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The lichen-rich coastal heath vegetation on the isle of Anholt, Denmark – description, history and development

Christensen, Steen N.[1] **& Johnsen, Ib**[2]

[1]*Botanical Museum, University of Copenhagen, Gothersgade 130, DK-1123 Copenhagen K, Denmark; Fax +4535322210; E-mail steennc@get2net.dk;* [2]*Ecological Physiology Research Group, Botanical Institute, University of Copenhagen, Øster Farimagsgade 2D, DK-1353 Copenhagen K, Denmark; Fax +4535322321; E-mail ibj@bot.ku.dk*

Abstract. The marine foreland called Ørkenen (= the desert) at Anholt is covered by lichen-rich *Empetrum nigrum-Corynephorus canescens* heath vegetation on beach ridge systems formed during the elevation of land after the Weichsel ice age and *Stereocaulon saxatile*-rich *Ammophila arenaria- Corynephorus canescens* vegetation on semi-fixed aeolic dunes. The development of the vegetation at Ørkenen is the result of various kinds of human exploitation, with its maximum in the 16th and 17th century. After the cessation of human use, a slow succession towards closed vegetation with mainly *Empetrum nigrum* and *Corynephorus canescens* began. The present heath ecosystem, developed on sandy substrate with very little organic matter and a small nutrient supply, is a high priority habitat in Europe.

Keywords: Beach ridge; *Calluna vulgaris*; *Corynephorus canescens*; Dune; *Empetrum nigrum*; Exploitation; Heath; *Juniperus communis*; Lichen; Pine forest; Shingle.

Nomenclature: Hansen (1981) for vascular plants; Andersen et al. (1976) for mosses; Santesson (1993) for lichens.

Introduction

The 22 km^2 large island of Anholt in the Kattegat is composed of two different parts: moraine hills in the west, Vesterlandet, and a 19 km^2 large marine foreland in the east, Østerlandet, called Ørkenen (= the desert). The moraine hills are built of layered sand and the surface consists of a mixture of moraine sand and moraine clay mixed with stones of different sizes.

During the last Ice Age most of Denmark was glaciated. The ice cap retreated about 14 000 yr ago. From about 13 000 years before present to about 10 000 yr before present, Denmark was one continuous land mass, including the western part of the Kattegat with the present day islands of Anholt and Læsø (Wienberg Rasmussen 1970; Binderup 1994). The subsequent rise in sea level resulted in a transgression of the sea over much of the former land and at its maximum ca. 6000 to 5000 before present, the sea level of the Littorina Sea had risen to ca. 10 m above the present level (Heller 1973; Binderup 1994). Only the moraine hills were then above the sea (Heller 1973; Christiansen 1976). The post glacial uplift of land, in combination with the westerly winds and currents that predominate in the middle of the Kattegat, has during the last 5000 yr resulted in the development of a marine foreland of successive beach ridges deposited east of the moraine hills. These deposits have created the whole eastern part of Anholt: the beach ridge system, Ørkenen, the spit, Totten, and the reef, Anholt rev (Trap 1963; Schou 1969, p. 84; Christiansen 1976) (Fig. 1). At present the beach ridge plain is 12 - 13 m above sea level in the oldest western part gradually falling towards east (Heller 1973). The geomorphologic processes and features of Ørkenen are very much like those of the eastern peninsula of the other sandy Kattegat island, Læsø (Hansen 1995).

Ørkenen on Anholt is an almost level plain, composed of a system of old beach ridges of stones and pebbles with sandy depressions in-between. These shingle ridges run basically S-N in the western part, while in the southern and eastern part, they run SW-NE, more or less parallel with the present southeastern coastline (Fig. 1).

Superimposed on this system of ridges we find scattered, up to 25 m high aeolic dunes (Fig. 2). The dunes in the eastern part of Ørkenen are the largest and most mobile, while in the western part, which is in lee of the prevailing winds by the western moraine hills, the inland dunes are few and small. These aeolic dunes are today more or less fixed, as the vegetation cover of today prevent large scale sand drift episodes (Figs. 2, 3 and 4). In places aeolic sand have smoothed the contours of the beach ridge system (Fig. 3) or resulted in more or less flat stretches of sand.

The soil of Ørkenen is among the most leached and nutrient-poor vegetation substrates in Denmark. With exception of the dwarf shrub vegetation, the humus content of the soil is very low and there is practically no organic top soil formation.

Fig. 1. The island of Anholt. The moraine hills, Vesterlandet, make up the westernmost one fifth of the island, while the marine foreland, Ørkenen, constitute the remaining eastern part. The orientation of the beach ridges is clearly seen except where obscured by aeolian dunes. Two dune plantations appear as dark angular patches. South of the moraine hills and southwest of the air strip (light coloured rectangular patch) a large *Pinus mugo* thicket is seen (same as in Fig. 6). Aerial photo 14 May 1998, copyright Kort og Matrikelstyrelsen.

