRIOPOULOS (1962), however interesting they may be from a phytogeographical point of view, have to be abandoned. As far as GAMISANS' (1975) theories about the population of the alpine zones are concerned: though the rotation of the Sardo-Corsican complex is widely accepted by now, they do not agree with some of the geological and palaeobotanical data. In fact, the height of the mountains is supposed to have been rather modest still during the lower Miocene and palaeoecological research suggests a temperate subtropical flora rather than an alpine one for the time in question. Thus we are left with long-distance dispersal as the sole answer, unless a more satisfactory solution can be found.

The Messinian

The term "Messinian" designates the very last period of the Miocene, from approximately –5.5 Mio to -.4.5 Mio years.

In the history of the Mediterranean the Messinian represents a very important phase. Already the discovery of Messinian Evaporite deposits at various points around the Mediterranean (Sicily, Calabria, North-Africa) suggested the particular nature of this era. These Evaporites were then thought to be local occurrences, deposited by lagoons during a period of extreme aridity (OGNIBEN, 1957; PERRODON, 1957; NESTEROFF, 1971).

A further indication of the exceptional character of this era was given by a series of submerged canyons along the Mediterranean coasts. These canyons, whose ground is covered by Plio-Quaternary sediments, are carved into the continental shelf for a length of several hundred meters, ending on the floor of the basins. They generally follow a course in continuation of the rivers of nowadays, Rhone and Nile being classical examples thereof (BOURCART & al., 1948; LE PICHON & al., 1971).

Exploratory drilling in the Mediterranean by oil companies revealed oil-bearing layers of Messinian age alternating with Evaporite deposits, which signifies successions of normal marine and evaporite-forming conditions within a relatively short time-span.

A satisfactory explanation for these findings, however, could only be found when new techniques such as seismic recording and deep-sea-drilling became available. It was the "Deep-Sea-Drilling-Project" (= D.S.D.P.) of the American National Science Foundation that finally yielded the crucial geological data for a better understanding of the Messinian events.

Seismic recordings proved the omnipresence of a particularly hard, strongly reflecting layer in the whole of the Mediterranean. This "M-Reflector" (RYAN & al., 1973) was identified as late Miocene Evaporite, in fact, it turned out to be the uppermost zone of Messinian Evaporite-deposits. The continuity of the "M-Reflector" allowed to generalize the results of local drillings. According to seismic profiles the maximum strength of Evaporite-deposits reaches between 1500 and 1800 meters, giving a strong impression of the enormous amounts of water involved and the catastrophic character of the events, particularly if we consider that these Evaporites were deposited in the whole of the Mediterranean in not much more than a million years (RYAN & al., 1973).

Deep-sea-drilling further revealed a series of laminae in the Messinian Evaporites that are typical of alternations in conditions from marine to evaporite-forming: cycles of evaporation were interrupted temporarily by marine transgressions. Calculations based on the "Solfifere gessose" of Sicily suggested at least ten such cycles. The lamination does not agree with the continuous climatic development in this time and thus cannot be ascribed to climatic variations.

There is, on the other hand, a very distinct line between Messinian Evaporites and Pliocene marine sediments, indicating a very sudden and drastic transition from evaporite-forming to permanent marine conditions at the end of this period.

The most surprising evidence was brought to light by drillings in the actual floor of the deep basins: a typical "sabkha-facies", the formation of which is usually attributed to a coastal desert environment subjected to periodical inundations (SHEARMAN, 1963), was found. Similarly spectacular was the variety of sediments encountered, testifying all sorts of conditions for sedimentation: deserts, torrents, fresh water- and salt-lakes, lagoons with stagnant waters and, finally, a marine environment. The discovery of a typical "bull's eye pattern", the arrangement of Evaporite sediments found in salines (SCHMALZ, 1966, 1969, 1971), added the last clue for the conviction of an extensive desiccation of the Mediterranean during the Messinian.

Thus the D.S.D.P. had furnished sufficient arguments to support the theory of catastrophic events in the Messinian: within a very short time-span (1-2 Mio years), the Mediterranean underwent repeated cycles of evaporation and inundation, which led to the build-up of enormous amounts of Evaporites. With the beginning of the Pliocene, this phase was finally interrupted by a sudden and permanent marine transgression (RYAN & al., 1973).

Geological models

The geological data led to a number of different hypotheses that have been critically reviewed by SCHMALZ (1966, 1969), HSÜ (1972a) and DROOGER (1973). There are three main models to explain the Messinian events.

