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The Beech in the Crimea, its systematic position and origin.

By *E. V. Wulff*, Moscow.

I. Determination of the area.

The Crimean peninsula is the only region in eastern Europe inhabited by the beech, entirely isolated from the continuous west-european area by the Black Sea and steppes, whose northern part, covering the plains is predominantly saline. On its other extremity this crimean area of the beech is separated from its dwelling place in the Caucasus *) by the likewise saline region of the Kerch peninsula, the Kerch straits and the steppes of the Taman peninsula. On the south it is separated from the habitat of the beech in Asia Minor by the waters of the Black Sea.

Thus the range of the beech in the Crimea represents at the present time an island area, whose origin and previous connection with the bodies of beech forests situated in the countries surrounding the Crimea offers a most interesting problem still waiting its solution.

At the present time the beech covers approximately 12 per cent of the whole forest area of the peninsula, forming a rather narrow band which stretches across the mountainous part of the Crimea in the direction from west to east.

This latter is intersected by three mountain chains also stretching from west to east, their elevation above sea level and geological age increasing from north to south. The northernmost third chain is the lowest and at the same time the youngest of them, consisting of Tertiary rocks. It is followed by the second one formed chiefly of chalky deposits and finally by the first consisting mainly of jurassic limes and loamy shists.

The third and second chains of the Crimean range are covered with oak forests or show traces of their former presence. Where

*) It is absolutely erroneous to connect by a continuous line the areas of *Fagus orientalis* in the Crimea and the Caucasus as is done by Lämmermayr (Pflanzenareale I, Reihe H. 2, Karte 18).

the forests spread over the Jurassic deposits of the first chain the oak is becoming replaced by the beech which first begins to appear on the southern slopes of the second chain at an altitude of 450—500 m. above sea level as a constituent of mixed forests. Only farther southward at a higher elevation these mixed stands give way to beech forests reaching the border of the table land which forms the summit of the Crimean range, the socalled Yayla, and in some places cover its surface up to an altitude of 1400 m. above sea level. On the southern slope of the main chain the beech in some places forms the upper forest limit being at the lower horizons replaced by the crimean pine, *Pinus laricio* var. *Pallasiana*, the latter in places being succeeded by the common pine, *Pinus sylvestris*.

These interrelations are determined, as we shall see farther on, by the history of the forest, while the general character of the habitat of the beech in the Crimea is due to edaphic and climatic factors.

2. Altitudinal limits.

The elevation of the main mountain chain of the Crimea is not the same throughout. It reaches its highest point, 1544 m. (the Roman-Kosh peak) near the middle of its extension and then gradually becomes lower towards its western and eastern extremities. The highest peak in the west reaches an altitude of about 640.1 m. and that in the east from 1152.1 m. to 714.7 m.

The following table shows the altitude to which the beech reaches in the mountains of the Crimea and the highest elevation of the respective part of the range.

Name of Yayla	Name of peak.	Maximum elevation of place in m.	Vertical limit of beech in m.	Difference in elevation in m.
Ay-Petri.	mt. Domus-Charysk	1258.8	1258.8	0
"	mt. Ay-Petri.	1258.8	1237.4	21.4
Babugan-Yayla	Roman-Kosh	1543	1360	183
"	Plateau, average	1451-1492		91-132
Chatyrdag	East slope — Eklisi-burun	1525	1400	125
"	Lower plateau.	1251.4-1280.2	1024.0-1252.2	227.4-28.0
Demerji-Yayla	mt. Demerji	1357	1280.2	76.8
Karabi-Yayla	Kara-tau	1258.8	1254.5	4.3

From these data it may be seen that at the western and eastern extremities of the range the beech not only reaches its upper rim but in some places occupies a part of the plateau, while in the center it does not attain its highest points, the distance between its upper limit and the most elevated point of the range varying from 4.3 to 283 m. The limit of the beech in the Crimea above sea level lies within the range of 1250—1400 m. the latter figure indicating the highest point.

Thus it may be said that the beech reaches the highest point of its vertical distribution only in an inconsiderable part of the mountain range, the central high Yaylas of the Crimea. Here, as shown by Mrs. Poplawskaya*), the beech assumes in the upper belt of its distribution the form of a bush, the result of the dying of the central trunk which is replaced by a number of secondary ones starting from the roots. These beeches resemble large bushes, each formed by 2—15 stems arranged in a circle and having a diameter of 20 to 43 cm. at breast height, as measured on 13 such stems.

These bush forms are moreover injured by the weight of the snow cover, wind, water currents, rolling down rock fragments, eating back of the shoots by cattle and by wild animals such as deer and goats. Such bush forms of the beech may be observed in the Crimea rather frequently on the spurs of the main range.

In many places of the range, in its lower regions, the beech, though it reaches up to the very crest, does not however assume such altered forms but disappears abruptly, leaving the impression as if its upper part approaching the summit had been cut off by a sharp razor. This circumstance and many others are evidence that the limit of the beech in the Crimea is an artificial one, due to the agency of man, chiefly the pasturing on the summits of the range of flocks of sheep numbering many thousands, goats, cattle and horses **) which have destroyed the arboreal vegetation over a considerable extent of the summit plateau.

It may be therefore stated that the limit of beech forests in the Crimea lies at approximately 1400 m. above sea level, but this is

*) H. I. Poplawskaya. On the character of the upper limit of the beech in the Crimea. Journ. of the Russian Bot. Soc. v. 10. 1925.

**) E. V. Wulff. The vegetation of the eastern Yaylas of the Crimea 1925.



Photo H. Poplawska.
Fig. 1. Bush forms of beeches in the higher belt of the chief mountain chain of the Crimea.

not the upper limit of the forest in general, since here the beech undoubtedly ought to give place above to pine forest. This is confirmed by the presence of isolated tall pines (*Pinus silvestris*) occurring on all the high Yaylas, and particularly by the fact that after 7 years protection from pasturing one of the areas of such a Yayla has become covered with pine saplings (1940—9250 specimens per hectare).

3. Climatic conditions.*)

Under the conditions prevailing in the Crimea the beech grows within the limits of the following temperatures:

January from -3° (Alabačh, 1250 m.) to 1° (Yaman-Kala).

July from 16° (Alabačh) to 21° (Yaman-Kala).

Precipitation fluctuates from 500 mm. (Karabi-Yayla, 974 m.) to 1000 mm. (Ay-Petri, 1180 m.).

Average yearly relative humidity varies from 70 per cent (Crimea State reservation, 685 m.) to 75 per cent (Yaman-Kala, Ay-Petri).

The wind conditions vary between 23 m/s (3) Crimea State reservation and 6,9 m/s (3) Karabi-Yayla, the winds occurring in the latter case every month and frequently.

The snow cover persists on the higher areas for 3 to 4 months (January—April).

The conditions of temperature and partly those of precipitation are those characterizing the beech climate according to Koeppen. The same cannot be said of humidity, particularly when we pass from the usual characteristic humidity to the cases when it falls below a certain level. Thus for Alabačh, situated at the upper timber limit 80 cases during one year are recorded when humidity was below 30 p. c., among them 30 cases when it was 20 p. c. In isolated cases humidity may fall below 1—4 p. c. We do not meet with such phenomena in the plain even in the desert. Here they are explained by south winds blowing from the free atmosphere.

Attention is drawn by the fact that the beech forests are peculiar

*) By S. S a p o z h n i k o v a from the data of the Division of Agricul. Metereology of the Institute of Plant Industry of the Lenin Academy of Agronomy and those of the Meteorological Division of the Crimean Water Service.

to the northern slopes. Unfortunately no figures are available that would characterize the influence exposition exercises on variations in climate. There is only the indication that the southern slopes differ from the northern ones by often losing their snow cover during the winter. The structure on the southern slopes points to the greater rôle played by evaporation. As a result the soil of the northern slopes and its vegetation are better protected by the snow cover from frost (reaching 24°) and dry winds; besides that they preserve at the beginning of the growing season a considerably greater part of the winter precipitations than the southern slopes.

Owing to the difference in the degree of heating existing between the northern and southern slopes, the relative humidity of the adjoining strata of the air will be different. Thus on sunny days the relative humidity in a beech forest exceeds by 5 per cent that at the meteorological station of the state reservation situated in the vicinity on the gentle southern slope of a small ridge. A comparison of steeper slopes would probably show a still greater difference. The difference in relative humidity determines also the difference in evaporation.

The above considerations may to a certain extent explain the preference shown by the moisture-loving beech for the northern slopes.

The light conditions in the beech stands of the Crimea have been studied by Prof. I v a n o v *) who comes to the following conclusions.

1. The intensity of radiation in the shade under the canopy averages 0.05 gr. cal. per 1 cm² in 1 mm. which is to evaporation in open places in the ratio of 1/20—1/25.

