Recent progress in the botanical exploration of Greece

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It is indeed a great honour to receive this award, which is a token of appreciation from respected colleagues. It is a particular pleasure that it takes place in these magnificent surroundings. If I am not mistaken two Danish architect brothers, Hans Christian Hansen and Theophilus Hansen, were involved in building the old University of Athens at the time of King Otto. In spite of his Greek-sounding name, Theophilus Hansen was pure Danish, but his parents were members of the philhellenic movement of the early 19th century – western intellectuals who admired everything Greek and supported the Greek struggle for independence. Thus the name Theophilus, given to their son who was born in 1813.

I have had the pleasure and privilege to work on the Greek flora for more than 50 years. [photo] Here is a young couple on their first joint trip to the Aegean islands in the mid-1960. I am proud to say we are still married, and Barbro is sitting in this hall today.

[photo] This photo was taken about ten years later. On this occasion the elderly gentleman in the middle, Karl Heinz Rechinger, received an honorary doctorate from the University of Lund in Sweden. On his left-hand side is a much younger version of your present speaker. The Austrian botanist Karl Heinz Rechinger was born in 1906. His father was also a botanist in Vienna and a friend of Svante Murbeck, who at that time was professor of botany in Lund. Towards the end of the First World War, when living conditions in Vienna were difficult, the 12-year-old boy was sent as a Kriegskind to live with Svante Murbeck (“uncle Svante”) and earned his first money by mounting pressed plants at the Lund Botanical Museum. During the Second World War, after the annexation of Austria to Nazi Germany, Rechinger like everybody else of his age was drafted into the Army. He was a member of a small group of German and Austrian botanists, one of whom had friends in high places. Probably thanks to these contacts they managed to avoid being send to the Russian front, and instead were sent to Greece to collect plants. The official task was to collect wild relatives of cultivated plants, to be used in long-term breeding projects. Rechinger interpreted this very widely, saying “that means all flowering plants”. And so he spent the whole spring and summer of 1942 in Crete as a German soldier, studying and collecting plants. It was certainly not Rechinger’s own choice to come to Greece in German uniform – politically he was rather the opposite of the ruling ideology at that time. In spite of the unfortunate circumstances of this visit, he remained a true friend of Greece all his life. He died in 1998, at the ripe age of 92.

[photo] Partly inspired by Rechinger, the Swedish botanist Hans Runemark started a series of investigations of the Aegean flora and built up a research group at the University of Lund in the 1960s. Here is Runemark in the field, together with Dimitrios Skopelitis, captain on the kaiki Panormitis which was our base for several of these expeditions. A few newly discovered species have been named after Runemark, including this beautiful Omphalodes on the left which is endemic to a small area in south-eastern Peloponnisos.

Fifty years later a group of Runemark’s former student made a jubilee trip to Naxos and Amorgos. [photo] In the harbour of Naxos we found to our delight that the small ferryboat travelling the route between Naxos and Amorgos is now named Express Scopelitis, after the old captain. After arriving in the harbour village of Katapola on Amorgos we went for a walk in the surrounding. [photo] Passing the nekrotafio, our attention was drawn to a new and beautifully decorated grave. [photo
Coming closer we could see that the person laid to rest here is none other than Dimitros Skopelitis (1926-2014). With him he had got two of his most important attributes, the anchor and the violin.

The nineteen-sixties was also a time of much botanical activity at Greek institutes. A successful research group was built up at the University of Patras by Dimitrios Phitos, including prominent botanists such as Theodoros Georgiadis, Gregory Iatrou, Dimitris Tzanoudakis, Rea Artelari, Dimitris Christodoulakis and others. Almost all of these are now retired, and because of the economic crisis there has been little new recruitment. Fortunately there are now reasons to be cautiously optimistic about the Patras institute as my friend Panayotis Dimopoulos and some of his co-workers have now moved there. Good botanical research is also carried out in Athens, Thessaloniki and elsewhere.

