SOME TAXONOMIC INVESTIGATIONS ON THE GENUS *RHINANTHUS*

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PREFACE

This paper represents part of a thesis accepted for the Degree of Doctor of Philosophy of the University of London. The work was carried out at Queen Mary College with the aid of a maintenance allowance from the Department of Scientific and Industrial Research.

The author's comments and conclusions on *Rhinanthus* are based on study of the specimens in Herb. Mus. Brit.; on field observations at numerous British, and several Swiss localities; on cytological investigations; and on experiments in which *Rhinanthus serotinus* (Schönh.) Oborny (British and Finnish), *R.* cf. *angustifolius* C. C. Gmel. (Swiss), *R. hirsutus* Gremli (Swiss), and *R. minor* L. (from a number of British localities, one Swedish and one Swiss locality) were cultivated from seed in England.

The following material is represented in the author's private herbarium:—

65 gatherings from Britain (nos. 1-65), 10 sheets of British and European specimens cultivated in England (nos. 66-75), 2 sheets of Swedish specimens (nos. 76-77), 11 sheets of Swiss specimens (nos. 78-83 and 100-104) and 16 sheets of Canadian specimens (nos. 84-99); of these nos. 1-38 and 78-83 are from populations studied in the field by the author.

The material of the original thesis has been considerably abridged. A fuller account of the investigation may be obtained by reference to the original thesis in the library of the University of London.

INTRODUCTION TO THE LITERATURE

Linnaeus provided the original generic and specific names for *Rhinanthus* in 1753 when he published the name *Rhinanthus crista-galli*. *Rhinanthus* is a critical genus. J. Sterneck, who published his "Monographie der Gattung *Alectorolophus*" in 1901, listed 51 species for which as many as 179 synonyms were given ; the number of synonyms for single taxa ranging from 0-15. Other continental workers, notably Chabert, Soó and Poverlein, published taxonomic papers on the genus *Rhinanthus* ; references to their works appear in the Bibliography. Druce (1901), Marshall (1903) and later Wilmott (1940, 1942 and 1948) produced papers on the British forms of *Rhinanthus*, Wilmott's 1940 and 1942 papers being the last major taxonomic works published on the genus. Wilmott gave an account of the literature in relation to British *Rhinanthus* in his paper "Some Remarks on British *Rhinanthus*" (1942, 361-379).

THE TWO MAIN TAXA IN BRITAIN

The genus *Rhinanthus*, even within the British Isles, cannot here be studied in its entirety. The field has been limited therefore to one (*R. minor* L.) of the two species which are easily distinguished by their corolla morphology. These species are *R. minor* L. and *R. serotinus* (Schönh.) Oborny, the names replacing the extensively used *R. minor* Ehrh. (non L.) and *R. major* Ehrh. (non L.) respectively, both of which are to be rejected as later homonyms.

Evidence was presented in detail in the original thesis to show that the two taxa could only be separated satisfactorily on corolla characters. Characters such as bract form and colour, and shape and colour of the corolla teeth were found to be variable in both taxa, the degree of variability overlapping ; both white and violet teeth, for example, occur in each taxon. Bract shape and toothing have been mentioned by various writers e.g. Wilmott (1942) and Warburg (1952) as diagnostic characters.

Plate 9 illustrates the bracts from specimens of *R. minor* and *R. serotinus* from a Kentish

chalk quarry (at Halling) and a plant grown from seed from Easthaven, Angus (in a London greenhouse), respectively. Considerable similarities are evident. The toothing is equally deep in members of both series, whilst bracts of similar shape occur on each plant.

The corollas of *R. minor* and *R. serotinus* (Fig. 1) may be easily distinguished, the most conspicuous difference being the upcurving of the corolla in *R. serotinus*.