Fig. 2. The northern central part of Ørkenen showing the beach ridge system and the aeolian inland dunes. In the upper left corner, the sea, the beach and the coastal dunes are seen. Oblique aerial view, 7 Aug. 1999.

Due to the coarse soil texture, the field capacity is very low, thus contributing to leaching of the soil as well as to the drought stress situation for the plant cover of Ørkenen, resulting in a very low primary productivity. Soil pH at Ørkenen measured in August 1999 varied from 4.2 to 7.2 (Table 1). Only where some humus had been formed soil pH reaches levels around and below 5.

The climate of Anholt reflects its small size and its position in Kattegat, midway between Jutland and Halland. The winters are mild followed by a cool spring, with even June having the relatively cool mean temperature of 14.5 °C. The mean temperatures in July, 17.2 °C, and August, 16 °C, however, are relatively high. The fall is also relatively warm. Only February has a mean temperature below zero, – 0.6 °C. The mean annual precipitation is relatively low: 536 mm, distributed over only 138 days, while fog occurs on 42 days, which is relatively often. In comparison to mean Danish climatical conditions, the climate of Anholt is relatively warm and dry (Nielsen 1975; Karsten 1982).

The vegetation of the central part of Anholt, Ørkenen, is dominated by two plant communities on the aeolian dunes and the beach ridge system, respectively. The aeolian dunes are characterized by *Ammophila arenaria*, *Corynephorus canescens* and a ground cover of cryptogams, especially *Stereocaulon saxatile* and *Cladonia* spp. (Table 2). Dwarf shrubs are absent from the aeolian dunes. The beach ridge system is characterized by *Corynephorus canescens*, *Empetrum nigrum* in patches and a species-rich ground cover of cryptogams, in particular *Cladonia* spp. (Table 3, Fig. 3). *Corynephorus canescens* is almost the only vascular plant on the sandy plains between the ridges, except for the most western part of Ørkenen, where more continuous *Empetrum-Calluna* heath occurs (Table 5, Fig. 5). *Empetrum nigrum* forms a more or less continuous cover along the shingle ridges (Table 4, Fig. 4). *Ammophila arenaria* is only occasionally present in the beach ridge system vegetation.

Calluna vulgaris heath occurs mainly in the SW part of Ørkenen on more or less level, gravelly ground (Table 6, Fig. 6), as well as in the slacks behind the foredunes. With the exception of the dominating dwarf

Table 1. pH of soil samples of Anholt, August 10th 1999. 10 g dry matter of soil was suspended in 50 ml water, stirred and left to settle for 2 hr, and pH(H_2O) was measured in the supernatant with glass electrode meter PHM340, Radiometer, Copenhagen.

Vegetation type	Soil depth (cm)	pH(H_2O)
Corynephorus-Stereocaulon vegetation on inland dunes (see Table 2)	0-1	6.2
	5-10	7.2
Ammophila-Cladonia glauca vegetation on inland dunes (see Table 2)	0-1	5.2
	5-10	6.6
Corynephorus heath with scattered *Empetrum* patches (see Table 3)	0-1	6.3-6.6
	5-10	6.4-7.2
Empetrum-heath on old beach ridge (see Table 4)	0-1	5.8
	5-10	6.1
Empetrum-Calluna heath, mineral soil covered with algae (see Table 5)	0-1	5.1
	5-10	5.3
Empetrum-Calluna heath, *Cladina*-gap (see Table 5)	0-1	4.2
	5-10	4.4
Empetrum-Calluna heath, *Polytrichum*-gap (see Table 5)	0-1	5.0
	5-10	5.8
Empetrum-Calluna heath, below *Empetrum nigrum* (see Table 5)	0-1	4.9
	5-10	5.4
Calluna heath, below *Calluna vulgaris* (see Table 6)	0-1	4.5
	5-10	4.6

Table 2. The vegetation of the inland dunes exemplified by analysis from the dune Storhøj. The north slope is exposed with an unstabilized vegetation dominated by *Corynephorus canescens* and a large amount of minerophilic lichens (*Corynephorus-Stereocaulon* vegetation). The south slope is stabilized and is dominated by *Ammophila arenaria* and organophilic lichens on the litter (*Ammophila-Cladonia glauca* vegetation). UTM 32 V PH 568 886. 12 Aug. 1999. Pin-point analyses of each vegetation type was based on 10 to 30 1-m^2 squares with a 20-cm^2 mesh, i.e. 16 cross points. p = present in the 1-m^2 phrames but not recorded by the cover analysis. np = not present.

