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A Taxonomic Revision of the Genus Sibthorpia L.

By OLOV HEDBERG
Institute of Systematic Botany, University of Uppsala

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I. Introduction

Sibthorpia L. is a genus of small, creeping herbs, belonging to the tribe *Rhinanthoideae - Digitaleae* of *Scrophulariaceae* (Wettstein 1891 p. 82). In his survey of the genus Bentham (1846 p. 427) recognized five species: *S. europaea* L., *S. africana* L., *S. pichinchensis* H. B. et K., *S. retusa* H. B. et K., and *S. peregrina* L. Later on another nine species have been added: *S. nectarifera* Wedd., *S. parvifolia* Mart. et Gal., *S. repens* (Mutis ex L.) O. Ktze, *S. conspicua* Diels, *S. americana* Sessé et Moc., *S. balearica* Knoche, *S. australis* J. Hutch., *S. triandra* Suesseng., and *S. pelia* Beauverd et Topali. The genus occurs in the oceanic parts of Western Europe, in mountains in Greece, Ethiopia ("Abyssinia"), East and West Tropical Africa, and S. Rhodesia; on the Baleares, Madeira, and the Azores; and furthermore along the Cordilleras of Central and South America. It has earlier been reported also from South Africa and Eastern Asia. The first record from S. Africa was published by Thunberg (1800 p. 104, 1823 p. 481) and concerned *Sibthorpia europaea* L., but was probably erroneous (Harvey 1838 p. 254, Hiern 1904 p. 125). No specimen is to be found in Thunberg's herbarium at

Uppsala (UPS).[1] — A sheet in Paris (P), labelled "Caput b. Spei, collection de l'Abbé Pourret" evidently belongs to *S. africana* L. (Knoche 1922 p. 390) and must probably have been confounded in some way, that species being apparently endemic to the Baleares in the Mediterranean. Finally, there is in the Stockholm Herbarium (S) a collection of *Sibthorpia peregrina* L., labelled "Afr. austr.: Cap. B. spei, Wahlberg". Many ships bound for S. Africa would make a stop at Madeira, where this species is endemic, and confusing of locality or label appears probable also in this case. No authentic find of *Sibthorpia* from S. Africa is known to the author. — The species reported from East Asia, *Sibthorpia pinnata* (Wall.) Benth., is nowadays considered generically distinct from *Sibthorpia* and is called *Ellisiophyllum pinnatum* (Wall.) Makino (cp. Bentham 1846 p. 428, Maximowicz 1871 p. 223, Makino 1906 p. 91, and Brand 1913 p. 28).

When attempting to identify some *Sibthorpia* material from East Africa the author found considerable difficulty in disentangling the taxonomy and nomenclature of this African plant. Since it was subsequently found that the same uncertainty prevailed regarding European and — still more — American material it was found desirable to attempt a revision of the whole genus. Much of the confusion prevailing as to the taxonomy of this genus seems to have arisen because new species have been described from inadequate material — sometimes one single collection — and without sufficient knowledge of the variability of the living plant and of the relevant literature. Study of a comprehensive material shows that some of the characters used in the past for taxonomic distinction in this group are so variable as to be of little use for taxonomy. It may therefore be useful to start with an examination of some of these characters.

II. Examination of some Taxonomic Features

The number of stamens is in most groups of phanerogamic plants a feature of considerable taxonomic importance and was used by Linnaeus as one of the main criteria in his artificial system. Accordingly, a South American plant of this group with only three stamens was described by Mutis (ex Linné 1771 p. 153) as a new genus, called *Willichia* (nowadays included in *Sibthorpia*). Much later Suessenguth (1935 p. 18) regarded trimery of the flower as the main criterion in

[1] The abbreviations for herbaria have been adopted from Lanjouw and Stafleu 1954.

distinguishing his "*Sibthorpia triandra*". In this particular genus the number of stamens is very variable, however. Thus in *Sibthorpia peregrina* L. the number of stamens usually varies between 5 and 8 (Linné fil. 1781, Curtis 1794, Bentham 1846 p. 427). Ruiz and Pavon (1798 pp. 6—7) reported that in their "*Veronica rotundifolia*" (=*Sibthorpia repens*) the number of stamens is 3 or 4, and Cambessedes (1827 p. 118) that in "*Disandra africana*" (=*Sibthorpia africana*) the stamens are 4 or 5. Kuntze (1898 p. 239) stated that in *Sibthorpia repens* the number of stamens is 3—5, and that in *S. europaea* and *S. africana* the flowers are tetramerous or pentamerous. On British material of *Sibthorpia europaea* in cultivation at Kew Gardens the present author found flowers with 4 stamens and those with 5 to be about equally common. — Apparently the number of stamens is too variable in this genus to be used for separation of species.

The surface structure of the seeds has sometimes been used as a distinctive feature. It has in most cases been described as "white foveolate" or "white reticulate", sometimes as papillate or smooth (cp. Knoche 1922 p. 390, Beauverd 1937 p. 265). Study of living material of *Sibthorpia europaea* revealed some interesting details in this respect. Living seeds that were almost ripe, being blackish brown in colour, proved to have their surface cells very turgescent, the distal part of each cell projecting a little to make the surface slightly mamillate. When the surface dried, which occurred a few minutes after the seeds were removed from the capsule, and which process could be studied under the microscope, the surface cells shrank in about the same way as the marginal cells of a common fern sporangium. Their lateral walls were apparently thicker and more resistant than the rest and remained, forming the well-known white-foveolate structure (cp. Svensson 1928 p. 475 regarding a similar texture in the seed surface of *Limosella*). When the seeds become fully ripe before drying the surface cells may sometimes become more resistant, the seed surface becoming smooth or showing a faint alveolate or reticulate structure in black. As a matter of fact seeds with white reticulum and seeds with smooth black surface are often found in different capsules on the same specimen. This feature can evidently not be used for species discrimination in *Sibthorpia*.

All species of *Sibthorpia* have reniform or orbicular, crenulate leaves. The average number of leaf crenules and their shape (retuse, truncate, rounded, or apiculate) have been used by some authors for distinguishing species (cp. e.g. Bonpland, Humboldt and Kunth 1817 p. 390—391,

Martens and Galeotti 1845 p. 11). But these features, as well as the degree of pubescence of the plant and the length of the petiole, are apparently much influenced by the habitat and may display considerable variation within the population of one district and even in a single specimen (cp. Bentham 1846 p. 428). The leaf size is also very variable and difficult to use for taxonomic distinction (cp. Kuntze 1898 p. 239).

Occurrence or non-occurrence of nectaries in the flower has been used by some botanists for species discrimination in this genus (Weddell 1858—1862 p. 11, Diels 1906 p. 428). In flowers from an isotype of *Sibthorpia nectarifera* Weddell at Kew no trace of nectaries could be found on dissection, although these were used as one of the main specific criteria for that plant. Such nectaries can probably be appropriately studied only in living material, and far too little is known about them in most of the species so far described to allow a proper judgment of their taxonomic significance.

The colour of the corolla appears to be a useful criterion in some cases, though apparently it shows some variation, e.g. in *Sibthorpia europaea* (cp. Bentham 1846 p. 427). Too much importance should not be attached to different shades of red, since they are often impossible to judge from herbarium specimens and since the way of describing colours varies so much with different collectors. — In American material the colour of the corolla seems to be more variable than in that from the Old World.

The relation between the lengths of peduncle and petiole seems to provide a good characteristic in European and African material, whereas in the American material it appears to break down as a distinctive feature. Similarly, in Old World material the seed size offers a reliable distinction (cp. Tab. 1 and Fig. 1), whereas the New World material displays a continuous variation in seed size (l.c.). The number of flowers per node affords a fairly good criterion in the Old World material, whereas American material displays wide variation also in this respect.