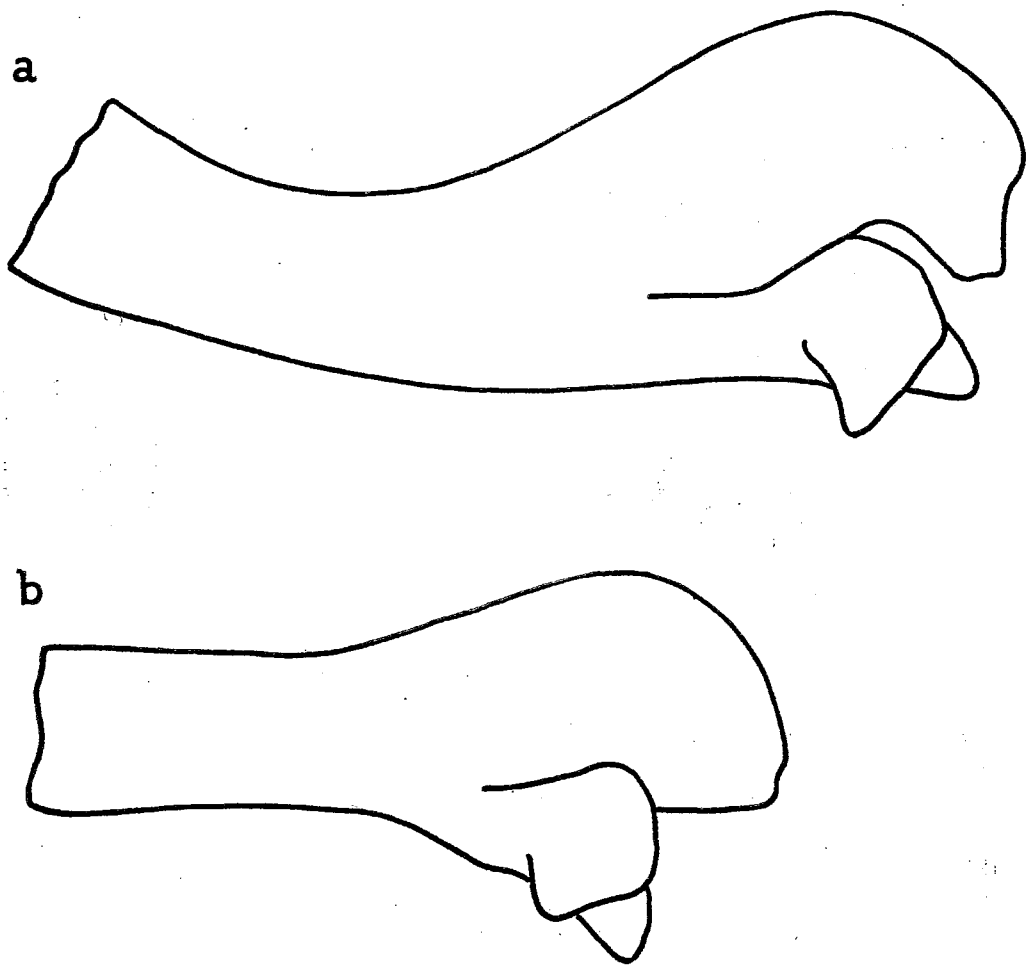
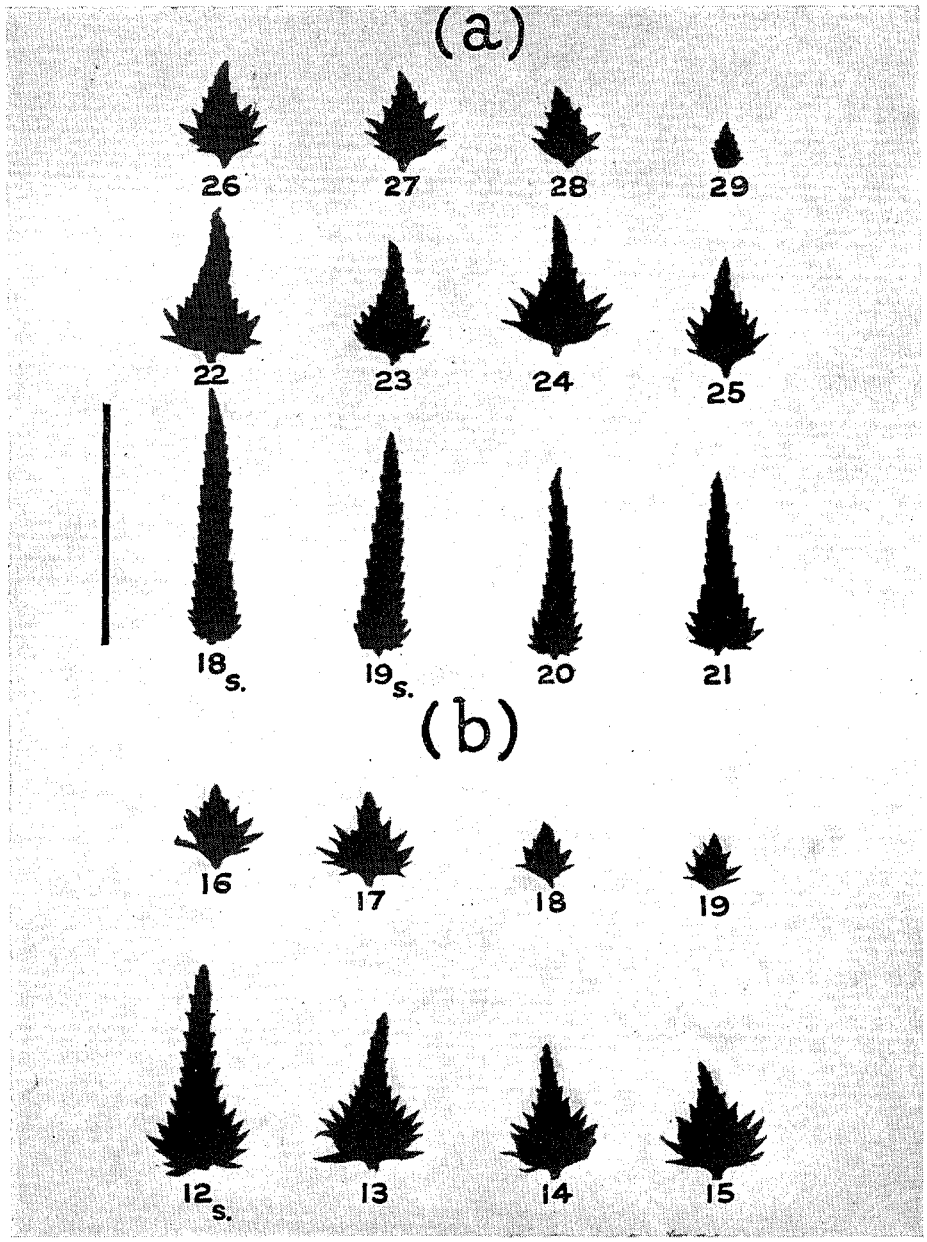


Fig. 1.
a = Corolla of *R. serotinus* (Schönh.) Oborny. (Cultivated specimen; seed from Scotland.) × 10
b = Corolla of *R. minor* L. (From Kent.) × 10

The Present State of the Taxonomy of Rhinanthus minor L. in Britain

The most recent taxonomic publications on British *Rhinanthus* are those of A. J. Wilmott. The number of British taxa with a straight corolla-tube which he recognised is uncertain, but he appeared to accept the following : *R. minor* Ehrh., *R. minor* var. *robustus* Druce, *R. stenophyllus* (Schur) Druce, *R. borealis* (Sterneck) Druce, *R. spadiceus* Wilmott, *R. spadiceus* subsp. *orcadensis* Wilmott, *R. borealis* var. *calvescens* Wilmott, *R. lintoni* Wilmott, R. *lochabrensis* Wilmott and *R. vachellae* Wilmott, that is a minimum of eight species, all of which are covered by Linnaeus' diagnosis of *R. minor* L. Of the species mentioned above, *R. minor*, *R. stenophyllus* and *R. borealis* are the only ones which do not appear to be endemic. Soó (1929, 185) described various taxa belonging

PLATE 9.



(a) Bracts of *R. serotinus* (Schönh.) Oborny.

(b) Bracts of *R. minor* L.

Numbers indicate node numbers from stem base.
s = sterile bract (intercalary leaf).

Vertical line shows length of bract 18a.

to the " Minores " and Wilmott (1942, 367) wrote " Once again, I must admit that I cannot fit the characters given by Soó to the British material I have seen : all sorts of intermediates seem to occur." Wilmott, however, described the existence of forms intermediate between some of the species which he appeared to accept as occurring in Britain. Wilmott's species were described from herbarium material and, even whilst applying new names, he suggested that descriptions might need alteration. Quotations in the following paragraph illustrate some of his doubts.