An important development in the mid-1960 was the establishment of a Natural History Museum in Kifissia by Angelos and Niki Goulandris. Their most prominent plant collector for several decades was Elli Stamatiadou. Here are Kiria Niki on the left and Kiria Elli on the right, photographed in the foothills of Mount Parnassos. The plant in the foreground is a rare and beautiful one: [photo] *Paeonia pannassica*, first collected already in the 1850s by the Greek botanist Orphanides, but recognized as an independent species only much later.

Just as the history and civilization of Greece has long attracted foreign scholars, so has the rich and interesting flora of this country. [photo] One of the leading explorers in the 19th century was Theodor von Heldreich, a German botanist who arrived in Athens as a young man in 1842 and stayed for the rest of his life. He married a Greek woman of a well-known family and had two daughters. The Heldreich family grave is in the central cemetery of Athens, and there is even a street named after him (lower left). In his long career Heldreich collected about 700 new species, for instance, the beautiful *Aquilegia amaliae*, named after Amalia, Queen of Greece and wife of King Otto. Several species have been named in honour of Heldreich, for instance, the famous *Jankaea heldreichii*, an endemic of Mount Olympus.

A Greek contemporary of Heldreich and equally important as a botanical explorer was Theodoros Orphanides. He may not look like a field botanist in this photo, but in fact he traveled to remote mountain areas and made several spectacular discoveries, such as *Biebersteinia orphanidis* and *Adonis cyllenea*, both rare endemics of northern Peloponnissos, long believed to be extinct but recently rediscovered. Another of Orphanides’ discoveries was *Galanthus reginae-olgae* (also named after a Queen). Contrary to most snowdrops it flowers in the autumn, with leaves developing later and seeds ripening in the spring. Several species have been named after Orphanides, such as the beautiful tulip on the lower right.

My first major work on the Greek flora was a study of the genus *Nigella* on the Aegean islands. [photo] This group has an interesting pattern of differentiation with recognizable local populations on almost every major Aegean island [5 photo shifts]. These are annual plants, well suited for cultivation and experimental studies. The map on the right shows the results when plants from Naxos were experimentally crossed with plants from other island and mainland populations. The numerals and the thickness of the lines indicate the percentage of well developed pollen in the hybrids, and is a measure of the genetic similarity between the parents. Values below c. 50 mean in practice that there is no seed-set and further gene exchange is thus prevented. As you can see, populations from different Kikladian islands are closely related and must be considered to belong to the same species, whereas there are sterility barriers between the Kiklades and the Greek mainland as well as between the Kiklades and the East Aegean Islands. It appears, for instance, that crossing a plant from Naxos with one from Karpathos produces a hybrid with low fertility value. They are like
horse and donkey; they can be crossed and produce a mule, but this is sterile so there will be no further gene exchange and we are consequently dealing with separate species.

[photo] For most northern Europeans this is probably the quintessential picture of Greece. But there is also a different Greece. [photo] This photo was taken a few months ago in the Prespa National Park in the northwest corner of the country, showing the pontoon bridge in Lake Mikri Prespa to the island of Agios Achilleios. Few European countries have a diversity similar to that of Greece. Comparing, for instance, the high mountain flora of Lefka Ori in western Crete with that of Rodhopi on the Bulgarian border there is a similarity of zero – not a single species in common.

After I moved to Copenhagen in 1973, a research group was built up there with special reference to the Greek mountains. [photo] This map shows localities where members of the Lund/Copenhagen group have collected, photographed or observed plants from the early 1960s onwards. A Flora Hellenica Database, started in 1989, now comprises almost one million records – not only our own but also many specimens gathered by Greek and German colleagues as well as literature reports.

[photo] In 2013 a group of five Greek and three foreign botanists led by Panayotis Dimopoulos published an annotated checklist of the vascular plants of Greece. This is an important reference work, listing 5,572 species in tabular form, with brief data on their distribution, ecology and life form. There are also long lists of synonyms as well as a photo appendix.