Species	North slope Cover %	South slope Cover %
Empetrum nigrum	p	1.3
Thymus serpyllum	p	np
Ammophila arenaria	22.5	83.6
Corynephorus canescens	40	22.5
Hieracium umbellatum	np	1.3
Cetraria muricata	3.8	1.3
Cladonia arbuscula	p	np
Cladonia cervicornis	np	p
Cladonia chlorophaea	np	3.8
Cladonia coniocraea	5	2.5
Cladonia diversa	23.8	5.0
Cladonia floerkeana	p	p
Cladonia foliacea	np	p
Cladonia glauca	30.0	17.5
Cladonia gracilis	p	np
Cladonia macilenta	p	1.3
Cladonia merochlorophaea	p	11.3
Cladonia phyllophora	p	1.3
Cladonia portentosa	np	p
Cladonia ramulosa	1.3	1.3
Hypogymnia physodes	p	p
Stereocaulon saxatile	15.0	np
Trapeliopsis granulosa	np	p
Cephaloziella divaricata	p	6.3
Dicranum scoparium	2.5	1.3
Klebsormidium spec.	1.3	np
Litter	p	1.3
Sand	10.0	p

Fig. 3. Lichen-rich *Corynephorus canescens* heath with scattered *Empetrum nigrum* patches on marine foreland overlain by aeolian sand (Table 3). Inland dunes are seen in the background. Central part of Ørkenen north of the dune Bassen. 1 Aug. 1998.

shrubs, the floras of the *Empetrum* and the *Calluna* heath are similar. The *Calluna* heath is dealt with in more detail below.

The vegetation types of Ørkenen are presented in detail in Christensen (1997) and Johnsen (1997). Large unbroken areas of undisturbed lichen-rich heath vegetation on acidic, nutrient-poor sandy substrate as found in Ørkenen, are rare in present-day Europe. In large parts of western Europe areas with such vegetation are directly threatened by building and recreational activities, as well as changing their composition and dynamics due to air pollution from agriculture and industrial activities and invasion of non-indigenous highly competitive species.

Ørkenen at Anholt has great aesthetic, scientific and conservational value and large parts of the area are without any direct anthropogenic influence at present. The main purpose of the present paper is to demonstrate that the present vegetation is the result of centuries of human over-exploitation of the original vegetation cover and the subsequent successional processes.

History of land-use and its impact on vegetation

Analysis of historical sources from the 15th to the 20th century

Knowledge of the land-use history of a habitat is essential to understand the development of the present day vegetation and is indispensable when defining the appropriate management of the area (Dolman & Sutherland 1991). Therefore, the few and scattered notes on the vegetation of Ørkenen and its utilization found in historical sources are presented below.

Anholt was originally a forested island. The forest consisted mainly of Scots pine (*Pinus sylvestris*), but there was probably some oak too, judging from sub-fossil remains in fens (Steenstrup 1896; Jessen 1897 cited in Karsten 1982).

Tradition tells that in the east Blåskoven was found (the blue forest or the black forest, depending on the age of the name), and one of the larger dunes still carry the name Blåhøj (the blue/black hill), while in the west there was a mixed forest of hazel, birch and oak (Kristensen 1891).

Fig. 4. Shingle beach ridge rich in epilithic and epigeic lichens. The phanerogamic vegetation is characterized by *Corynephorus canescens* expansions and *Empetrum nigrum* patches, the latter more or less following the ridges. The transect line follows the orientation of the ridge (Table 4). The central part of Ørkenen south of the dune Bassen. 14 Nov. 1997.

Due to the many ship wrecks caused by the reefs around the island, king Frederik II of Denmark ordered in a letter of 8 June 1560 a light to be established. A beacon lit by wood was established. Already 18 April 1564, the king required in a letter the fuel for the beacon to be provided from elsewhere, as the pine forest on Anholt was heavily overcut (Hobolt 1946). About 1583 a lamp lit with tallow was established (Kleiminger 1995). 1592 the Danish king Christian IV wrote that seafaring men complained about the reduction of the forest, which they used for landfall, and he referred to his fathers command not to cut in the forest (Paulsen 1898; Heide 1914; Hobolt 1946). In 1631 king Christian IV asked the light keeper to use Scottish coal, as the forest had now almost disappeared (Hobolt 1946).

The written sources differ in opinion but it seems that the destruction of the forest was not only due to the beacon, but also to the inhabitants ruthlessly cutting the forest for wood tar (Bynch 1801b; Becker 1841; Trap 1963) and for fire-wood in households. The wars with the Swedes during 1700-1721 and the pirate period thereafter finally destroyed the Anholt forest. The forest was told once to have been on fire for seven days and nights (Kristensen 1891). By the mid 18th century, the forest was replaced by *Juniperus* thickets that were high and dense enough for all the cows of the island (between 70 and 90 – see below) to hide in (Bynch 1801b). These thickets disappeared around 1800 (Bynch 1801b).