In his description of *R. spadiceus*, Wilmott stated that he was ". . . not completely satisfied as to the status of this plant. In some localities it is found comparatively uniform and unmistakable, and seems to deserve the rank of species which it has been given "; in his description of *R. vachellae* he remarks " . . . whether it is really a distinct species, must await further material. Meanwhile, however, it needs a name . . ." In his paper in the *Journal of Botany* (1940) Wilmott wrote " The characters given for the new forms here described, being based on a limited number of specimens, also require testing in the field . . .", and " It may be useful to add determinations of, or remarks on, the remaining gatherings in Herb. Mus. Brit. which have been identified as " *Drummond-Hayi*," in one or other nomenclatural combination. Some of them do not agree with *R. borealis*, *R. Lintoni*, and *R. lochabrensis*, and whether the descriptions of these require modification or whether there remain still further forms to be described, must await further investigation." Wilmott mentioned intermediates between *R. stenophyllus* and *R. minor*. He stated (1948, 84) that *R. vachellae* is " somewhat intermediate " between *R. stenophyllus* and *R. spadiceus*, but no indication of the manner in which it is intermediate was given. He stated that *R. borealis* is " somewhat like " except in pubescence of the calyx " the small chalk-down form of *R. minor* ", and mentioned a series which " contains some specimens with normally puberulous calyx and one with glabrous calyx (except, of course, on the ciliate margin), and various degrees of glabrescence between the two extremes are shown by the remaining specimens "; Wilmott called the intermediate forms *R. borealis* var. *calvescens*. It might also be noted at this point that Wilmott indicated that *R. vachellae*, a species " with pubescent calyx ", " looks extremely like some of the plants collected near Affric Lodge, which had glabrous calyces." The above quotations indicate some of the difficulties which confront the orthodox taxonomist and which made it necessary for Warburg to write in 1952 (*Flora of the British Isles*, 889) " Experimental work on the genus, and on this aggregate (*R. minor* agg.) in particular, is badly needed."

Before beginning an experimental study of a genus, it is useful to assess how far orthodox taxonomy has succeeded in separating morphologically distinct forms. The characters in general taxonomic usage for the genus have been scrutinised, and a check has been made on Wilmott's descriptions and diagnoses of British species by a comparison of these diagnoses with one another, and by reference to the holotype specimens in the herbarium of the British Museum. (It should be noted here that a herbarium sheet labelled "Holotype " exists in Herb. Mus. Brit. for each of the *Rhinanthus* species named by Wilmott. He usually labelled one of the specimens on each sheet as the holotype. Three unlabelled specimens are on the sheet of *R. vachellae* ; the best-developed specimen will be regarded here as the holotype.) Some reference to other species recorded for the British Isles has also been made. Various characters used in the taxonomy of *Rhinanthus* will now be considered in turn and an attempt will be made to assess the value of each.

Floral Morphology with particular reference to the corolla.

The characters of the corolla which have been used in the taxonomy of *Rhinanthus* are length, shape, and features of the corolla teeth. These will be discussed in turn.

The greatest variation in corolla length in the described British forms is small; all fall into the range 13-15 mm. I consider this character to be of extremely doubtful value since I have found it to be affected by environmental influences ; for example plants cultivated in the absence of a host plant produced corollas smaller than those typical of plants of similar origin which were attached to hosts.

The descriptions of the British species named by Wilmott were made mostly from dried material (see, for example, Wilmott, 1942, 374). It must therefore be expected that corolla morphology might not have been easily discernible. For example, in the description of *R. spadiceus* subsp. *orcadensis* (Wilmott, 1942, 369), it is stated that " the corolla . . . in the dried plant, seems to be broader and the lower lip looks larger." My own field notes relating to plants with a general similarity in habit to the type specimens of this taxon, and which were collected from heathland on Orkney Mainland, indicate that the corollas of these plants were similar to those of larger specimens of *R. minor* growing elsewhere. The only other description of corolla shape which is given in Wilmott's papers on *Rhinanthus* appears to be a reference to the " large and peculiar-shaped " corolla of *R. lochabrensis* which was mentioned in his paper describing *R. vachellae* (1948, 84). No measurements appear to have been published of the corolla of *R. lochabrensis*, and no qualifying statement seems to have been made.

My own observations of the corollas of living British and Continental specimens support my conclusion that a group of the genus, *R. minor*, is characterised by a more or less uniform corolla morphology and appears to be adapted by the ultimate position of the stigma for self-pollination. The slight variations in the proportions of the lobes of the corolla which may occur are such that they do not lend themselves to written description. It is, in any event, evident that the morphology of the corolla, which might be expected to provide some of the strongest evidence for specific differences, has received little more than casual attention in the diagnosis of British endemic taxa.

The length and shape of the corolla teeth have been used in diagnoses and descriptions of British *Rhinanthus*; it is difficult, however, to consider specimens in relation to diagnoses where no standard is given. For example, the teeth of *R. lochabrensis* are " more projecting than in *R. Lintoni* " (Wilmott, 1940, 212), whilst the teeth of *R. lintoni* are " narrow scarcely projecting " (Wilmott, 1942, 374). In my experience, the variation in the shape of the corolla teeth in *R. minor* appears to be continuous from the condition in which the teeth are so short as to be scarcely recognisable, to that in which they are about 1 mm. in length. There is some evidence that tooth-shape, at least in part, reflects genetic differences, since plants from different localities (when cultivated under similar conditions by the present writer) were found to be distinguishable by their corolla teeth. However, it is evident that written descriptions, such as appear in the diagnoses of the British endemic forms, are inadequate for use in the practical determination of species.

Shape and Measurements of the calyx

The shape of the calyx appears to have been regarded as important in the diagnoses of British *Rhinanthus* species by Wilmott, as does the measurement of length and breadth. Descriptions of the shape and measurements of the calyx are published in Wilmott's specific diagnoses, and in the descriptions of species given by Warburg in the *Flora of the British Isles* (1952). I have examined critically the published figures and have compared them with the written descriptions of shape, and, where type material is available in Herb. Mus. Brit., I have compared the published data with my own measurements of this material. My measurements were of the maximum dimensions of the most mature calyx of each holotype specimen (to the nearest 0·5 mm.).

In order to facilitate comparison of the various sets of data, length and breadth measurements may be combined into a simple shape index " S " calculated from the equation:

$$S = \frac{\text{Breadth of calyx}}{\text{Length of calyx}} \times 100$$

Indices derived from measurements published in the literature will henceforth be referred to as " S_L", whilst indices derived from measurements of the holotype specimens will be referred to as " S_T". These indices, together with the measurements from which they were derived, are given in Table I below.

Key—*Warburg (1952, 890).
†Wilmott (1942, 373).

TABLE 1.

Measurements and shape indices for the calyces of British Rhinanthus " species."

Species	*Holotype Length*	*Specimen Breadth*	S_T	*Literature Length*	*Literature Breadth*	S_L
R. minor Ehrh.	—	—	—	—	—	—
R. stenophyllus (Schur) Druce				14–16	10–12*	71·43–75·00
R. calcareus Wilmott	11·50	8·50	73·91	c.12	9–11	75·00–91·67
R. spadiceus Wilmott	11·50	10·50	91·30	11	8	72·73
				12	9	75·00
				11	10	90·91
				(14	9½)	(67·86)
subsp. *orcadensis* Wilmott	8·00	7·50	93·75	—	—	—
R. borealis (Sterneck) Druce				18	17†	94·44
var. *calvescens* Wilmott	15·50	13·00	83·87	—	—	—
subsp. *salmoni* Soó	11·00	8·50	77·27	—	—	—
R. lintoni Wilmott	11·00	9·00	81·82	12	9½	89·15
				9½	10	105·26
				13	11	84·62
R. lochabrensis Wilmott	13·00	11·00	84·62	13	11½	88·46
				17	13½	79·41
R. vachellae Wilmott	10·00	8·00	80·00	—	—	—

Measurements from the literature are those given in the original diagnosis of each taxon except where indicated in Key. All measurements are given in mm.
— indicates no measurement available.