2. The relative content of physiological radiation in full radiation under the canopy in shaded places is always lower (23—24 p. c.) than in illuminated ones (32—45 p. c.) which indicates that light which has passed through the leaves takes a considerable part in the illumination under the canopy.

3. Even in places which in the absence of young growth and grass cover are at noon in the deepest shade the heliograph reveals

*) I v a n o v L. Light conditions in the beech stands of the Crimea, according to the observations made at the Crimean reservation. Bulletin of the Leningrad Forestal Institute. 1927.

at other hours and under a clear sky the action of direct rays. The duration of their action amounts on the average to one half of what it may be in open places while the intensity is no less than one third.

4. On comparison with the elements constituting a beech forest, illumination under the canopy appears to be connected chiefly with the number of trees on the sample plot, in other words, with the distance between the trunks. The connection with the continuity of the canopy, determined at sight, as well as with its density (according to the planes of intersection) is less apparent.

5. In the plots under investigation there was observed a close connection between the distribution of young beech growth and illumination.

4. Edaphic conditions.*)

The lower third (in places the lower half) of the main Crimean range is composed of clayey schists (shale) of the so called Tauric formation (upper Trias and lower Jura). The upper portion of the mountains is covered by thick deposits of Jurassic limestones, which crown the main range with a narrow, bare, even summit plateau named Yayla. Between the limestones (above) and the schists (below) there may be observed outcrops of sandstones and conglomerates covering a small part of the slopes and being of considerable extent only in several places on the northern slopes. Slips and faults of Jurassic limestone are forming here and there on the southern as well as the northern slopes and ridges, descending far down. Outcrops of intrusive rocks in the shape of isolated laccolites are in the Crimea of less frequent occurrence.

The distribution of beech stands in the Crimea is connected with the outcrops of limestone and partly of with those of igneous rocks. This connection appears with particular clearness on the southern slopes but in places where ridges of limestone or igneous rocks reach down to a lower level the beech follows them (especially on shaded declivities) as low as 450—500 m. above sea level. Development of beech stands is but rarely to be observed on carbonate-free loamy schists, limestone and conglomerates on the southern or even on the northern slopes.

*) By I. Antipov-Karatajev.

During recent years the expedition of the Academy of Sciences under the direction of Prof L. I. Prasolov *) has carried out a survey of the soils of the Crimea. According to the data of this expedition the soils of part of the Crimea covered with forest are referred to Ramann's brown earth type. The brown earth overlying limestone and covered with beech forests falls into three different categories:

Par 1. dark coloured humus soils (the analogue of rendsins) on continuous limestone rubble, developed on the steep slopes beneath the Yayla in the upper belt of beech forests. These soils form a very narrow band as measured vertically; their horizon is scarcely differentiated, the clotted granular dark brown mass of the soil directly overlies the limestone rubble, without any clearly expressed intermediate layer of limestone eluvium; it is free of carbonates owing to leaching, but possesses an active acidity (p. H. about 6.0) approaching the neutral, great absorption capacity (40—45 milequivalents per 100 gr. of soil) and a considerable content of organic substance (about 13 p. c. in the upper horizon of the soil). In some places these rendsins of the brown earth region form patches and tongues protruding into the next, median region of beech forests, where it occupies the steepest declivities littered with débris of limestone. Higher up they pass into the chernozem like soils of the Yayla, covered with mountain meadows.

Par 2. brown (dark brown) soils on reddish brown clayey limestone eluvium with underlying limestone; they form a thin layer (not more than 50—70 cm. deep) leached free of carbonates but having p. H. of nearly neutral or faintly acidic value (about 6.0). They are of a clotted granular texture. These soils are those most approaching Ramann's brown earth but from their character they must be referred to underdeveloped mountain soils in which the

*) Report on the activity of the Academy of Sciences of USSR for 1927, p. II Leningrad 1928. Id. for 1928 p. II Leningrad 1929. Id. for 1929 p. II Leningrad 1930.

I. N. Antipov-Karatayev. Soil types of the southern coast of the Crimea. Monograph: The soils of the Nikitsky Garden. Bull. of the Division of Soil science of S. I. A. B. vol. 4, 1929.

L. I. Prassolov. The Brown Earth of the Crimea and Caucasus. Priroda No. 5 1929. (russ.).

N. N. Sokolov. Some new data on the relief and soils of the Crimea. «Krym». N 1/9, 1929.

influence of the mother rock, the limestone, is rather well expressed. The upper horizon of these soils contains a considerable quantity of humus (up to 8—9 p. c.); they are also saturated with bases, chiefly Ca. These are the most typical soils of beech forests in the Crimea. They are less developed on the southern than on the northern slopes of the main mountain range of the Crimea, occupying its less steep parts.

Par 3. podzolized brown earths or light brown soils developed on thicker and moister reddish brown clays, the product of the decomposition of limestone, mostly along gullies and gorges; they cover a very small area, have an inconsiderable humus horizon with an underlying yellowish brown podzolized layer gradually passing into a reddish brown illuvial horizon, which lies directly on the limestone rubble; the reaction of the upper horizons of the podzolized brown earths is slightly acid or acid (p. H. below 6.0); the texture of the podzolized yellowish brown horizon is also lumpy; in a moist condition the soil mass by its consistency reminds one of rubber; the absorption capacity of the podzolized brown earth is not constant throughout: in the podzolized horizon a slight decrease in its value is observed which reminds one somewhat of the analogous picture presented by podzol soils; thus in one of the typical cross sections through podzolized brown earth under a typical beech forest on a slope at the level of 550 m. we have the following content of absorbed bases:

Absorbed bases p. c. of milequivalents

No. of cross section and its depth in cm.	p. H.	Ca.	Mg.	H.	absorption capacity.	Humus in %
50 1—6	6,68	27,0	2,9	—	29,90	8,29
6—15	6,35	13,1	2,5	1,16	16,76	2,06
20—30	5,96	26,0	3,3	1,13	30,43	0,98
50—60	5,63	31,0	2,5	not det.	33,50	0,63
85—95	7,59	not determined				0,49

Approximately the same subdivision into different soils, with the exception of the rendsins may be observed under beech forests on effusive rocks. The only region exhibiting this feature is the Chamny-burun-Uraga ridge near Alushta. Here under the south



Photo H. Poplawska.

Fig. 2. Forest of tallgrowing beeches in the Crimea.

and north slopes typical brown earths have developed; they have a great absorbing capacity for bases, are leached, even somewhat undersaturated, containing an inconsiderable quantity of humus (up to 10 p. c.), and clayey; on the northern and north-eastern slopes in addition to typical brown earths, podzolized brown earths are observed. These are distributed over an inconsiderable area forming isolated patches and spots in places receiving the greatest quantity of moisture, which in its turn is due to stagnation of water proceeding from precipitation and retained owing to the greater thickness of the clayey mass from which the podzolized brown earths develop.

5. Character, size, interspaces between the trees, age.

The beech forests of the Crimea do not exhibit a homogeneous appearance in their whole extent. In places with a greater amount of moisture, gorges, mountain valleys and particularly the upper course of mountain rivers and where the forest has suffered little injury from cutting and pasturing, the trunks are tall. In other instances, where moisture is less abundant particularly on the open southern slopes situated in the neighbourhood of settlements and therefore more affected by the agency man the trunks are very thick but short and bear a low and wider spreading crown. This type of beech forest is in the Crimea of wider distribution than the first one.

The size of the trees and the distance between them vary greatly in dependence on the conditions of growth and on their height above sea level, as illustrated by the data obtained by Poplawsk a.*)

Area ¼ hectare.

Elevation above sea level in m.	Total number of trunks	Average diameter of trunks	Average height of tree	Number of bushes	Average number of trunks in bush	Number of solitary trees	Dead wood.	Number of trunks per ha.
725	60	44	25	—	—	—	—	240
1060	132	28	22	10	2	112	7	528
1200	189	26	18	18	2	153	11	756
1290	357	15	12	81	3	110	11	1428

*) H. I. Poplawsk a. Materials for the study of the vegetation of the State reservation. 1925.

The maximum trunk diameter obtained by measurement of individual specimens of 31 m. in size, at breast height was equal to 135 cm., while the maximal diameter usually varies between 70 and 100 cm.



Photo E. Wulff.

Fig. 3. Forest of lowgrowing beeches in the Crimea.

As to the maximal age of the beech trees in the Crimea, it must be considered to be about 200—220 years in mountainous regions of difficult access where virgin forests still occur.

6. Regeneration of the beech together with the forest.

The regeneration of beech stands takes place by means of seeds and when the trees are cut down also from shoots proceeding from the stems and roots. According to data of the forester Uglitskich*)

*) Uglitskich A. Report on the management of the Beshuy forest district, Tauride prov. 1915.