The deep-water deep-basin model (SCHMALZ, 1966; SELLI, 1973a)

According to these authors, the depth of the Mediterranean basins at the time of the Messinian was practically equal to that of today. To explain the Evaporite-deposits, they suggest a high rate of evaporation, an extreme concentration of the sea-water and hence an increase in salinity to the degree of precipitation. However, all the evidence of a desertification of the basins, as well as the actual pattern of sedimentation, have been disregarded and this particular model therefore must be rejected.

The shallow-water shallow-basin model (NESTEROFF, 1973a + b)

This model is based on the presupposition that the Mediterranean basins were no more than a few hundred meters deep during the Miocene as yet. These epicontinental basins are thought to have been cut off from the Atlantic repeatedly in the course of the Messinian, leading to the cyclic deposition of Evaporites. The lack of plankton- and benthos-species in the Evaporites does not allow for a continuous connection with the Atlantic. Simultaneously a rapid and continuous subsidence of the Mediterranean basins was initiated, reaching 1000 to 2000 meters in the Messinian alone. The continent, on the other hand, was marked by the onset of a period of intense orogenesis. The submerged canyons and terrestrial sections of Evaporites are explained by Plio-Quaternary morphogenetic adjustments.

The shallow-water deep-basin model (RYAN & al., 1973)

This model has been proposed by the scientists participating in the D.S.D.P. We are giving a short review here. For detailed information we refer to the publications of the authors HSÜ (1972a + b, 1973, 1978), HSÜ & al. (1973, 1977b), RYAN (1973) and CITA (1973).

According to this model, the continuous subsidence of the Mediterranean basins since the beginning of the Oligocene had led, at the time of the Messinian, to a state close to the present one, post-Messinian modifications being limited to regional readjustments. In a first phase of the Messinian events, the connections between the Mediterranean and the Atlantic became limited such as to prevent a compensation in salinity, causing considerable Evaporite-deposition in the Mediterranean. The interruption of this last contact with the Atlantic resulted in a drastic lowering of the sea-level. This, in turn, led through the change in mass-proportions to considerable isostatic readjustments, affecting particularly the margins of the basins. It is during this period of desiccation mainly, that the rivers have carved the now submerged canyons into the margins of the continental plate.

A new, cataract-like connection with the Atlantic, according to MULDER & PARRY (1977) in the region of Gibraltar, opening and closing in response to a complicated equilibrium between erosion and emergence, marked the following period of cyclic changes. Phases of evaporation that culminated in desert-conditions alternated with inundations causing a marine environment in cycles of about 10 000 years each. Again, isostatic responses, similar to the Quaternary ones in Scandinavia, had to be expected.

Towards the end of the Messinian a new outlet of the north-east European Paratethys directed waters into the eastern Mediterranean, leading to a whole series of fresh water- and salt-lakes that have been named "Lago Mare". The pattern of "Lago Mare" as it has been reconstructed from sediments reflects the palaeogeographical complexity of the Mediterranean. The period of "Lago Mare" lasted approximately 100 000 years.

"Lago Mare" and with it the Messinian were ended by geomorphological adjustments and the sudden marine transgression from the Atlantic that marked the onset of the Pliocene.

Both the "shallow water" models are based on the "bull's eye pattern" of the "sabkha-facies", i.e. on a desertification of the Mediterranean basins, the salinity crisis. The sedimentological, palaeontological and tectonic data is controversial and allows for different interpretation. The bone of contention is obviously the depth of the basins at the time in question.

In its efficiency, simplicity and completeness in what concerns the explanation of the Messinian events in all their complexity the "deep basin" model of Ryan & Hsü is the much more convincing one. Furthermore, some of the data can hardly be explained by Nesteroff's "shallow basin" model, as for example:

- the absence of stratigraphic deformations in the Evaporite-deposits;
- the admittedly controversial presence of deep-sea organisms in the pre- and post-Messinian sediments;
- the formation of the canyons, which requests extremely complex tectonic movements according to Nesteroff's theory.

It seems therefore justified to use the Ryan & Hsü-model as the basis for a working-hypothesis in floristic and systematic research.

