Studies on *Maculinea alcon* (Schiff.) - *rebeli* (Hir.) (Lep. Lycaenidae) with Reference to the Taxonomy, Distribution, and Phylogeny of the Group

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Contents.

Introduction.

For some years the author has collected Danish Lycaenids to study their local geographical variation. Rather early it became evident from the information concerning the Danish population of *Maculinea alcon* (Schiff.) that this species still required a great amount of investigation, not only in Denmark, but also in the adjacent faunal areas. In Denmark *alcon* was not recognized until 1923, and the present knowledge concerning its Danish distribution is far from complete. In addition, there are many unsolved problems in its Danish and European variation. Thus a number of years ago in Belgium (Berger 1946) attention was called to the remarkable Danish range of variation, which was associated with both *Mac. alcon* and its closely related Central

European form *rebeli* (Hir.), the taxonomical problems of which have not yet been elucidated. But in spite of a comprehensive Danish material of the species, which is rather common in certain parts of this country, the study of it has to a certain extent been neglected, and even the latest views concerning its relations in the Danish area (Langer 1960) rest on insufficiently supported assumptions.

The primary purpose of this study was consequently to elucidate the identity and taxonomy of the Danish population, with special regard to the specimens with outer resemblance to forma *rebeli* (Hir.). As Scandinavia furthermore contains a Swedish population of the species, which has hitherto been referred to as *alcon* (Nordström 1955), this population was naturally included in the primary studies.

As the problems of the Scandinavian population were satisfactorily clarified during this work it also proved necessary to include the neighbouring regions in Central Europe in the study, as it seemed possible to solve the hitherto complicated problem on the relationship between *alcon* and *rebeli* from entirely different and more simple lines than those previously suggested. For this reason the present work has been divided into two main sections, the first of which only deals with the Scandinavian population of *Mac. alcon* and its taxonomy, while the second makes an analysis of the European populations of the entire group based on the Scandinavian findings and the comprehensive literature which since 1946 has been published in many European countries. Based upon this analysis the phylogeny and taxonomical problems of the group are discussed separately.

Introductorily it might be useful to summarize the development of the problems regarding the group, especially in view of the progress made since they were brought up in 1946. In that year L. Berger carried out a divison of the Belgian *alcon*-population into two groups with apparently well-defined morphological differences. The first group showed an outer resemblance to the typical race of the species and was in Belgium found in damp areas with *Gentiana pneumonanthe* L. The other group, however, was found on dry biotopes with other *Gentiana* species, especially *cruciata* L. and seemed according to the European literature to have a wide distribution. It was the first time reported from the Styrian Alps under the name of *Lycaena alcon*

var. *rebeli* (Hirschke 1904) and was consequently mentioned by Berger as specifically different from *Mac. alcon* under this name. Furthermore, the Central European population of this new species was separated as a distinct geographical race, subsp. *xerophila*.

The study was soon cited in a number of European countries including Denmark (Hoffmeyer and Knudsen 1947). However, the following authors in France (Bernardi 1947) and in Switzerland (Beuret 1949) were not able to confirm the significance of the originally chosen morphological differences, but to a certain extent the different ecological niches of both forms. On account of this, the differences between them in their opinion should be considered an example of ecological subspeciation.

The specificity of f. *rebeli* has later on been asserted again, to a certain extent for the same reason, viz. the divergent ecology compared with *alcon* (Forster-Wohlfahrt 1956). Schulte (1958) has tried to confirm this statement on account of certain divergences in the shape of the male genitalia, findings which, however, have not been confirmed later on (Ebert 1961). At present great uncertainty prevails in Central Europe regarding the problem. This uncertainty is increased by observations from Holland (Lempke 1942), Czechoslovakia (Schwarz 1950) and Germany (Bergmann 1952, Ebert l. c.) reporting the occurrence of *alcon*, but not of *rebeli*, on dry biotopes in Central Europe.

A complete picture of the ecological and taxonomical relations of the entire group is consequently becoming urgent but has so far been obscured by the apparent lack of applicable features of f. *rebeli;* thus it is not yet evident whether this form represents an ecological race of *alcon* or whether another type of diverging evolution has taken place. As the Danish population has been associated with both *alcon* and *rebeli*, it must by virtue of its variation be capable of supplying important information in the present situation.

Part I. **The identity of the Scandinavian population.**

A. **Material and methods.**

As mentioned in the Introduction re-examinations of the group proved that many of the originally selected morphological features showed such a wide range of variation that their taxonomical value became doubtful (Beuret 1949, p. 26). This apparent lack of specific features in f. *rebeli* shows that its problems should be

attacked on a broader basis than hitherto. For that reason the present work has been based on group examinations, in which primary taxonomical significance is attached to the variation of the group. To be ideal the scope of the study-material will easily become so extensive that collections up till now in Denmark and Sweden are insufficient for its purpose. The lack of material from Sweden has in fact been perceptible.

The object of the study is the local population (deme in sensu Simpson 1961), and within this field the material is delimited in easily definable groups. The peculiar ecological requirements of the species, which in Scandinavia are almost exclusively satisfied on not too dry parts of moors with *Gentiana,* particularly *Gentiana pneumonanthe* L., have — in connection with a comprehensive cultivation — separated its recent occurrence in many comparatively well-isolated localities. Most of these are of small extent, with the exception of the remaining large moorland districts on the islands of Läsö and Fanö, and in Western Jutland between Klitmöller and Hansted. Specimens collected in the latter large areas have therefore been taken together in the following.

For practical reasons and to give a more illustrative picture of the variation, the total area of distribution in Scandinavia has been sub-divided into 10 districts where the following localities are situated (see Fig. 1).

I. Denmark.

District 1: Southern part of Jutland: 1. Frøslev (6 ♂ 6 ♀), 2. Løjt (23 ♂ 5 ♀), 3. Gallehus (1 ♂), 4. Arrildmark (2 ♂ 5 ♀), 5. Stensbæk-Gånsager (1 ♂ 4 ♀), 6. Fanø (49 ♂ 47 ♀).

District 2: Western Jutland: 7. Esbjerg (1 ♂ 1 ♀), 8. Oksby plantation (13 ♂ 12 ♀), 9. Tarm (2 ♀), 10. Brande (4 ♀), 11. Vedersø (2 ♂ 2 ♀).

District 3: Southern part of the Limfjord area: 12. Klosterhede (34 ♂ 25 ♀), 13. Lemvig (10 ♂ 5 ♀), 14. Holstebro (10 ♂ 3 ♀), 15. Havris hede (16 ♂ 12 ♀), 16. Nørre Lemhede (12 ♂ 10 ♀), 17. Venø (68 ♂ 93 ♀).

District 4: Northern part of the Limfjord area: 18. Legind, Mors (15 ♂ 13 ♀), 19. Dover plantation (3 ♂ 2 ♀), 20. Stenbjerg (1 ♂), 21. Hansted sanctuary (26 ♂ 31 ♀), 22. Thisted (1 ♀), 23. Østerild plantation (1 ♀), 24. Svinkløv (1 ♀).

District 5: Vendsyssel: 25. Ulveskov (1 ♀), 26. Hammer bakker (23 ♂ 17 ♀), 27. Hune (1 ♂), 28. Hirtshals (1 ♂ 1 ♀), 29. Hvims (5 ♂ 6 ♀), 30. Ålbæk (1 ♀), 31. Voerså (1 ♂).

District 6: 32. Læsø (105 ♂ 68 ♀).

District 7: Himmerland: 33. Lendrup (1 ♂), 34. Lille Vildmose (4 ♂ 1 ♀), 35. Udbyhøj (4 ♂ 1 ♀).

II. Sweden.

District 8: Skåne: 36. Höganäs (1 ♀), 37. Arild (20 ♂ 9 ♀).
District 9: Halland: 38. Landa (2 ♂), 39. Frillesås (17 ♂ 24 ♀).
District 10: Västergötland: 40. Göteborg (2 ♂ 1 ♀), 41. Landvetter (1 ♂).
    In that way the material comprises 480 males and 416 females.

The populational analysis tries to ascertain the extent and distribution of rebelid, alconid and other features in Scandinavia compared with data available from Central and Western Europe. In the subsections stress has mainly been put on graphic representation, concluded with short summaries.

B. Variation of the upper side.

In the present literature relating to the *alcon-rebeli* problem a number of differences in marking and colouring have been stated and discussed, and the features studied in the following are as regards f. *rebeli* based on sources as Hirschke (1904), Berger (1946) and Beuret (1949) and as regards *alcon* mostly on
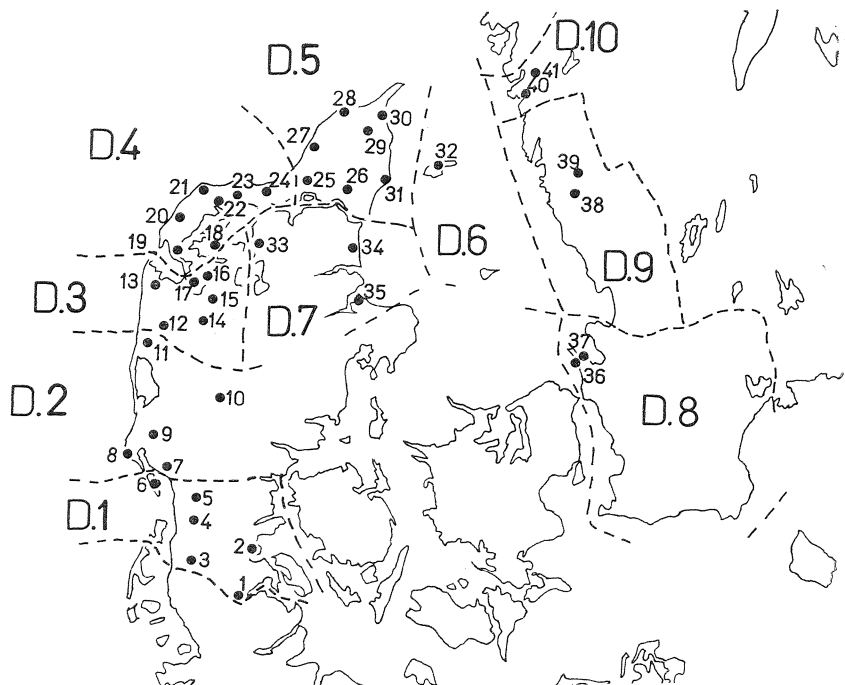

Fig. 1. Scandinavian area of *Maculinea alcon* Schiff., subdivided into 10 minor districts, with number and mutual position of localities examined.

the same sources besides Lempke (1955) and Beuret (1957). Accordingly, the influence of the following characters on the local variation has been registered.

Characters examined (Figs. 2 A and 2 B).

I ♀: markings on the fore wing: shape and number of submedian spots
    A: all punctated in regio cubitalis—analis, diameter ≦ 1 mm
    B: 2 or more elongated in regio cubitalis—analis, diameter > 1 mm
    C: total number from 0—4, constantly lacking in cells 1 A and 1 B
    D: total number over 4, constantly present in cells 1 A and 1 B

II ♀: markings on the hind wing in relation to ground colour
    E: terminal spots surrounded by a light contrast zone
    F: terminal spots indistinguishable from ground colour

III ♀: extent of blue suffusion on fore wings
    G: the blue suffused area, irrespective of density, reaches and exceeds the submedian spots in regio cubitalis—analis
    H: the blue suffused area reduced to the base or lacking

I ♂: shape of the border of males with intact ciliae
    K: border of hind wing linear with an interval of variation of 0—1 mm
    L: border of hind wing banded, unclearly defined basally with an interval of variation of more than 1 mm.