As late as around 1800, Bynch (1801a, b) told that lots of stumps were present in the dunes and that the roots if cut still smelled of resin. The stumps were excavated and used by the inhabitants (Becker 1841). Still in 1866, Ørkenen was called Skoven (= the forest) and stumps of pine could be found here and there in the drifting sand (Boye 1877).

There are only few indications of the composition of the flora and vegetation of Ørkenen in historical times. Pontoppidan (1768) mentioned solely 'Marhalm' (presumably *Ammophila arenaria*; see below) and *Juniperus communis*, and Bynch (1801b) also mentioned the former species in the coastal and inland dunes and tells that it avoids the old beach ridges. Imprints of *Leymus arenarius*,

Ammophila arenaria, Elytrigia junceiforme, Carex arenaria, Trifolium medium, Galium boreale, Hieracium umbellatum, Iris pseudacorus, Pinus sylvestris, Quercus robur, Alnus glutinosa, Corylus avellana and *Salix repens* have been found in caked clay conceivably used to cover charcoal or tar stacks (Heide 1914, Friis 1981).

Lange (1978) speculated that part of Ørkenen may be old heath, devastated by turf cutting and over-grazing. It was practice (e.g. on Læsø; Pontoppidan 1768) to hack turf into the dung heap in order to improve the manure. It also is conceivable that after the destruction of the pine forest, the inhabitants of Anholt had to change to turf for heating, removing all the organic contents and most of the nutrients of the soil, thereby exposing the sandy subsoil to the wind. In 1643 the sand drift got out of control (Pontoppidan 1768; Boye 1876) and in 1680 the town barely avoided being buried in sand (Jørgensen 1871; Hobolt 1946). Oral tradition (Bunch 1801b; Kristensen 1891), as well as an account by the owner of the island (Jørgensen 1871), tells about fields that were covered by sand.

The use of cow and sheep dung for fuel (Kristensen 1891) and the use of the underground parts of *Salix arenaria* for fire-wood as late as around 1900 (Svendsen 1915) is indicative of the over-exploitation of the organic resources of the island.

The major part of Ørkenen could not be cultivated due to the sand- and stone-rich substrate characteristic of the old beach ridges covering the isostatically elevated land area. References to agricultural practices are, hence, few and scattered in the historical sources. In 1683 a taxation commission recounted that the 16 farms on the island, which were situated in Vesterlandet (the moraine hills), had poor growing (Mackeprang 1904). The productivity of the fields was poor and the total production of the 16 farms was equivalent to that of a single farm in many other places in Denmark; the farmers, therefore, supplemented their earning by fishery and seal hunting (the lord of the island in an account to the king 1716, ref. by Jørgensen 1871).

Around 1800 the 16 farms each had 3-5 horses, 4-5

Table 3. *Corynephorus canescens* heath with scattered *Empetrum* patches in the central part of Ørkenen. UTM 32V PH 575 882. 10 Oct. 1997. Pin-point analyses of each vegetation type was based on 30 1-m^2 squares with a 20-cm^2 mesh, i.e. 16 cross points per square.

Species	Cover %
Empetrum nigrum	22.5
Carex arenaria	0.2
Corynephorus canescens	15.6
Buellia aethalia	0.2
Cetraria muricata	3.8
Cladonia arbuscula	0.6
Cladonia cervicornis	3.5
Cladonia ciliata	0.2
Cladonia diversa	10.6
Cladonia floerkeana	0.6
Cladonia foliacea	1.5
Cladonia furcata	2.1
Cladonia glauca	10.4
Cladonia macilenta	0.6
Cladonia merochlorophaea	1.3
Cladonia portentosa	2.7
Cladonia pyxidata	2.9
Cladonia ramulosa	1.7
Cladonia squamosa	1.9
Cladonia subulata	0.4
Cladonia uncialis	4.0
Hypogymnia physodes	1.9
Placynthiella oligotropha	0.4
Platismatia glauca	0.8
Polysporina simplex	1.9
Pseudevernia furfuracea	0.4
Rhizocarpon obscuratum	4.6
Stereocaulon saxatile	5.4
Trapeliopsis granulosa	0.8
Dicranum polysetum	0.2
Dicranum scoparium	0.8
Pleurozium schreberi	0.2
Polytrichum piliferum	1.5
Racomitrium lanuginosum	0.2
Zygogonium ericetorum	10.4

Table 4. *Empetrum* heath on old beach ridge in the central part of Ørkenen. UTM 32V PH 573 875. 14 Nov. 1997. Pin-point analyses of each vegetation type were based on 20 1-m^2 squares with a 20-cm^2 mesh, i.e. 16 cross points per square.