III. The Old World Species

When surveying the European and African material of *Sibthorpia* we may conveniently start with the three species described by Linnaeus in Species Plantarum (1753 p. 631): *Sibthorpia europaea, S. africana,* and *S. peregrina.* Incidentally, these seem to cover all of the material at hand from this part of the world even today. Beginning with *S. afri-*

cana, which has been the most problematic one of the three, we find only a very short original description and the reference: "Chrysosplenii foliis planta aquatica, flore flavo pentapetalo. Shaw afric. 149 f. 149." Also the description given by Shaw in his "Travels" (1738) is rather meagre, and his picture is very schematic. The locality given by Linnaeus is "Africa", and Shaw's travels concerned mainly North Africa. No *Sibthorpia* has later been found in North Africa, however, and the origin of Shaw's specimen appears doubtful (cp. Knoche 1922 p. 391). The type collection at Kew is furthermore very scrappy, containing some stem fragments with a few bruised leaves and the remains of two fruits. The interpretation of Linnaei *Sibthorpia africana* has accordingly been uncertain. Some have identified it with a plant endemic to the Baleares, e.g. Cambessedes (1827 p. 177 ff., as "*Disandra africana*"); others have used this name for the strain of *Sibthorpia europaea* occurring in Tropical Africa, as Richard (1851 p. 122), Hooker (1864 p. 208), Engler (1892 p. 379), Hemsley and Skan (1906 p. 353), Mildbraed (1914 p. 286), Fries (1916 p. 289), and Robyns (1947 p. 230). Hooker (l.c.) and Engler (l.c.) both independently reduced this "*Sibthorpia africana*" to a variety of *S. europaea,* and most later authors have followed them in that respect. Finally, some authors have apparently confused both the plants mentioned under the name *S. africana,* as Bentham (1846 p. 427) and Hayek (1929 p. 155). — However, a thorough study of the type material made it possible to identify it securely with the plant from the Baleares, lately described by Knoche (1922 p. 390) as "*Sibthorpia balearica*". Thus five seeds extracted from a fruit of the type specimen are of exactly the same size as is normal for the Balearic plant, being considerably larger than in *S. europaea* (cp. Tab. 1 and Fig. 1). The shape and pubescence of the leaves also agree best with the former, the leaf crenules often having a small apiculum. The two peduncles present in the type material, though damaged, are far longer than is usual in *S. europaea,* and besides spirally coiled, a feature that is common in the Balearic plant, but hardly occurs at all in (European or African) *S. europaea.* Furthermore, Shaw's original description states that the peduncles are long (this is also evident in his otherwise very schematic figure) and the corolla yellow, both features matching the Balearic plant but not the African one. Accordingly, the name *Sibthorpia africana* L. belongs to the plant endemic to the Baleares, which has also been called *S. balearica* Knoche, and which is a well-defined species with comparatively small variability.

Sibthorpia peregrina L. is a very characteristic plant endemic to Madeira; its taxonomy has given no trouble.

The remaining one of the Old World species is *Sibthorpia europaea* L., which in contrast to the preceding two species has a very wide distribution. It occurs in Western Europe from Ireland and England to Spain and Portugal, in Greece, the Azores, Ethiopia, East and West Equatorial Africa, and S. Rhodesia (cp. Fig. 3). It is apparently confined to areas with moist and cool climate, being in temperate regions a decidedly oceanic plant, whereas at lower latitudes it is an equally pronounced mountain plant. — From Greece was recently described a new species of *Sibthorpia, S. pelia* Beauverd et Topali (Beauverd 1937 p. 265), stated to differ from *S. europaea* mainly in the calyx lobes being "apice longe ciliati", in its larger, red corolla ("cinnabarina nec carnosa"), and in having papillate seeds instead of foveolate ones, with the two small protuberances of the concave side much closer together than in *S. europaea.* On examination of the type collection (from Geneva) I found it to fall in every respect within the normal variation range of *Sibthorpia europaea.* The colour of the corolla is of course difficult to judge from herbarium material, but I found no difference between the type specimen and much of the British material of *S. europaea.* Accordingly, *Sibthorpia pelia* Beauverd et Topali must be regarded as a synonym of *S. europaea.*

Whereas the *Sibthorpia europaea* of Europe has presented comparatively little difficulty to taxonomists, the strain occurring in Tropical Africa has been more ambiguous. Some botanists considered it to be specifically distinct from *S. europaea,* and named it "*S. africana* L." (Richard 1851 p. 122, Fries 1916 p. 289). Others have treated it as a variety of *S. europaea,* called "var. *africana*" (Hooker 1864 p. 208, Engler 1892 p. 379, Hemsley and Skan 1906 p. 353, and Robyns 1947 p. 230). As demonstrated above (p. 165) the name *Sibthorpia africana* L. belongs to another plant, and accordingly cannot be used for this one. Hutchinson (in Hutchinson and Dalziel 1931 p. 221) described a new species on material from West Africa, *Sibthorpia australis,* but apparently he did not want to include all African *Sibthorpia* material under that name. Some of the collections quoted by him undoubtedly differ habitually to some extent from the *S. europaea* of Western Europe, but he gives no distinctive characteristics between them. It is true that the African material tends to be more pubescent and to have a larger number of lobes on each leaf than European specimens, the lobes being accordingly more crowded and often slightly

overlapping. In African material the form of the lobes will usually be rounded, sometimes with a small apiculum, whereas in European material they will more often be truncate or retuse. When studying an extensive material, however, one will find some African specimens that almost exactly match British ones, and furthermore all kinds of intermediates between the latter and the "*australis*"-type of Hutchinson. Besides, the whole range of variation may apparently occur within the same small district, e.g. on one of the East African mountains (cp. e.g. the specimens Dummer 3521, K; Taylor 3485 and 3589, BM; Hedberg 183 and 270, UPS; all from Mt. Elgon). Accordingly it seems impossible to maintain taxonomic distinction between the European and African series of populations of this plant; they should all be called *Sibthorpia europaea.*

IV. The New World Species

In the New World *Sibthorpia* occurs as a montane genus along the Cordilleras of Central and South America from Mexico in the North to Argentine in the South. In this part of the world the genus displays a very considerable range of variation in a number of characters. But whereas the Old World material of the genus can be easily distributed into three distinct species, the American material constitutes a very critical group, showing more or less continuous variation in almost all features. This is adequately exemplified by the variation in seed size (Tab. 1 and Fig. 1) and size of pollen grains (Fig. 2). Some other variable features unfit for taxonomic distinction in this case have been discussed above (p. 162 f.). — From American material has been described no less than 7 species: *Sibthorpia pichinchensis* H. B. et K. (1818), *S. retusa* H. B. et K. (1818), *S. parvifolia* Mart. et Gal. (1845), *S. nectarifera* Wedd (1855—1857), *S. americana* Sessé et Moc. (1894), *S. conspicua* Diels (1906), and *S. triandra* Suesseng. (1935). Besides two other species originally placed in other genera also belong here: *Willichia repens* Mutis ex Linné (1771), and *Veronica rotundifolia* Ruiz et Pavon (1798). The application of most of these names has been uncertain, and I soon found it best to try first to arrange the available plant material into natural groups and then to establish the proper name for each group. By this method it was found that most of the material forms an almost continuous variation series. The only species showing a discontinuity from the rest is *Sibthorpia conspicua* Diels, which is distinguished by its larger habit, wider flowers, and multi-

crenate leaves. The remaining part of the American material apparently belongs to one single, though very polymorphic, species. The oldest validly published specific epithet relating to it is *S. repens* (*Willichia repens* Mutis ex L. 1771, *Sibthorpia repens* O. Ktze 1898), which must accordingly be used for specific name. — Though the range of variation is very considerable in a number of characteristics, such as pubescence, leaf size, number of leaf lobes, relative length of peduncle and petiole, size and colour of corolla, etc., the different variates show so little correlation that it appears futile to try any definite subdivision of the species. A more detailed study of this plant, based on living material and comprising ecology and cytogenetics may of course provide possibilities for taxonomic segregation in the future.