Some considerations of written descriptions of shape in relation to shape indices follow :

1. From the table it is evident that all the species listed fall, with regard to S_L, within the range for *R. spadiceus*, i.e. between 67·86 and 90·91. The S_L of 105·26 calculated for *R. lintoni* is probably a result of a misprint (see 4 below) and has been ignored here, whilst I consider the S_L of 91·67 calculated for *R. calcareus* to be negligibly in excess of the highest figure for *R. spadiceus*. From these considerations it appears that the description of shape of the mature calyx which is given in the diagnosis of *R. spadiceus* should cover all the other species here listed. Since all the descriptions in the literature cited are worded differently it is difficult to judge whether this is in fact the case.

2. The description of *R. lochabrensis* (Wilmott, 1940, 212) indicates that the calyx is at all times " considerably longer than broad "; the maximum S_L for this species is 88·46.

The minimum S_L calculated for *R. lintoni* is 84·62, and the description for this species runs " nearly as broad as long " (Wilmott 1940, 210). From these examples, it would appear that the written descriptions are at variance with the published measurements, since if a calyx whose breadth measurement is c. 89% of its length is " considerably longer than broad ", one with a corresponding percentage of c. 85 can hardly be described as " nearly as broad as long ". It is also relevant to note that at least one of the specimens on the holotype sheet of *R. lochabrensis* has $S_T = 100$, i.e. an almost round calyx. The description of the calyx of *R. lochabrensis* would therefore appear to be inaccurate, although the italics used by the author indicated that he attached considerable importance to it.

3. The description of the calyx of *R. calcareus* appears to be at variance with the published measurements. The smallest value for S_L in this case is 75·00 which is 4·41 less than the smallest value for *R. lochabrensis* whose calyx is " considerably longer than broad "; the description of the calyx as slightly longer than broad in *R. calcareus* (Wilmott 1940, 203) cannot be upheld since the figures indicate that it should be more elongated than that of *R. lochabrensis*.

4. For *R. lintoni* part of the diagnosis runs " Calyx juvenilis aliquantum, maturus paululum vel vix longior quam latus, parvus (e.g., 12 × 9½, 9½ × 10, 13 × 11 mm.) " (Wilmott 1940, 209). It can only be assumed that the length and breadth figures have been accidentally reversed or misprinted in the second example, since the written description is obviously at variance with this example. Omitting this second example this series falls within the ranges of S_L of both *R. spadiceus* and *R. calcareus*, despite the differences in the wording of the descriptions of the three species.

It must be concluded from the observations above, that the published calyx measurements and descriptions of calyx shape are of exceedingly doubtful value as diagnostic characters for subdivision of *R. minor* L.

Internode Length

Internode length has been mentioned in the diagnoses of each of the *Rhinanthus* species of Wilmott. Although written descriptions of length are given, in only one instance —that of *R. calcareus*—is any measurement given. Owing to the use of terms such as " upper ", " lower ", and " even below the topmost branches " to define the position of internodes, and of terms such as " short ", " long " and " elongated " to describe their length, the meanings of most of the descriptions are obscure.

In order to provide a numerical basis for discussion, every internode on each of the holotype specimens in the Herbarium of the British Museum has been measured.

The following paragraphs are an attempt to demonstrate some of the apparent inconsistencies in the descriptions of various species.

1. The description of *R. calcareus* (Wilmott, 1940, 202) runs " lower internodes about 8 mm. long, those between the intercalary leaves greatly elongated averaging 5 cm. long." It was evident from my measurements that the lengths of the internodes of the holotype specimen increase gradually (with minor irregularities) from the first to the eighteenth. Only two (the third and fourth) could be described as "about 8 mm. long", being 7 and 9 mm. long respectively. I have investigated the " lower " internode lengths of a number of specimens of *R. calcareus* determined by Wilmott in Herb. Mus. Brit. These showed considerable diversity and supported my conclusion that it is not possible to apply this description even to authenticated specimens.

The description quoted above is ambiguous, since it is uncertain whether the word " averaging " is intended to refer to the average for a single plant, or for the taxon in general. The average length for the four internodes " between the intercalary leaves " on the holotype specimen is 4·4 cm. although the longest of these was found to be 5·2 cm. An

investigation of the internode lengths of thirty specimens in Herb. Mus. Brit. was carried out. All these plants had been identified as *R. calcareus*, and the gatherings (from nine different localities) had in most cases been mentioned in one or both of Wilmott's 1940 and 1942 papers. In only three of the thirty specimens was any internode between intercalary leaves 5 cm. or longer, and, in these three, the mean length of these internodes was found to be 4·4, 4·5 and 4·8 cm. respectively. No arrangement of the data from these plants would give an " average " of 5 cm.

2. *R. lochabrensis* is described as possessing ". . . internodes elongated even below the topmost branches, longest between the middle intercalary leaves ", but the intercalary leaf numbers are given as " (rarely 1, 2)3(4) pairs " (Wilmott, 1940, 211). If the usual intercalary leaf number for the taxon is 3 pairs it is diffcult to see how the two characters are compatible since there can be only one " middle " leaf pair.

3. The inflorescence of *R. calcareus* was described by Wilmott (1940, 203) as " lax ". My measurements of the holotype specimens indicate that the mean length of the internodes between the three lowest flowering nodes is *greater* in the cases of *R. spadiceus*, *R. vachellae*, *R. lintoni* and *R. borealis* var. *calvescens* than in *R. calcareus*. It is somewhat difficult to see the reason for the inclusion of the term " lax " in the description of this species.

Other examples in the original thesis indicated similar anomalies in respect of the descriptions of other taxa including *R. spadiceus*, *R. spadiceus* subsp. *orcadensis*, *R. lintoni*, *R. vachellae* and *R. borealis* var. *calvescens*.

The evidence from these investigations indicates that it is by no means certain whether absolute or relative internode lengths were intended in the various diagnoses, and it is evident that whichever one was intended in the diagnoses by Wilmott, it has not been used consistently.

Internode Numbers along the axis and the character of " Intercalary Leaves "

Descriptions of internode numbers or node numbers which appear in diagnoses of British *Rhinanthus* taxa are in some cases specific, referring to a particular region of the stem, and in others general, referring perhaps to the entire stem. Specific reference to the number of nodes bearing " intercalary leaves " is given in all the diagnoses of British species by Wilmott, and reference to the number of flowers appears in some diagnoses.

There are no references to the total number of nodes in precise terms.