Species	Cover %
Calluna vulgaris	4.4
Empetrum nigrum	51.3
Corynephorus canescens	5.6
Alectoria sarmentosa var. *vexillifera*	0.6
Cetraria muricata	1.3
Cetraria aculeata	3.1
Cladonia arbuscula	0.6
Cladonia cervicornis ssp. *cervicornis*	2.5
Cladonia cervicornis ssp. *verticillata*	1.3
Cladonia coniocraea	0.6
Cladonia diversa	19.4
Cladonia floerkeana	1.9
Cladonia furcata	3.8
Cladonia glauca	13.1
Cladonia gracilis	5.6
Cladonia merochlorophaea	8.8
Cladonia portentosa	6.3
Cladonia pyxidata	5.6
Cladonia ramulosa	1.9
Cladonia squamosa	0.6
Diploschistes muscorum	0.6
Hypogymnia physodes	2.5
Platismatia glauca	0.6
Polysporina simplex	1.9
Porpidia tuberculosa	0.6
Pseudevernia furfuracea	2.5
Rhizocarpon geographicum	0.6
Rhizocarpon obscuratum	5.6
Stereocaulon saxatile	2.5
Trapeliopsis granulosa	0.6
Dicranum scoparium	1.9
Polytrichum piliferum	5.6

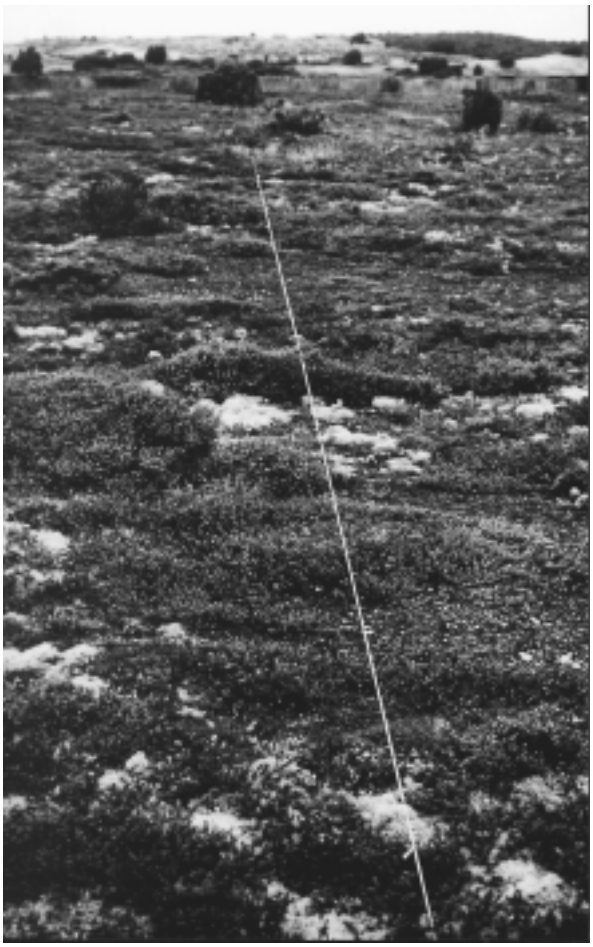

Fig. 5. Lichen-rich *Empetrum nigrum* heath (Table 5). The *Cladonia portentosa* cushions are clearly seen. To the upper right, behind the inland dunes, the northern of the dune plantations is seen (cf. Fig. 1). The western part of Ørkenen north of the path Ørkenstien. 30 Aug. 1997.

cows and 10-16 sheep (Bynch 1802). The at that time nine crofters each had a few geese and sheep and some a single cow (Bynch 1802). When a farmer had more than one son, only one could take over the farm. The others became crofters and were given any vacant house. Because all the land of the moraine hills was occupied, the bailiff assigned a piece of land in Ørkenen in case no houses were available; here a house could be build and a kitchen garden established. The sandy soil of the garden was fertilized with seaweed (Bynch 1802). Around 1800, four such houses were present in Ørkenen near the town (Bynch 1802). 'Marre-halmb' (= *Leymus arenarius*, but most likely referring to *Ammophila arenaria*) was an essential supplementary winter fodder (Bynch 1801b; Mackeprang 1904). It was also used for thatching (Bynch 1801b). By tradition the major part of the dunes were cut in September (Kristensen 1891; Hobolt 1946). Paulsen writes that *Ammophila arenaria* formerly and at least until around the end of the 19th century, was mowed and used for cattle fodder (Paulsen 1898 – he writes in the present tense!). The crofters, who had no hayfields on the moraine hills, tethered their only cow in the dunes (Kristensen 1891). One track in the inner part of Ørkenen was as late as 1924 called Fævejen (the cattle road), along which the cattle was driven to grazing in the farther dunes (Friis 1981). Around 1900 sheep-grazing was still practised in Ørkenen and young *Juniperus* individuals were pulled up to improve the grazing. The grazing ceased, however, before 1915 (Svendsen 1915). Friis (1981), however, observed a few sheep browse the small heather patches below the southern moraine hill Sønderbjerg in 1924. In the 1970s short-lived sheep-keeping with a few hundred sheep was established.