Separately or together the above-mentioned characters express the possible alconid and rebelid features of a population, as the characters I ♀ A and C, II ♀ E, III ♀ G and I ♂ K have been considered typical of the *rebeli* variation, whereas I ♀ B and D, II ♀ F, III ♀ H and I ♂ L should characterize the *alcon* variation. Some of these rebelid features have moreover been

Fig. 2. Upper side variation in Scandinavian *Mac. alcon* Schiff.
A: Male types. a: type K. b: type L (ad type K). c: type L (extreme).
B: Female types. 1 a: type ACE(G) extreme immaculate type
                 1 b: type ACE(G) common type
                 1 c: type ACF(H) extreme immaculate type
                 2 a: type ADE(G) trans ad ACE(G)
                 2 b: type ADE(G) common dark type
                 2 c: type ADF(H) common type
                 3 a: type BDE(G) common type
                 3 b: type BDF(G) common bright type
                 3 c: type BDF(H) common type

Fig. 3. Under side variation in Scandinavian *Mac. alcon* Schiff.
    a. Bright and well-marked male under side, in addition var. *novopuncta* Whli., typical of the southern Danish area i. e. districts 1-2, partly 3.— b. Dull female under side with reduced markings, typical of the northeastern Scandinavian area i. e. districts 3 (partly) and 4—10.
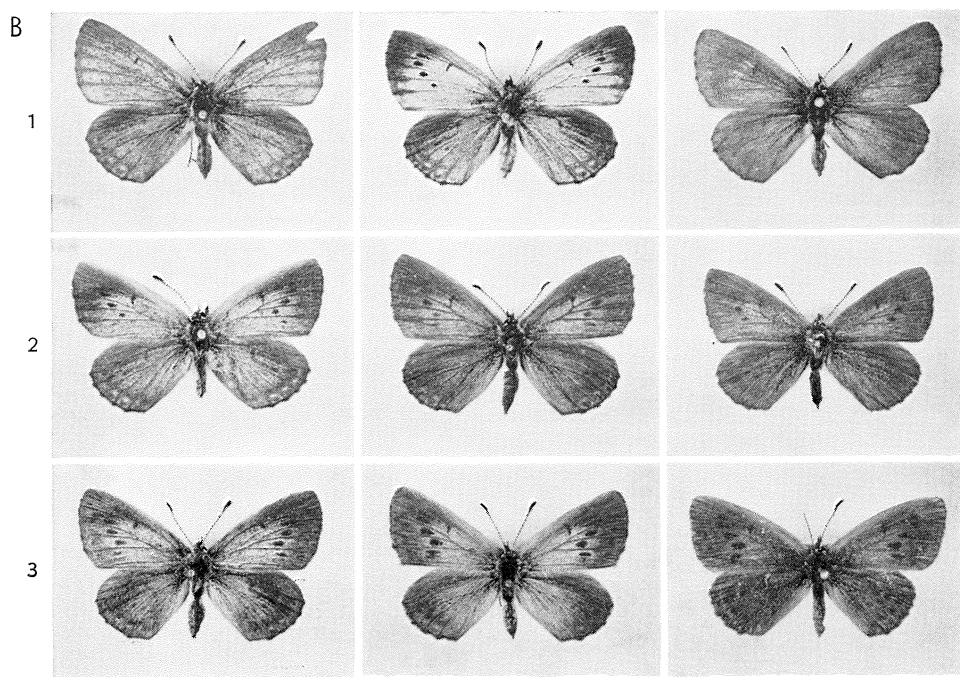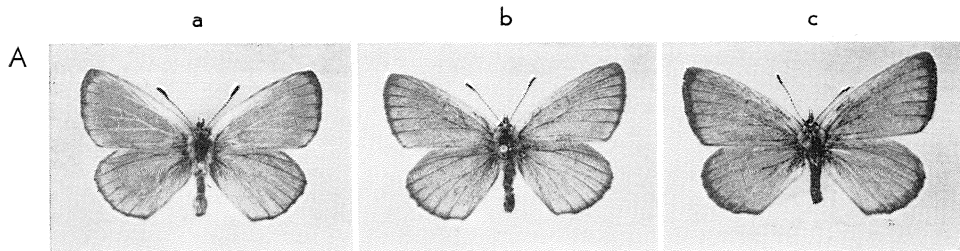
a   b   c
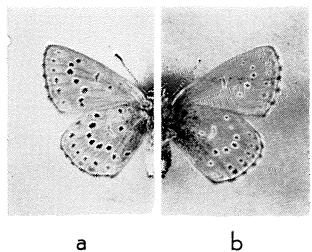
A

B

1

2

3

Fig. 2 A and B (above)

Fig. 3.

Upper and under side variation in
Scandinavian *Maculinea alcon* Schiff.
Legend opposite.

a   b

described as aberrant individual forms of *Mac. alcon*, as for instance the characters II ♀ E and II ♀ G under names such as *lunulata* Warn., *coerulescens* Lpk. and *coerulea* Vorbr. As each female may possess a total of four characters, it is easy to list in code pure rebelid and alconid type-variation for each locality together with the equally interesting intermediate variation and through the distribution of the female types available to illustrate the local geographical variation. According to the abovementioned characters a primary *rebeli* female is registered as type ACE(G) and a primary *alcon* female as type BDF(H), while the other theoretically possible types either denote rebelid, alconid or intermediate variation according to the main content of their characters. By means of this registration it is furthermore possible to analyse the correlation between the single female characters.

The error of method, which will always be present in a natural material, in which the borderline between the antagonizing characters is fluctuant, has in this study been reduced as much as possible by choosing characters with the least possible tendency of overlapping, by excluding worn specimens, and by identifying the few questionable types against the local trends in the variation. The potential sources of error are of course not excluded

Table I: Variation in Scandinavian *Mac. alcon* Schiff., ♂ and ♀. Upper side, I: Proportions in the occurrence of rebelid, intermediate and alconid types in districts 1—10.

Distr.	♂	Rebelid types K	Alconid types L	♀	Rebelid types ACEG	ACFG	BCEG	Intermediate types ACFH	ADEG	ADFG	BDEG	Alconid types ADFH	BDFG	BDFH
1	81	28	53	67	3	2	2	1	3	8	13	4	13	18
2	8	3	5	21	2	2	0	0	3	3	4	0	5	2
3 A*)	79	72	7	55	8	6	0	1	13	10	9	1	7	0
3 B**)	48	46	2	78	55	6	0	3	5	0	6	1	2	0
4	44	44	0	49	40	6	0	0	3	0	0	0	0	0
5	27	23	4	26	17	3	0	1	3	1	1	0	0	0
6	105	101	4	68	32	13	1	0	15	1	5	1	0	0
7	8	8	0	2	1	1	0	0	0	0	0	0	0	0
8—10	42	40	2	35	17	7	0	2	5	1	0	0	3	0

*) Distr. 3 A = localities 12—16 (incl.). **) Distr. 3 B: locality 17 (Venø).
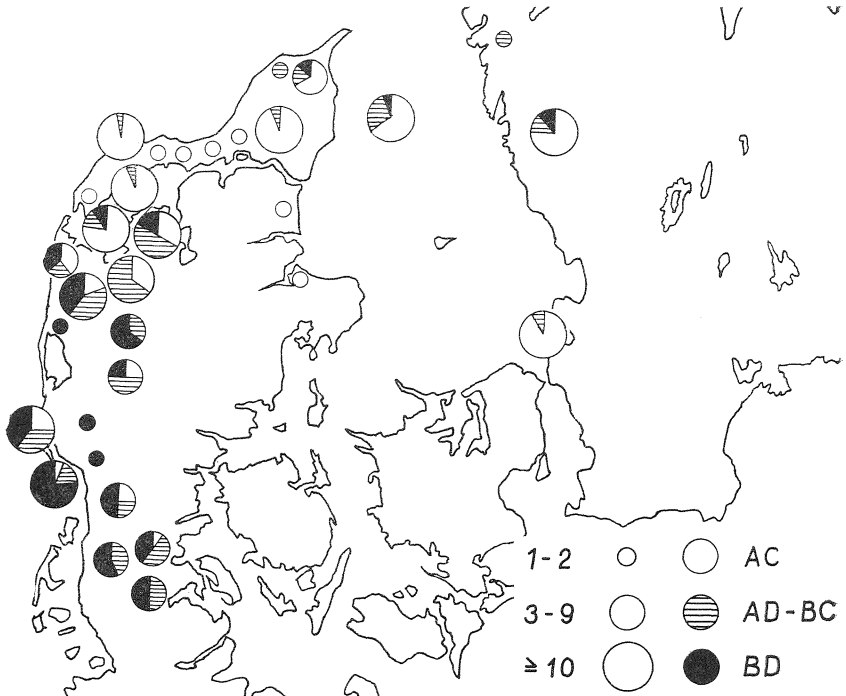
Fig. 4. Variation in Scandinavian *Mac. alcon* Schiff., ♀. Upper side, II: Pie-chart illustrating range of variation regarding size and number of submedian spots of the fore wing.

by his, but their real influence may only be of minor importance.

Type-variation and formation of clines in the area.

Table I and Fig. 4 and 5 illustrate the geographical variation within the area. From this a distinct centric distribution of the above-mentioned rebelid characters is observed in Districts 4—10 with marked dominance of the characteristic *rebeli* female type ACE(G), as a positive correlation between the characters I ♀ A and C, II ♀ E and III ♀ G is evident (Table I). The variation in the Danish and Swedish parts of this area follows the same lines, but the Swedish part and Läsö often show deviations in the female variation, the characters I ♀ D and II ♀ F being more frequently represented here than in the other part of this area.