Intercalary Leaves

Intercalary leaves, first named by Sterneck (see Wilmott, 1940, 201), are leaves between the topmost branches and the lowest bracts. Careful investigation of the buds in the axils of intercalary leaves reveals that they are, in most cases, aborted flower buds. Intercalary leaves are thus analogous to bracts, a fact which appears to have escaped previous notice. Simple-stemmed plants may possess pairs of such leaves which will here be referred to as " sterile bracts ". Since, however, by definition, intercalary leaves must occur above the topmost branch, it is impossible for a simple-stemmed plant to possess intercalary leaves. As the possible presence of intercalary leaves on unbranched plants has not previously been considered, it will be seen that like cannot always have been compared with like in diagnoses of simple-stemmed and branched species.

Wilmott (1940, 211) in the diagnosis of *R. lochabrensis* gave the stem habit thus " Caulis . . . simplex vel ramis paucis . . ." and the intercalary leaf-pair number as

(1-2-)3(-4) ", with no mention of plants without intercalary leaves. The simple-stemmed examples of the species must, however, lack intercalary leaves (in Sterneck's sense). The diagnosis of *R. lochabrensis* is therefore contradictory. If the figure " 0 " is in fact included in the diagnosis of *R. lochabrensis*, the range of intercalary leaf-pair numbers for the species covers almost the entire range recorded in the literature for British *Rhinanthus*, that is 0-4. The only species recorded as possessing a greater number of intercalary leaves is *R. calcareus*, which is described as possessing " (2-)4-5(-6) pairs " (Wilmott, 1940, 202).

In view of the facts reported above and the fact that a range of intercalary leaf numbers is indicated for each species, it is difficult to find adequate reason for regarding this character as of any great importance in existing taxonomic diagnoses.

Flower Number

Several criticisms may be made of the use of this character in the diagnoses of British *Rhinanthus* taxa where it is used by Wilmott, and in other descriptions e.g. those in *Flora of the British Isles*.

The following remarks represent a summary of the more important points presented in the original thesis:

1. It is noticeable that the number 5 is included in the ranges published for each of the British species by Wilmott or Warburg, except in the case of *R. stenophyllus* for which Warburg gives the range 6-12.

2. A specimen on the holotype sheet of *R. spadiceus* bears three flowers more than the maximum of five indicated in the diagnosis.

3. Examination of the various holotype specimens indicated that the description of the flower number of *R. lintoni*, that is (2-)3-4(-5), would cover them all.

4. Observations of cultivated plants of *R. minor* indicated that the flower number of *Rhinanthus* is considerably affected by environmental conditions.

There is thus evidence that the range of flower number in *R. minor* is continuous and cannot be of value for subdivision of this taxon.

Height

Height has been mentioned in diagnoses and descriptions of British *Rhinanthus* species. Fig. 3 shows the published ranges of height for various taxa. The first point which is evident from the figure is that there is a continuous range of heights.

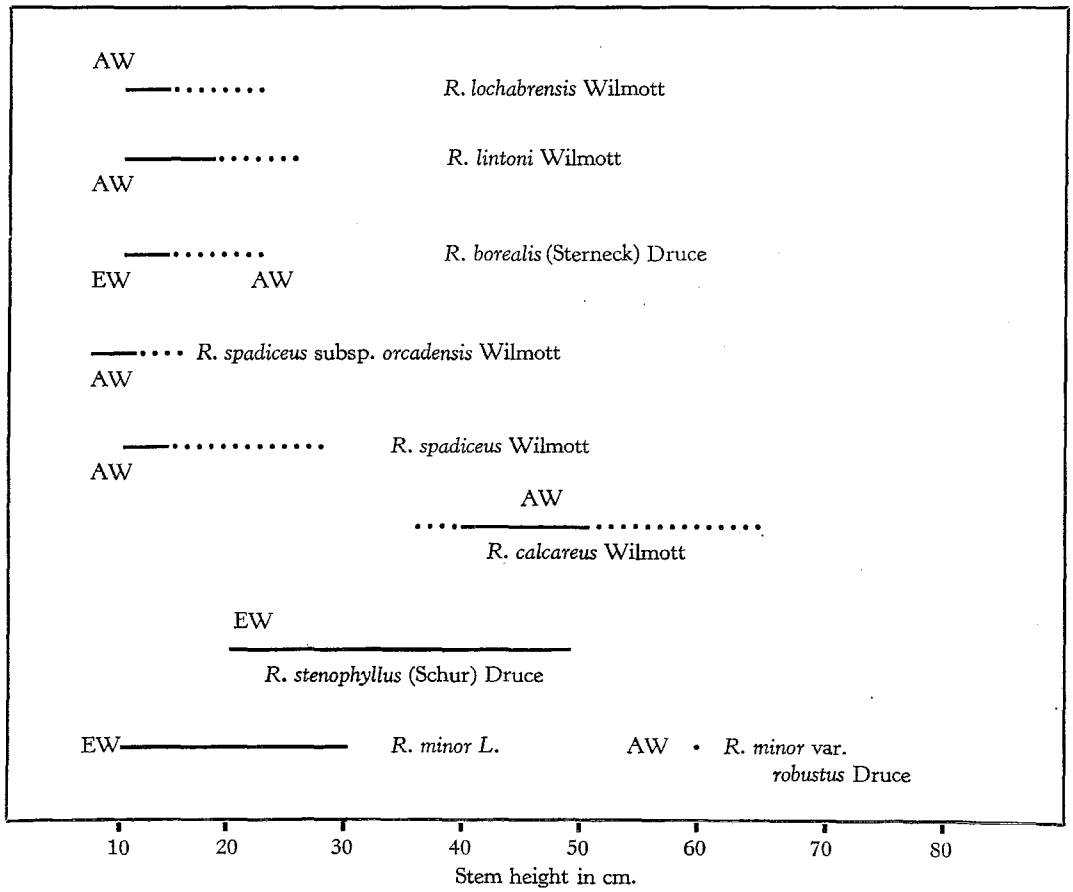
Space does not permit an exhaustive study of height in relation to the taxonomy of *Rhinanthus*, but the following is a summary of results presented in detail in the original thesis.

Height frequency histograms were prepared from data obtained from ten samples (the sample numbers varying from 25 to 72) of *R. minor* from localities ranging between Cornwall and Shetland. These histograms were each consistent with the view that height distribution was approximately normal within each population. The following points emerged:—

1. Two samples with overlapping height ranges (from The Lizard, Cornwall, and Tingwall, Shetland) have a total height range extending almost to the upper limit of the total range of published heights for British species, and *below* the lower limits of this range.

2. The Lizard specimens could not be identified (owing to the width of their leaves) as *R. calcareus* or *R. stenophyllus* and, therefore, do not correspond with any of the published diagnoses for British *Rhinanthus*.

Fig. 3. Published height ranges for British *Rhinanthus* species.