Climatic implications and palaeontological evidence

From the Burdigalian onwards the climate of the Mediterranean area was marked by an ever-increasing aridity that reached its maximum in the late Miocene, affecting considerable parts of Central Europe as well (Benda, 1973). Though palaeobotanical evidence is scarce, it has been established conclusively that in this period a flora of steppic character extended through the above areas (Berger, 1953, 1958). A great affinity between the local floras of the Mediterranean has been proved for this era (Bertolani-Marchetti & Cita, 1975) and signs of "modernism" could already be found (Trevisan, 1967; Benda 1973).

The results of the D.S.D.P. allowed for extremely interesting palaeoecological reconstructions of the upper Messinian: pollen-analytic evidence suggested cyclic variations in conditions with their respective changes in the composition of the flora and in types of vegetation. Furthermore, it was shown that the montane and consequently the "alpine" zone too were considerably lowered at times, forcing the thermophilous vegetation to retreat. At site 132 e.g., in the actual Tyrrhenian basin, pollen-analysis implied a typical montane forest, indicating a fairly cool climate (Bertolani-Marchetti & Cita, 1975). This is in accordance with the cooling-phase of the late Miocene (Bandy, 1973; Hsü, 1973), which is considered to be an effect of the desiccation (Ryan & al., 1974). With the general lowering of average temperatures, the coastal areas of nowadays would have become plateaus.

It is important to notice that evidence of a vegetational cover has been found in the actual basins. The results of pollen-analysis suggest a whole variety of facies subject to frequent changes in response to environmental oscillations (BERTOLANI-MARCHETTI & CITA, 1975).

These palaeoecological and palaeobotanical studies call to our attention the importance of the salinity crisis for the flora, and hence for floristics. It is possible to generalize from this data and draw conclusions also for species that cannot be traced in the actual sediments.

Significance of the salinity crisis: the Messinian Model

The geological theory of a salinity crisis in the Mediterranean during the late Miocene allows to look at the floristic connections from a totally new, even revolutionary point of view:

Already the increasing aridity of the climate must have caused an upheaval in the Arcto-Tertiary flora of rather subtropical character. Many species were forced to emigrate or condemned to extinction. The Mediterranean flora thus became more and more impoverished and its stability was no longer granted. At the same time young and agressive floristic elements, orophytic and steppic plants of eastern origin, conquered the soils of Europe in connection with the continuing formation of alpine chains and the extension of steppes.

The desiccation of the Mediterranean offered new ground for colonization where, through the lack of an established vegetational cover, competition was negligible. In Figure 1, we are giving an impression of Messinian vegetation and its altitudinal distribution according to the data of BERTOLANI-MARCHETTI & CITA (1975) and BERGER (1958) from the Tyrrhenian basin. This reconstruction cannot be but a flash on a limited area at a particular point in time and ought not to be generalized.

Along the exposed sides of the basins conditions at times were apparently favourable to a lowering of the vegetational zones, allowing for the growth of e.g. deciduous and coniferous forests far below their usual altitudinal limits. Through this lowering of the vegetational zones the "alpine" character of the higher regions became accentuated. The coasts were turned into plateaus and islands, as e.g. Corsica, were effectively peaks of at least 4000 meters in height in correlation, whilst the "alpine" aspect of the continental areas was stressed by isostatic readjustments. The vegetation was hardly homogeneous though, with all sorts of habitats being offered: depending on differences in morphology, exposition, soil etc., a whole variety of local facies must have developed (e.g. cliffs, ravines). The considerable erosive action continuously supplied new terrain for colonization. Only the abyssal plains, the actual floor of the basins, would have remained more or less sterile, their distinct character of desert or semi-desert allowing for a halophytic vegetation at the most. Their margins, finally, would favour a steppic flora or, where the water-supply was granted, riparian and delta forests.