Ivanenko B. Types of the stands in the Crimean State Reservation. 1925.

seed years occur every 5—7 years and are attended by the production of enormous quantities of seeds. The capacity for fruiting continues in the beech up to a very great age. The number of young beech saplings, as determined by counting, fluctuates between 1800 to 9000 specimens per hectare at the age of 10—20 years while specimens of 40—50 years occur in isolated cases. The young growth reaches the size of 2 m. looking in these instances crooked and stunted.

The young growth is unequally distributed over the forest and sometimes altogether wanting. This is due to its dependence on illumination but the unequal distribution has no effect on the regeneration of beech forests. Natural regeneration is effected by the beech itself. After clear cutting the young growth may be observed to be constituted of a great variety of species. On a sample plot 150 m. long and 2 m. wide chosen for her observations by Poplaw ska (l. c.) 511 specimens of young growth belonging to different species of trees were found, whose percentage in the composition was the following:

Beech	20 p. c.
Carpinus betulus	48,9 p. c.
Fraxinus excelsior }	17,3 p. c.
Fraxinus oxycarpa }	
Tilia oxyphylla	0,7 p. c.
T. cordata	0,9 p. c.
Acer hyrcanum	2,3 p. c.
Pinus silvestris	3,7 p. c.
Pinus laricio	0,9 p. c.
Populus tremula	1,3 p. c.
Ulmus montana	1,3 p. c.

7. Degree of domination of the beech, admixture of other trees and transition to other types of forest.

Pure beech stands are of rare occurrence; they mostly contain an admixture of a greater or smaller quantity of hornbeam — *Carpinus betulus* — and isolated specimen of other species — *Fraxinus excelsior* and *oxycarpa*, *Acer hyrcanum*, *Tilia cordata*, *Ulmus*

montana, *Populus tremula*, *Sorbus torminalis* and *aucuparia*, *Taxus baccata*. The character of exploitation prevailing in the beech forests of the Crimea promotes the increase of the number of hornbeam, since clear cutting of great areas renders regeneration of beech stands difficult. Therefore transition to hornbeam = beech forest may be observed.

According to the count made by Ivanenko (l. c.) on sample plots of 0,25 hectare within the limits of the Crimean reservation, the ratio of species was the following:

Plots.	Number of trunks.					
	Beech	Horn-beam	Ash	Acorn	Elm	Lime tree
VI	1124	—	8	—	—	—
VII	720	352	32	16	16	16
VIII	178	14	—	—	—	—
IX	738	—	—	—	—	—

8. Undergrowth of bush under the forest canopy.

Owing to deficient light the second stratum is in the beech forest entirely absent or only very feebly developed. It consists of the named trees and fruticose vegetation represented by an inconsiderable number of species, which never form a closed stand but only occur singly. The species of shrubs are the following:

Sambucus nigra
 Euvonymus latifolia a. verrucosa
 Crataegus oxyacantha
 Corylus avellana
 Ligustrum vulgare
 Rosa canina
 Rhamus frangula
 also Hedera helix
 and Clematis vitalba.

9. Herbaceous vegetation.

Investigation into the composition of the herbaceous vegetation in the beech forests of the Crimea has shown it to be somewhat heterogeneous in dependence on the alterations produced in the

composition of species by increased altitude above sea level, greater humidity and by edaphic causes.

Since these latter may vary within the limits of a very inconsiderable area in dependence on changes in the relief, which is of common occurrence in mountainous countries, it is very difficult to draw a sharp line of demarcation between associations and this has to be done with great caution.

Poplawska (l. c. 1925) distinguishes seven associations occurring in the beech forests of the Crimea:

1. Fagetum dentariosum
2. Fagetum herbosum
3. Fagetum carpinosum
4. Fagetum subalpinum
5. Fagetum saniculosum
6. Fagetum muscosum
7. Fagetum vallense.

The number of these associations may be reduced as they differ chiefly in the quantity not the quality of the constituent species. Therefore in our opinion only two associations deserve to be singled out: *Fag. dentariosum* and *subalpinum* *), which are characterized by successions of herbaceous vegetation depending on elevation above sea level.

The subjoined list contains the enumeration of the species constituting this association: **)

Name of plant	Association: <i>Fagetum dentariosum</i>		Association: <i>Fag. subalpinum</i>	
	Percentage of occurrence 570-1000 m. above sea level	1000-1100 m. above s. level	Percentage of occurrence 1100-1350 m. above s. level	
1. Cephalanthera rubra .	80	30	0	
2. Carex digitata	60	30	10	
3. Polygonatum polyanthemum	60	40	0	

*) The name given by the author to this association is not happily chosen, since alpine vegetation exists nowhere in the Crimea.

**) Poplawska H. On certain beech associations in the Crimea succeeding each other. Leningr. 1929.

4. <i>Dentaria quinquefolia</i> . . .	55	50	10
5. <i>Planthanthera montana</i> . . .	50	30	0
6. <i>Neottia nidus avis</i> . . .	50	30	10
7. <i>Asperula odorata</i> . . .	40	70	60
8. <i>Cynoglossum germanicum</i>	40	10	20
9. <i>Euphorbia amygdaloides</i>	30	70	50
10. <i>Epipactis latifolia</i> . . .	30	10	0
11. <i>Hedera helix</i> . . .	25	10	0
12. <i>Poa nemoralis</i> . . .	25	40	90
13. <i>Galium spurium</i> . . .	20	30	30
14. <i>Moehringia trinervia</i> . . .	20	40	40
15. <i>Aspidium filix mas</i> . . .	20	30	60
16. <i>Carex silvestris</i> . . .	15	0	0
17. <i>Arum orientale</i> . . .	15	20	10
18. <i>Monotropa hypopitys</i> . . .	15	10	0
19. <i>Corallorrhiza innata</i> . . .	15	30	0
20. <i>Cynanchum scandens</i> . . .	10	0	0
21. <i>Epipogon aphyllus</i> . . .	10	0	0
22. <i>Bromus ramosus</i> . . .	10	10	0
23. <i>Galanthus plicatus</i> . . .	10	30	10
24. <i>Lathyrus inermis</i> . . .	10	0	0
25. <i>Mercurialis perennis</i> . . .	10	50	80
26. <i>Primula acaulis</i> . . .	10	10	20
27. <i>Scilla bifolia</i> . . .	10	10	0
28. <i>Viola odorata</i> . . .	10	20	20
29. <i>Alliaria officinalis</i> . . .	5	10	0
30. <i>Carex pendula</i> . . .	5	20	20
31. <i>Dactylis glomerata</i> . . .	5	10	20
32. <i>Galium mollugo</i> . . .	5	10	30
33. <i>Lactuca muralis</i> . . .	5	30	50
34. <i>Lathyrus aureus</i> . . .	5	0	0
35. <i>Lapsana grandiflora</i> . . .	5	0	20
36. <i>Luzula nemorosa</i> . . .	5	0	20
37. <i>Milium effusum</i> . . .	5	10	10
38. <i>Salvia glutinosa</i> . . .	5	40	50
39. <i>Satureja grandiflora</i> . . .	5	20	30
40. <i>Viola silvestris</i> . . .	10	0	10

41. <i>Cephalanthera alba</i> . . .	10	0	0
42. <i>Convallaria majalis</i> . . .	5	0	0
43. <i>Ranunculus anemonae-</i> <i>folius</i>	5	0	20
44. <i>Bromus variegatus</i> . . .	0	10	0
45. <i>Geranium Robertianum</i> .	0	0	50
46. <i>Chaerophyllum aureum</i> .	0	0	30
47. <i>Poa pratensis</i>	0	0	30
48. <i>Corydalis Marschalliana</i> .	0	0	10
49. <i>Scrophularia nodosa</i> . . .	0	0	10

10. The mosses of the beech forests of the Crimea.

Owing to the considerable humidity and moderate temperature of the soil and air the zone of beech forests is the habitat of two thirds of the 40 species of mosses occurring in the Crimea. Most of them belong to those growing under conditions of shade and humidity. In old beech forests the crowns of the trees form a continuous canopy, creating semi-darkness, and the ground is littered with dead leaves. In such sections of the forest the conditions necessary to the growth of the vegetation of the lower strata including mosses are deficient; these latter occurring only in places where interruptions in the canopy admit the penetration of light.

The mosses of the Crimean beech forest have been studied rather thoroughly by A. Sapegin *), who established their composition and distribution according to the conditions of their habitat.

I. Growing on earth.

cc **)

<i>Homalothecium sericeum</i>	<i>Dicranum scoparium</i>
<i>Stereodon cypressiformis</i>	<i>Brachythecium velutinum</i>
	c.
<i>Thuidium salebrosum</i>	<i>Fortella tortuosa</i>
<i>Bryum capillare</i>	

*) S. Sapegin. The mosses of mountainous Crimea. Bull. of the Novorossiysk, Society of Naturalists 1910.

**) cc — très commune, c — commune, ac — assez commune, r — rare, ar — assez rare, rr — très rare.

ac.