Note—Continuous lines indicate the published " typical " ranges whilst dotted lines indicate exceptional (?) extensions of the range.

Key— AW = Range given by A. J. Wilmott, 1940.
EW = Range given by E. F. Warburg, 1952.

3. A sample from a population at c. 1,400 feet on Ben Nevis, Inverness-shire, was found to have a majority of plants with pubescent calyx, and a modal height of 10 cm.; this is at the lowest limit of the published height range for any of the British species with pubescent calyx, and the lowest limit of the height range in this sample (4 cm.) was well below the lower limit of any of the published ranges for these species.

4. Each of the ten samples mentioned above possessed a different modal height, these modes forming a gradually ascending series between 10 cm. and 43 cm. There was a continuous range of height between the shortest and the tallest plant recorded in this investigation.

The final conclusion must be that there is a continuous height range in British *R. minor* L., and further, that the subdivisions of this range bounded by " round numbers" are not valid for discrimination of taxa.

Bract Shape and Length

A bract may be defined as a leaf in the axil of which arises a flower or branch of an inflorescence. Warburg (1952, 888) wrote that intercalary leaves (see p. 107) " are often

transitional between the lower leaves and bracts in shape and toothing " and he defined the bracts used in his descriptions of species as excluding " the two lowest pairs which are often transitional to the leaves." There appears to be a more or less gradual change in the shape of leaves in the widest sense of the term (i.e. including bracts) from the base to the apex of the stem in any *Rhinanthus* plant. In general, there is a widening of the base of the leaves and an increase in the divergence and length of the leaf teeth associated with the flowering part of the axis. The leaves of a specimen with numerous flowering nodes are usually triangular in the lower part of the inflorescence, and become more ovate towards the apex of the inflorescence. Frequently only one flower is borne on a node, but there is no great difference in the shape of the two bracts at this node (although sometimes the sterile bract is slightly the smaller). In the lower part of the inflorescence, flowers may be borne in the axils of bracts which are almost identical in shape to the sterile bracts (intercalary leaves) which occur below them. Sterile bract-pairs in the lower part of the inflorescence should be included in the orthodox descriptions of bract shape, since, using Warburg's system mentioned above, it is possible, for example, that comparison of the third bract pair of an inflorescence without "intercalary leaves " might be made with the fifth bract pair of an inflorescence with two intercalary leaf pairs. Such a comparison is hardly justifiable. In British *Rhinanthus* it appears that the main differences in shape indicated between the bracts of different species are such as occur between successive bracts in a single inflorescence of a well-developed plant.

My observations on cultivated plants have indicated that environmental factors influence the number of flowers produced by *Rhinanthus*, and that plants dwarfed, for example, by cultivation without a host plant, produce fewer flowering nodes than luxuriant specimens, and may fail to produce the more ovate bracts characteristic of the upper part of the inflorescence, although genotypically capable of doing so. It is, therefore, unwise to place too great an emphasis on bract shape as a diagnostic character for subdivision of *R. minor* L.

Leaf Measurements

Careful study of the type specimens and of field populations of *Rhinanthus* indicated that the range of leaf measurements in *R. minor* is continuous. The ranges published by Wilmott in his diagnoses are small, and in some instances smaller than the range shown by single local populations. Discrepancies occur between the holotype specimens and descriptions in several cases; for example, a leaf of the holotype of *R. vachellae* was found to be 3 mm. wide, 1 mm. greater than the figure published in the diagnosis; similarly a leaf of the holotype of *R. lintoni* was found to be at least 2 mm. broader than the 3 mm. indicated in the diagnosis, despite the fact that shrinkage in drying has undoubtedly occurred.

It was concluded after a detailed investigation (reported in thesis) that no importance can be attached to the published leaf measurements for discrimination of British *Rhinanthus* taxa.

Leaf Shape

From the published diagnoses and descriptions of leaf shape in British *Rhinanthus* taxa, considerable differences between taxa might be expected. From the remarks of Sterneck (1901, 107-8), translated by Marshall (1903), it is evident that a very considerable variation may occur even within a single *Rhinanthus* population. My observations on *R. minor* populations (see thesis) strongly support this. Variation in the shape of leaves

from the base to the apex of the stem was noted by Chabert (1899), who remarked that the lower leaves were often shorter and more obtuse than the upper ones. My observations indicate that different populations are often characterised by different numbers of nodes below the inflorescence, and that certain phases of leaf shape, present in plants with numerous internodes, are omitted from plants with fewer nodes. It might, therefore, not be comparing like with like, when the upper leaves of plants with few nodes are compared with those of plants with numerous nodes. It would, therefore, have been preferable in orthodox taxonomic diagnoses to have compared node numbers rather than leaf shapes, whose differences are subjectively determined and which depend partly on factors (e.g. position on the stem) which have only been arbitrarily defined in the literature.

Measurement of the holotype specimens of Wilmott's seven taxa indicates that the topmost stem leaf (excluding intercalary leaves and bracts), which was taken as a standard, tapered from near the base in each case. The diagnoses of *R. calcareus*, *R. spadiceus* and *R. lintoni*, which indicate that the leaves are " linear " for the first species and " linear-lanceolate " for the second and third, cannot be accepted.

In view of the considerable variability in shape which in some populations is much greater than the entire range of the holotype specimens under discussion, it is doubtful whether species may be diagnosed by such a character, the variation of which is probably due in part to segregation of factors affecting allometry and to genetic or environmental control of the number of nodes below the first bracts. It is not surprising that some populations may appear more uniform than others (e.g. a sample from Ben Lawers had a very small range of shape (see thesis)), since (excluding the effects of any mutation) any genetically controlled variability will depend ultimately on that inherent in the original ancestor(s) (which may be very few) of any spatially distinct population.

If this brief investigation has demonstrated the inadvisability of attempting to distinguish British *Rhinanthus* species on the character of leaf shape it will not have failed in its object.

Pubescence

The character of pubescence of various organs has been mentioned in a number of taxonomic diagnoses of British *Rhinanthus* species. Soó (1929, 82) considered the pubescence of the calyx to be very important. He distinguished four main types of calyx pubescence, only one of which, " the quite short-hairy " type, occurs in Britain according to Wilmott (1942, 372). The description of hairiness refers to the calyx surfaces, excluding the margin which appears to be hairy in all British forms. The pubescence of organs other than the calyx does not appear to have been regarded by taxonomists as of such importance as that of the calyx. A brief mention of such considerations and assessments of their importance will now be made, with a more detailed discussion of calyx pubescence.

Stem: the descriptions of stem pubescence for British *Rhinanthus* species are somewhat vague in the few cases where they are given in the literature. It might be noted, however, that environmental factors considerably influence the apparent degree of pubescence of the stem. Plants dwarfed, e.g. by cultivating them without a host plant, appear more pubescent on the stem than larger specimens with longer internodes.