Whereas most specimens of *Sibthorpia repens* are very unlike the less polymorphic *S. europaea,* we may occasionally find specimens of the former which are morphologically very similar to the latter. Such specimens have been collected in Mexico, Costa Rica, and Ecuador.

V. Key to the Species of Sibthorpia

A Corolla large (at least 4 mm long or 6 mm wide); fullgrown leaves usually more than 30 mm wide.
  B Corolla yellow; seeds more than 1 mm long; Madeira .... *S. peregrina*
  BB Corolla purple or dark red; seeds about 0.5 mm long; Argentine and S. Bolivia ..... *S. conspicua*
AA Corolla small (less than 4 mm long or 6 mm wide); fullgrown leaves usually less than 30 mm wide.
  C Peduncles flexuose; corolla yellow; Baleares ..... *S. africana*
  CC Peduncles not flexuose; corolla reddish or white but not yellow.
    D Corolla not longer than $^4/_3\times$ calyx; fruit shorter than calyx; sepals erect in fruit; peduncles usually shorter than petioles; West and South Europe, Azores, and mountains of Tropical Africa ..... *S. europaea*
    DD Corolla usually longer than $^4/_3\times$ calyx; fruit usually longer than calyx, or sepals reflexed in fruit; peduncles often longer than petioles; Central and South America ..... *S. repens*

VI. Enumeration of the Species

1. *Sibthorpia europaea* L. Sp. pl. p. 631 (1753).

Type: "Habitat in Cornubiae, Devoniae, Lusitaniae, udis aggeribus"; specimen 793.1 in Linnaean Herbarium (LINN, lecto.).

Syn. *S. prostrata* Salisb. Ic. stirp. rar. p. 11 (1791), nom. illegit.

S. africana auctt. non L. Sp. pl. p. 631 (1753). — *S. europaea* var. *africana* Hook. Journ. Linn. Soc. Bot. 7 p. 208 (1864); Engl. Hochgebirgsfl. trop. Afr. p. 379 (1892).

Table 1. Seed length in Sibthorpia.

Normally 10 seeds were measured in each collection, to the nearest $^1/_{40}$ of a mm (an * indicates that only 5 seeds were available). The table gives only average value and range of variation.

Origin of collection	Seed length
S. europaea L.	
England, St Just, Falmouth, Collett (K)	0.50 (0.45—0.53)
France, Cherbourg, Corbière (G)	0.53 (0.48—0.58)
„ , Brest, St Anne, Mercier (G)	0.59 (0.50—0.63)
„ , Manche, Biville, Corbière (G)	0.53 (0.48—0.58)
Spain, Cadiz, Sierra de Palma, Reverchon 124 (K)	0.56 (0.55—0.60)
Greece, Thessalia, Mt Pelion, 1200 m, De Heldreich 32 (G)	0.48 (0.43—0.53)
„ , „ , „ , Topali (G)	0.46 (0.43—0.50)
„ , „ , „ , „ (G; lectotype of "*Sibthorpia pelia* Beauv. et Topali")	0.44 (0.40—0.45)
„ , Crete, Enneadivia, 450 m, De Heldreich (K)	0.53 (0.50—0.55)
Azores, San Miguel, Goodman (K)	0.49 (0.45—0.55)
Ethiopia, Mt Bouahit, 3950 m, Schimper 1310 (K)	0.49 (0.45—0.53)
Kenya, Elgon, 3000 m, Hedberg 183 (UPS)	0.50 (0.45—0.55)
Tanganyika, Mt Meru, 3150 m, Hedberg 2410 (UPS)	0.48 (0.43—0.50)
Uganda, Ruwenzori, 3450 m, Hedberg 623 (UPS)	0.57 (0.50—0.63)
Fernando Po, 2300 m, Mann 1455 (K)	0.48 (0.43—0.53)
S. africana L.	
"Shaw's afric. 149"=holotype (K; locality uncertain)	0.78 (0.75—0.85)*
Baleares, Kennedy 106 (K)	0.79 (0.70—0.83)
„ , Mallorca, Boissier (G)	0.74 (0.65—0.85)
„ , „ , Bourgeau (G)	0,92 (0.80—1.00)
„ , „ , „ 2781 (K)	0.86 (0.80—0.90)
„ , „ , Ferrer 52 (G)	0.82 (0.75—0.90)
„ , „ , Chodat (G)	0.80 (0.70—0.85)
„ , „ , Gros (S)	0.81 (0.75—0.90)
„ , Minorca, Rigo (K)	0.78 (0.75—0.80)
S. peregrina L.	
Madeira, Mandon 186 (K)	1.25 (1.10—1.40)
„ , „ „ (S)	1.21 (1.10—1.33)
„ , „ „ (S, second sheet)	1.14 (1.00—1.28)
„ , Favrat (G)	1.13 (1.08—1.20)
„ , „ 15 (G)	1.11 (1.00—1.25)
„ , Radlof (S)	1.06 (1.00—1.15)
Unlabelled specimen (S)	1.12 (1.05—1.20)
S. repens (Mutis ex L.) O. Ktze	
Mexico, Baja California, Brandegee (NY)	0.49 (0.45—0.58)
„ , Temascaltepec, Hinton et al. 1717 (NY)	0.60 (0.55—0.68)
„ , „ , „ „ „ 4069 (NY)	0.55 (0.48—0.58)
„ , „ , Cumbre, 2800 m, Hinton et al. 6410 (NY)	0.49 (0.45—0.53)
„ , Chiapas, Mt Tacana, Matuda 2372 (NY)	0.60 (0.58—0.65)
„ , „ , „ „ , 2100 m, Matuda 2959 (NY)	0.50 (0.45—0.55)
„ , Puebla, Boca del Monte, Purpus 3005 (NY)	0.56 (0.53—0.60)
„ , Mexico Valley, Bourgeau 1247 (G)	0.81 (0.65—0.90)
„ , „ „ , „ 988 (K)	0.75 (0.70—0.80)
„ , Coulter 1313 (K)	0.70 (0.65—0.75)
„ , Lyonnet 168 (K)	0.57 (0.55—0.60)
„ , Sierra de Clavellinas, 2700 m, Pringle 4992 (K)	0.56 (0.53—0.60)

(Tab. 1. Seed length in Sibthorpia, contd.)