Tortula subulata

Thuidium recognitum
Hylocomium splendens
Rhytidadelphus triquetrus
Eucalypta contorta

Brachythecium rutabulum
Bryum argenteum
Rhytidium rugosum
Polytrichum juniperinum
Politychium formosum
Mnium spinosum
Mnium undulatum
Brachythecium albicans
Ctenidium molluscum
Hypnum Schreberi
Catharinea undulata
Tortula mucronifolia
Thuidium Philiberti
Brachythecium populeum
Bryum badium
Bryum cuspidatum
Scerapodium purum
Campylium Sommerfeldtii

r.

Isothecium myurum
Ceratodon purpureus
Tortula ruralis

rr.

Campylium protensum
Tortella inclinata
Polytrichum piliferum
Polygonatum urnigerum
Climacium dendroides
Districhium capillaceum
Racomitrium canescens
Barbula fallax
Barbula unguiculata
Pterigynandrium filiforme
Weisia viridula
Amblystegium varium
Amblystegium serpens
Eurhynchium valutinoides
Webera cruda
Anomodon attenuatus
Rhodobryum roseum

These species are unequally distributed and do not grow everywhere. Not unfrequently one or several species in some areas predominate, ousting the others. On humid soils and humid layers of earth covering stones and rocks the species represent the following composition:

c.

Mnium undulatum

ac.

Mnium stellare

ar.

Mnium affine

Fumaria hygrometrica

r.

Mniobryum albicans

Mnium cuspidatum
Fissidens taxifolius
Barbula unguiculata
Mnium punctatum
Mnium serratum
Bryum capillare
Eurhynchium striatum
Amblystigium serpens
Mnium spinosum
Bryum cirratum
Bryum bimum
Bryum pallens
Bryum turbinatum
Bryum badium

rr.

Amblystegium varium
Dicranella rufescens
Dicranella varia
Hygroamblystegium filicinum
Brachythecium mildeanum
Brachythecium velutinum
Polytrichum formosum
Dicranum scoparium
Webera nutans
Catharinea undulata
Oxyrrhynchium Swartzii
Rhabdoweisia fugax
Fissidens adiantoides
Bryum cuspidatum

On stones and rocks without soil covering.

cc.

Homalothecium sericeum

Stereodon cupressiformis

Anomodon viticulosus
Orthotrichum anomalum

Ctenidium molluscum

Pseudoleskeia atrovirens

Bryum capillare
Schistidium confertum
Leskeella nervosa
Tortula subulata
Tortula ruralis
Pterigynandrum filiforme

c.

ac.

Schistidium apocarpum

ar.

Brachythecium velutinum

r.

rr.

Ptychodium tauricum
Grimmia pulvinata
Grimmia anodon
Neckera crispa
Neckera complanata
Anomodon attenuates

<i>Pseudoleskeela catenulata</i>	<i>Anomodon longifolius</i>
<i>Neckera Besseri</i>	<i>Dicranum scoparium</i>
<i>Ciriphyllum velutinoides</i>	<i>Polaisia polyantha</i>
<i>Homalothecium philippeanum</i>	<i>Bryum caespiticium</i>

The majority of the enumerated mosses grow also at the bases of trees. Only a few of the species may be considered to be dependent on the proximity of tree trunks for their habitat. These are:

<i>Isothecium myurum</i>	<i>Anomodon viticulosus</i>
<i>Pterigynandrium filiforme</i>	<i>Anomodon attenuatus</i>
<i>Isopterygium silesiacum</i>	<i>Dicrinum tauricum</i>
<i>Leskeela nervosa</i>	<i>Neckera complanata</i>

On the trunks of trees the following species grow epiphytically:

	c.
<i>Orthotrichum affine</i>	cc.
<i>Leicodon sciurooides</i>	ar.
<i>Pterigynandrum filiforme</i>	r.
<i>Leskeela nervosa</i>	<i>Anomodon viticulosus</i>
<i>Brachythecium sericeum</i>	<i>Orthotrichum leiocarpum</i>
<i>Orthotrichum anomalum</i>	<i>Anomodon attenuatus</i>
<i>Oethotrichum obtusifolium</i>	<i>Anomodon longifolius</i>
<i>Orthotrichum pumilum</i>	<i>Pylaisia polyantha</i>
<i>Orthotrichum fastigiatum</i>	<i>Pseudoleskeea atrovirens</i>
<i>Stereodon cypressiformis</i>	

It must be noted that the mosses grow on tree trunks relatively rarely. Out of 195 species of mosses indicated by S a p e g i n for mountainous Crimea 132 occur within the limits of the beech forest zone, 24 of them being met with in the Crimea nowhere else but in the beech forests. These are the following:

<i>Dicranella rufescens</i>	<i>Mnium medium</i>
<i>Grimmia anodon</i>	<i>Mnium orthorhynchum</i>
<i>Orthotrichum pallens</i>	<i>Disphyscium sessile</i>
<i>Orthotrichum pumilum</i>	<i>Pogonatum urnigerum</i>
<i>Orthotrichum speciosum</i>	<i>Anomodon attenuatus</i>

<i>Orthotrichum stramineum</i>	<i>Campylium protensum</i>
<i>Rhabdoweisia fugax</i>	<i>Ptychodium tauricum</i>
<i>Ulota crispula</i>	<i>Brachythecium populeum</i>
<i>Webera nutans</i>	<i>Cirriphyllum velutinoides</i>
<i>Bryum inclinatum</i>	<i>Eurhynchium striatum</i>
<i>Rhodobryum roseum</i>	<i>Eurhynchium striatum</i>
<i>Mnium hornum</i>	

The lichens and fungi of the Crimea, those of the beech forests in particular, have not yet been studied as a whole.

II. The associates of the beech forest.

Only a few species are in the Crimea connected with beech forests. The most important of them are enumerated in the following list. The most constant associates of the beech being marked by a cross.

<i>Aspidium Robertianum</i>	+	<i>Dentaria quinquefolia</i>	
<i>Aspidium spinulosum</i>		<i>Corydalis Marschalliana</i>	
<i>Athyrium filix femina</i>		<i>Cypripedium calceolus</i>	
+	<i>Poa nemoralis</i>	+	<i>Mercurialis perennis</i>
	<i>Luzula nemorosa</i>	+	<i>Primula officinalis</i>
	<i>Carex vesicaria</i>		<i>Sanicula europaea</i>
+	<i>Arum orientale</i>	+	<i>Cynanchum scandens</i>
+	<i>Euphorbia amygdaloides</i>	+	<i>Salvia glutinosa</i>
+	<i>Epipogon aphyllus</i>	+	<i>Satureja grandiflora</i>
+	<i>Corallorrhiza innata</i>	+	<i>Verbascum spectabile</i>
+	<i>Neottia nidus avis</i>	+	<i>Lathraea squamaria</i>
	<i>Nectaroscordum Dioscoridis</i>	+	<i>Monotropa hypopitys</i>
	<i>Cephalanthera grandiflora</i>	+	<i>Asperula odorata</i>
	<i>Moehringia trinervia</i>	+	<i>Circaeae lutetiana</i>
	<i>Ranunculus lanuginosus</i>		

12. Is the beech forest an indivisible whole or does it consist of separate components.

Although the composition of the herbaceous vegetation of the beech forest is not always an absolutely constant one, undergoing alterations in dependence on the conditions of illumination, the thickness of the litter of dead leaves and the altitude of the locality

above sea level, the beech forest must be nevertheless considered as an indivisible whole, since notwithstanding all the alterations which may occur in the herbaceous cover, it is the beech that determines the character of the forest. Our conception of «beech forest» is something quite definite, evoking always an identical association of images, not purely subjective. The composition of the herbaceous vegetation is to a considerable extent dependent on various accessory conditions, among which the agency of man in its manifold forms, such as pasturing of cattle, removal of the litter of dead leaves, cutting off single trees and thus improving the conditions of illumination under the canopy, etc., plays a very important rôle and it cannot, therefore, be considered as a decisive factor in determining the conception of »beech forest».

13. Exploitation of the forest and the alterations caused by it.

The system of exploitation of the beech forests in the Crimea used to consist in normal years in cutting the high stands 2—3 times during a period of 10—30 years; this secured regeneration of the forest, since under such a method of cutting a young growth of beech would arise, and the relation between the species remained the same.

During the years of the Revolution, clear cutting was practised, and, in privately owned forests, particularly those belonging to village communities, also in prerevolutionary times. When the cut area had a width of only 30—40 m. succession of species would take place, finding expression in the admixture of a large percentage of other species chiefly hornbeam, but also ash, aspen etc. When the cut area is 200—400 m. wide, regeneration of the beech does not take place evenly throughout.

Regeneration of the forest through shooting from the cut trunks is inconsiderable in high stands where the trees are 150—200 years old, but is of much greater importance in younger stands with lower trees. These are situated chiefly in the higher regions of the mountain range, and where, in normal years, the forests were not exploited because they were under special protection.