Leaves: *R. lintoni* is the only British species for which a record of distinctive leaf-pubescence exists. The hairs on the " midrib (and sometimes veins) beneath " are described (Wilmott, 1940, 210) as " longer." It is interesting to note that the holotype specimen of *R. lintoni* is on a sheet in Herb. Mus. Brit. with other specimens of the original gathering, some of which are labelled " *borealis* " with the signature of the late A. J. Wilmott. It seems probable that the presence or absence of the slight elongation of hairs indicated in

the diagnosis could easily be due to simple allelic differences between members of a single population, and that it is not a character likely to be associated with cross-fertility barriers within such a population. It is further obvious that it was necessary to select individuals with particular combinations of characters from the type population in order to describe them as a new species.

Bracts: in British *Rhinanthus* the scabrousness of the foliage decreases towards the apex of the inflorescence, the upper bracts of plants with numerous flowers being almost glabrous. The descriptions of bract pubescence in British literature must be considered in relation to this fact, since it might be expected that all the bracts of few-flowered forms would exhibit pubescence; it must be remembered that these may be comparable with the lower bracts only of larger specimens. In the light of these remarks, it is evident that no significant references have been made with regard to bract pubescence in the diagnoses of British species.

Calyx: Wilmott appeared to recognise five taxa with a shortly pubescent calyx surface in the British Isles ; these are *R. borealis* (Sterneck) Druce, *R. lintoni* Wilmott, *R. lochabrensis* Wilmott, *R. vachellae* Wilmott and *R. borealis* var. *calvescens* Wilmott. It is evident from the literature that considerable similarities exist between some plants with a pubescent calyx-surface and others without, and that there are some intermediate forms e.g., *R, borealis* var. *calvescens* (see p. 103; and Wilmott, 1940, 209).

It might be argued that when there exists a complete series (such as Wilmott himself indicated) between two extremes in a single locality, it is unwise to take a sample midway between these extremes and name it as a new variety.

R. vachellae was described by Wilmott in 1948 as " another British *Rhinanthus* with pubescent calyx ". Some of his doubts about this taxon have been indicated on p. 103.

Chabert, in 1899, wrote that the character of pubescence of the calyx in *Rhinanthus* varied with age . . . " The calyx is very accrescent between the opening of the flower and the maturation of the seeds, its surface becoming doubly and occasionally triply extended. As it does not give rise to new hairs, those which exist become very much less dense and in consequence are relatively smaller in number. . . " (translated). Marshall, in a letter to Linton (1903), indicated another type of alteration in pubescence . . . " In some of my flowering specimens of *R. borealis* the whole surface of the calyx is densely pubescent. As they grow old the calyces lose their hairs gradually, at last becoming almost glabrous." I have confirmed these observations, since both phenomena occurred in Swedish *R. minor*, which was cultivated in England in 1955. Any description of calyx pubescence, should, therefore, indicate the age of the specimen. Apart from such disadvantages, if, as Wilmott (1948, 84) wrote, ". . . the hairy calyx may be a variable character in some species of *Rhinanthus* ", it may be argued that it cannot be a reliable character by which to separate one species from another, and it cannot be of such fundamental importance in the taxonomy of *Rhinanthus* as Soó (reported by Wilmott, 1942, 372) thought.

Various facts indicate that the glabrousness or " quite short hairy " pubescence of the calyx may depend on a pair of allelomorphs, which can segregate and re-combine with numerous combinations of genes, affecting other taxonomic characters. The description of populations of *R. groenlandicus* by Ostenfeld (1901, *Bot. Faroes*, 51-55), quoted by Wilmott (1942, 371), shows " that among a large number of Arctic specimens there are always some with a hairy calyx, but the greater part with glabrous, though the specimens do not otherwise differ from each other in any respect." Dr. N. Hylander, in a letter to the present writer, described collections in the Herbarium of Uppsala Universitets Institution För Systematic Botanik which came from " Northernmost Finland " and " Northernmost Norway " thus: "it must be stressed, that in many of these collections only some specimens have pubescent calyx, whilst the rest have glabrous; apparently both types

occur together in one and the same population without any ecological differentiation at all." The considerable similarity recorded by Wilmott (1948, 84) between *R. vachellae* and *R. stenophyllus* and *R. spadiceus* except in the pubescence of the calyx of the former species might also be taken to indicate that pubescence of the calyx may sometimes represent merely an allelic difference between otherwise similar forms.

Although *R. borealis* was described as a " circumpolar Typus " by Sterneck (1901, 333), and although there is evidence that the character of pubescent calyx is associated with mountain or boreal habitats (i.e. in Britain it is only recorded from Scotland and the northern islands in the literature, whilst specimens sent to me by Mr. Evan Roberts from Moel Siabod, Wales, at 2,000 feet indicated that the character occurs in the Welsh mountains), it is not necessarily at great selective advantage in such regions. This is indicated by the remarks of Hylander above and the record of *R. borealis* subsp. *salmonii* Soó (a taxon with glabrous calyx surface) at 2,000 feet (Wilmott, 1942, 373). It is interesting to note that the character of " shortly hairy calyx " occurs in *Rhinanthus* of non-montane regions in the New World and extends, according to Sterneck's map (1901, Taf. 111), as far as the southernmost limits of the genus; here it occurs in *Alectorolophus kyrollae* Chabert and *A. pacificus* Sterneck. The reasons for the present geographical and altitudinal distribution of forms with shortly hairy calyx and those with glabrous calyx remain obscure, as their ecological tolerance ranges appear to overlap considerably.

Corolla: pubescence of the corolla appears to have been mentioned only in connection with *R. vachellae* amongst the British species. The corolla of *R. vachellae* was stated by Wilmott (1948, 84) to be much more pubescent than that of *R. lintoni*; no mention of this character appears in the diagnosis of *R. lintoni*. Examination of the holotype specimens does in fact indicate that the lateral surface of the hood only of the one well-preserved corolla of *R. vachellae* on the type sheet has somewhat more conspicuous pubescence than *any* of the other holotype specimens of Wilmott's species. However, in view of the difficulties in estimating degree of pubescence (which appears to vary continuously) it is not possible to place much reliance on such subjective comparisons for identification of critical species.

Conclusion Regarding Pubescence

The ultimate conclusion must be that differences of pubescence in *R. minor* L. need considerably more study before their value in the subdivision of this taxon can be assessed.