Origin of collection	Seed length
Mexico, Schaffner 359 (G)	0.73 (0.68—0.78)
„ , „ (K)	0.50 (0.45—0.55)
Costa Rica, Vara Blanca 1500—1750 m, Skutch 3121 (NY)	0.57 (0.50—0.63)
„ „ , Poás, Kupper 32 (MU; holotype of *Sibthorpia triandra* Suesseng.)	0.62 (0.60—0.65)
„ „ , Tonduz 12637 (K)	0.47 (0.45—0.50)
Colombia, Cundinamarca, Sibaté, 3000—3100 m, Pennell 2498 (NY)	0.63 (0.55—0.73)
„ , „ , El Peñon, 2800—3000 m, Pennell 2669 (NY)	0.58 (0.53—0.65)
„ , „ , Fusagusuga, 1800—2300 m, Pennell 2691 (NY)	0.49 (0.45—0.50)
„ , „ , Tequendama, 2400—2500 m, Pennell 2654 (NY)	0.55 (0.53—0.60)
„ , Cauca, Mt Puracé, 3400—3600 m, Pennell and Killip 6528 (NY)	0.72 (0.60—0.80)
„ , „ , „ „ , 3450 m, von Sneidern 1904 (NY)	0.57 (0.50—0.63)
„ , „ , Paletará, 2950—3100 m, Pennell 6973 (NY)	0.64 (0.60—0.68)
„ , Tolima, 3200—3400 m, Pennell 3079 (NY)	0.72 (0.65—0.80)
„ , Santander, 2000—2500 m, Killip and Smith 15560 (NY)	0.54 (0.50—0.58)
„ , Norte de Santander, 2900 m, Killip and Smith 20667 (NY)	0.70 (0.65—0.75)
„ , Bogota, Jameson 160 (K)	0.65 (0.63—0.68)
Venezuela, Tovar, Fendler 914 (K)	0.64 (0.63—0.68)
Ecuador, Pichincha, 4500 m, Hall (K)	0.85 (0.78—0.95)
„ , „ , 3000—4250 m, Jameson (NY)	0.64 (0.60—0.70)
„ , „ , Jameson 75 (K)	0.63 (0.60—0.65)
„ , Chimborazo, André 1084 (K)	0.55 (0.53—0.58)
„ , Pilyhun, Jameson (K)	0.72 (0.70—0.75)
„ , Azuay, 3000—3200 m, Camp E-2010 (NY)	0.72 (0.70—0.75)*
„ , André 3149 (K)	0.62 (0.60—0.68)
„ , Spruce 5437 (K)	0.56 (0.50—0.63)
„ , „ 5849 (NY)	0.72 (0.65—0.78)*
Bolivia, Unduavi, N. Yungas, 3300 m, Buchtien 2977 (NY)	0.69 (0.60—0.75)
„ , „ , „ , „ , „ 95 (K)	0.65 (0.58—0.78)
„ , „ , „ , „ , „ 9041 (NY)	0.69 (0.65—0.75)
„ , „ , 2500 m, Rusby 1245 (NY)	0.62 (0.58—0.68)
„ , Larecaja, 2700—3000 m, Mandon 470 (K)	0.62 (0.53—0.65)
„ , „ , Mandon 471 (K)	0.73 (0.65—0.78)*
S. conspicua Diels	
Argentine, Catamarca, Hieronymus (NY)	0.48 (0.45—0.53)

S. australis J. Hutch. Fl. W. Trop. Afr. 2 p. 221 (1931). Type: Cameroons Mt, 2150 m, Dec. 1862, Mann 1963 (K, lecto.)

S. pelia Beauverd et Topali Candollea 7 p. 265 (1937). Type: Greece, Thessalia, Mt Pelion, 1100 m, 18.9.1936, S. Topali (G, lecto.)

Distribution: Widespread in the oceanic parts of W. and S. Europe, on the Azores, and on high mountains in Tropical Africa. — Occurs in

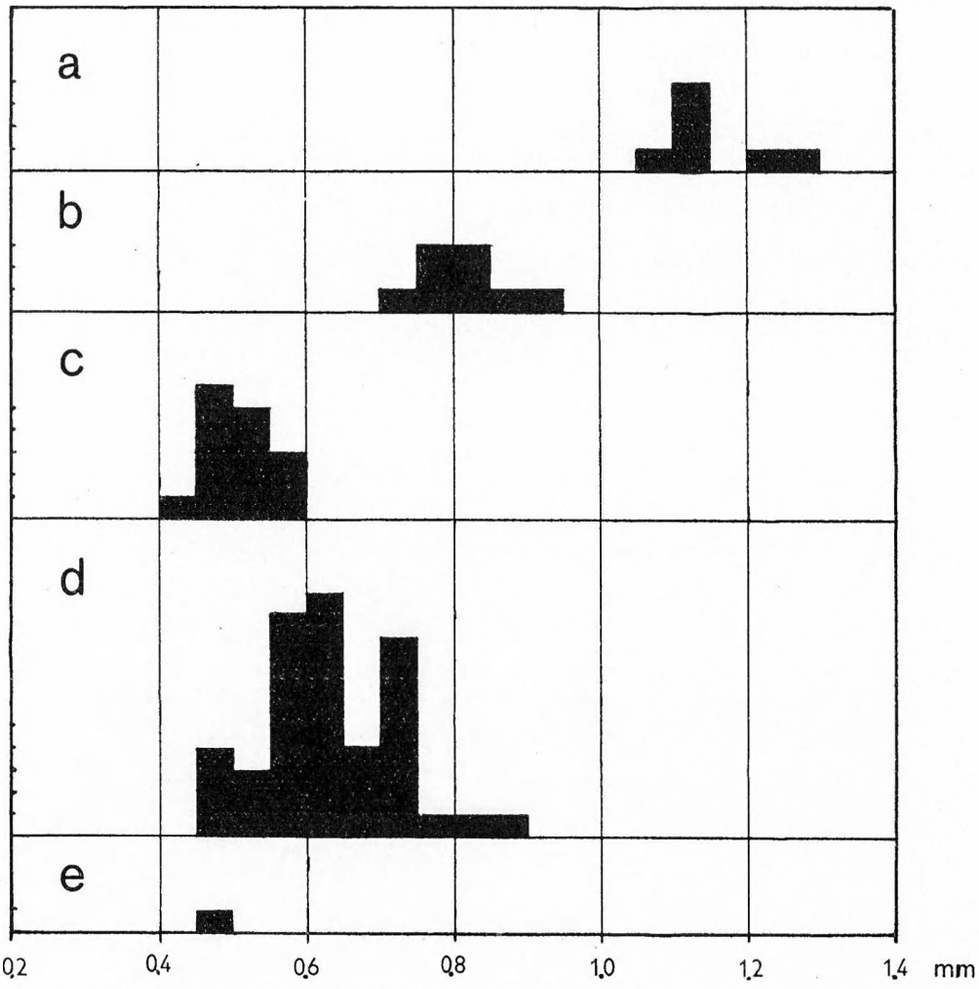

Fig. 1. Diagram illustrating variation in seed size in the species of *Sibthorpia,* based on the average values from Tab. 1. The horizontal axis gives the seed size in mm (class width 0.05 mm), the vertical axis the number of collections in each size class. a = *Sibthorpia peregrina,* b = *S. africana,* c = *S. europaea,* d = *S. repens,* e = *S. conspicua.*

moist and shady places along streams and marshes, on damp rock walls, etc.; often mixed with mosses.

Azores. *Terceira,* Fayal, June 1838, Guthnicht (BR, K). *San Miguel,* 22.8.1894, Trelease 657 (K); id., May 1838, Hochstetter 27 (G); id., 1865, Godman (K); id., Furnas, June 1937, Allorge (S).

Ireland. *Kerry.* N. slope of Connor Hill, 1805, Mackay (BM, K). Connor Hill near Dingle, Sept. 1842, Andrews (BM, K). Connor Hill, 20.8.1851, Webb (UPS); id., Sept. 1906, Druce (S). S. side of Connor Hill, Dingle, 300 m, 6.7.1938, Ross, Sealy and Burtt (K). Connor Pass, Aug. 1897, Gamble (K). Connor Hill Pass, 350 m, 21.5. 1936, Hall (K); id. 11.6.1937, Lousley (K).

Wales. *Glamorgan,* June 1938, Vachell (BM). *Carmarthen,* Abergarloch, banks of River Cothi, 1.6.1947, Eastwood (BM).