In contrast herewith Districts 1—3 are characterized by a heterogeneous local variation, with a larger spectrum for the
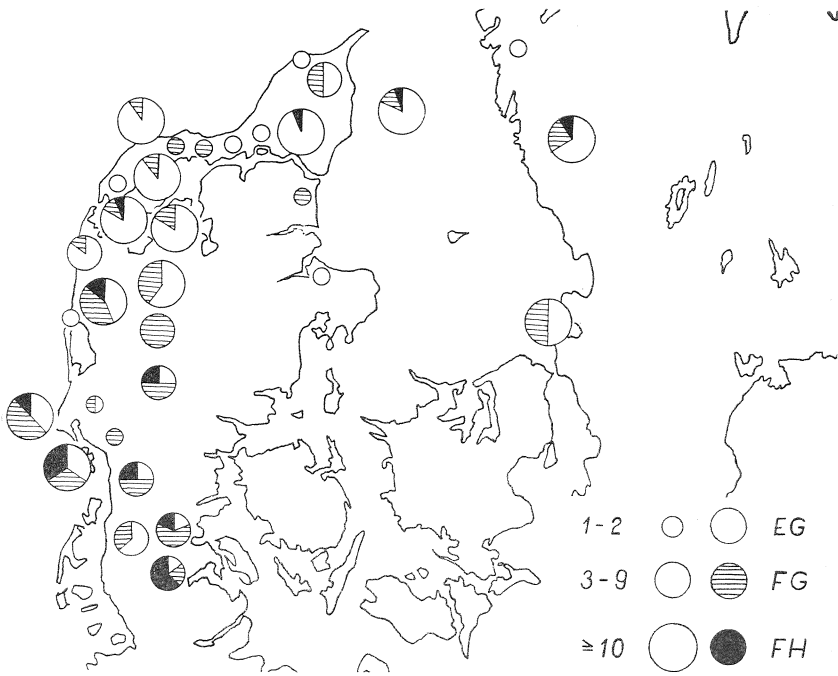
Fig. 5. Variation in Scandinavian *Mac. alcon* Schiff., ♀. Upper side, III. Pie-chart illustrating range of variation regarding terminal spots of the hind wing and their relation to the colouring of the upper side. Characters EG = var. *lunulata* Warn. and characters FH = var. *nigra* Wheeler.

various female types (Table I, Figs. 4—5). In general, the area is marked by a distinct clinal variation, as all the characters studied show more or less stepped north-southgoing clines. Together with the decrease of rebelid features in this area a marked cumulation of alconid features forming oppositely directed clines in the local female variation is noted, most pronounced in the marking characteristics I ♀ B, I ♀ D and II ♀ F.

Among other upper side features in colouring and marking, which have earlier been discussed from a taxonomical point of view, the following have been investigated here: the median cell spot on the fore wing of the male, the colouring of the ciliae and the shade of the blue side suffusion. The median cell spot shows no geographical variation, being present in most specimens, even if only indicated. The colouring of the ciliae, however, shows trends of a geographical variation in agrement with

the above-mentioned characters: in Districts 4—10 they are often white and distinctly barred in their basal parts whereas in Districts 1—2 they are frequently darkly suffused, especially in females of type H. The blue shade varies in the material predominantly according to irrelevant factors such as wear and age of the specimens in question.

Most commonly the butterfly in the greater part of Scandinavia is of a round- and broad-winged type which, however, in the southernmost parts of Denmark (District 1) appears together with more long- and narrow-winged types, which are furthermore distinguished by their pronounced alconid features, the males often representing type L and the females types BDF(G) or BDF(H).

Curiously enough, the collections at the Zoological Institute in Lund include some old, insufficiently labelled specimens, which in appearance and marking clearly disagree with the ordinary broad-winged rebelid type in Sweden. The specimens in question are one male and one female, labelled Sc. coll. C. G. Thomson, and two males and one female labelled Ldgst $^8/_7$ 87 coll. J. Østerberg. Considering the rare occurrence of the species in Sweden, they are obviously some mislabelled Central European *alcon* specimens. It is interesting to note in this connection that Svenska Fjärilar (Nordström and Wahlgren 1941, Pl. 47, Fig. 14) brings a picture of a similar specimen, which on account of its band-shaped border and other appearance was determined as *Mac. alcon* by Berger (l. c. p. 100). As non-Swedish material was used in several instances for illustrations in this work it was tempting to assume that the same had been the case with this specimen. An investigation of i. a. this matter proved, however, that the specimen was really Swedish, originating from Göteborg, July 1933 (Bryk and Nordström 1946).

To try to solve the problem I approached the present owner of the specimen, Dr. Fr. Nordström, Stockholm. Dr. Nordström informed me (i. l. 1961) that the male in question is not Swedish after all and kindly lent the labels pertaining to the specimen for me to verify. The original label is almost illegible, but the date 14-7. 1875 clearly shows that this is not the specimen referred to by Bryk and Nordström (l. c.). Consequently, the Swedish origin of this specimen as well as the afore-mentioned specimens with insufficient labels should be rejected, and old spe-

cimens from Sweden ought to be re-examined based upon the experience gained here before they can be accepted.

In summary, the upper side variation of the Scandinavian population indicates the presence of two groups with different appearance and a characteristic geographical distribution. One, localized in Districts 4—10, shows a variation which in most of the local populations is closely correlated with statements for f. *rebeli* in Central Europe. Certain localities in this area (Districts 6 and 8—10) show, however, deviating characteristics, as for instance an increase of the dark suffusion and the size and number of the dark eye spots in the female, but with regard to the main trends in their variation they clearly belong to this area. In Districts 1—3 the variation is heterogeneous, partly due to the formation of north-southgoing clines in the rebelid characters studied, and partly to an increase in the alconid characters, forming similar oppositely directed clines in the area.

C. **Variation of the underside.**

Whereas several marking elements of the upper side seem applicable in characterizing both forms, only few features have been elicited in connection with the underside variation. Berger (1946) stated a number of minor differences in ground colour, size and number of the dark eye spots. These differences were not confirmed by Beuret (1949) who, however, did not express any opinion on the taxonomical significance of the basal spot of the fore wing, which by Berger as well as by later French authors (Bernardi 1947, Cleu 1950, Bernardi and Gaillard 1951) has been considered of some importance, being frequently present in *alcon*-specimens and often completely absent in *rebeli*-specimens.

Based upon these observations it has been interesting to study the frequency of this inconspicuous eye spot, annually as well as geographically, to the extent possible in the comprehensive Scandinavian material. As the basal spots are subject to the same general trends in variation as other underside markings it may be important to mention these first.

In the southern area of Denmark (Districts 1 and 2) the ground colour is light, ranging from brown to greyish-white (especially in Danish West-Coast demes (for instance (6) Fanö and (8) Oksby) with well-developed, coarse dark-eye spots (Fig. 3 a). This

type is gradually changing in District 3 into a partially anta-
antagonizing type with dark grey ground colour, especially in
the male, with an evident tendency of reduction in the marking
of the dark eye spots, whereby the light marginal zone of these
becomes the contrasting clement to the ground colour (Fig. 3 b).
This type of underside predominates in the remaining localities
in the area of investigation (Districts 4—10).

This tendency of reduction has a marked influence on the
appearance of the basal spot of the fore wing, which is often
delineated only as a light eyeless spot. In the countings for Table

Table II: Variation in Scandinavian *Mac. alcon* Schiff. Under side: Annual
frequency of specimens in Scandinavian demes belonging to var.
novopuncta Whli. (*basinovopuncta* Courv.).

Distr.	Locality	Year	Number of Specimens	Number of novopuncta		
				Uni-lateral	Bilateral	%
1.	1. Frøslev	1934	10	1	2	30
1.	2. Løjt Kirkeby	1960	15	2	5	48
1.	6. Fanø	1923	31	9	13	65
-	6. Fanø	1947	23	1	10	50
-	6. Fanø	1951	10	1	6	70
2.	8. Oksby pl.	1961	24	4	7	46
3.	12. Klosterhede	1949	21	3	5	40
-	12. Klosterhede	1951	10	1	3	40
3.	13. Lemvig	1941	10	0	4	40
3.	14. Holstebro	1947	13	1	4	38
3.	15. Havris hede	1961	21	3	3	28
3.	16. Nr. Lemhede	1961	20	1	2	15
3.	17. Venø	1949	59	3	4	12
-	17. Venø	1950	43	0	6	14
-	17. Venø	1951	29	0	5	17
4.	18. Legind, Mors	1961	27	1	0	4
4.	21. Hansted, Thy	1961	43	2	1	7
5.	26. Hammer bkr.	1925	10	1	0	10
5.	29. Hvims	1961	11	1	0	9
6.	32. Læsø	1957	51	0	4	8
-	32. Læsø	1958	58	0	5	8
8.	37. Arild, Skåne	1948—1953	29	0	5	(17)
9.	39. Frillesås, Hall.	1940—1948	42	0	5	(12)

II, possible cases of doubt have therefore been recorded as having basal spots. Rather constantly it appears unilaterally without any geographical variation in the ratio between unilateral and bilateral occurrence. In no instances has presence of double basal spots been noted, a feature which is rather frequently observed in specimens of typical *alcon* (Beuret 1957, p. 212).

Table II gives the annual frequency of specimens in the Scandinavian populations with basal spots (var. *novopuncta* Whli.). To prevent the percentages from being too much disturbed by incidental variation the numerical minimum requirement for the annual series has been fixed at 10 specimens. The comparable annual values seem to indicate a certain annual constancy. Thereby the geographical variation becomes interesting, as it brings out two different groups in Denmark, a southern group (Districts 1—2) with high percentages and a northern and eastern (Districts 4—7) with low percentages.* The area between the two groups, the northern populations in District 3, shows transitional values. The Swedish material, which is too sparse to provide any concrete conclusions as to its variation in this respect, seems, however, to be more closely connected with the north-eastern Danish area.

Supplementary to the comments made on the earlier-mentioned, incompletely labelled specimens in Lund, it should be noted that the female in the series (Ldgst. $^8/_7$-87, coll. J. Østerberg) shows bilateral double basal spot. This little deviating feature, together with the aberrant upper side variation of the specimens, only confirms the assumption regarding their non-Scandinavian origin.

In summary, the examination gives evidence of deviating geographical variation in the Scandinavian population of *Mac. alcon* with the same delimitation as for the upper side variation. Both with its darker greyish colour and its spot reduction, which is clearly reflected in the low frequency of basal spots on the fore wings in its local populations, this northern area (Districts 4—10) shows conformity with Central and Western European

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* The individual findings from the Danish area of investigation also confirm this tendency, apart from one male in District 7 (Lendrup Str.) with bilateral basal spot. This locality is, however, situated in the neighbourhood of District 3, and the variation should therefore be considered on line with observations from that district.

observations concerning the variation of f. *rebeli*. Compared with
this the local populations in Districts 1—3 show a range of vari-
ation which in general connects them with the population of
Mac. alcon (Schiff.) in the neighbouring faunal areas as Holland
(Lempke 1955, p. 294).

D. **Variation of the androconial scales.**

The androconial scales show often in the single specimen a
pronounced constancy, or at any rate a limited variation so that
their morphology can be used as determinative character in
cases where outer difference is small. Among the Lycaenids, al-
ready Tutt (1907) called attention to their morphology, which at
that time was considered "always identical" for the single spe-
cies. Later examinations, however, have demonstrated a certain
range of variation within the different generations in several
species (Trübsbach 1939), occasionally also between races within
the same group (Beuret 1949).

Their morphological variation was in Berger's material an
important proof of the specificity of f. *rebeli*, but a thorough re-
examination did not confirm this point of view (Beuret 1949).
Nor have recent investigations (Ebert 1961) provided any taxo-
nomically applicable conclusions from the morphological varia-
tion of these scales in this group, and determinations based on
this have earlier resulted in an erroneous systematic position,
e. g. the local Swiss race *macroconia* Brt. being placed by Beu-
ret under *alcon* (1949, p. 34) and under *rebeli* (1957, p. 219).