The beech forests of the Crimea are being exploited chiefly for fire wood and the preparation of charcoal from the branches and boughs remaining after the removal of the trunks.

14. Effect of pasturing.

With the exception of goats pasturing is not practicable in beech forests owing to the insufficiency or total absence of a herbaceous cover; but on sultry days the herdsmen lead their cattle into the higher lying parts of forests, situated nearer to the summit of the range, and here the cattle will destroy the young growth, trample down the saplings and render the soil cover more compact.

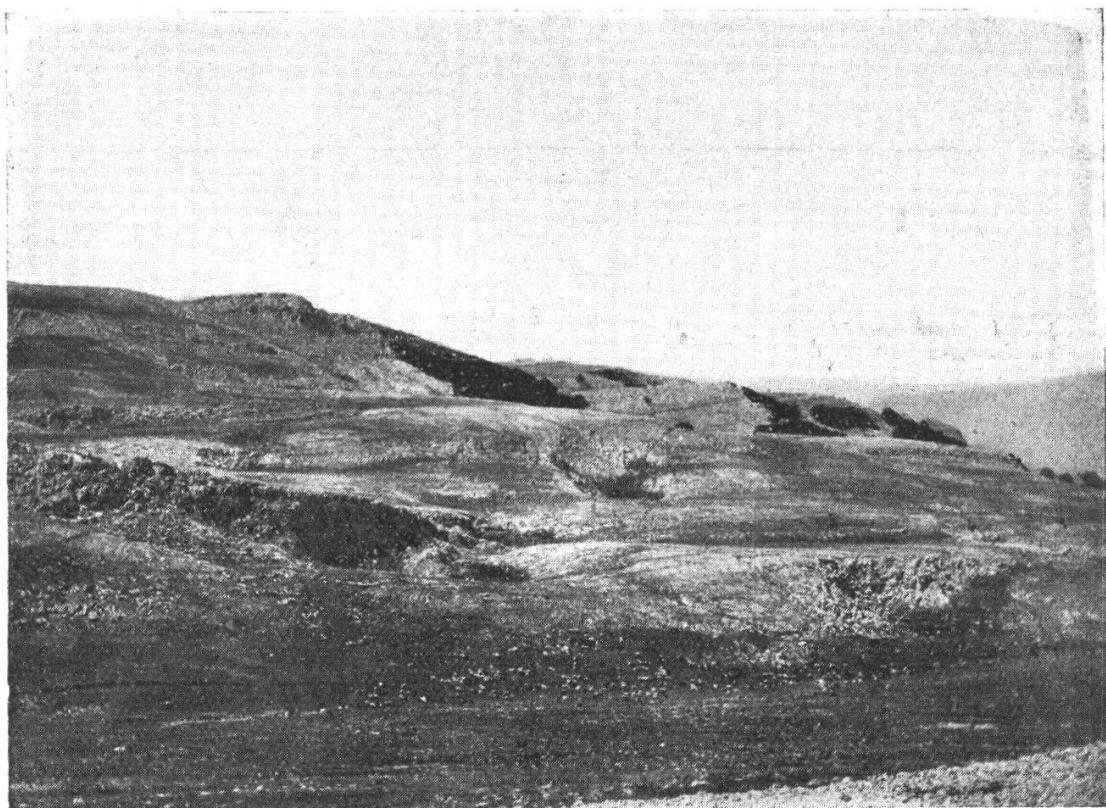


Photo N. Klepinin.

Fig. 4. Relicts of beech woods on the plateaux of the Crimean mountain-chains.
(Yayla.)

Such a forest is doomed to perish utterly when clear cut, and this explains the bareness of the summits and upper levels of the slopes of the Crimean range. This bareness, in its turn, has a catastrophic influence on the water economy of the peninsula.

The pasturing of swine is also injurious since these animals eat the beech nuts, and for this reason swine pasturing is prohibited in these forests.

Fires are of rare occurrence in beech forests since these grow only in regions of high humidity, abounds and the main body of beech is concentrated in the upper parts of the mountainous regions above human settlements. Fires are therefore without any significance in the life of the Crimean beech forests.

15. Influence of parasites.

Nearly all of the old beech trees in the Crimea are infested with the fungus *Polyporus fomentarius* which causes the pit to rot. Such trunks are easily broken by the impact of the wind, forming large tracts of windfall, which, seen from a distance, give the impression of wide clear cuttings made by man.

16. Succession of beech forest.

There is reason to suppose that during the Tertiary period the forests on the southern slope of the main range consisted of arborescent juniper. (*Juniperus excelsa*) oak (*Quercus pubescens*) and partly the Crimean pine (*Pinus laricio* var. *Pallasiana*). In the median belt the first two were both disappearing while the pine predominated, being succeeded by the common pine (*Pinus silvestris*) in the upper belt. In some parts of this slope these relations still continue, but in most cases their regularity has been disturbed by the beech, which has occupied the upper belt and is gradually supplanting the pine where this has not yet already happened. On the northern slope of the range vegetation during the Tertiary period seems to have been represented by an analogous composition of species — *Pinus silvestris* in the upper belt, *Pinus laricio* v. *Pallasiana*, *Juniperus foetidissima* in the median belt and *J. excelsa* with an admixture of broad-leaved species in the westernmost part adjoining the sea coast. At the present time the upper and median belts of the northern slope are occupied in their whole extent by beech forests. Individual groups of other species persist however within the beech forests, quite out of harmony with their surroundings, and bearing witness to the struggle between the forest species to the victory won by the beech.

But there is another stage intermediate between the Tertiary and the contemporary composition of forests in the Crimea and corresponding to the glacial and interglacial periods. The climatic conditions of the glacial periods, while they did not cause the formation of glaciers in the Crimea, no doubt produced a lowering of the temperature and an increase of precipitation leading to the development of moist and boggy places in the lower regions of mountainous Crimea. This change of climate promoted the development and wide distribution of northern elements, in the first place of the birch — *Betula verrucosa*. At the present time within the beech forests there occur islands formed by these relicts of northern vegetation. Thus the birch, numbering a few hundred specimens, is found but in one region doubtless representing a climatic and formation relict within the beech forest. There is however evidence of its wide distribution in the Crimea during the interval between the Tertiary and present period. This evidence consists in small pieces of charcoal found among the remains of fire places dug out by Bonč-Osmolovskij in the caves of the Crimea where paleolithic man probably lived between the first and the second glacial periods. These caves are situated near the limits of the contemporary distribution of beech forests in the Crimea and bear witness to a wide distribution of the birch at the time when they were inhabited by prehistoric man, since the percentage of birch in the charcoal is very high, sometimes forming the bulk of it.*)

Thus in the Crimea we have a repetition of the same picture of the distribution of the beech that we have in western Europe.**) During the Tertiary period the beech appears to have been a constituent of the mixed forests of mountainous Crimea. After the glacial period had set in it probably survived only within the limits of the main range, since among the charcoals above mentioned the beech

*) Bonč-Osmolovskij G. Le paléolithique de Crimée. Bull. de la Commission pour l'étude du quaternaire de l'Acc. d. Sc. U. S. S. R. No. 1. 1929.

Hammermann A. Kohlenreste aus dem Paläolithikum der Krim. Höhlen Ssjurenj I. und II. Ibid.

Palibin W. u. Hammermann A. Kohlenreste aus dem Paläolithikum der Krim. Höhle Kiik-Koba. Ibid.

Wulff E. The Paleolithic in the Crimea. Priroda No. 2. 1930 (russ.).

**) See f. i. Vaupeil C. De l'invasion du hêtre dans les forêts du Danemark. Ann. d. sc. nat. Ser. 4. Botan. VII, 1857, p. 86.

is entirely wanting. At the close of the glacial period the beech, just as in western Europe, begins to take possession of the area, becoming free to do so owing to the disappearance of the northern vegetation which was dying out under the influence of the greater warmth of the climate and decreasing humidity. The Tertiary elements in the forests of the Crimea were supplanted in the places where they still persisted and continuous beech stands were formed. This process has not yet come to its close and we are now witnessing one of its last stages.

17. Systematics of the Crimean beech.

After De Candolle had pointed out the difference between the beech of western Europe (*Fagus silvatica*), and the eastern beech, which latter he justly separated as a distinct form, (*f. asiatica*), and particularly after Lipsky ¹⁾ in 1898 had finally established the difference of the Caucasian from the west European beech, describing the former as *Fagus orientalis* Lipsky, and Stojanoff and Stefanoff ²⁾ had proved that both the species (*Fagus orientalis* and *F. silvatica*) occurred in the Balkan Peninsula, it became necessary that the systematic position of the Crimean beech should be cleared up. That it was uncertain had been repeatedly indicated. Thus Büsgen ³⁾ says: «Die Buchen, welche in der Krim auftreten, sind nicht mit Sicherheit als echte Rotbuchen anzusprechen, da fruchtende Exemplare von dort nicht beschrieben wurden. Likewise Ascherson and Graebner ⁴⁾ point out in their description of *F. orientalis*: «Ob die Buche der Krim und von Nord-Syrien (Amanus) zu dieser Unterart gehört, ist noch festzustellen.»