The westernmost part of Ørkenen, close to the town, was by the turn of the 19th century for the most changed into fields, particularly potato, carrot and rye fields (Paulsen 1898).

The total clearing of the forest, probably followed by turf cutting, and the heavy exploitation of the vegetation by hay cutting and grazing, resulted in a man-made wasteland: "…a sand sea .. here and there covered with scattered *Ammophila* …; yellow sand hills and grey stone flats are all that meets the eye..." (Becker 1841). Photographic illustrations from the latter part of last century and the beginning of this century show an almost completely denuded landscape in Ørkenen (Paulsen 1898: Figs. 2 and 3; Grøntved 1931: Figs. 1 and 2).

The presence of large amounts of reddish coloured

Table 5. *Empetrum-Calluna* heath in the central, western part of Ørkenen. UTM 32V PH 563 876. 30 Aug. 1997. Pin-point analyses of each vegetation type were based on 10 1-m^2 squares with a 20-cm^2 mesh, i.e. 16 cross points per square.

Species	Cover %
Calluna vulgaris	17.6
Empetrum nigrum	31.3
Cetraria aculeata	3.5
Cladonia cervicornis	2.7
Cladonia cornuta	1.2
Cladonia diversa	6.6
Cladonia foliacea	0.8
Cladonia glauca	2.0
Cladonia gracilis	19.9
Cladonia merochlorophaea	2.7
Cladonia portentosa	18.0
Cladonia ramulosa	1.6
Cladonia uncialis	0.8
Hypogymnia physodes	0.8
Stereocaulon saxatile	0.8
Dicranum scoparium	4.3
Polytrichum piliferum	7.0

Fig. 6. Lichen-rich *Calluna vulgaris* heath on gravelly flat (Table 6). The transect line is being established by the second author. The pin-point phrame is seen beside the rucksack. In the background a selfsown thicket of *Pinus mugo* is visible (cf. Fig. 1). The south western part of Ørkenen west of the air strip. 28 Aug. 1997.

sand in the inland dunes indicates former leaching of, e.g. iron compounds, from a previous organic top soil layer in a wide spaced original pine forest or heathland.

Since the deterioration of the former forest at the island, the previous mor layer has thus completely disappeared or has been covered with massive layers of aeolian sand. During the recent three centuries, a weak humus formation has taken place mainly below the dwarf shrub vegetation.

The distribution of Calluna vulgaris and Juniperus communis over the past 150 years

In the southwestern part of Ørkenen, *Calluna* was only scarcely present in 1867 (Paulsen 1898, reference to map by Hans Pedersen). A few years later, 1870, *Calluna* occurred here and there, but was not common and never formed an unbroken cover (Jacobsen 1879). An almost unbroken *Calluna* shrub of 500-600 paces in circumference surrounded by younger, isolated bushes was, however, present at the turn of the century (Paulsen 1898). In this little heathland, reindeer lichens occurred and in places seemingly out-competed the *Calluna* shrubs. Species of *Cladonia* and *Cetraria* (*Coelocaulon*),

Table 6. *Calluna* heath in the SW part of Ørkenen. UTM 32V PH 561 868. 28 Aug. 1997. Pin-point analyses of each vegetation type was based on 10 1-m^2 squares with a 20-cm^2 mesh, i.e. 16 cross points per square.

Species	Cover %
Calluna vulgaris	44.1
Empetrum nigrum	3.5
Cetraria muricata	2.7
Cladonia arbuscula	1.2
Cladonia cervicornis	2.0
Cladonia chlorophaea	4.3
Cladonia ciliata	1.6
Cladonia diversa	2.7
Cladonia foliacea	1.2
Cladonia furcata	1.2
Cladonia glauca	0.8
Cladonia gracilis	7.8
Cladonia merochlorophaea	2.0
Cladonia portentosa	2.3
Cladonia ramulosa	2.3
Hypogymnia physodes	1.2
Stereocaulon saxatile	1.2
Dicranum scoparium	8.2
Pleurozium schreberi	0.8
Polytrichum piliferum	4.7

Thymus serpyllum, Lotus corniculatus, Corynephorus canescens, Antennaria dioica, Carex arenaria, Empetrum nigrum and *Juniperus communis* occurred in the openings of the *Calluna* carpet (Paulsen 1898). In 1924 a few scattered wretched *Calluna* heath patches occur below the moraine hill Sønderbjerg (Friis 1981). This *Calluna* heath was still expanding NE and E in 1961 (Hansen 1962). Karsten (1982) confirmed the expansion of the *Calluna* dominated vegetation since the time of Paulsen (1898) without any reference to its present extension. He does, however, describe one further *Calluna* patch more to the east, in Pakhusbugten, where *Calluna* and *Empetrum* are co-dominant, and argues that it must be a new growth of *Calluna* since Paulsen (1898) did not refer to it (Karsten 1982). Today *Calluna vulgaris* is established in many places along Pakhusbugten, the southeast coast, and colonized far east (personal observations). The soil conditions support the theory of the young age of the *Calluna* communities: only a weak podsol profile is developed (Karsten 1982).