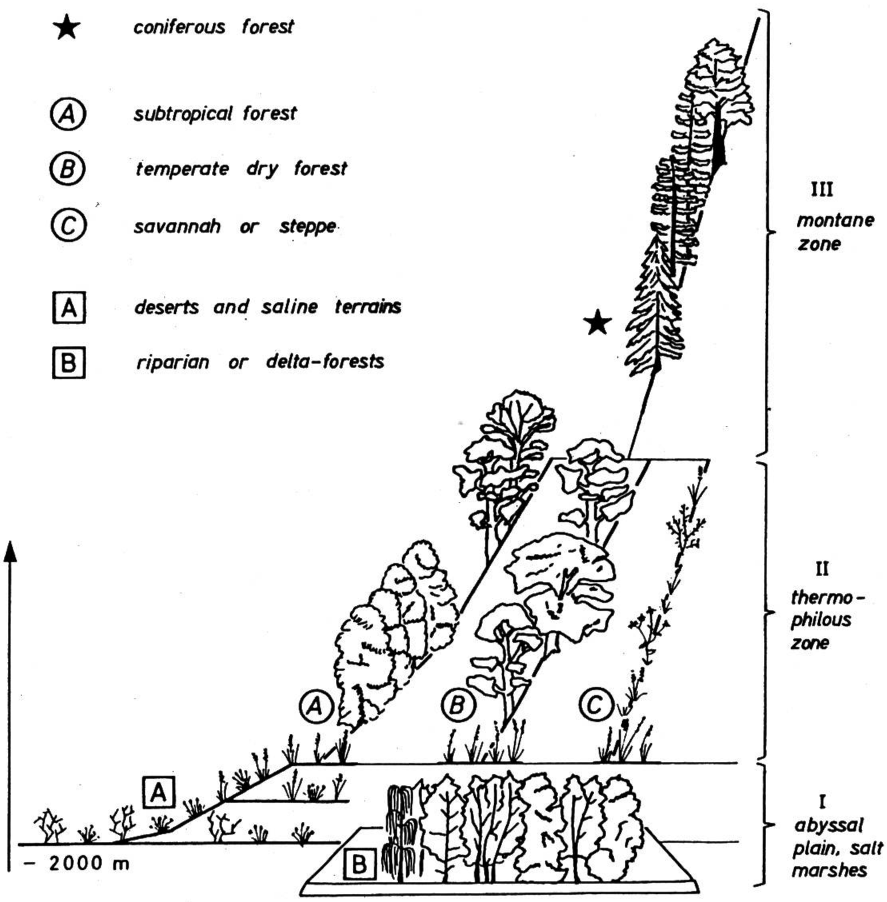

Fig. 1. – Reconstruction of vegetational zones and their altitudinal distribution in the Tyrrhenian basin during the Messinian (according to the data of BERTOLANI-MARCHETTI & CITA, 1975, and BERGER, 1975).

Typical representatives:

I. [A] *Cyperaceae, Chenopodiaceae, Poaceae.*

[B] *Liquidambar, Alnus, Salix.*

II. According to exposition and local conditions on the slopes:

(A) *Magnolia, Liquidambar* (lower altitudes, humid, e.g. ravines).

(B) *Quercus, Ulmus, Carya, Juglans.*

(C) *Poaceae, Asteraceae, Fabaceae.*

III. ★ *Pinus, Picea, Abies, Cedrus, Tsuga.*

The cyclic phases of desiccation with the accompanying changes in the environment evoked dynamic responses in the flora: changes in composition and extension of the various plant-communities would have resulted.

Not only did the morphological and ecological upheaval of the salinity crisis strike the last blow to the already disconcerted Arcto-Tertiary flora, it also allowed for new and significant floristic exchanges. Multiple paths between the various Mediterranean basins opened up along the bared "submerged" chains leading to a veritable explosion in migrations, to the profit of, above all, aggressive species possessing sufficient genetic plasticity. At the same time, through the expansion of steppes and the continuing formation of the Alps, new transcontinental connections were established, with Africa and Asia for example. The lack of competition in these new conditions would have particularly encouraged the immigration of alpine taxa from the east and also favoured an expansion of their altitudinal limits. The lowering of the vegetational zones furthermore explains the presence today of "alpine" species on the Atlantic chains.

The complexity of the geological events, the environmental conditions and the morphology of the emerged chains encouraged the exchange of floristic elements while at the same time acting as a filter, allowing for certain species to pass only. The result was a thorough re-distribution of floristic elements, though local conditions would have imposed a particular direction on their migration.

With the deterioration of the climate, the Pliocene "diluvium", and the Quaternary glaciations proper the pattern left by these floristic connections became disrupted. Only a certain number of species bear witness of that distant past. Their study, however, will not only allow for an evaluation of this model but also elucidate some of the mysteries of the European flora, and the Mediterranean one in particular.