England. *Scilly Isles.* St Mary's, on the shore near Watermill Cave, 24.7.1939,

Lousley 261 (K); id., Porgis Lane, 24.7.1939, Lousley 289 (K). *Cornwall.* St Levan, Aug. 1883, Brown (BM). Newlyn and Penzance, July 1894, Steuart (BM). Newlyn near Penzance, July 1922, Worsdell (K). Near Penzance, 1836, Polwin (K); id., 1798, Hurlock (BM). Penzance, Duncan (K); id., Aug. 1845, Russell (G); id., May 1860, Torrance (BM); id. July 1886, Steuart (BM). Falmouth, June 1836, Squire (UPS). St Just, Falmouth, July 1896, Collett (K). Truro, Penryn and Falmouth, July—Sept. 1835, E. A. W. (K). Tintagel, 1846, Pascoe (UPS). Rocky Valley near Tintagel, 15.9. 1948, Meikle (K); id., 2.7.1915 and 19.8.1925, Thurston (K). Rocky Valley between Tintagel and Boscastle, 14.9.1882, Churchill (K). St Blarey and about Boscastle, Aug. 1794, Maton (BR). Boscastle, 18.9.1882, Churchill (K). Stream W. of Boscastle, 10.7.1915, Thurston (K). Newquay, July 1901, Dixon (BM, K). Kerris Moor, June 1896, H. G. (BM). St Ives, 25.9.1890, Clarke 47621 (G, K). Lostwithiel, 29.7.1947, Taylor 1053 (K). Bridges, Sept. 1900, Green (K). St Austell, 1845, Pascoe (BM, LD). Withiel, 1868, Chandler (BM). *Devon.* Lynmouth, June 1885, Fry (BM). Torrington, 18.9.1882, Ley (K). Little Torrington, 14.7.1924, Hiern (K). Tavistock, July 1835, Ralfs (K). Horsebridge, Aug. 1929, Edwards 4 (K). Kingsbridge, Churchill (K). Plym Valley, 12.7.1882, R. P. M. (BM). By a stream between Roborough Down and Buckland Monarchorum, 7.6.1871, Briggs (BM). *Somerset.* Porlock, 4.9.1883, Murray (BM). Holford, Aug. 1893, Thomas (BM); id., 2.8.1902, White (K); id. 10.8.1933, Thompson (K); id., 24.8.1937, Makins 1454 (K). Wiveliscombe, Bollard Lodge, 1864, Prior (K). Minehead, Grabbish Hill, 15.9.1887, R. P. M. (BM). *Sussex.* Cross-in-hand, 1892, Farr (BM). Burnt House between Cross-in-hand and Buxted, Aug. 1833, Kippish (BM). Waldron, 1849, Forster (BM); id., Cherrill (BM). Cuckmere Distr., Heathfield Park, 14.8.1880, Roper (K); id., 5.9.1882, Haviland (K). Heathfield and Dallington forest, Aug. 1878, Jenner (BM). Hurstmanceaux Park, Sept. 1898, T. H. (BM).

Channel Isles. *Jersey.* St Ouen, July 1894, Gray (K). St Brelade, 21.7.1928, Louis-Arsène (K). Rozel Lane, 13.10.1894, Dymes (K). Les Vaux, July 1842 (BM). Greve de Lecq, Nov. 1862, Herb. Hookerianum (K). St Larionis Valley, July 1900, Gray (K). *Guernsey,* St Peter's Valley, 23.5.1893, M. Dawber (BM).

France. *Manche.* Biville, 7.8.1896, Corbière (G). Octeville near Cherbourg, 19.8. 1897, Corbière (G). Cherbourg, 1847, Le Jolis (G); id., Aug. 1849, Le Jolis (LD); id., June and July 1853, Le Jolis (K, S, UPS). Mortain, Saint-Hilaire-du-Harcouet, July—Oct. 1855, Brehier (BR, K, S). *Calvados,* Vire, July 1837, Lenormand (G, K); id., Limage (S). *Orne,* Berson, Husnot (BR). Near *Paris,* Huet du Pavillion (G); id., Bernet (G). *Finistère.* Environments of Brest, 21.8.1855, Kiener (G); id., Lambezellec, July 1870, Tourlet (G); id., S:t Anne, 12.8.1835, Kiener (G). St Jean du Doight, 28.5.1909, Gadeceau (G). Le Huelgoat, 27.8.1897, Gadeceau (G). Morlaix, 20.8.1884, Miciol (K). Portz-an-Trez near Morlaix, Aug. 1880, Miciol (G); id., Sept.–Oct. 1884, Miciol (BR, G). *Côtes-du-Nord.* Brieuc, environments of Painpol, Oct. 1856, A. de Villejean (K). Dinan, Aug. 1850, Lemann (BM); id., June 1862, Mabelle (UPS). *Ille-et-Vilaine.* St Malo near St Coulomb, Jeanpert (G). Pont Réan, June 1907, Humbert (G). Environments of Fougeray, May 1872, Gadeceau (BM). Forêt de Painpoul, 24.5.1876, Gadeceau (BM). *Morbihan,* Vallée de Tréauray near Ste Anne d'Auray, 7.8.1883, Bouvet (K). *Loire inférieur.* Tegréac, 10.5.1874, Gadeceau (BM). Nantes, 30.6.1869, Lloyd (UPS); id., M. de Bonnemaison (G). Chateaubriant, 29.8. 1931, Charrier (LD). *Aveyron,* Entrague, 2.10.1889, J. de Puyfol (BR, G, LD, S).

Basses-Pyrénées. Above Birriatou, foot of escarpment W of Mt Chaldogoganan, 26.6. 1898, Neyraut (K). Between Béhobie and Birriatou, 14.7.1900, Neyraut (LD).

Portugal. *Minho,* Arcos de Vale-de-Vez, 15.6.1944, Fontes, Myre and Rainha 338 (G). *Oporto,* 1855, S-n (UPS); id., July 1891, Buchtien (LD, UPS); id., July 1855, Sjögren (S); id., Mattosinhos, 12.6.1881, Johnston (BM), *Beira Litoral,* Pedrogão Grande, 17.7.1947, Fontes & Rainha 2005 (G). *Beira Baixa,* Valesim, foot of Mt Herminio, Aug. 1881 (BM). *Estremadura,* Serra de Cintra, 1848, Welwitsch 207 (BM, G); id., Cruz Alta, 500 m, 29.5.1938, Rothmaler (G, S). *Algarve.* Cabeço, near Monchique, 22.6.1853, Bourgeau 1974 (G, K, LD).

Spain. *Galicia,* Lugo, 1851—52, Lange (K, UPS). *Asturias.* Corias near Cangas de Cineo, July 1864, Bourgeau 2688 (BM, G). Llanos, 20.7.1835, Durieu 251 (G, K). *Cadiz.* Algeciras distr., foot of Sierra de Palma, 16.5.1924, Ellman & Hubbard (K); id., 25.6,1887, Reverchon 124 (G, K, LD, UPS); id., 21.4.1926, Lindberg 756 (LD).

Gibraltar. Valley N. of Waterfall Valley, 15.5.1913, Wolley-Dod 2006 (K).

Greece. *Thessalia.* Mt Pelion, 1200 m, 28.7.1882, De Heldreich 32 (BM, G, LD, S, UPS); id., 1300 m, 14.6.1935, Beauverd (G); id., E. slope, Oct. 1936 and July—Aug. 1937, Topali (G); id., E. slope between Zagora and Pouri, 1.8.1937, Topali (G); id., between Kissos and C. Col of Pelion, 1100 m, 18.9.1936, Topali (G). *Crete.* W. Crete, June 1846, De Heldreich (BM, K). Enneachoria, 450 m, June 1846, De Heldreich (BM, G, K); id., 350 m, July 1932, S. C. Akeley 1426 (K). Between Vonkolies and Paleochora, 600 m, 24.9.1938, Ripley and Barneby (K).

Ethiopia. Mt Bouahit, 4000 m, 23.3.1840, Schimper II: 1310 (BM, G, K, S). Mt Silke, Schimper 598/1853 (BR).