Based on field work in 1981, Karsten (1982) gives the following description of the *Calluna* heath in the SW part of the island. The *Calluna* heath here is established on a deflation plain covered with pebbles. The most common species in the vegetation is *Calluna vulgaris* (see our Table 6). It grows in approximately 20 cm high, dense shrubs scattered on the deflation plain (Figure 6). The shrubs have a broad age spectrum, from seedlings, which predominantly occur on bare mineral soil, to older shrubs with central cavities. Self-sowing is rather heavy, about 42 seedlings per m^2. In other areas of Ørkenen where *Calluna* is dominant or co-dominant, seedlings are rarely seen. *Empetrum* plays only a minor role in the vegetation (see Table 6) and seems to prefer the higher, stony, old beach ridges, where *Calluna* is less vigorous. The soil consists of gravely sand with a 4-6 cm thick illuvial horizon at 30 cm depth. No Hard pan develops, just a reddening of the sand. Only under the dwarf-shrubs is a slightly developed mor-layer present in some places, but most of the organic matter on the soil surface is just drifted litter (Karsten 1982).

Juniperus thickets were present in Ørkenen around 1760 but had disappeared around 1800 (Bynch 1801b). On the moraine hills, however, "...some bushes of *Juniperus* spread their branches over the ground..." (Bynch 1801b). In 1866 miserable *Juniperus communis* bushes grew only near the town (Boye 1876). Later that century, *Juniperus* had its maximum density in the southwestern part of Ørkenen and was only thinly scattered in the rest of Ørkenen (Paulsen 1898). This was probably the result of grazing management, where young *Juniperus* bushes were pulled up to improve grazing for sheep. After the cessation of grazing shortly before 1915, *Juniperus* started to spread in Ørkenen (Svendsen 1915). Today, *Juniperus communis* is very common throughout most of Ørkenen particularly in the western part (Figs. 3, 4 and 5).

Afforestation during the 20th century

After 1885, widespread afforestation commenced in Vesterlandet, i.e. on the moraine hills (Wolsing 1973). Mainly *Pinus mugo* and *P. sylvestris* were used to prevent sand drift and over-sanding of the fields (Svendsen 1915). Today, Vesterlandet is, with the exception of agricultural land, mainly pastures, mostly covered with forest (Nielsen 1975). In Ørkenen, afforestation took place in the beginning of this century (Karsten 1982). The 16 ha large plantation, Hermansgave, established in 1908, consists of *Pinus sylvestris* and *Quercus robur*. The pines were in 1982 5-6 m high, while the oaks were merely bushes. A comparable plantation exists SW of the lighthouse (Karsten 1982). Stands of Scots pine and oak several metres in height occur at present. Northeast of the town, a minor stand of *Pinus nigra* and some *P. sylvestris* are in bad condition, especially *P. nigra* fails to flourish (Karsten 1982).

Aside from the planted stands in Ørkenen, extensive thickets of self-established *Pinus mugo* occur (Fig. 6). In some places, self-established *P. sylvestris* and *P. contorta* are found, but they do not spread to the same degree as *P. mugo* (Karsten 1982). *P. mugo* is the only tree capable of establishment in these harsh conditions of poor soil, low precipitation and heavy winds (Fodgaard 1995). By 1924, the *P. mugo* thickets were small and scattered below the moraine hill Sønderbjerg (Friis 1981), but since then the self-sown thickets have expanded considerably, at present by 30-40 m per year (Fodgaard 1995). Seed-sources are partly the plantations and partly the *Pinus mugo* hedges established around summer cottages.

The most extensive self-established thickets in Ørkenen occur along Nordstrand and Pakhusbugten, where depressions behind the foredunes often are covered with trees. In the drier places, *Pinus mugo* dominates, while in damper situations the indigenous *Betula pendula, Alnus glutinosa* and *Populus tremula* are prominent. In parts of Ørkenen, especially in the western part and in the vicinity of Hermansgave, the vegetation has changed from dune vegetation to impenetrable *Pinus mugo* thickets (Karsten 1982).

Due to the high conservation value of the open landscape, Århus Amt supported by the EU LIFE programme commenced clearing of the self sown *Pinus* thickets during 1995-1996.