The purpose of studying the morphology of these scales on
a Scandinavian material has been to obtain information concern-
ing their range of variation in this area and to compare the ob-
servations with information already available from Central Eu-
rope, especially from Belgium. An examination without use of
actual slides is simple: a suitable number of scales are removed
from the area around the median cell of the fore wing with a
soft brush, and the sample is examined microscopically by 100×
magnification. For the present investigation samples have been
taken from a large number of males, as far as possible in series
of 4—8 specimens, from localities distributed all over the Scan-
dinavian area in order to lay down the framework for and the
tendencies in their variation. Specimens from the following loca-
lities have been examined: (1) Frøslev, (6) Fanö, (8) Oksby,

(12) Klosterhede, (17) Venö, (18) Legind, Mors, (21) Hansted, (26) Hammer bakker, (29) Hvims, (32) Läsö, (34) Lille Vildmose, (35) Udbyhöj, (39) Frillesås, (41) Landvetter.

On the whole the specimens examined are moderate in their range of variation with a clear tendency of concentration on one of three types of scales, either a pear-shaped type with flat top (type A), or a more ovoid type (type B), or a more intermediate type, pear-shaped but with a rounded top (type AB) (Fig. 6). The general variation in the material is mainly concentrated on type AB, tending towards type A. Several of the localities examined show, however, dominance of the ovoid type B, as for instance localities (8) Oksby, (29) Hvims, (32) Läsö and (35) Udbyhøj. On the whole, however, the uniformity of variation in the area is remarkable: even males of a rather different appearance show the same variation in this respect. Control examinations carried out on Eastern European (Polish) specimens of a pronounced alconid type (ex coll. Nat. hist. Mus. Aarhus, and coll. Kaaber) show a variation which agrees with the above-mentioned variation and on the whole with information available for *Mac. alcon*.

Fig. 6. Androconial scales (×100) in a male from district 4, loc. 18: Legind bj. left: type A, middle: type AB, right type B.

The variation in the part of the Scandinavian area (Districts 4—10) where the outward characters are of a rebelid type, is as regards the androconial scales too diverse and so highly marked by features corresponding to *Mac. alcon* that no taxonomical significance can be attached to it.

E. **Variation of the genitalia.**

The variation of the sclerotized parts of the genitalia in the group have also been examined by several authors (Berger 1946, Bernardi 1947, Beuret 1949, Schulte 1958, Ebert 1961) to elucidate the taxonomy of f. *rebeli*, but so far without decisive results. This may mainly be due to the fact that closely related forms with simply built genitalia often show a marked variation in details so that seeming differences only express the range of a wide normal variation in the group. In such cases reported differences should often be evaluated with certain reservations and not used as single-characters in determination. This wide normal variation seems to play an important part within several

groups among the Lycaenids, for instance in the two closely re-
lated groups *Aricia agestis* Schiff.—*cramera* Eschh. and *Ar. al-
lous* Hb.—*inhonora* Jach.—*montensis* Vrty (Beuret 1960), in *Lycae-
ides idas* L. and *Lyc. argyrognomon* Bergstr. (own investigations)
and to a great extent in the *Mac. alcon*—*rebeli* group.

With the broad uncus and edged valves of the males, the lat-
ter group is a typical representative of its tribus *Glaucopsychidi*.
This simple morphology connected with a pronounced variation
has so far made reported differences problematic in as much as
f. *rebeli* only seems to have a few and conditionally applicable
features compared with *Mac. alcon*, as for instance more rough-
ly shaped valves (Bernardi 1947, Schulte 1958) and a more strong-
ly sclerotized antevaginal plate in the female of the subsp.
xerophila (Berger 1946). However, Ebert's findings have not con-
firmed the male differences, and Beuret has shown that most of
the local alpine races, irrespective of outer type, have slightly
sclerotized antevaginal plates (Beuret 1949, p. 18 and Pl. V).

Due to these facts it has been necessary first to elucidate
the extent of the local variation in the area (Districts 4—10)
where the outer *rebeli*-appearance according to the previous state-
ments is evident, before making comparisons with the remaining
part of the area (Districts 1—3). For this reason the investiga-
tions have been carried out on a number of series of varying
size. A foreign control material, comprising German, Polish and
Austrian specimens, has been available, but only of *alcon*-types.
Because of lack of material on f. *rebeli* the conclusions here rest
on the authors quoted above.

Most of the preparations used are from the author's own col-
lections; in addition a number of preparations made by Dr. S.
Hoffmeyer in 1947, now the property of the Natural Museum in
Aarhus, and five belonging to Mr. G. Pallesen, Aarhus, have
been examined. For embedment of the dissected parts, Canada
balsam and the synthetic resin Celodal II have been used; in
the latter the prepared parts can be mounted without previous
dehydration, whereby distortion from shrinkage is avoided. The
risk of this, however, does not seem to be of importance for
species with strongly sclerotized structures as these Lycaenids.
The following characters have been particularly studied: in the
male the shape of the valve, in the female the sclerotization of
the antevaginal plate.

From the material as a whole, the following general features are observed: a tendency to asymmetry in the contours on the right and left valves in the same specimen, and a positive correlation between length of valves and span of the fore wings, so

Fig. 7.   Fig. 8.

Fig. 7. Male genital variation in Scandinavian *Mac. alcon* Schiff.
left: a left valve ($\times$25) type I. Male, district 4, loc. 21 Hansted.
middle: a left valve ($\times$25) type II. Male, district 1, loc. 6 Fanø.
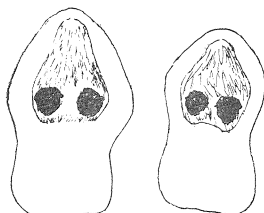right: a left valve ($\times$25) type III. Male, district 3, loc. 17 Venø.

Fig. 8. Female genital variation in Scandinavian *Mac. alcon* Schiff.
left: antevaginal plate ($\times$25) strongly sclerotized type. Female,
          district 6, loc. 25 Ulveskov.
right: antevaginal plate ($\times$25) strongly sclerotized type. Female,
          district 1, loc. 1 Frøslev.

that large males generally have longer valves than small ones. Furthermore in the whole material investigated presence of a varying number of small "teeth" is noted between the dorsal and distal part of the valve, allthough as a rule they are better developed in valves from the northern Scandinavian districts (3—9). Moreover three main types of valves are represented: a coarse and broad one, the dorsal side of which is either convex or straight (type I A) or clearly concave (type I B), a more tapered type in which the proximal and especially the distal part is narrower compared with type I B (type II). Between these main types intermediates with narrowing either proximally or distally are noted (type III), see Fig. 7.

The females examined show presence of strongly sclerotized antevaginal plates (Fig. 8, and Table III).

The shape of the valve has been studied on drawings transferred to a paper by a draw-
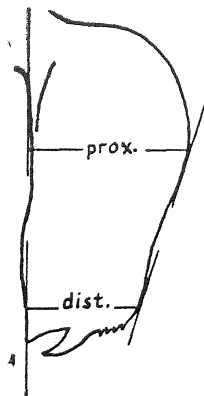

Fig. 9. Measuring areas in male genitalia. Proximal and distal width of valve.

Table III: Variation in Scandinavian *Mac. alcon* Schiff. Male and female genitalia: Origin and number of material examined with range of variation in outline of the valves and sclerotization of the antevaginal plate.

Distr.	Locality	♂	Valves examined	Broad type (I)	Intermediates type (III)	Slender type (II)	♀	Antevaginal sclerotization of plate: strong or weak
9.	39. Frillesås	1	2	2	0	0	1	strong
7.	35. Udbyhøj	1	2	0	2	0	-	
	34. Ll. Vildmose	1	2	2	0	0	-	
6.	32. Læsø	9	18	14	4	0	3	strong
5.	26. Hammer bkr.	10	18	15	2	1	1	strong
	25. Ulveskov	0	0	0	0	0	1	—
4.	21. Hansted	5	10	8	2	0	1	strong
	18. Legind bj.	5	10	9	1	0	1	
3.	17. Venø	5	10	8	2	0	2	strong
	14. Holstebro	5	10	8	2	0	-	
	12. Klosterhede	5	10	4	6	0	1	—
2.	9. Tarm	0	0	0	0	0	1	strong
	8. Oksby	5	10	4	2	4	1	—
1.	6. Fanø	8	15	5	7	3	2	strong
	1. Frøslev	3	5	2	2	1	2	—
	Northwestern Germany	3	6	0	6	0	-	
	Northeastern Germany	2	4	0	3	1	-	
	Poland	2	4	0	0	4	-	

ing-apparatus mounted to a microscope at 50× (ocular 2, objective 40 mm., distance from ocular to paper: 320 mm.). The greatest proximal and distal width has then been measured at right angles to a tangential plane of the ventral valval side (Fig. 9).

Judging from Table III and Fig. 10 a distinct tendency to geographical variation in the Scandinavian material is found, with a more frequent occurrence of valve-types with narrowing of the distal part (types III and II) in the southern Danish districts 2 and 1, while in the northern districts 4 to 9 the coarse and broad type I predominates. The valves from the foreign area south and
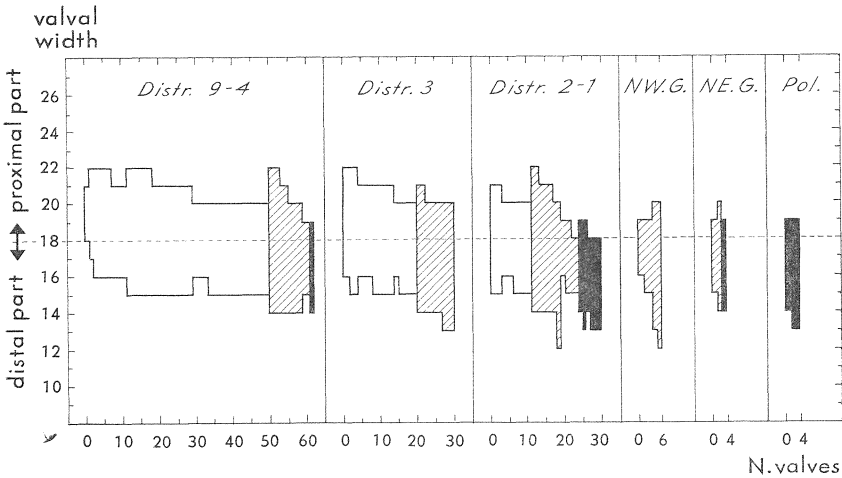
Fig. 10. Variation in Scandinavian *Mac. alcon* Schiff. Male genitalia: Diagram illustrating proportions in occurrence of the three various valve-types in Scandinavian males, compared with males from Northwestern Germany (NWG), Northeastern Germany (NEG) and Poland (Pol.). Units of the ordinate are millimeters used to measure the projections of the valves.

> White area: valve-type I. prox. width: $\geqq 20$, distal width: $\geqq 15$
> black area: valve-type II. prox. width: < 19, distal width: < 14
> hatched area: intermediate valve-types III.

east of Denmark are of the same slender types as in southern Denmark.

Comparing these trends with the information available from other parts of Europe a clear relationship between the Scandinavian females and the Belgian females of subsp. *xerophila* is noted. In the males a similar relationship is noted between the males from the districts 4—9 and information about f. *rebeli*, especially subsp. *xerophila* through the presence of the valve type I (compare illustrations given by Bernardi l. c., Schulte l. c.). Regarding the evident distal narrowing of the valves being found in southern Denmark it is interesting to note that this feature according to Beuret (1949 pl. IV and 1957 pg. 206) and Schulte (l. c.) seems to be typical to *alcon* (s. str.), a suggestion being supported by the above variation of the Eastern European males. The wide range in the southern Danish districts makes it, however, difficult, if not impossible to use this feature as anything more than a supporting mark.