Belgian Congo. Mts W. of Lake Kivu, 2000 m, Febr.—March 1929, Humbert 7762 (BR). *Virunga Volcanoes.* Ninagongo, 3000 m, 22.12.1911, R. E. Fries 1650 a (UPS). Mikeno, S. slope 2200 m, Kikeri marsh, April—May 1929, Humbert 8115 (BR); id., 2250 m, Aug. 1937, Louis 2193 (BR) and Lebrun 7230 (BR). Mikeno, S. slope, 2400—2600 m, Aug. 1937, Lebrun 7294 (BR); id., 3000—3400 m, April 1929, Humbert 8054 (BR, K). Karisimbi, 2400 m, Febr. 1932, Lebrun 5007 (BM, BR); id., N. slope, Rukumi Plateau, 3650 m, Aug. 1937, Louis 5409 (BR) and Lebrun 7455 (BR). Id., 3800 m, 24.8.1947, Hauman 1211 (BRLU). Muhavura, 3450 m, June 1929, Humbert 8546 (BR). *Ruwenzori,* W. slope, foot of Mt. Emin, 3900 m, July—Aug. 1932, Hauman 453 (BRLU).

Uganda. *Virunga Volcanoes,* Muhavura, W. slope 3400 m, 3.10.1948, Hedberg 2063 (UPS). *Ruwenzori.* Bulanuka, Scott-Elliott 7848 (BM, K). Bujuku Valley near Bigo, 3450 m, 1.4.1948, Hedberg 623 (UPS). Lamia Valley, 3950 m, March 1932, Humphreys 1364 (BM). *Elgon,* W. slope 3350 m, Jan. 1918, Dummer 3521 (K).

Kenya. *Elgon.* E. slope above Japata Estate, 3000 m, 1.3.1948, Hedberg 183 (UPS); id., 3300 and 3400 m, Febr. 1935, Taylor 3485 (BM) and 3589 (BM). E. slope in lower part of alpine belt, 3450 m, 3.3.1948, Hedberg 270 (UPS). *Aberdare.* Kinangop, below Karati Falls, 2150 m, April 1933, Coryndon Museum 2728 (K); id., 2800 m, 25.10.1934, Taylor 1209 (BM).

Tanganyika. *Kilimanjaro.* Above Mamba, 2600 m, Sept. 1893, Volkens 785 (BM, G, K). SE. slope, 2700 m, 18.2.1934, Schlieben 4813 (BM, BR, G, S). SE. slope at upper limit of forest belt, 2800 m, 7.3.1934, Schlieben 4951 (BM, BR, G, S). SE. slope below Peter's Hut, 3350 m, 21.6.1948, Hedberg 1334 (UPS). *Mt Meru,* W. slope, 3150 m, 31.10.1948, Hedberg 2410 (UPS). *Uluguru Mts.* Mgeta River, Hululu Falls, open area between large rocks on wet ledges, 15.3.1953, Drummond and Hemsley

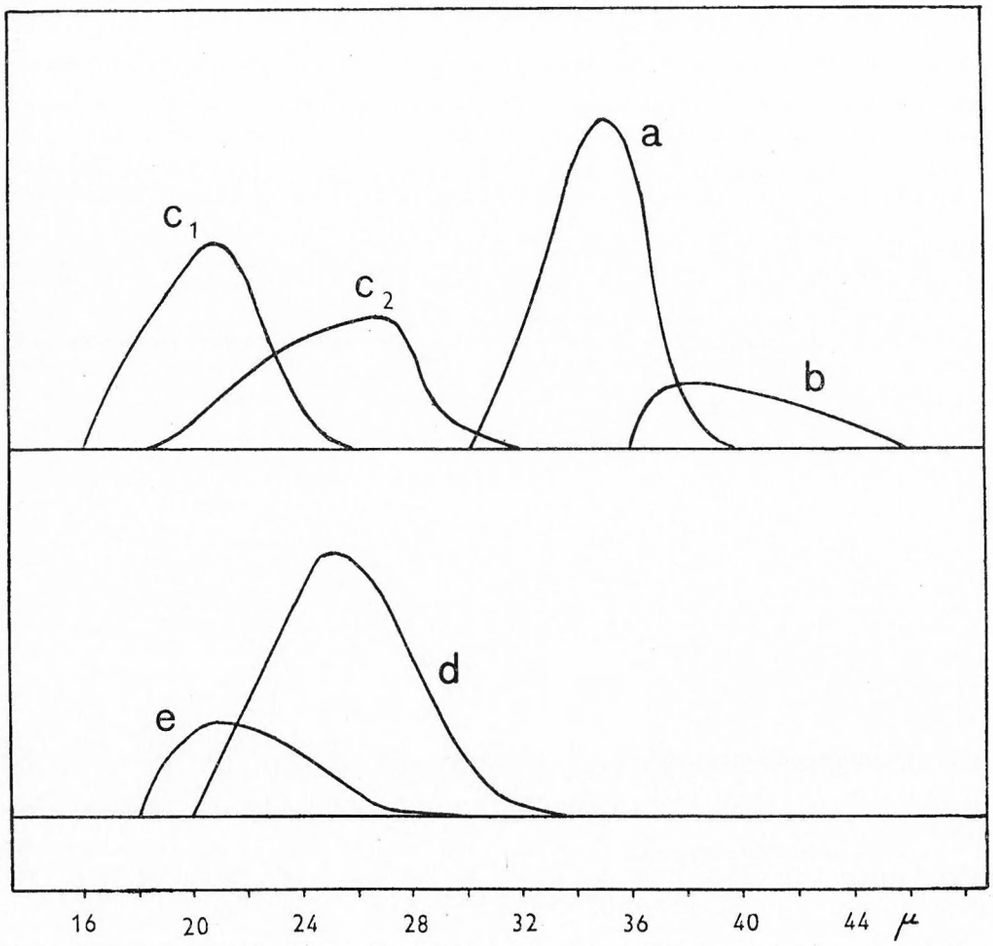

Fig. 2. Frequency curves for size of pollen grains in the species of *Sibthorpia*. The curves are based on measurements (to the nearest μ) of 10 pollen grains in each of 10 collections of *Sibthorpia peregrina* (a), 3 collections of *S. africana* (b), 7 collections of *S. europaea* from Europe (c_1), 6 collections of *S. europaea* from Africa (c_2), 11 collections of *S. repens* (d), and 4 collections of *S. conspicua* (e). The measurements were made on lacto-phenol preparations as described in Hedberg 1952 (p. 257).

1587 (K). Lukwangule Plateau, above Chenzema Mission, 2500 m, bog in valley on plateau, 13.3.1953, Drummond and Hemsley 1572 (K).

British Cameroons. *Cameroons Mt,* 2000 m, June 1891, Jungner 152 (UPS); id., 2150 m, Dec. 1862, Mann 1963 (K); id., Nyanga camp, 2300 m, Dec. 1930, Maitland 1197 (K); id., Mokunda, 2350 m, Febr. 1931, Maitland 1322 (K).

Fernando Po. Clarence Peak, 2400 m, 1862, Mann 1455 (K).

S. Rhodesia. Inyanga, Pungwe River, 1800 m, 21.2.1946, Wild 851 (K); id., 2100 m, 19.10.1946, Wild 1390 (BR, K).

2. *Sibthorpia africana* L. Sp. pl. p. 631 (1753).

Type: "Shaw's afric. 149", ex herb. Goodenough (K, holo.).

Syn. *Disandra africana* Reichard Systema pl. 2 p. 137 (1779); Cambessedes Enum. Bal. p. 18 (1827).

Sibthorpia balearica Knoche Fl. Balear. 2 p. 390 (1922). Type: Not stated by author; Baleares: Mallorca, Barranco de Soller, 16.5.1864, Bourgeau 2781 (K, lecto.).

Distribution: Endemic to the Balearic Islands. — In moist and shady localities, on damp rocks and screes, etc.