Discussion

Long-distance dispersal has often been used as a last resort in attempts to resolve floristic enigmas. First proposed by ENGLER in 1879 for the case of Corsica, this theory has gained momentum since all the many models had to be rejected on grounds of geological or floristic evidence. With the rotation of Corsica dating from the Oligo-Miocene, it appeared to be the only explanation for the presence of "modern" and alpine species on Corsica.[1]

However, many authors have now cast doubts on the efficiency and importance of long-distance dispersal. Thus, according to LEVIN & KERSTER (1974), the range of wind-dispersal is generally no more than a few hundred meters. VAN DER PIJL (1969) confines the predominance of wind-dispersal to floristically impoverished areas and oceanic islands such as Hawai, where distances of several

[1]Though the lowering of the sea-level during the glaciations (GUILCHER, 1968) might just have allowed for a temporary connection between Cap Corse and the Continent, it would have been a lagoon at the most and hence be of local and very limited interest only.

kilometers may be achieved. As for distribution by animals: RUNEMARK (1969) and MÜLLER (1977) consider it of very limited importance over long distances.

RUNEMARK (1969) in fact came to the conclusion that even short distances provided an effective barrier to distribution by birds. In his work, he showed that new arrivals are doomed to failure in any balanced vegetation. Naturally, the glaciations must have caused some disturbances on Corsica too, facilitating the immigration of new species. However, according to RUNEMARK (1969), even a disturbed habitat is adverse to the establishment of a haphazard isolated intruder. The correlation between the efficiency of dispersal-mechanisms and the actual area occupied is thus small in Angiosperms (WULFF, 1950). If, on the other hand, a whole section of a flora ("cortège floristique") is advancing on new terrain, the necessarily young and aggressive character of these elements would turn them into a phalanx that could easily win the upper hand over the long-established species. The multiple connections of the desiccated Mediterranean basins would have encouraged this kind of migration. It is particularly the presence of whole floristic elements on Corsica, the definable floristic connections, combined with the lack of adaptive radiation that cannot be explained by an immigration through long-distance dispersal.

The presence of "modern" taxa on Corsica is generally ascribed to Quaternary immigration. However, the typically alpine taxa of Nordic origin (KULCZINSKI, 1923), whose establishment in Central Europe can be traced to the time of the glaciations, are absent on Corsica. Other fairly recent introductions to the Mediterranean (GREUTER, 1970) are poorly represented: e.g. *Primula* L., *Gentiana* L., *Pedicularis* L., *Poaceae* L., *Cyperaceae* L. The argument of "overcrowding", i.e. a limit to the number of taxa an area can support, is of no avail. In fact, PARRIAT (1951), who observed the same lack of Nordic taxa in the moss-flora of the Corsican mountains, considers this to be due to a Tertiary colonization rather than to the effects of competition. It would certainly be hard to explain why it always had to be the Nordic taxa that were defeated by competition. The lack of these Nordic taxa, on the contrary, gives an indication to the time of immigration: with a Tertiary colonization of Corsica it would have to be expected.

The presence of alpine species on Corsica, on the other hand, can easily be explained with the Messinian Model: because of the alpine orogenesis, the climatic changes and the lowering of the vegetational zones in the Mediterranean, alpine taxa of Asian provenance could expand westwards and also establish themselves on "islands" such as Corsica (Fig. 2).

We do not exclude certain isolated cases of long-distance dispersal, but we agree with WULFF (1950) that they ought to be supported by data about the mechanism of transport and the possible path of migration. For Corsica the only well documented case apart from introductions by man is *Menyanthes trifoliata* L. (REILLE, 1975).

As for what concerns the stage of development of the Messinian flora: though palaeobotany cannot prove it directly, the existence of a large number of "modern" taxa is certainly in full agreement with the theories about the evolution of the Angiosperms (CAIN, 1944; TAKHTAJAN, 1954; AXELROD, 1970). WULFF (1950) thought that alpine elements existed already in the Tertiary and according to BRAMWELL & RICHARDSON (1973), the period from −10 Mio to −1 Mio years was an important phase in the differentiation of the various types of mountain vegetation. For the flora of the Aegean islands, in particular, the dating

Fig. 2. – Model for the migration of orophytic plants in the western Mediterranean during the salinity crisis.

proposed by various authors (SNOGERUP, 1967; GREUTER, 1970, 1971; RUNEMARK, 1971) is in perfect accordance with our model. Greuter, for example, sets the isolation of Crete in the order of 10 Mio years, thus explaining the large number of Tertiary relict, though not necessarily endemic, species in its flora. KÜPFER (1974), moreover, proved the existence of a Tertiary basis, common to the Pyrenees and the Alps, for the boreal species that invaded Spain during the glaciations. The flora of the southern hemisphere, let it be recalled, even dates back to the Lower Tertiary (VAN STEENIS, 1971; BECK, 1976).