[photo] An Atlas of the Aegean Flora appeared in 2016, in two volumes – a total of 1,578 pages or 6.2 kilos. It comprises distribution maps and brief descriptions for all species and subspecies with reliable records from at least one Aegean island – 3,362 maps in all. [photo] Here is an example from the map volume on the left and the corresponding part of the text volume on the right. About 400 of the most interesting and photogenic species are illustrated in a photo appendix. [photo] Here is one example: The autumn-flowering *Cyclamen graecum* (left) is widespread in southern Greece, whereas the spring-flowering *Cyclamen persicum* (right) is an East Aegean species. The epithet *persicum* is a mistake by Linnaeus; this species which is the wild progenitor of most of the cultivated cyclamens does not occur in Persia, but is in fact restricted to the East Aegean islands, western and southern Anatolia and Cyprus.

[photo] This map shows the number of species recorded from Aegean islands and peninsulas. The numbers range from 1965 on Crete down to a few hundred on the smallest islands. Only one year has passed since the publication of the Aegean Atlas, but there have already been important amendments for islands such as Rodhos, Astipalea, Amorgos and Thasos.

[photo] The island of Crete has more than 200 local endemics. Some are rare and have a very restricted distribution (such as *Anchusa cespitosa* in Lefka Ori), others are relatively common over most of the island (such as *Ebenus cretica* and *Phomis lanata*).

[photo] The East Aegean islands also have a rich and interesting flora, including some local endemics and many Anatolian species. *Fritillaria rhodia*, for instance, is a local endemic of Rodhos, discovered as late as 1960. *Convolvulus coelesyriaus* has only one locality on Greek territory, on the small island group of Kastellorhizo, and otherwise occurs in the adjacent South Anatolia.

[photo] The Athos peninsula is a unique place, both with respect to culture and to natural history. As you know, it constitutes a semi-independent monastic community off limits not only to women but also to female domestic animals. For that reason there has been no grazing by cows, sheep or
goats for several centuries, so much of the peninsula is still *pragmatiki fisi* of great interest to botanists. As you can see, many of the species have names such as *athoa* or *sancta*.

[photo] Many botanists have the impression that Crete has the richest and most interesting flora in Greece. This is both true and false. Due to isolation and the presence of high mountains it has many unique species, but with respect to the total number of species it is surpassed by mainland areas of the same size: 1965 species in Crete as compared to 2600-2800 in areas of the same size in the northern parts of the mainland. In fact, the central Balkans may have the highest botanical diversity anywhere in Europe. Altitudes range from sea level to nearly 3000 meters, and there is much variation in climate, geology, soil conditions and land use.

[photo] From the Flora Hellenica Database we have calculated the number of species recorded in grid squares of 20 x 20 minutes of latitude and longitude throughout Greece. The ten top-scoring squares have here been highlighted. As you can see, they are all in mountainous areas of the mainland and northern Peloponnisos.

[photo] This is a similar map for grid squares of 10 x 10 minutes, colour coded from light yellow for squares with the lowest number of species through dark yellow to orange and red for the richest squares. At this scale the map reflects not only the actual diversity but also the degree of botanical exploration. It can be seen, for instance, that squares in the far north-east are light yellow, certainly because this part of Greece has been relatively poorly explored.

[photo] A Greek friend helped me produce this map showing the number of range-restricted species per 10 x 10 minute squares. The concept of “range-restricted” was introduced in the Vascular Plant Checklist, and simply means a species where the linear distance between the furthest points of occurrence is less than 500 km (that is approximately the distance from Kalamata to Alexandroupolis). There are hotspots almost throughout Crete and then in mountainous areas from Taigetos to the northern borders. Studies of this kind will help identify areas where resources are best used for conserving biodiversity.