Spain: Baleares. *Mallorca.* Alcudia, Chodat (G). Between Andraitz and Estallenchs, 200 m, 1.3.1936, Martindale 187 (K). Calvia, Barranco de Soller, 200 m, 25.5.1934, Gros, Fl. Iberica sel. I: 83 (BM, K, S, UPS). Barranco de Soller, 16.5.1869, Bourgeau 2781 (BM, BR, G, K); id., 550 m, 3.7.1936, Kennedy (K). Near Soller, 28.4.1897, Bicknell (BM, G). Deya, 200 m, 10.2.1921, Goodman 109 (BM). Escorca, 8.6.1948, Ferrer 52 (G). Fornaluitz, 150 m, 25.3.1929, Edmonds (K). Olumalluch, 600 m, 2.6. 1928, Jahandiez (BM). Pollenza, 120 m, 22.10.1934, Martindale 77 (K); id., 5.5.1899, Bicknell (K). Puig Mayor, 1000 m, 9.6.1912, Knoche X B 101 (K); id., Barranco de Bini, 1000 m, 30.6.1936, Kennedy (K). Valdemosa, 700 m, 6.4.1932, Kennedy (K); id., 600 m, 30.5.1933, Kennedy (K); id., 9.5.1922, Sjöstedt 195 (LD). *Minorca.* Barranco d'Algendar, 27.4.1885, Rigo (BM, G, K, UPS).

3. *Sibthorpia peregrina* L. Sp. pl. p. 631 (1753).

Type: Specimen 475.1 in Linnean Herbarium (LINN, lecto.).

Syn. *Disandra prostrata* Murray Syst. Veg. ed. 13 p. 290 (1774); Reichard Syst. Plant. 2 p. 136 (1779); L. fil. Suppl. pl. p. 214 (1781); Curtis Bot. Mag. 7: 218 (1794).

Distribution: Endemic to Madeira. — On moist, shady rocks, grassy roadsides, etc.

Madeira. Round Funchal, May 1837, unknown collector (BM, K). Funchal, Ribeiro Fres, 1894, Menezes (BR). Above Funchal, 7.7.1892, Murray (BM); id., 850 m, 22.5.1913, Sprague and Hutchinson (BM, K). Near the Mount Church, 14.6. 1895, Murray (BM). Between Funchal and Camara, Aug. 1853, Welwitsch 5925 (BM). Caramujo, Aug. 1935, Lundblad (S). Jardin de Serra, 800 m, May—Aug. 1865, Mandon 186 (BM, G, K, S). Nossa Senhora do Monte, 150 m, 25.5.1874, Agnér (UPS). Pico de hacho, rocky summit, 30.4.1875, Love 155 (K). Ribeira Fria, Levada de Jõas Gõmes, 3.8.1936, Dahlgren (UPS). Ribeira de S:a Luzia, 10.12.1887, Favrat 15 (G); id., 1000—1400 m, 10.7.1900, Bornmüller 1038 (BR, G, LD, S). Rio de Bento, 8.8.1929, Tutin 2003 (BM). St' Anna, Aug. 1888, Favrat (G). Valley of S. Vicente, 600 m, 30.4.1924, Riley 56 (BM, K).

4. *Sibthorpia repens* (Mutis ex L.) O. Kuntze Rev. Gen. 3: 2 p. 239 (1898). — *Willichia repens* Mutis ex L. Mantissa pl. p. 558 (1771).

Type: Mexico, Mutis; specimen 475.4 in Linnean Herbarium (LINN, lecto.).

Syn. *Veronica rotundifolia* Ruiz et Pavon Fl. Peruv. 1 p. 6 (1798). Type: "Habitat copiose in Peruviae uliginosis ad Pillao vicum". (Not seen.)

Sibthorpia pichinchensis H. B. et K. Nov. gen. et sp. 2 p. 390 t. 176 (1818). Type: Ecuador, Pichincha, "inter planitiem Verdecucho et Chorro de Cantura", Bonpland & Humboldt. (Not seen.)

S. retusa H. B. et K. Nov. gen. et sp. 2 p. 391 t. 177 (1818). Type: Mexico, "in frigidis juxta Tiangillo", Bonpland & Humboldt. (Not seen.)

S. parvifolia Mart. et Gal. Bull. Acad. Brux. 12: 2 p. 25 (1845). Type: Mexico, Zacuapan, Galeotti 7040. (Not seen.)

S. nectarifera Weddell Chloris Andina 2 p. 111 (1859). Type: Bolivia, La Paz, Sorata, Mandon s. num. [Not seen, but possibly the same as Mandon 470 (BM, G, K, NY, S) or 471 (BM, G, K, NY, S).]

S. americana Sessé et Moc. Fl. Mexic. ed. 2 p. 145 (1895). Type: Mexico, "Heremo P. P. Carmelitarum". (Not seen.)

S. triandra Suesseng. in Fedde Repert. 39 p. 18 (1935). Type: Costa Rica, Poàs, March 1932, W. Kupper 892 (M, holo.).

Distribution: Widespread along the Cordilleras of Central and South America from Mexico to Bolivia, mainly between 2000 and 4000 (1450—4500) m altitude. — Moist and shady places in montane forest, banks of streams, etc., at higher levels in open páramo.

Mexico. *Baja California,* Sierra de la Laguna, Oct. 1899, Brandegee (NY). *Durango,* San Ramón, Apr.—May 1906, Palmer 209 (NY). *San Louis Potosi.* 1877, Schaffner 359 (M); id., 1800—2400 m, 1878, Parry and Palmer 681 (K). *Hidalgo.* Between Pachuca and Minerae del Chico, 2500—2700 m, 10.12.1931, Fröderström and Hultén 18 (S). *Mexico.* Mexico Valley, San Nicolas forest, 27.9.1865, Bourgeau 988 (BR, K, NY, S). Mexico Valley, 3.11.1865, Bourgeau 1247 (G). Temascaltepec distr., Las Cruces, 3350 m, 21.9.1932, Hinton 1717 (NY); id., Cumbre, 2800 m, 28.8.1934, Hinton 6410 (NY); id., Pantoja, 3.6.1933, Hinton 4069 (NY). *Morelios,* Loma S:ta Maria, Nov. 1909, Arsène (G). *Puebla.* Boca del Monte, March 1908, Purpus (BM, NY). Manzanilla, 2200 m, 24.11.1908, Arsène 1636 (K). San Franzisca, 27.11.1909, Nicolas (G). *Vera Cruz.* Orizaba Mt., 3500 m, June—Oct., Galeotti 7046 (BR, G, K). Orizaba, 3000 m, 1839, Linden 1404 (G, K). Vera Cruz to Orizaba, Müller (K). Orizaba, Aserradero de Santa Cruz, July 1853, Müller (NY). *Oaxaca.* Cordillera, 2700 m, Aug. 1840, Galeotti 7165 (G, K); id., Moran Forest, 2100 m, June—Oct. 1840, Galeotti 2729 (BR). Sierra de San Felipe, 2700 m, 5.6.1894, Pringle 4681 (BM, BR, G, K, M, NY, S); id., Aug. 1849, Galeotti 7165 (BR). Sierra de Clavellinas, 2700 m, 18.10.1894, Pringle 4992 (BM, BR, G, K, M, NY, S). *Chiapas.* Tacana Volcano, N. slope 2100 m, 2.4.1939, Matuda 2959 (K, NY). Mt Tacana, Aug. 1938, Matuda 2372 (NY). *Unidentified localities*: Mineral del Oro, 30.6.1829, Schiedel and Deppe (M). Zimapan, Coulter 1313 (K). La Cima, 3000 m, Aug. 1904, O. Kuntze (NY). Gajalpa, 1800 m, Aug. 1904, O. Kuntze (NY). Bosque del Desierto de los Leones D. F., Jan. 1927, Lyonnet 168 (NY).