Pigmentation

From diagnoses of *Rhinanthus* species it would often appear that differences of pigmentation have been regarded as important. The colour of the corolla teeth has been used in most specific diagnoses and has, in some cases, led to controversy (see Wilmott, 1942, 363). The pigmentation of stem, bracts and calyx has been used in taxonomy. Wilmott, for example, wrote of *R. minor* " The stems may be quite green, or black-striolate, or suffused with some form of (reddish to violet and blackish) anthocyanin ", and " many . . . forms of *R. minor* tend to be suffused with purple-violet on the bracts, calyces, and even stems." He suggested that, as these colorations had been used in descriptions, the variation in the field should be noted in case these colorations should prove to be associated with morphological differences, and that the colour of the corolla needs study from week to week to see if it changes.

The following is a brief summary of the main points which have emerged from observations on cultivated plants and natural populations.

The colour of the corolla tooth in a single Kentish population of *R. minor* varied

from plant to plant, Spinel pink $0625/_2$, Aconite violet $937/_3$ and Dauphin's violet $039/_1$ (the colours are from Wilson's 1938 Colour Chart) being among the colours recorded.

The teeth of successive corollas on a single plant may vary between white and violet in *R. minor* (and in *R. serotinus*). The violet teeth of a single corolla may fade almost to white before the corolla falls. The coloration of the corolla tooth and striolation of the stem are genetically controlled characters which are not necessarily linked. Rubescence of the stem, bracts and calyx, stem striolation and in some cases pigmentation of the corolla teeth appear to be enhanced by dry conditions.

In view of the evidence presented it is concluded that corolla tooth colour, striolation of the stem, and rubescence of the upper parts of the plant are not good taxonomic characters for discrimination of *Rhinanthus* species.

The "treacle-brown" colour (see Wilmott, 1942, 368) of the corolla in *R. spadiceus* is due to the development of reddish or purple anthocyanin in epidermal cells of the corolla (which also contain yellow plastids) as it matures. A corolla will appear " treacle " or " fuscous spotted " (cf. *R. perrieri* Chabert) depending on whether a majority of cells contain anthocyanin or whether this pigment is mainly confined to more particular groups of cells. Both conditions may occur in a single field population, and the spotted condition is probably often a transitional stage to the completely treacle corolla. The exact shade of the mature corolla depends on the concentration and colour of anthocyanin present. Similar development of pigment in the corolla occurs in other *Rhinanthus* taxa and the process has been followed in Swiss *R.* cf. *angustifolius* C.C. Gmel. which was cultivated in London in 1955. The corollas of two plants were Dresden Yellow 64 (Wilson's Colour Chart standard) at the time of opening. The corollas became mottled with red on the lower lips soon after they had expanded fully, and finally became orange in colour before becoming detached from the plant. This coloration had previously been observed in the field at the locality (near Zermatt) from which the seeds were collected in 1953. Development of diffuse anthocyanin pigmentation of the corolla is undoubtedly an inherited character in *Rhinanthus*, but in view of the fact that I have observed it in taxa as distinct as *R. serotinus* (Swiss plants), *R.* cf. *angustifolius* (Swiss) and *R. minor* (Swiss and British) it seems unlikely that this would be a valuable character for the subdivision of one of these taxa. This is borne out by the fact that I have observed the character in various combinations with other characters within *R. minor*, e.g. in plants with glabrous calyces (Malham, Yorks; Shetland; Orkney; Dover, Kent) and plants with pubescent calyces (Ben Lawers, Perthshire).

A variable number of black or brown anthocyanin spots occurring on some *Rhinanthus* corollas have been found to be genetically controlled, although environmental factors have some effect on their intensity. They occur in *R. minor*, *R.* cf. *angustifolius* and *R. serotinus*.

The conclusion must be that the varying anthocyanin pigmentation in *Rhinanthus* does not provide any sound taxonomic character.

Conclusions and Discussion

It has been shown in the first part of this paper that British *Rhinanthus* may be satisfactorily split into two taxa by the use of floral characters only. These taxa agree with the original diagnoses of *R. minor* L. and *R. serotinus* (Schönh.) Oborny, respectively. The latter species has not been considered in detail in the present paper.

The group of plants possessing the corolla characters of *R. minor* has been divided into a number of species, including several supposedly endemic British ones, described by Wilmott. The investigations recorded in the present paper indicate that descriptions

of these species are unsatisfactory in a number of respects : some of the descriptions fail to agree with the type material : inconsistencies and ambiguities have been discovered in the descriptions of some individual characters in the various diagnoses : some taxonomic characters have been shown to vary within single populations; some characters have been mentioned in the diagnosis of one species and not in another, and so on; the individual conclusions need not be repeated here. It is evident that division of *R. minor* L. into species has not been satisfactory with regard to British forms. Since one of the main objects of orthodox taxonomy must be to provide a method for recognition of similar forms, it is essential that the descriptions of such forms shall be mutually exclusive; this necessitates, especially in the taxonomy of critical groups, a precision in diagnosis which has been lacking in descriptions of *Rhinanthus* under discussion.

It is evident from my investigations that existing diagnoses do not cover all the British forms of *Rhinanthus*, and it appears that each *Rhinanthus* population might have a combination of phenotypic characters which renders it distinct from every other population. This might be expected if, in fact, the total British *R. minor* population included various combinations of genetically controlled characters, some of which might be modified by environmental influences. It would require independent assortment of genetic factors controlling only four such characters (e.g. calyx pubescence, habit, leaf shape and shape of corolla teeth) for sixteen " species " to be produced. If certain individuals or populations became genetically isolated, for example, by transference of seed to new localities, different environmental influences acting on the various populations might allow genetic drift to take place along different paths (the variability of an isolated population would depend in the first instance on the homozygosity or otherwise of the initiator(s) of that population). This situation might lead to production of forms differing to a lesser or greater degree, whilst any subsequent breakdown of barriers to outbreeding between isolated populations might give rise to further phenotypic variability. The complex series of phenotypes which undoubtedly exists in British *Rhinanthus* might have arisen in this way. Attempts to provide a name for every phenotype would result in a very great multiplicity of names, as has been pointed out by Marsden-Jones and Turrill (1954, 183) in relation to their studies on *Centaurea*.

This paper has been an attempt to assess the value of existing descriptions of British *Rhinanthus*. It has become evident that the diagnoses of certain species cannot be used with any degree of confidence for identification of even the type specimens.

It is relevant to note here that a number of *Rhinanthus* populations have been examined cytologically and that no evidence has been found of varying chromosome numbers either within *R. minor* (a number of forms have been investigated) or between *R. minor*, *R.* cf. *angustifolius* and *R. serotinus*. All so far examined were found to possess $2n = 22$ chromosomes (original thesis and Hambler, 1953 and 1954). The diploid complement of 14 large and 8 much smaller chromosomes is somewhat unusual; the fact that it is common to all *Rhinanthus* forms so far examined may be taken as evidence of their recent evolutionary divergence.

My investigations lead me to the conclusion that the type specimens of the British *Rhinanthus* taxa described by Wilmott merely represent minor genetic variants, and should all be regarded as belonging to the species *R. minor* L.

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