In connection with my researches into the origin of the flora of the Crimea and its relation to the floras of the Caucasus, Asia Minor and the Balkan Peninsula, conducted for several years, this uncertainty prompted me to undertake a critical study of the Crimean beech. For this purpose, in collaboration with my assistant T. Zyrina, I collected in 1924, special material from various re-

¹⁾ Lipsky V. Acta Horti Petropol. XIV/1897/300.

²⁾ Stojanoff N. and Stefanoff B. Flora of Bulgaria I/1923/317.

³⁾ Büsgen in Kirchner, Loew u. Schroeter. Lebensgeschichte der Blütenpflanzen Mitteleuropas II, 1/1911/3.

⁴⁾ Ascherson und Graebner. Synopsis d. mitteleuropäischen Flora IV/1908—1913/440.

gions of the Crimea. Study and comparison with materials from the Caucasus showed ⁵⁾ that part of it had an unmistakable resemblance to *F. orientalis*, while in another part of it no essential divergence from *F. sylvatica* could be discovered. A number of specimens among the material exhibited moreover features intermediate between the two species, so that it was impossible to refer them to either. In 1925 another collection was made from 126 trees in 26 stations in different mountainous regions of the Crimea. Investigation ⁶⁾ of this material confirmed the heterogeneity of the Crimean beech and established beyond doubt the identity of some of the Crimean specimens with the Caucasian beech, *Fagus orientalis*.

At about the same time the study of the Crimean beech within the limits of the State reservation were undertaken by H. I. Poplawsk a number of whose previous investigations, as already mentioned, had been devoted to the systematic position of the Crimean beech. The degree and character of the variability of the distinctive features was statistically studied on a very large material collected from different altitudes, but unfortunately in one region only.

These investigations have shown the variability of the Crimean beech to be of three different kinds: 1. variability of characters in the single tree; 2. Individual variability in trees growing beside one another under the same conditions and 3. variability related to ecological conditions, particularly to elevation above sea level.

As to the first kind of variability it was established that the variability of characters in a single tree was of a quantitative nature, its limits being more restricted than those of individual variability. This latter was very considerable, but no special correlation between the characters could be detected. Each tree exhibited various combinations of all the characters and there were instances in which trees standing side by side showed a closer relation to the European beech, in some of their characters, while in others they appeared to be nearer to the Caucasian species.

The variability of characters related to ecological conditions,

⁵⁾ Wulff E. und Zyrina T. Die Buche in der Krim. Oesterreich Bot. Zeitsch. Nr. 10—12/1924/276.

⁶⁾ Wulff E. and Zyrina T. Materials for the study of the Crimean beech. Bullet. de la Soc. d. natur. d. Crimée VIII/1925/75. (russ.)

chiefly altitude above sea level, manifested itself in the following ways: 1. at higher elevations the leaves were smaller, more rounded and their broadest part shifted from the upper third towards the center of the leaf; further the number of leaf veins decreased with increasing altitude and finally the leaf stalk became a little shorter.

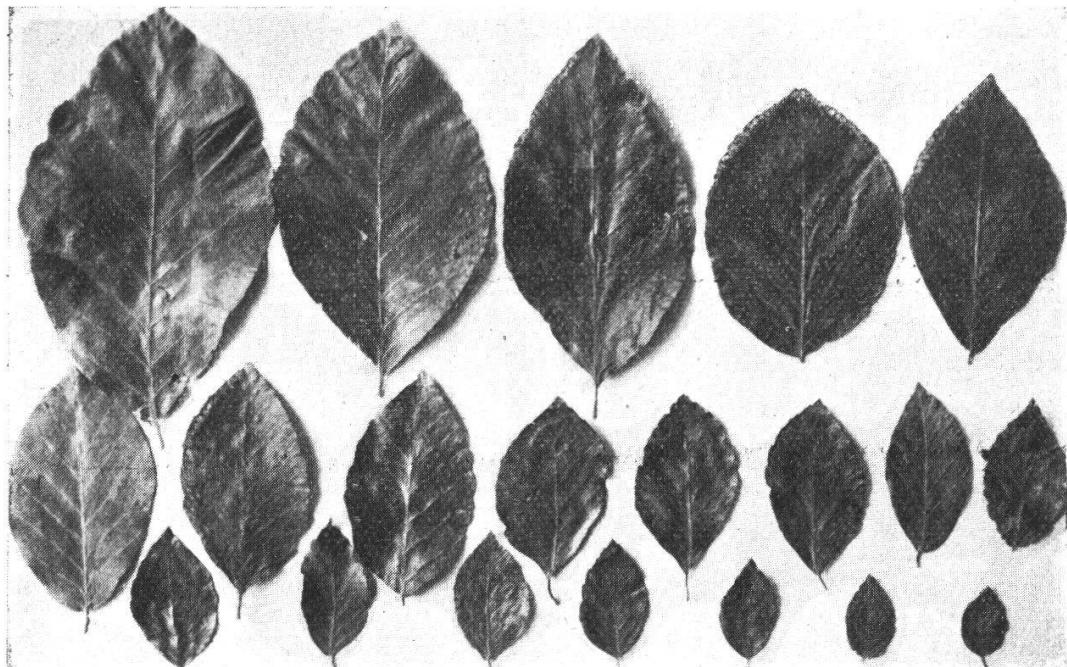


Photo E. Wulff.

Fig. 5. Leaves of the Crimean beech.

Thus the leaf of the beech in the upper regions of its distribution not only diminishes in size but changes its form. The perianth in the male flower becomes smaller in the upper and lower parts of the beech zone, particularly where it borders on the Yayla and so to a considerable degree does the relative size of the teeth. In correspondence with the size of the perianth that of the stamens also decreases. The nuts likewise become smaller towards the upper and lower parts of the beech zone, the largest nuts occurring in the middle region. Thus the fruit as well as the flower are of maximal size in the center of vertical distribution of the beech, i. e. in the optimum zone of vegetative growth, decreasing towards its upper and lower limit, while the leaves continue to decrease as the habitat becomes more elevated.

The result of these investigations Poplawskia has summarized in the following table:

<i>Altitude above sea level.</i>			
<i>Trunk</i>	490 to 600	600 to 1100	1100 to 1300
1. Average diameter	44 cm.	22 cm.	15 cm.
2. Average height	23 to 25 m.	22 m.	18 m.
3. Percentage of bushy beeches	0	0	10,5 to 42,4%
<i>Crown</i>			
Attachment of crown	Median	High	Low
<i>Leaves</i>	cm.	cm.	cm.
1. Length	8,5	7,5	6,5
2. Ratio of width to length	1,89	1,70	1,54
3. Coefficient of form of leaf	0,53	0,56	0,52
4. Number of lateral veins	10	9	8
5. Length of petiole	0,76	0,66	0,67
<i>Male flowers</i>	mm.	mm.	mm.
1. Length of perianth	5,06	6,26	5,30
2. Ratio of width to length	1,34	1,31	1,30
3. Length of teeth	2,57	2,42	3,04
4. Length of stamens	1,0	2,5	2,3
<i>Nuts</i>	mm.	mm.	mm.
1. Length	13,2 to 14,2	13,6 to 15,2	13,4 to 14,1
2. Ratio of length to width	1,5 to 1,8	1,7 to 2,0	1,4 to 1,8

Unfortunately such measurements are not available either for *Fagus orientalis* in the Caucasus or, as far as I know, for *Fagus sylvatica* in western Europe, a comparison with the data obtained for the Crimean beech and the establishment of the difference between them being thus impossible. Poplawskia was however able to give the data obtained from the measurement of the leaves of *Fagus orientalis* from Caucasus. They proved to differ from the leaves of the Crimean beech in their greater length, lesser width and greater number of lateral veins (12—13 on the average, up to 15 in isolated specimens, while in the Crimean beech they measured 8—10, though 12 lateral veins not infrequently occurred). The shape of the leaf and the length of the petiole in the Caucasian beech rather approached the figures obtained for the Crimean beech. Poplawskia nevertheless considers the Crimean beech as a form intermediate

between *F. silvatica* and *F. orientalis* and proposes its separation as an independent species, *F. taurica* n. sp.

The material studied by me and Zyrina was considerably less extensive than that investigated by Poplawskia, but while the latter had collected her material in one region only (the Crimean State reservation) ours was taken from 26 stations scattered over the whole area of distribution of the beech in the Crimea. This is of great importance since the conditions of the habitat and the habit of the beech vary greatly in the different regions.