To sum up, some trends to a geographical variation are noted in the male genitalia in the Scandinavian material corresponding

with the other above examined features, and in agreement with information from Central Europe about the two forms. In the females greater uniformity is observed, corresponding with subsp. *xerophila* of the *rebeli*-group.

F. Discussion.

By their variation the Scandinavian *alcon* are naturally divided into two groups, one in the Districts 1—3, the other in the Districts 4—10. As appears from the previous sections of this article, the latter group is not only habitually but in the males also genitally characterized by features which in Europe are common to a group of forms collectively named *rebeli* (Hir.). These features are so pronounced that they cannot be explained as incidental convergence, but indicate the presence of a population in Scandinavia belonging to the *rebeli*-group. Hereby previous assumptions (cf. the Introduction) are definitively confirmed.

The Scandinavian *rebeli*-population is in appearance closely related to the Central European race subsp. *xerophila* Berg., which, however, is not observed farther north than the neighbourhood of Hannover (Schulte 1958) and in Belgian Limburg (Berger 1946). Thus there are distinct common features as a large average size (normal span of the fore wings in males: 32—34 mm, in females: 34—36 mm) and a high frequency of darkly suffused females (var. *arcasoides* Berger), and the sclerotization of the antevaginal plate agrees fairly well with the Belgian variation. In other respects, however, the Scandinavian population seems to diverge by its clear tendency of coarser spot marking, not only on the upper side but also on the under side, a feature which does not seem to be the case in Belgium (Berger l. c., p. 101). In other respects the under side also differs by its darker grey colouring and blurred marking. At this stage, however, it would be more reasonable to note the important common features between the two populations and to treat the Scandinavian population as a form of *rebeli* belonging to the Central European race subsp. *xerophila*.

Most conspicuous are the ecological differences between these two areas. While the Central and Western European *xerophila*-population through its attachment to dry biotope-types is clearly distinguished from *Mac. alcon*, the Scandinavian population is attached to the biotope and plant customary to this species, viz.

Gentiana pneumonanthe. During his years of collecting in Northern Jutland the author has often seen oviposition on the leaves and flowers of this plant, an observation which is confirmed by other Danish and Swedish collectors.

This deviation from the normally known ecology makes it possible to form a more definite opinion regarding the taxonomy of the entire group. The great uniformity of variation in the Scandinavian *rebeli*-area shows a close positive correlation with the male and female *rebeli*-characters in other parts of Europe with different ecological requirements. Like the Belgian *xerophila*-population the Scandinavian female variation is predominated by the blue suffused type ACE(G) and the darker alconid *arcasoides*-type ACF(G), and the male variation by the narrow-bordered type K. The outlines of the valves are also in agreement with observations for subsp. *xerophila* from Northern France and partially with observations for subsp. *rebeli*. The uniformity in this respect of the Scandinavian, Central European and alpine *rebeli*-populations thus clearly shows that the form possesses a number of genotypical features which are not the result of an ecological speciation as assumed by Central European authors. The symphily with ants of the entire group, whereby the susceptible pupal stages are passed in the climate of an ant-hill might also reduce the influence of environmental factors on the phenotypic variation between *alcon* and *rebeli*. The diverging evolution in the group, which is clearly expressed by the marked features of f. *rebeli* should therefore be ascribed to other factors than ecological ones.

The different ecology in the Scandinavian area compared with Central Europe makes it easier now than earlier to analyse its assumed specific position compared with *Mac. alcon*. The evident clines of the rebelid features in Southern Denmark (Districts 1—3) which geographically is connected with areas where only *alcon* has been observed (Warnecke 1956) solves this problem. The southward direction of the clines with a gradual increase of alconid features indicates that the entire population of this area should be considered a *rebeli*-population whose characters are being assimilated by a gradual infiltration of alconid features owing to migration from the south. This phenomenon is well known under terms as "secondary intergradation" (Mayr 1942) or "introgressive hybridization" (Anderson 1953), but in

the present instance it is of particular interest because of the taxonomical position of f. *rebeli* up till now. In Denmark the relationship between *rebeli* and *alcon* is only that of two geographical races belonging to the same species.

The cline shows a clear uniformity in pattern in the hybridal zone, as in the populations nearest the *rebeli*-area (District 3) it only penetrates in the female variation by an increasing frequency of characters I ♀ B and D, analogous with a similar tendency to numerical increase in dark eye spots on the under side (Fig. 3 a and Table II). The other features in marking and colouring show rebelid variation. South of this area — in District 2 — this tendency increases and besides the variation of characters II ♀ E and F and III ♀ G and H clearly shifts towards the melanic alconid character. The alconid variation now penetrates in the male, both in the upper side variation and in the variation of the outlines of the valve. In District 1 the increase of these alconid features is more predominant and the distinctive *rebeli*-character II ♀ E — the terminal spots surrounded by a light contrast zone — is decreasing (Fig. 5). The rebelid features, however, still penetrate in the females by a high frequency of characters I ♀ A and III ♀ G, just as in the genital variation.

Acknowledging this introgression of *Mac. alcon* in the Danish *rebeli*-population and its rate of penetration in the various demes it is easier to analyse the taxonomical problems of f. *rebeli* than previously, but before this another factor should be discussed: Judging from the range of variation in the Scandinavian *rebeli*-population it is remarkable that several peripherally situated localities (Nos. 29, 32, 37, and 39) show a range comprising intermediate and alconid features besides the usual *rebeli*-pattern, cf. the occurrence of the female types AD and BD often combined with type F in Districts 5—6 and 8—10. The Central European subsp. *xerophila* to which the Scandinavian *rebeli*-population belongs is through these features less well-differentiated than the alpine subsp. *rebeli* whose populations almost exclusively comprise the primary female type ACE(G) (Hirschke 1904, Beuret 1957). This convergency towards *Mac. alcon* must, however, be due to other factors than the secondary intergradation, which has modified the populations in the hybridal zone.

Thus the problems on the taxonomy of f. *rebeli* (s. l.) lie pri-

marily in the wide range of variation in subsp. *xerophila* being stated above, secondly in the presence of intermediate populations resulting from the secondary intergradation between *Mac. alcon* and it. In this way the only feature applicable to ensure a safe determination of a deme in question is the proportion between rebelid, intermediate and alconid characters measured through a variational analysis of a representative section of it. According to the delimitation from the geographical variation in the Scandinavian area a relationship with f. *rebeli* (s. l.) is thus indicated if (1) type AC represents 66—100 $^0/_0$ and (2) type ACE(G) represents 50—100 $^0/_0$ of its females, and (3) if the under side shows a spot-reduction expressed by lack of basal spots on the fore wings in 90—100 $^0/_0$ of the specimens in an annual series of a suitable size. The *rebeli*-features of the male may also be used, but only as supporting marks as they remain unaltered in some parts of the introgressional zone.

The clinal variation in Southern Denmark also illustrates the taxonomy of *Mac. alcon*, but as no local populations with a similar homogeneous alconid type-variation in the females are found, at most hybridal populations with predominance of some alconid features, it is not possible here to delimit the normal range of variation in a typical *alcon*-population.

The presence of these various types of variation in the group in Denmark makes it possible, too, to delimit the range of hitherto uncertain variation in other parts of Europe, as the direction of the clines gives a clear indication of continuing outside the Danish area.

Part II. Maculinea alcon (Schiff.) — rebeli (Hir.) in Europe.

A. Introgressive hybridization and typical populations.

As stated in the previous section, the main part of the Scandinavian population of *Mac. alcon* shows a clear relationship with the Central European race *xerophila* Berg. of the *rebeli*-group. In the south-western parts of Denmark the population must — partly because of its upper side variation — be conceived as a hybridal zone between *xerophila* and a later invasion of *Mac. alcon*. As the entire Danish population is connected with the Central European *alcon*-population it may be possible to trace the intermediate features further into areas where the species has the

same ecology as in Denmark. Theoretically the decreasing clines from the Danish *rebeli*-area should have a similar influence on the population of the adjacent countries as in the Danish hybridal zone, partly penetrating the female variation by frequent occurrence of specimens with reduced spot-size and increased blue colouring of the upper side and partly by occurrence of aberrant forms with typical rebelid features.

From Northern Germany, i. e. the area between the Danish border and the Lower-Elb, only little information is available on the variation of *alcon*. The important var. *lunulata* Warn., which combines typical rebelid features in its appearance (characters I ♀ A, I ♀ C, II ♀ E and III ♀ G in the above registration, see Fig. 2 B, 1 a-b, 2 a) has, however, been described from this area (Warnecke 1956), but it is rare, which was also to be expected in view of the observations from Southern Denmark. A small North German material, which the author had the opportunity of seeing at Dr. Warnecke's during a visit to Hamburg, showed pronounced alconid features in the males, whereas the few female specimens were of the typical Danish intermediate type ADF(G).

In Northern Germany *alcon* is also found in the eastern parts, though more rarely at the border of its former north-eastern German occurrence in Pomerania (Urbahn 1939), and information from the literature is still sparse. On request Dr. Urbahn, Zehdenick, has kindly given information and material from this area. The variation is marked by typical alconid features, and forms as var. *lunulata* are not known (Urbahn i. l. 1962). The male specimens from this area were of an *alcon*-type, both in appearance and genitally (cf. Part I, Section G), and the single female (Prerow, Darss 1951 H. & E. Urbahn leg.) was of a true var. *nigra*-type with completely dark suffusion of the ciliae.

In the north-eastern German area the intermediate features are seemingly replaced by typical *alcon*-variation, but in the north-western European area variation seems to agree fairly well with the Danish observations. Thus detailed studies have been made on the individual and geographical variation of the species in Holland (Lempke 1955), from which it is evident that the normal range is much wider here than that of the typical Austrian form. Of special interest in the present study are the local Dutch races, the moor-race *ericae* Lpk. and an isolated dune-

race *arenaria* Lpk. The moor-race, whose racial character compared with the typical form is reduction in spot-size of the female upper side submedian band, shows besides this other features in its variation corresponding to those forming north-south-
going clines from the Danish *rebeli*-area. Thus extreme specimens
with the rebelid character I ♀ A are referred to as *supracaeca*
Lpk. (Fig. 2 B, 1 a), with the characters II ♀ E as *lunulata* Warn.
(Fig. 2 B, 1 a- b), and III ♀ G as *coerulescens* Lpk. and *coerulea* Vorbr.,
and specimens with tendencies of reduction in the marking of
the under side as *infraparvipuncta* Lpk. and *cecinae* Horm. Similar
features, though less pronounced, are found in the dune-race
arenaria Lpk., which in this connection may be considered an
extreme form of *ericae*. Features similar to those of the *ericae*-
population also seem to prevail in the Belgian *alcon*-population,
which at any rate clearly differs from the typical form by the
tendency of its females to show increased blue colouring of the
upper side (cf. Berger 1946, p. 99) and to smaller spot-size in
the submedian band.