[photo] Greece in general and the Aegean area in particular is of great biogeographical interest and an ideal area for studying evolution and speciation. Here are three examples of distribution patterns demonstrating some of the biogeographical borders. *Ostrya carpinifolia* is a deciduous shrub which is widespread in SE Europe, extending to the islands of Thasos, Samothraki and Evvia, but not further into the Aegean archipelago. *Nigella doerfleri* is an annual herb, neatly restricted to the Kiklades and Crete. *Dianthus elegans* is a perennial herb of the East Aegean Islands and Western Anatolia. The phytogeographical border between the Kiklades and the East Aegean Islands is rather distinct and in actual fact constitutes the biological borderline between Europe and Asia. I am sorry to say to our East Aegean friends that biogeographically they belong to Anatolia.

[photo] According to the theory of island biogeography, if you plot the size of islands on the horizontal axis and the number of species on the vertical axis, and use logarithmic scale on both axes, then the dots should appear on a straight line. In practice islands differ not only in size but also in ecological complexity and degree of botanical exploration. In this diagram, for instance, the difference between Samothraki and Limnos is at least partly explained by the fact the Samothraki has been subject to detailed botanical study whereas Limnos is comparatively poorly explored. Also according to theory, remote islands should be poorer in species than those close to the mainland. In the diagram the Kiklades (which are relatively far from the mainland) have been marked with open circles and other islands with black dots. There is a slight tendency for the open circles to be below the regression line, but it is not particularly significant.
The picture becomes clearer if you visualize species numbers like this. For each of the five regions there are two numbers: The first indicates the total number of species, and the second indicates the number of species not extending across the dotted line into the neighboring region. For instance, 2410 species have been recorded on the East Aegean islands; 937 of these have not been found in the Kiklades. A total of 1661 species have been recorded on the Kikladian islands; only 188 of these do not extend into the East Aegean area. Looking around we can see that the second figure in each pair is consistently higher outside the dotted line than inside. The Kikladian islands are almost as rich in total number of species as other islands of the same size, but this is mainly due to the presence of many omni-Mediterranean species which are evenly distributed throughout the area. With respect to species with biogeographical borderlines in the area, the Kiklades are indeed somewhat impoverished.

The Flora Hellenica Database, which has been built up over a period of almost 30 years, now comprises about 940,000 geo-referenced records. This makes possible many kinds of statistical studies of biogeography and evolution. Here is a simple example: The island of Karpathos is situated half-way between Crete and Rodhos. Is the flora more similar to that of Crete or that of Rodhos? Comparison of floristic lists gives an index value of 60 for Karpathos-Crete and 33 for Karpathos-Rodhos. The Karpathos flora thus has greater similarity with that of Crete.

This conclusion is not new. In fact, my friend Thomas Raus pointed out already in an article in 1991 that the flora of Karpathos is European rather than Anatolian. But here is a firm statistical basis for the claim. The background is paleogeographical. One of the earliest events in the breakup of a large Aegean land block was the penetration of a sea arm between Karpathos and Rodhos at a period when there was still land connection between Karpathos and Crete. With the nearly one million geo-referenced records in the database we can now make similar studies throughout the area.

I hope to be able to work with the database for a few more years. The whole dataset will then be handed over to younger Greek colleagues who are more skilled with modern statistical methods and biogeographical theory. Undoubtedly there is still much to be extracted from the database, especially when compared with databases for climate, geology, soil conditions and other ecological parameters. But this is better left to younger forces rather than retired professors. One of the positive developments in Greece in recent years is an increased appreciation of the natural heritage of the country and a steadily increasing pace of botanical exploration. No less than 180 new species and subspecies have been described from Greece in the 12-year period since 2005. Perhaps not all of them will become generally recognized, but it certainly indicates that there is still much to be discovered. In addition to the basic taxonomy, floristics and biogeography, much remains to be done in the fields of ecology, evolution and conservation.

According to a recent search in the database, my field days in Greece amount to 1,482, or a little more than four years. It has been a pleasure and a privilege to work in this country where I have always felt welcome and have obtained many friends. I would like to conclude with a bunch of wild tulips from an olive grove on the island of Chios.