Rapid and brutal though the environmental changes during the Messinian may have been, their impact on the vegetation needs not have been fatal. The Quaternary developments, palynologically well documented, were of the same order of magnitude. Furthermore, KERSHAW (1974) found cycles of regression and expansion in the Australian subtropical forests that lasted 10 000 to 15 000 years, time intervals comparable to those inferred for the Messinian events.

Having studied in detail *Aconitum napellus* L. subsp. *corsicum* (Gayer) Seitz, *Armeria fasciculata* (Vent.) Willd., *Brassica insularis* Moris, *Cynara corsica* Viviani, *Digitalis gyspergerae* Rouy, *Digitalis lutea* L., *Echinophora spinosa* L., *Gentiana lutea* L., *Helichrysum frigidum* Willd., *Morisia monanthos* (Viv.) Ascherson, *Onopordon horridum* Viviani, *Onopordon illyricum* L., *Pycnocomon rutifolium* (Vahl) Hoffmanns. & Link and *Silene corsica* DC. as test-cases, we come to the conclusion that the Messinian Model is not only in full agreement with their distribution and relationships, it is the only plausible explanation. The surprising similarity of the Messinian Model with the hypotheses of continental bridges is noteworthy. In the former, however, the well-defined floristic connections are no longer associated with an abstract "geological geometry", they are the logical consequence of the paths of migration, intimately linked to the structure of the Mediterranean basins in the Messinian. The key-note of BRAUN-BLANQUET'S (1926) model for Corsica, a palaeogen flora developed "in situ", is taken up in the Messinian Model, which finally provides a satisfactory and credible explanation for the chorological complexity, the various floristic elements and their obvious connections, without being in contradiction to geological and palaeontological evidence.

Of course the possibilities for an application of the Messinian Model go beyond Corsica. From a systematic point of view the case of the *italica/patula*-group in the genus *Silene* L. merits mentioning: this large circum-Mediterranean steppic complex together with the closely related, highly endemic, chasmophytic species is a prime example for a distribution- and relationship-pattern that can be explained easily and with surprising elegance using the Messinian Model. The situation and systematic position of the representatives of *Digitalis* L. in the Spanish sierras becomes comprehensible with an immigration of "alpine" elements in the Atlantic chains as a result of the lowering of vegetational zones during the salinity crisis (Fig. 2). Furthermore, the puzzle of the "African connections" (*Erica* L., *Helichrysum* Miller, *Silene* L.) is given a new aspect by the expansion of montane steppic environments over vast areas, which acted as a bridge between the different regions during the Messinian. As a general effect the striking number of pioneers amongst the true Mediterranean plants (e.g. *Morisia monanthos* (Viv.) Ascherson, *Trifolium subterraneum* L., *Physanthyllis tetraphylla* (L.) Boiss. and various species of *Digitalis* L. and *Silene* L.) might be seen in connection with the Messinian events, particularly if we consider the extent of erosion implied. There is, finally, the somewhat exaggerated xeromorphism of the typical Mediterranean plants.

Could this phenomenon be a remainder and reminder of the extreme aridity in Messinian times?

Conclusions

Our first applications of the Messinian Model (some of which will be published in detail shortly) are certainly convincing. Fast as geological research is moving nowadays, some minor adjustments of the theories and consequently the Messinian Model are to be expected, though we very much doubt that fundamental changes will be necessary. Obviously, more research will be needed to finally establish the value of the Messinian Model, i.e. the impact of the salinity crisis on the flora. Our projects concentrate on the western Mediterranean. However, the eastern parts with the Aegean flora in particular ought to be reconsidered too under this new aspect. The coincidence of theories (e.g. GREUTER, 1970) is very promising. The trans-continental connections, especially with Africa, also deserve attention.

Further palaeobotanical evidence from coastal and submerged areas could yield crucial information about the state and character of the flora at the time.

Detailed climatic studies and particularly meteorological computations for local situations will be indispensable in view of the importance not only of the climate in general but the actual weather-conditions too (fog-zones, inversions, etc.).

Zoological research, so far depending on the geologically unsatisfactory Tyrrhenian continent. could also profit from the theory of the Messinian salinity crisis and, last but not least, the coincidence of the transition from the forest-dweller Ramapithecus to the savannah-hunter Australopithecus (PILBEAM, 1972; HSÜ & al., 1977b) with the expansion of steppes in the Messinian is remarkable after all.

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