In Northern and Eastern France *xerophila*-populations instead
prevail (Bernardi 1947, p. 64), but intermediate *alcon*-types are
represented here, too, as shown by Bernardi (l. c. Pl. 1, Fig. 6)
from the Department of Eure named *rebeli xerophila;* and the
information concerning the appearance of "*rebeli*" in Normandy
(Olivier 1948) suggests that the specimens flying on the dry biotopes in this area instead are intermediate forms of *alcon*, analogous with this type. On the other hand, the population found
in Western France on biotopes with *Gentiana pneumonanthe* obviously contains a form which in almost all features corresponds
to the typical *alcon*, with which it has also been identified in
the literature up till now (Bernardi l. c., Beuret 1957, p. 209).

According to the above it is, however, clear that in a large
area — stretching from the Limfjord in Denmark to the north,
into German towards south and west, and from there through
Holland-Belgium — the resident *alcon*-population must in future
be considered an intergradational zone between an original *xerophila*-population of the *rebeli*-group and a later invasion of *Mac.
alcon*, which is now gradually assimilating the original rebelid
features. Consequently these are still predominant in the northern parts where the intergradation has been working only for
a short time. This theory is better motivated than the expla-

nation accepted so far, which ascribes the divergent variation in parts of the area (i. e. Holland) to differences in the ecological conditions (Lempke l. c., p. 291). The occurrence of the Dutch dune-race *arenaria* on the dry-soil gentian *G. cruciata* L., which is the usual Central European host to *xerophila* might be explained by assuming that the colonization of the dune localities did not take place until the intergradational process in the main Dutch area was so far advanced that the local variation in the dunes, conditioned by a later isolation, was onward marked predominantly by alconid features (cf. Lempke 1947).

While the approach to the problem in Central and Western Europe has so far been based on the presumed ecological divergences between the two forms, the regularity demonstrated here in the variation of the species, irrespective of type of biotope, indicates that the nature of the whole problem is changing. In the northern parts of Central Europe two different forms of *alcon* are found, which are able to replace each other on dry and damp biotopes without changing their typical features — except for some extent of local variation in the representative of f. *rebeli* in Scandinavia and in *alcon* in Holland. The predominating factor in determining their relative distribution is, as shown in the previous section, the inability of the *rebeli*-group to maintain sympatric populations with *alcon* on biotopes with *Gentiana pneumonanthe*. This gentian is the most common one in the northern parts of Central Europe where dry-soil species as *G. cruciata* are either lacking or are found only sporadically. In the southern parts the ecological conditions are rather opposite to those prevailing in the northern area, for which reason a study of the variation of *alcon* in this area on the same lines as in the foregoing might elucidate many hitherto obscure problems. In the literature it has been possible to follow the species from Czechoslovakia (Schwarz 1950). through Middle and Southern Germany (Bergmann 1952, Ebert 1961) via the north-western parts of Switzerland (Beuret 1949, 1957) to Eastern France (Bernardi l. c.), the species following *G. cruciata* — and to some extent *Gentiana campestris* L. too — in the entire area.

While the imaginal variation in the eastern part (Czechoslovakia) seems to correspond closely to the typical *alcon*, information from Thuringia and Northern Bavaria gives proof of a distinct strain of rebelid features — in Northern Bavaria also

genitally in the male — in the local variation, compare the figures given by Bergmann (l. c., Pl. 52, Figs. A 2 and B 2), Beuret (1957, Pl. 12, Fig. 12), and Forster-Wohlfahrt (1955, Pl. 24, Figs. 27 and 32). In Switzerland these features change into the interesting race *cruciata* Brt., whose range of variation is so wide that it has already been considered an intermediate race between *alcon* and *rebeli* by Beuret (1949, p. 51), a point of view which is fully confirmed by this review. In Eastern and Northern France this intermediate variation passes into a *xerophila*-variation of a more uniform *rebeli*-type.

Occurrence of populations with intermediate variation is also noted from other parts of Central and Southern Europe. In accordance with the premises in Part I, the high-alpine Swiss races, *alpicola* Brt., *magnalpicola* Brt. and *macroconia* Brt., represent typical *rebeli*-forms analogous — if not identical — with the typical *rebeli* Hir. from the Styrian Alps in Austria. Other Swiss races, as *gadmensis* Brt., show, however, indistinct, intermediate features, which may well be the result of an introgressive hybridization, though they may also reflect a lower degree of differentiation of the population in agreement with some of the local Scandinavian populations of *xerophila*. It is remarkable, however, that the features dominating the outer variation in the Alps are of an entire rebelid, and not alconid type.

On the southern side of the Alps and in Southern Europe the trends of the variation can also be fitted into this pattern. Thus the Middle Italian mountain race *peninsulae* Vrty. shows a well-defined rebelid pattern in appearance (Verity 1943, Pl. 8, figs. 50—52). The other local races from this area are, however, more closely connected with *alcon* than with *rebeli*. The typical *alcon* has its border of occurrence in the eastern part of Northern Italy, but its characters may be followed farther westward in the Swiss races *haurii* Brt. and *pseudoroboris* Brt. and in the Italian *turatiana* Vrty. — and *nestae* Higs. (Higgins 1930). In Southern and Eastern France the local races in Hautes and Basses Alpes, however, prove a distinct outer relationship with the alpine *rebeli*-forms, an appearance which in the Southern French mountain forms from the Cevennes and Gard — the local races *taranis* Cleu (Cleu 1950) and *aigoualensis* Gaill. (Bernardi and Gaillard 1951, Gaillard 1952) — gradually changes into clearly intermediate features with increasing alconid tendencies in the

western part. The westernmost French population at the Atlantic is, as above mentioned, marked by a typical outer *alcon*-appearance. However, there still seems to be great gaps in the knowledge on the distribution of the group in Middle France.

According to this variation it is possible to unite the various types in groups according to the outer appearance, completely disregarding differences in ecology, which have apparently a minor influence on the different phenotypes. Most simply the European populations can be combined into three groups: a primary *alcon*-group, a primary *rebeli*-group, and a group with secondary (intermediate) features.

The primary *alcon*-group is represented by the typical Austrian form. As the concepts regarding the normal range of variation in *Mac. a. alcon* have hitherto been obscured by the various authors in Central Europe by including forms with evident hybridal features, it is not possible here to give an exact delimitation of this range. According to Part I the following characters seem to be typical to specimens in a population belonging to this form: In the male: the upper side most frequently with band-shaped borders (character I ♂ L). In the female: darkly suffused upper side with coarse submedian spots on the fore wing, complete in number (characters I ♀ B and D, II ♀ F); blue colouring of the upper side sparse, most frequently absent (character III ♀ H); the ciliae suffused with dark grey or brown; spot-marking of the under side coarse with a tendency to numerical increase, reflected by a frequent occurrence of basal spots on the fore wings, on account of which specimens with double basal spots are probably only present in such populations; furthermore, the outlines of the valve are strongly tapered in the distal parts. In a typical population the variation of these characters will presumably range only from slight to moderate, but further investigations on this subject are urgently needed.

The primary *rebeli*-group is represented by the following characters: In the male: upper side with narrow borders (character I ♂ K). In the female: intense blue colouring of the upper side, dark suffusion present only along costa and the border of the fore wing; the row of submedian spots on the fore wing reduced in number and size (characters I ♀ A and C, III ♀ G); the terminal spots on the upper side of the hind wing with distinct light contrast zone (character II ♀ E); the ciliae white, tending

to be barred basally; spot-marking on the under side with a ten-
dency to reduction, involving elimination of the basal spots on
the fore wings. The morphology of the male genitalia shows
edged, broad valval contours.

The *rebeli*-group is divided into two forms: a homogeneous
type from the Alps with absolute dominance of these features
in its populations, and a more heterogeneously varying type in
Central Europe, the *xerophila*-type. As will appear from the ana-
lyses in Part I, the latter shows a number of clearly alconid
features in its populations, not only in the female variation, but
also in the range of the male genital variation. Its main cha-
racter, however, is rebelid (cf. the Discussion in Part I, p. 298).

The secondary group is even more heterogeneous in its vari-
ation, combining as a rule both alconid and rebelid features in
the same specimen. Exponents of this variation are populations
with a content of female types possessing both the coarse spot-
marking of *alcon* and the extensive blue upper side colouring
of f. *rebeli* (type BDE(G)), or lack of the blue colouring of *alcon*
combined with the reduced or lacking spot-marking and white
ciliae of *rebeli* (type ACF(H)). A differential-diagnosis between
populations of this type and subsp. *xerophila* may be quite intri-
cate, but according to the discussion in Part I it seems possible
to separate local populations in question mainly by studying the
range of the female type-variation and its content of alconid,
rebelid and intermediate types.

By comparing the distributional areas of the primary groups
the dispersed pattern for both of them is remarkable (Figs. 11
and 12). Thus areas containing populations with typical alconid
features are noted from the French Atlantic Coast but from
there not until from lowland parts of Eastern Europe, western-
most in East Germany and Poland, through western Czechoslo-
vakia (Polacek i. l. 1963), the eastern parts of Switzerland and
Northern Italy (Beuret 1957, Verity 1943). From here the area
stretches continuously towards the east via Balkan and Southern
Russia (Beuret l. c.), northernmost to Leningrad (Kaisila 1962,
p. 407) and onward to Pamir and Tibet (Seitz 1909, 1930, cf. Fig. 11).
Within this area only one local race has been reported from
Kaukasus, viz. *monticola* Stgr. (Staudinger-Rebel 1901), the name
of which in earlier European literature was used mainly to de-
signate the alpine races of *rebeli*-appearance.

The occurrence of f. *rebeli* is, however, located in Western
Europe and here in three main areas: a Southern European in
the middle of Italy (Verity 1943), a large and partially connect-
ed mountainous area in the Alps, stretching from the Styrian Alps
(Hirschke 1904) to the western parts of Switzerland and South
Eastern France (Beuret 1957, Bernardi 1947). This area is con-
nected with a greater one in the western part of Central Europe
and North-Eastern France consisting of populations of the race
xerophila Berg. Isolated though still continuous with this area
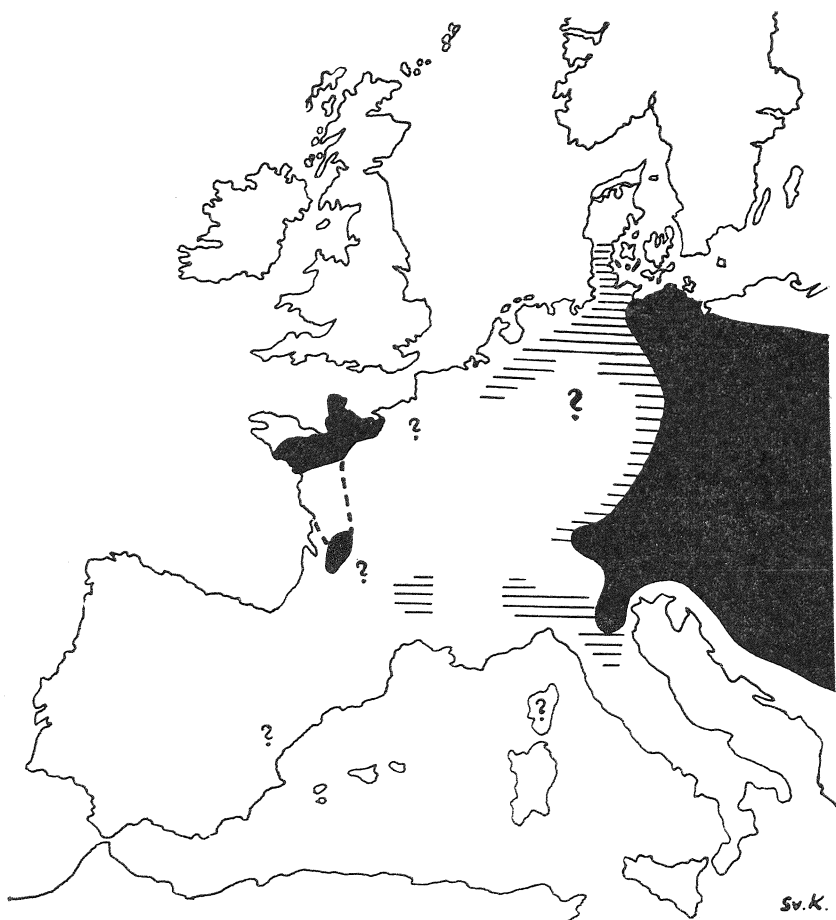
Fig. 11. European distribution of the *alcon*-group: black area: primary
(=typical variation); hatched area: secondary variation with predominant
outer alconid appearance.

during clinal variation *xerophila*-populations are found again in Southern Scandinavia (Fig. 12).