Discussion

The relation between the history of land-use and the actual vegetation

The vegetation development of Ørkenen during historical times is not known in detail, but from the rather few historical sources cited above, one likely scenario is the following:

1. The island was from prehistoric times to the Middle Ages covered by Scots pine forests with elements of deciduous trees, notably oak. A dwarf-shrub vegetation might have been present on the forest-floor, at least in more open places.
2. The forest was cut for fuel and other purposes during the Middle Ages up to around 1600. *Juniperus* thickets developed when the forest was cleared. Expansion of dwarf-shrub heath became possible. Sand drift began and accelerated.
3. After the total destruction of the forest around 1600, it is conceivable that the inhabitants cut turf for fuel, and also for fertilizing the fields and other purposes, as was common practice in other sandy areas of Denmark (Højrup 1975; Odgaard 1994). This, in combination with possible overgrazing, the removal of young junipers to improve grazing, possible cutting of old junipers bushes for fire wood and other purposes and digging up underground parts of *Salix arenaria* for fuel, destroyed any original vegetation, depleted the soil of its nutrients and created a wasteland dominated by *Corynephorus canescens* and lichens (about 1600 to about 1900).
4. The cessation of grazing resulted in the spread of *Juniperus* in Ørkenen and the spread of what little *Calluna* heath that might have been left. Afforestation with *Pinus*, especially *P. mugo*, gave rise to considerable self-sowing and a build up of extensive thickets of this species, particularly in the depressions of the southern part of Ørkenen (about 1900 to about 1995).
5. The cutting of the *Pinus mugo* thickets (1995-1996).

On the other sandy Kattegat island, Læsø, Hansen (1995) describes a comparable scenario for the destruction of the pine forest there; the forest of Læsø was mainly cut for fuel for the extraction of salt from brackish water. Also in the Veluwe area, The Netherlands, a vast desert-like landscape of drifting sand with lichen-rich *Corynephorus* vegetation developed as a result of human over-exploitation of former oak woods and heathlands on poor, dry Pleistocene sands (de Smidt and Koster, respectively, cited by Daniels 1990).

Human exploitation as prerequisite for the development of the ecosystems of Ørkenen

Losses of organic matter and nutrients by the burning of the forest, and maybe also the ground cover and peat layer, may have been considerable and the time required to replace these losses may be decades or even centuries (Vestergaard & Alstrup 1996). Further, the extraction of organic matter by the local population additionally depleted the area of nutrients.

The characteristics of the ecosystem of Ørkenen are the lack of soil formation and, hence, the low nutrient level of the sandy soils. As a result, the vegetation, which mainly is in early succession stages containing many pioneer species of low competitive ability, is mainly due to human over-exploitation for centuries. The expansion of the *Calluna* patches and the spread of *Juniperus* in recent times are the results of the cease of exploitation and signs of recovery through progressive succession.

Conclusion

Interaction of land use and environmental conditions

In all likelihood, human over-exploitation was the agent that caused the development of the present nutrient-poor and dynamic conditions of the beach ridge and dune systems of Ørkenen. Grazing and hay extraction of the dunes increased the mobility of this inherent dynamic system, as evidenced from historical reports of oversanding of fields and the threat of the town. The later cease of these uses have resulted in a state where the natural internal perturbations of the, by nature, dynamic dune system creates a mosaic of vegetation in different succession stages. This gives room for species and communities with low demands for nutrients and poor competitive abilities, such as lichen-rich *Corynephorus* vegetation and lichen-rich *Ammophila* vegetation.

In the beach ridge system conceivable turf cutting and the uprooting of woody plants, as well as grazing, resulted in depletion of the nutrients and organic matter, giving rise to nutrient-poor mineral soils of low water-holding capacity. These conditions are suitable for the same type of species as mentioned above, and for epilithic lichens, which colonize the stones and pebbles of the beach ridges. The dwarf shrubs also benefited from the halt of the exploitation of Ørkenen and is slowly spreading. The natural succession of these shingle ridges (Randall & Doody 1995, cited by Packham & Willis 1997; Fig. 8.7) will probably result in a reduction of the epilithic lichen cover through the expansion of the dwarf shrubs.

Conservation value of Ørkenen in light of its background

This subject is treated in more detail in Christensen & Johnsen (2001), hence, in the following only a few principal points will be briefly dealt with.

The internal dynamics caused by the inherent nature of the dune and beach ridge systems and the overall succession trends, albeit slow, resulting from the human over-exploitation and its cease, makes this large and at present undisturbed marine foreland highly valuable aesthetically, scientifically and educationally. The fact that Ørkenen is one of the largest and least affected by agricultural pollution, e.g. deposition of atmospheric nitrogen compounds, of the European lichen-rich, nutrient-poor ecosystems on acidic sandy soil gives it high conservation value, both from a Danish and a European standard. The main threats against the vegetation of the marine foreland of Anholt are invasions of especially *Pinus mugo* and atmospheric pollution, and more locally by encroachment by *Rosa rugosa* and tourist wear.

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