Our material was carefully investigated and after measuring the parts of the male and female flowers we came to the conclusion that the leaves vary in relation to the conditions of their station to such a degree that they are unable to contribute anything to the elucidation of the specific differences between the beeches under consideration. According to our observations the dimensions and compactness of the leaf blade vary considerably in relation to the humidity and shade of their stations: in valleys and in dense stands, i. e. where there is sufficient humidity and shade they are large, rather thin, and elongated, while in open places with a drier atmosphere and particularly in trees standing alone they are small and leathery.

It is but natural that in the Caucasus with its high humidity (both high precipitation and particularly great saturation of the atmosphere) which by far exceeds that prevailing in the Crimea, the leaves should be larger and therefore it is not surprising that their lateral veins are more numerous than in the Crimea.

We therefore directed our attention to other characters which might serve to establish the systematic position of the Crimean beech, those of greater significance in the organization and less dependent on the conditions of the habitat, namely the leaflets of the cupule and particularly the structure of the perianth in the male flower.

These distinctive characters exhibit in *F. orientalis* and *F. silvatica* the following divergences: in *F. silvatica* the leaflets of the cupule are very narrow and for the most part *awl-shaped*, short, the lower not protruding over the upper; the cupule therefore does not

show a densely foliated character. In *F. orientalis* on the contrary the leaflets of the cupule, chiefly the lower ones, are linear, brownish, reaching in the flowering stage to the top of the cupule, often herbaceous, occasionally even provided with obvious veins, spade-shaped and up to 4 mm. vide.

In *F. orientalis* the leaflets are unequally distributed over the cupule, the lower ones (up to the middle part of the cupule) at a greater or less distance from one other, while the upper ones on the contrary are crowded. The lower part of the ripe cupule is often leafless, since the large herbaceous leaflets fall off soon after the flowering period ceased.

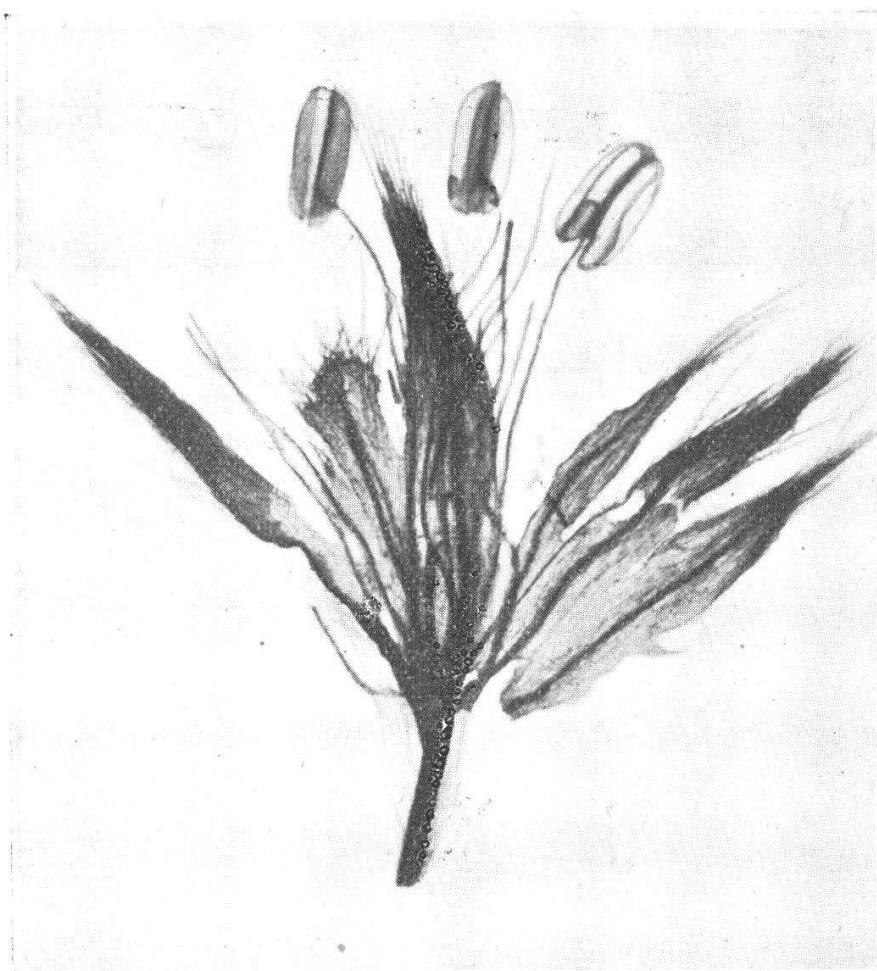


Fig. 6. Male flower of *Fagus silvatica* L. Crimea. $\times 9.6$.

As to the male flowers, the main difference in their distinctive features consists in the shape of the teeth of the perianth, the size

of the interspaces between them and the character of these. In *F. silvatica* the perianth has deep incisions and is divided into 5—6 long linear pointed, lancet like lobes, exceeding in length the tube of the corolla. In *F. orientalis*, on the contrary, while the perianth is also divided into 5—6 lobes the incisions are considerably less deep. The lobes are short, broadly egg shaped, with rounded points, only half the length of the tube or even shorter, and overlapping one another at the base. These lobes have a very characteristic shape in the flowers of *F. silvatica* where they converge at sharp angles towards the apex, and therefore look pointed, while in the flowers of *F. orientalis* the lobes are for the most part obtuse and rounded towards the apex.

Taking these fundamental characters as a basis, we investigated our entire collection of material but could not at all agree with the view that there occurs in the Crimea only an intermediate form between the Caucasian and the West European species. We had to divide the available Crimean material into three groups: to the first we referred the specimens closely approaching the Caucasian beech, in the structure of the male flowers and cupule, to the second the specimens closely related to the West European beech and in the third we left those which occupied, as it were, an intermediate position, and could not be referred to either of the former groups. This part of the material actually represented an intermediate form connecting these two species of beech.

The surveys made of the distribution of the above mentioned forms in the Crimea have not as yet resulted in a definite picture of the replacement of one of the species by the other, depending for instance on the altitude above sea level such as occurs in the Balkan Peninsula. But more detailed investigations may possibly reveal some regularity in their distribution.

The measurement of this material and its comparison with the measurements of analogous parts in *F. orientalis* from the Caucasus and *F. silvatica* from Germany (the neighbourhood of Breslau) collected for us by the courtesy of Prof. Winkler, have yielded the results given in the following table:



Fig. 7. Male flower of *Fagus orientalis* Lipsky Crimea. $\times 9.6$.

Dimensions*) in mm.	<i>Fagus silvatica</i> W. Europe	<i>Fagus silvatica</i> Crimea	Interme- diate forms	<i>Fagus orientalis</i> Crimea	<i>Fagus orientalis</i> Caucasus
Length of lower leaves on cupule	5—10	3—8	6—13	8—15	8—12
Width of ditto	0,25—0,5	0,25—0,5	0,25—1	1—4	—
Length of upper leaves on cupule	3—5	3—5	3—4	2—7	2,5—4
Length of male perianth	4—5	3—4,5	3—5	2—4	2,5—4
Length of its tube	1—2,25	1—2,25	1—3	1—2,5	1,5—2,25
Length of bend	2—3,5	1,5—2,5	1,25—2,25	1—2	1—2
Length of filament	3—6,5	4—7	4—6	3—6	5—6
Length of anther	1—1,5	1—1,5	1—1,5	—	—
Length of fruit stalk	20—30 (10)	17—30	10—27	12—40	22—40
Length of nut	16—17	13	—	12—17	12—17

*) All measurements are made on dry material.

This intricate picture of the systematics of the Crimean beechies, *F. taurica*, since instead of bringing us nearer to the explanations. *F. taurica*, since instead of bringing us nearer to the explanations of the causes of its heterogeneous morphological structure we should simply obscure the problem. Analogous uncertainty and intermediate morphological structure in the beech are observed also in the Balkan Peninsula. Stefanoff *) writes about it in his paper on the origin of the flora of Rhodope and Stoyanoff **) says: «Anscheinlich bildet die Buche im Preslaw-Balkan Übergänge zwischen *F. silvatica* und *F. orientalis* Lipsky, ebenso wie man es auch auf Karlik in den südlichen Rhodopen beobachtet.»

Gritescu ***) has shown that the beech occurring in the Dobruja must be referred also to *F. orientalis*; unfortunately the details of his analysis were not available. Finally there is reason to believe that on the outer margin of its distribution in the Caucasus, which has not yet been studied in detail, *F. orientalis* also produces forms approaching *F. silvatica*. This is categorically stated by Medvedev †), the eminent specialist in the arborescent vegetations of the Caucasus.