Between these insular European areas with primary variation the species appears in a number of intermediately varying forms, the appearances of which are connected with the nearest centre of primary variation. Only in the western part of Central Europe (Belgium, Hannover) and in North-Eastern France the entire occurrence may be divided into an *alcon*-type with inter-
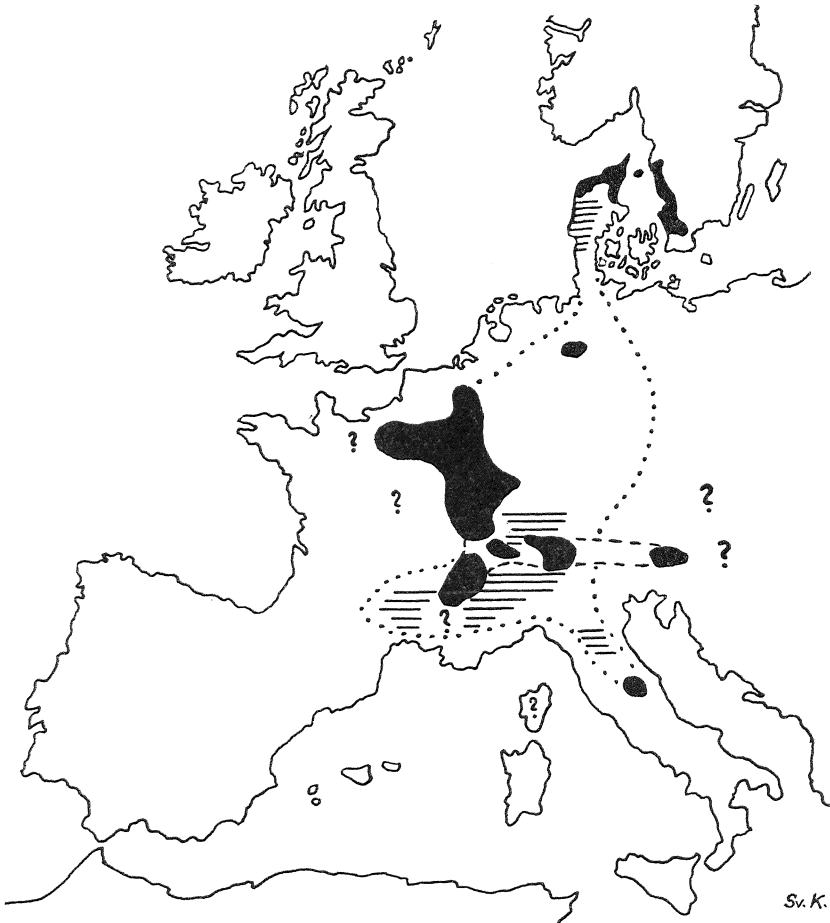
Fig. 12. European distribution of the *rebeli*-group; black areas: primary variation, including the ssp. *peninsulae* and *xerophila*; hatched areas: secondary variation with predominant outer rebeli appearance; dotted line: approximate border for intermediate variation, irrespective of outer appearance.

mediate features on damp biotopes and a *rebeli*-type on dry bio-
topes, separated, too, by different flying seasons. In the Alps the
two forms are also clearly separated by differences in their ver-
tical distribution. The continuity of the present isolated *rebeli*-
areas through the intermediately varying areas indicates, how-
ever, that this form has previously had a continuous European
distribution of considerable dimensions.

B. **Some features of the evolution and distribution of the group.**

The observations given above concerning the taxonomical,
geographical and ecological relations of the two primary forms
in Europe should make it possible (cf. Beirne 1952, p. 26) in the
following to reconstruct the probable principal features in their
evolution and distribution in this area.

The extensive clines in Central Europe combined with the
ecological replacement of both forms clearly prove that the taxo-
nomical divergences of f. *rebeli* are only of an intraspecific na-
ture. Schematically the mutual relationship between them can
best be illustrated as two branches of a phyletic line, between
which the degree of differentiation is not yet so great that an
exchange of genes has ceased under sympatric conditions but
is only hampered by special ecological conditions. As the segre-
gation is not, as hitherto assumed, caused by ecological influ-
ences it has probably been brought about by geographical iso-
lation, especially as this factor is generally recognized as the
most essential cause of diverging evolution within a species or
a species-group (Mayr 1942). Several features are in agreement
with this. Thus the restricted palearctic distribution of f. *rebeli*,
excluding the *xerophila*-populations mentioned above, shows a
centre inside the parts of Southern Europe which during the
most extensive glacial ages of the Pleistocene Period formed a
refugial area for certain parts of the recent European flora and
fauna (Reinig 1939, de Lattin 1950). Due to this, the form shows
far greater adaptability to cool-temperate conditions in these
areas than *alcon*, a feature which is clearly reflected in the dif-
ferences of their vertical distribution in the Alps where *rebeli*
is found at altitudes of 2000 metres or more as compared with
alcon, which does not exceed 1200-1500 metres (Forster-Wohl-
fahrt 1955, Beuret 1957). Furthermore, the geographical varia-
tion of the group seems to be more diversified and the character

of the local populations more homogeneous in this area where the selection-pressure has been active longer than in the postglacially settled parts of Central Europe. The primary *rebeli*-races in all probability originate from a population belonging to the archetype of the species, which after an interglacial phase of the Pleistocene was parted from the main population by a glacial epoch, and — geographically isolated — had to adapt itself to different ecological conditions in parts of this Southern European refugial area. However, the extent of the present taxonomical divergences proves that the duration of this period was not long enough to allow an evolution of sufficient isolational mechanisms against assimilation from *alcon* when the two branches met again.

This hypothesis is supported by a great number of analogous examples from various parts of Zoology, cf. Mayr (1942) and Huxley (1942), and from the Lycaenids, too. In this family the two closely related forms, *Philotes baton* Bergstr.—*vicrama* Moore form an example of principally the same type in their taxonomical and geographical relations (Hemming 1929, Beuret 1957). Another species as *Lycaeides argyrognomon* Bergstr. (*ismenias* Meig.) shows in its European geographical variation a remarkable analogy with this pattern, too, as it — at least north of the Alps — can be divided into two race-groups, a Western European with blue suffused females and an Eastern European with brown females (Heydemann 1955).

However, the other branch of the phyletic line, the primary *alcon*-form, does not show complete analogy with the picture of the entire group outlined above as of species with a continuous distribution in Europe and Asia and a more or less vicarious Western European form, as its European distribution is bicentric. To analyse the proper reasons for this distributional picture it is necessary first to compare the present geographical relations between the two primary groups. On account of the Northern European *rebeli*-population and the decreasing clines of its characters through Central Europe it is evident that the first postglacial invasion of the group has consisted of this form and not of *alcon*, as an invasion in reverse order is excluded because of the incomplete taxonomical divergence of *rebeli*. At that time the Western European *alcon*-population was still geographically isolated from its Eastern European area. Its distributional pattern can therefore be explained solely on the assumption that

during a later interglacial period — at a time when the descen-
dants from the first pleistocene wave, the present primary *rebeli*-
forms, had only a limited distribution in Southern Europe —
another advance towards west was made by the species. North
of the Alps this second *alcon*-invasion was able to spread as far
as to the Atlantic, but later on, owing to the climatic deteriora-
tion of another glacial period, its continuous European distribu-
tion was again separated into two areas, the recent eastern and
western centres.

This distributional pattern of a population separated into an
eastern and western European part without any significant geo-
graphical variation is not unique, being also found for a butter-
fly-species with partially the same ecological requirements, viz.
the Hesperiid *Heteropterus morpheus* Pall., whose European dis-
tribution (Picard 1949) in general outline corresponds closely
with that of the primary *alcon*-group.

While the taxonomical and geographical relations between
the primary forms of the group clearly elucidate the chronology
in the two pleistocene invasional waves, it is far more hypo-
thetical to establish the interglacial periods in which these ad-
vances did pass. The difficulties are mainly due to the fact that
a diverging evolution does not take place at fixed time-rates
but besides time depends on other important factors as the size
of the isolated population and the ecological divergences during
the isolation.

As the second pleistocene invasional wave, represented by
the Western European *alcon*-population, at present does not seem
to diverge morphologically from the typical form in Eastern Eu-
rope, it is easier to deal with its problems first. Based on the
above-mentioned general evolutionary considerations it may be
assumed that this conformity is due to the fact that the isola-
lation has taken place late in the Pleistocene and may have
comprised a large population in Western Europe, and that ap-
proximately analogous conditions prevailed in both areas during
the period of isolation.

The glacial conditions prevailing towards the end of the Plei-
stocene Period in Europe, i. e. the fourth Glaciation, were less
extreme than the earlier, and the climatic conditions of the
single glacial and interglacial phases are known in the main
(*vide* Zeuner 1946, 1958, Deevey 1949). Theoretically it has been

possible for *alcon* to spread over Europe during both Interstadial phases of this main Glaciation. A spreading during the second Interstadial phase (the Alleröd-Interval) is not likely, however, in spite of pollen-finds of *Gentiana pneumonanthe* L. in Denmark from this period (Iversen 1949), because the mean summer temperature in Central Europe was too low — 4—6 degrees of Celsius below the present (Firbas 1947) — to permit a massive spreading of the butterfly. The invasion has therefore probably taken place during the first Interstadial phase (the Warthe-Brandenburg- or Aurignac-Interval) in which the warmest periods correspond to the present European climate (Deevey l. c., p. 1323). At the beginning of the following glacial phase the continuous distribution of *alcon* north of the Alps was divided into two, one of which was forced towards the western and southern parts of Europe where it had to adapt itself to the maritime forest-climate prevailing in these ice-free parts (Poser 1947 a, 1947 b), while the other was forced eastwards.

The first pleistocene invasional wave to Western Europe — represented by the primary forms of the *rebeli*-group — most probably antedates these events, as the different morphology and alpine ecology of the form in its Southern European area indicate an isolation which at times has taken place under entirely different and more severe conditions and which has probably also been of a longer duration than that of the western *alcon*-population. The centre of distribution of the *rebeli*-group excluding the postglacial areas in Central Europe is situated in an area south of the Alps where the type of the glacial flora and fauna varied from cool-temperate to subarctic (Firbas 1947). However, the present adaptability of the form to analogous ecological conditions in the Alps at altitudes above 2000 metres proves that it has been able to survive even under such extreme glacial conditions in this Southern European refugial area. It is not possible, however, to establish when this first pleistocene invasional wave was isolated in this area, but further studies on the proper identity of the Southern European *alcon*-populations may throw more light on this important problem.

During the later phases of the fourth Glaciation these fore-runners of f. *rebeli*, owing to better adaptability to cool-temperate climatic conditions, have been able to spread in some of the icefree parts of Western Europe where *alcon* did not thrive, and

the peripheral segments of the two populations must have been able to intergrade during this period. The distinct intermediate feature already mentioned, which characterizes the Southern French *alcon*-populations, probably results from an intergradation between the two populations during this period. In a similar way it is possible to explain the intermediate features of the females of the *xerophila*-form in the northern parts of this area, features as an increased dark suffusion of the upper side and a tendency to spot augmentation which distinguish this *rebeli*-form from the alpine populations. The proper postglacial invasion from Western Europe has therefore in all probability consisted of a primary intergradational form with predominant outer rebelid features and an appearance which is recognized in the present Scandinavian *xerophila*-populations in which, as shown in Part I, the variation is in fact dominated by rebelid features, but with a content of distinct alconid features which in this way have a logic and natural explanation.

This postglacial invasional wave from Western Europe must have taken place rather early in the Boreal period, as the Swedish population is bearing evidence of a route via the northeastern parts of Denmark at the time when the Scandinavian Peninsula was still connected with Central Europe, since no populations are found on the Danish isles in spite of the presence of *Gentiana*. In Central Europe its distribution has reached far eastwards, intermediate variation being found as far into Germany as Thuringia. This spreading may, however, also have come from the south.

The postglacial re-invasion of *Mac. alcon* to Central Europe may in theory have taken place from both Western and Eastern Europe, but seems to have come exclusively from the eastern area. It is remarkable that *alcon* in the eastern part of Central Europe has intergraded into the *rebeli*-populations on the dry biotopes, whereas the analogous localities in the western part of Central Europe still contain *xerophila*-populations with distinct rebelid features, concurrently with intermediately varying populations on the damp biotopes. In this area a frail though effective barrier seems to separate these two forms, largely conditioned by differences in their flying seasons. This extensive Western European *xerophila*-area in Northern and Eastern France (and Belgium), geographically in close connection with the Western

European *alcon*-population, can only be taken as an indication that the latter, contrary to *rebeli*, has become static during its glacial isolation and has lost its expansional power. This point of view is supported by the Central European observations on *alcon*, which clearly deny the presence of any ecological barrier to its spreading as long as this takes place in areas situated at altitudes below 1200—1500 metres. This relation between the two European *alcon*-centres may therefore be compared with the different distributions of the diploid and tetraploid races of the cruciferous *Biscutella laevigata* L. in Central Europe, which as regards the diploid races are ascribed to a depauperisation during a pleistocene isolation (Manton 1934, 1937).

The eastern postglacial re-invasion of *alcon* has also taken place south of the Alps, which may account for the presence of the intermediately varying races in this area. Thus the pictures of the race *turatiana* published by Verity (Verity 1943, Pl. 8, Figs. 53—56 (incl.)) correspond closely to the author's specimens of intermediate *alcon* from Central Europe. This postglacial intergradation of *alcon* has south of the Alps as in Central Europe parted the originally continuous *rebeli*-population into the two present isolated areas in the Alps and the middle of Italy, which are now protected against intergradation because of their alpine ecology. Also here a remarkable analogy is observed between the distributional patterns and postglacial invasion-routes of *Mac. alcon* (s. str.) and *Heteropterus morpheus* Pall., both north and south of the Alps (cf. Picard l. c.).

The theory of isolation and intergradation outlined here solves a great number of hitherto contradictory features in the variation and distribution of the two forms, and makes the single parts of their taxonomy fit into a general pattern in agreement with both glacial-geological conditions prevailing in Europe during the later phases of the Pleistocene and the already known post-glacial invasional routes from the different European refugial areas in the latter part of the Pleistocene. But, as will appear from the above, much work has still to be done in extending the knowledge on many of the problems briefly mentioned here. The taxonomical relations between the two primary *alcon*-areas in Europe as well as between the two ecologically different groups in the northern and eastern parts of France are some of the most important problems calling for further investigation.

C. Systematic problems.

From the above it follows that *Mac. alcon* in the western parts of its palearctic area consists of two separately occurring forms, which in large areas primarily or secondarily intergrade into each other. These conditions together with an ecological replacement between them in the entire area prove that the hitherto stated specificity of f. *rebeli*, which has mainly been motivated by presumed ecological divergences, can not onward be maintained. Certainly its marked geographical variation and sympatric occurrence with intermediate *alcon*-forms in a relatively well-defined ecological niche in Western Europe indicate that for some reasons it may be considered a sibling species to *alcon* in this area. On the other hand, the clines formed by the rebelid features in large parts of the European area clearly show the apparent lack of specific divergences between them. Thus their mutual relations are only an interesting borderline case between the categories "species" and "subspecies" in perfect analogy with the concept "Rassenkreis" (Rensch 1929). This means that *Mac. alcon* is represented in Europe by two diverging subspecies, which in large areas intergrade into each other, partly subsp. *alcon* Schiff. and partly the geographically varying subsp. *rebeli* Hir. The named geographical local races of the latter entail that only a part of the population in the Alps may be represented by the *rebeli*-name while populations of more or less the same phylogeny from the greater part of the remaining area are to be recognized under other names as subsp. *peninsulae* and subsp. *xerophila*.

A special nomenclatorial problem is created by the intermediate variation, which in distinct clines represents the two primary forms in large parts of Europe. Huxley (1942, p. 226) has suggested that extensive clines should have their own subspecies names. For practical reasons it is reasonable to follow this point of view, allthough the two concepts belong to different fields, and to gather the intermediately varying populations of the same origin into main groups. In Central Europe there will be only one main group, viz. the recent population between the Eastern European *alcon*-area and the present isolated areas in Scandinavia and Western Europe of the once total *xerophila*-population. As mentioned above, the clines in the northern and southern parts pass over two different types of biotopes, and it

might be worth considering whether special features are present in the intermediate variation by comparing specimens from the different biotopes. According to the author's material of inter-mediate *alcon*-types from both areas, a moderate increase of the average size is found for the southern part (from Northern Ba-varia) living on dry biotopes, while colouring and marking of the females show almost identical variation. Accordingly the need of naming any actual ecoclinal variation does not seem indicated in this case. Among the Central European races with clinal features three have been described so far, viz. the Dutch *arenaria* Lpk. (1942) and *ericae* Lpk. (1955) and the Swiss *cru-ciata* Brt. (1949). In spite of the priority of the name *arenaria* it would be reasonable continuing to use this upon the isolated divergent dune-population and consequently to apply the follow-ing name *cruciata* to the main population of Central Europe with intermediate features. Accordingly it will be termed *Mac. alcon* subsp. (cl.) *cruciata* Brt. (primary synonym *ericae* Lpk.). With regard to the nomenclatorial problems of the intermediately varying populations in Southern and Western Europe it is not possible — owing to lack of material — to come to any conclu-sion at present.

The insufficient knowledge of the proper extent of the diverg-ing evolution of the *rebeli* group also precludes a discussion on the feasibility of considering its systematic problems in more de-tail than in this work. Owing to the special borderline case of the group it might be reasonable to transfer it to an optional category between species and subspecies which has been sug-gested by several recent authors, most frequently termed semi-species (Mayr 1942, Kiriakoff 1946). According to this a *rebeli*-race as *xerophila* should be termed *Mac. (alcon) rebeli xerophila* Berger, and the parenthetic term between the generic name and the species name should not compromise the usual bino-minal or trinominal combination, in agreement with the recom-mendation of the Nomenclature Commission for an optional cate-gory as the subgeneric one (Mayr, Linsley and Usinger 1953). Judging from the divergences in the Scandinavian material an ordinary subspecific nomenclature would, however, be prefer-able for the time being.

For the Scandinavian and Central European area the follow-ing nomenclature will be applicable: In the Scandinavian and

Central European *rebeli*-populations: *Mac. alcon xerophila* Berger. In the Eastern European *alcon*-population: *Mac. alcon alcon* Schiff. For the entire intermediately varying population in the greater part of Central Europe: *Mac. alcon cruciata* Brt.

Summary.

The study deals with a number of taxonomical, zoogeographical and evolutionary problems in the group of *Mac. alcon-rebeli*. On account of a population-analysis of a large Scandinavian material of the group, which in this area is predominantly found on biotopes with *Gentiana pneumonanthe* L. it is in Part I possible to elucidate the taxonomical significance of a number of previously discussed characters. The distribution in Scandinavia shows that f. *rebeli* in a dedifferentiated type belonging to the Central European race *xerophila* is found in the north-eastern parts of Jutland in Denmark and in the isolated Swedish area. In the western parts of Jutland this population intergrades with *alcon*.

In Part II an analysis of the structure of the European populations is made to elucidate their taxonomical and evolutionary problems. It is shown that the various races can be united in three groups: a primary *alcon*-group and a primarily varying *rebeli*-group, and a secondarily varying group containing forms whose characters are ascribed to the effect of an introgressive hybridization between the primary groups. The entire European distribution confirms this assumption, as such forms are found between the centres of primary variation. In some parts of Western Europe and the Alps, however, the forms tend to separate into ecologically diverging, partially sympatric populations.

On account of the recent distribution and the incomplete taxonomical divergence of f. *rebeli* a general outline on the evolution of the group is made. It is stated (1) that the *rebeli*-group in all probability originates from a population isolated under severe conditions during part of the Pleistocene in a refugial area in Southern Europe; (2) that the bicentric occurrence of the primary *alcon*-form in Europe indicates a formerly continuous distribution, probably in the first Interstadial phase of the fourth Glaciation, which was subsequently separated into the recent eastern and western areas; (3) that the intermediate features in the Western European races (including subsp. *xerophila*) indicate a primary introgression between the *rebeli*- and the *alcon*-group in this area during the later part of the fourth Glaciation; (4) that the postglacial recolonization of Central Europe started from the Western European area and consisted of a primary intergradational form with pronounced rebelid features (subsp. *xerophila*); (5) that the postglacial invasional wave from Eastern Europe consisting of primary *alcon*, due to its superiority at sympatric competition, by a secondary intergradation has infiltrated the original *xerophila*-area and split it into its present minor segments in Central and Northern Europe; (6) that this process can be followed only from the Eastern European *alcon*-centre, for which reason the western *alcon*-population is presumed to have lost the power of expansion during its pleistocene period of isolation.

In a systematic treatment of the group f. *rebeli* is included as a sub-species of *Mac. alcon*. For practical reasons the major part of the inter-mediately varying populations of Central Europe is collectively classified here under the name subsp. (cl.) *cruciata*.

Acknowledgements.

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