Thus it must be stated that where the areas of distribution of the two species of beech meet, i. e. at the western as well as the northern limit of *F. orientalis*, there occur intermediate forms, connecting the two species in addition to the typical forms of each.

The uncertainty as to the systematic position of these intermediate forms does not depend on the ecological conditions of the station and can be understood only by inquiry into the history of the origin of the two species of the beech, which we will now consider.

18. History of the Crimean Beech.

At the present time it may be considered proven by biogeographical and geological evidence that the mountainous part of the Cri-

*) Stefanoff B. The origin and development of the vegetation of the Rhodope. Sofia. 1927.

**) Stoyanoff N. Kritische Studien und kleine Mitteilungen. Mitt. d. Naturh. Inst. Sofia. II. 1929.

***) Gritescu G. Punica granatum si *Fagus orientalis* in flora Romanei. Bull. Grad. Bot. d. Cluj. VII. № 1—2/1924/57.

†) Medvedev v. The beech... and birches of The Caucasus. Bull. of the Tiflis Bot. Gar. № 17. 1910.

mean Peninsula, as late as the Tertiary and perhaps the beginning of the Quaternary period, was the peninsula of a mainland, which occupied the depression of the contemporary Black Sea, and was continuous with Asia Minor and Transcaucasia. Moreover in the western part of the Black Sea there repeatedly arose connections between the Crimea and the Balkan peninsula. From the beginning of the close of the Tertiary period the northern level part of the Crimea was becoming dry land and turned into a bridge, which has continuously connected from them up to the present time the mountainous part of the Crimea with the mainland of southern Russia. The past history and vicissitudes of the beech in the Crimea cannot therefore be considered independently of the countries which once formed a single whole.

As to the history of the beech during the Tertiary period it must be noted in the first place that all we know about the fossil beech is confined almost exclusively to imprints of its leaves. Our knowledge concerning the structure of the cupule is very scanty and we possess no data as to the structure of the flower. Thus there is wanting the most essential of characters which would enable us to establish the interrelations between the west European and eastern beeches during the Tertiary period.

According to Unger and Etinghausen all the contemporary beeches, not only of Europe and Asia but those of America as well, must be derived from the Tertiary beech, *Fagus Feroniae* (*F. Deucalionis*). At the same time Etinghausen and Krasan point out the extreme variety of form and structure observed in the leaves of the same tree, which change at different seasons of the year in dependence on the conditions of the habitat. This leads them to the conclusion that all the described beeches, instead of representing separate species, are only different stages in the variation of the Tertiary beech in the course of its transformation into the contemporary *F. silvatica*. «Der Typus der *F. silvatica* begann vielmehr schon im Eocän und vielleicht noch früher, und zwar in den verschiedensten Gegenden der Erde, sich auszubilden, unabhängig von den be-

stehenden Formelementen, und ist dieser Prozess wahrscheinlich heute noch nicht beendet.»¹⁾

In a later work²⁾ Ettighausen points out that during the Tertiary period the predominating forms of the beech were the normal form of *F. Feroniae* and the normal form of *F. Deucalionis*, form intermediate between them being observed during the whole Tertiary period. Forms of *F. Feroniae* make their appearance as early as the Miocene, although the normal form (typical *F. Feroniae*) predominated. Towards the end of the Tertiary period, in the Pliocene, the form *plurinervia* of this beech predominates, which is actually *F. Deucalionis* distinguished by the presence of up to 11 secondary nerves on each side of the leaf.

Among the described fossil forms their must also be mentioned *F. pliocenica* Sap. out of which according Saporta at the end of the Miocene and the beginning of the Pliocene «on voit enfin émerger et se dégager peu à peu le type non encore complètement fixe de *F. pliocenica* actuel».³⁾ On the strength of his comparisons Depape⁴⁾ comes to the conclusion that *F. pliocenica* is the form most closely related to the present *F. orientalis* Lipsky. Finally Palibin⁵⁾ has described fossil forms of the last mentioned beech, *F. orientalis* Lipsky f. *fossilis* Palib., found by him in the Caucasus, as evidence that as early as Pliocene there existed a beech identical with the one now inhabiting the Caucasus.

These data justify the conclusion that the oriental beech, whose habitat did not undergo climatic changes during the glacial period is a species which has come down to us possibly unaltered from the Tertiary period and that consequently *F. orientalis* is not a form that has detached itself from *F. silvatica*, as De Candolle

¹⁾ Unger F. Geologie der europäischen Waldbäume, I, 1869. Ettighausen u. Krasan. Beiträge zur Erforschung der atavistischen Formen, II. Folge. Denkschr. Ak. Wiss. Wien, B. 55, 1889.

²⁾ Ettighausen C. Die Formenelemente der europäischen Tertiärbuche (F. *Feroniae* Ung.). Denkschr. Ak. Wiss. Wien, B. 61, 1897.

³⁾ Saporta G. Origine paleontologique des arbres cultivés 1888, p. 152.

⁴⁾ Depape G. Recherches sur la flora pliocène de la vallée du Rhône. Ann. d. Sc. natur. 10 Ser. IV, 1922, p. 143.

⁵⁾ Palibine I. Trav. d. Jard. Bot. de Tiflis XII/2, 1913, p. 165 and Bull. Mus. Cauc. VIII, fasc. 3—4, p. 269.

supposed *F. silvatica* L. *f. asiatica* D. C.) but a Tertiary species probably older than the present west European beech.

Even more favourable to this view than the above mentioned paleontological data is the composition of the beech association in Transcaucasia, among whose constituents are such evergreen elements as *Buxus sempervirens*, *Rhododendron ponticum*, *Ilex aquifolium*, *Prunus laurocerasus*, as well as a number of herbaceous species. We quite agree with Lämmermayer and Mattfeld *) that the Tertiary forest should be distinguished by the variety of its composition whose remains are to be found at the present time in the forests of western Transcaucasia and the mountain systems of southern Bulgaria. The finding in the celebrated Göttingen brecia of beech and hornbeam together with *Rhododendron ponticum* is rather cogent evidence in favour of the relict nature of the beech forests in Transcaucasia and the Balkan peninsula. There cannot subsist any doubt as to the correctness of Mattfeld's conclusion: «demnach steht nicht nur als gesichert, dass das kolchische Waldgebiet ein Relikt der subtropischen Tertiär-Vegetation birgt, sondern es dürfte auch wahrscheinlich sein, dass hier noch ein Rest der Vegetation vorliegt aus der sich ein Teil der Flora und zum Teil der Vegetation des mitteleuropäischen Waldgebiets entwickelt hat.»

Let us now trace the history of the beech since the close of the Tertiary period. As shown by the data of palaeontology the beech had a very wide distribution during the Tertiary period, reaching far up into the north. Fossil remains of the beech have been found even in Greenland, Iceland and Spitzbergen. In the Quaternary period with the incipient glacial epoch begins the dying out of this Tertiary beech, proceeding farther southward as the climate became progressively colder.

As a result the beech persisted only in the mountain systems of Europe, chiefly to the south of 50° n. lat. and the adjoining parts of

*) Lämmermayer. L. Die Entwicklung der Buchenassoziation seit dem Tertiär. Repert. Spec. nov. Beih. B. XXIV, 1923.

Mattfeld J. Die pflanzengeographische Stellung Ost-Thrakiens. Verh. Bot. Ver. Brandenb., B. 71, 1929.

Asia Minor and Transcaucasia, which at that time were directly connected with the former. From this place of refuge the beech in the postglacial period began its advance towards the north, gradually reestablishing the former limits of its distribution.

The Crimea, although at the beginning of the Quaternary period it was already isolated from Asia Minor, likewise served as a refuge for the Tertiary beech, which experienced the unfavourable conditions of the glacial period in the mountains of southern Europe. According to Lämmermayr one of the chief refuges was the Dinaric mountain system of the Balkan Peninsula, connected on one side with the Carpathian Mountains and on the other with Asia Minor, and through it, perhaps even directly, with mountainous Crimea.

The map of these sheltering places of the beech, composed by the Lämmermayr (l. c.) contains sufficient evidence of the connection existing between these stations of the beech. And it seems to me that the question must necessarily arise: is not the beech in Asia Minor and Transcaucasia the descendant of the Tertiary beech which has undergone the least alteration; are not the intermediate forms in the Balkan Peninsula and the Crimea stages in the transformation of this Tertiary beech into the present *F. silvatica* and will not a more detailed investigation reveal the presence of such intermediate forms in other west-European asylums of the beech *); and finally, are not the mountain of the Balkan Peninsula and the Crimea the bridge linking the Tertiary *F. orientalis* with the post-tertiary *F. silvatica*? **).

*) Although Mattfeld (Aus Wald und Macchie in Griechenland. Ber. d. deutsch. Dendr. Ges. B. 38. 1927) considers the beech occurring in Greece to be identical with *F. silvatica*, his conclusions, drawn only from the habit, cannot be accepted as final.

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