Costa Rica. Mt Poàs, 2600 m, 27.3.1932, Kupper 892 (M). N. slope of Central Cordillera, Vara Blanca de Sarapiqui, 1500—1750 m, July—Sept. 1937, Skutch 3121 (K, NY, S). Around Raucho Floreo, 2000 m, 22.2.1890, Tonduz 2125 (S). Poàs, Achiote Forest, 2250 m, Nov. 1896, Tonduz 10830 (BR, G). La Palma, 1450 m, 25.9.1898, Tonduz 12637 (K). Trazu, 2000 m, 10.7.1891, Tonduz 4290 (BR, G). "Massif de l'Iscasée, vallée de los Archangeles", 1900 m, 27.5.1888, Pittier 263 (BR).

Colombia. *Norte de Santander,* Paramo del Hatico en route from Toledo to Pamplona, 2900 m, March 1927, Killip and Smith 20667 (BM, NY, S). *Santander.* Between Piedecuesta and Las Vegas, 2000—2500 m, Dec. 1926, Killip and Smith

15560 (NY). W. slope of Páramo Rico, 3300—3600 m, Jan. 1927, Killip and Smith 17745 (NY). *Tolima.* "Rosalita" near Páramo de Ruiz, 2800—3100 m, Dec. 1917, Pennell 2987 (NY). Páramo de Ruiz, 3700—3900 m, Dec. 1917, Pennell 3021 (NY). Below Páramo de Ruiz, 3200—3400 m, Dec. 1917, Pennell 3097 (NY). *Ibague,* 1300 m, André 2020 (NY). *Cundinamarca.* Sibaté, 3000—3100 m, Pennell 2498 (NY). Tequendama, 2400—2500 m, 28.10.1917, Pennell 2654 (NY). El Peñon, SW. of Sibaté, 2800—3000 m, 29.10.1917, Pennell 2669 (NY). Rio San Christobal, near Bogota, 2700—2800 m, 14.11.1917, Pennell 2681 (NY). Fusagusuga, 1800—2300 m, Nov. 1917, Pennell 2691 (NY). Boqueron de Bogota, André K. 741 (K, NY). *Cauca.* Cordillera Central, Puracé, 3450 m, Febr. 1938, von Sneidern 1904 (NY, S); id., 3900 m, Febr. 1938, von Sneidern 1905 (S). Cordillera Central, Paletará, 2950—3100 m, June 1922, Pennell 6973 (NY). Mt Puracé, "Canaan", 3400—3600 m, June 1922, Pennell and Killip 6528 (NY).

Venezuela. Merida, near Tovar, 1854—5, Fendler 914 (BR, G, K).

Ecuador. *Quito distr.* Ravines near the base of Pichincha, 1836, Jamesson 60 (NY); id., 3000—4200 m, Jamesson (NY); id., Cruz Loma, 3800 m, 9.1.1920, Heilborn 164 b (S). Pichincha, 4500 m, Hall (K); id., Atacatzo, 12.5.1920, Holmgren (S). At the foot of Pichincha, 1843, Pl. Hartweg. 1280 (LD). Caves in the Andes, 3000—4200 m, 21.1.1856, Jameson 67 (BM, G, K). *Chimborazo,* André 1084 (K, NY). *Azuay.* Along the Rio Mataderu, W. of Cuenca, 3000—3200 m, 3.3.1945, Camp E-2010 (NY). Páramo de Iusa, 3200—3400 m, Lehmann 5150 (K). Mt Guayaraporta, June 1858, Spruce 5434 (K). Ecuadorian Andes, Spruce 5437 (BM, G, LD, NY, S), and 5849 (BM, K, NY).

Peru. *Canta,* Huamantanga, April 1831, Matthews 503 (K). *Huaraz,* Cordillera blanca above Curaz, 3200 m, Weberbauer 3238 (G).

Bolivia. *La Paz.* Near Sorata, shore of the river Challasuyo, 2700—3000 m, 1818, Mandon 470 (BM, G, K, NY, S). Id., Lacatia, 3300—4000 m, Febr.—Apr. 1818, Mandon 471 (BM, G, K, NY, S). Sorata, 4000 m, Febr. 1886, Rusby (NY). Cordillera Real, 3600 m, Febr. 1926, Tate 271 (NY). *N. Yungas, Unduavi,* 2500 m, Oct. 1885, Rusby (NY); id., 3300 m, Dec. 1865, Pearce (BM, K); id., Nov. 1910, Buchtien 95 (G, K, NY) and 2977 (NY); id., Oct. 1931, Buchtien 9041 (NY).

5. *Sibthorpia conspicua* Diels Bot. Jahrb. 37 p. 428 (1906).

Type: S. Bolivia, Toldos at Bermejo, Nov. 1903, Fiebrig 2249 (BM, G, M, K, iso.).

Distribution: Confined to the Cordilleras of S. Bolivia and N. Argentine. — Moist and shady localities in montane forest.

Bolivia. S. Bolivia, Toldos at Bermejo, 1900 m, 26.11.1903, Fiebrig 2249 (BM, G, M, K).

Argentine. *Catamarca.* Quebrada de la Tala, Nov. 1872, Hieronymus 431 (G, NY); id., comm. Grisebach Dec. 1878 (K). Rio Pisavil, 1600 m, 30.1.1949, Brücher (LD). *Tucuman.* Valle de las Sosas, 18.10.1948, R. E. Fries (S). Valle de Tafi, 1400 m, 21.11.1949, Brücher (LD, S).

VII. Phytogeographical Discussion

From a taxonomic point of view the genus *Sibthorpia* forms a very natural and well-defined group. Its nearest relative is apparently *Ellisiophyllum pinnatum* (Wall.) Makino from SE. Asia, distinguished, i.a., by its entirely different leaf shape. Consequently *Sibthorpia* may be assumed to be a monophyletic group, and hence treated as a phytogeographical unit (cp. Good 1953 p. 95). — Study of a comprehensive material of this genus reveals that the intraspecific variation is different in different parts of the world. The strain of *Sibthorpia europaea* occurring in W. Europe is quite uniform, but the African material of the same species is rather variable (cp. p. 167 above and Fig. 2). The uniformity of the European strain appears quite natural in connection with the alleged general depauperization of biotypes in the European flora during the Quaternary glaciations. The African strain on the other hand would probably have found more favourable conditions on the high mountains during the corresponding pluvial epochs than at present (cp. Nilsson 1932, 1940, Fries and Fries 1948 p. 75 f.), and may well have occupied a larger area at that time. The South American *Sibthorpia* material displays an amazing range of variation, so wide that one can easily understand that several ± extreme forms of what is called here *Sibthorpia repens* were treated in the past as distinct species (cp. p. 167 above). *Sibthorpia africana* and *S. peregrina* are both island endemics with small distribution areas and comparatively small variation. *S. conspicua* also seems to have a comparatively small variation range; it is confined to the slopes of the Cordilleras in Argentine and S. Bolivia. It is apparently closely related to *S. repens*; the differences between these two are much less distinct than those between the three Old World species (cp. e.g. Figs. 1—2). It has already been mentioned above (p. 168) that *Sibthorpia europaea* and *S. repens* show great affinities. The most probable course of evolution in this group — to judge from morphology — appears to be that *S. europaea* and *S. repens* have been differentiated from a common ancestor, the latter in its turn giving rise to *S. conspicua*. *Sibthorpia africana* and *S. peregrina* were probably earlier differentiated from the same ancestral stock; at present they represent endemics of ± relic nature.

The total distribution of *Sibthorpia* (Fig. 3) is very interesting, showing a Middle-Atlantic disjunction. This distribution picture cannot be due to the activities of Man, because there are different species on different sides of the Atlantic. Furthermore all species seem to demand

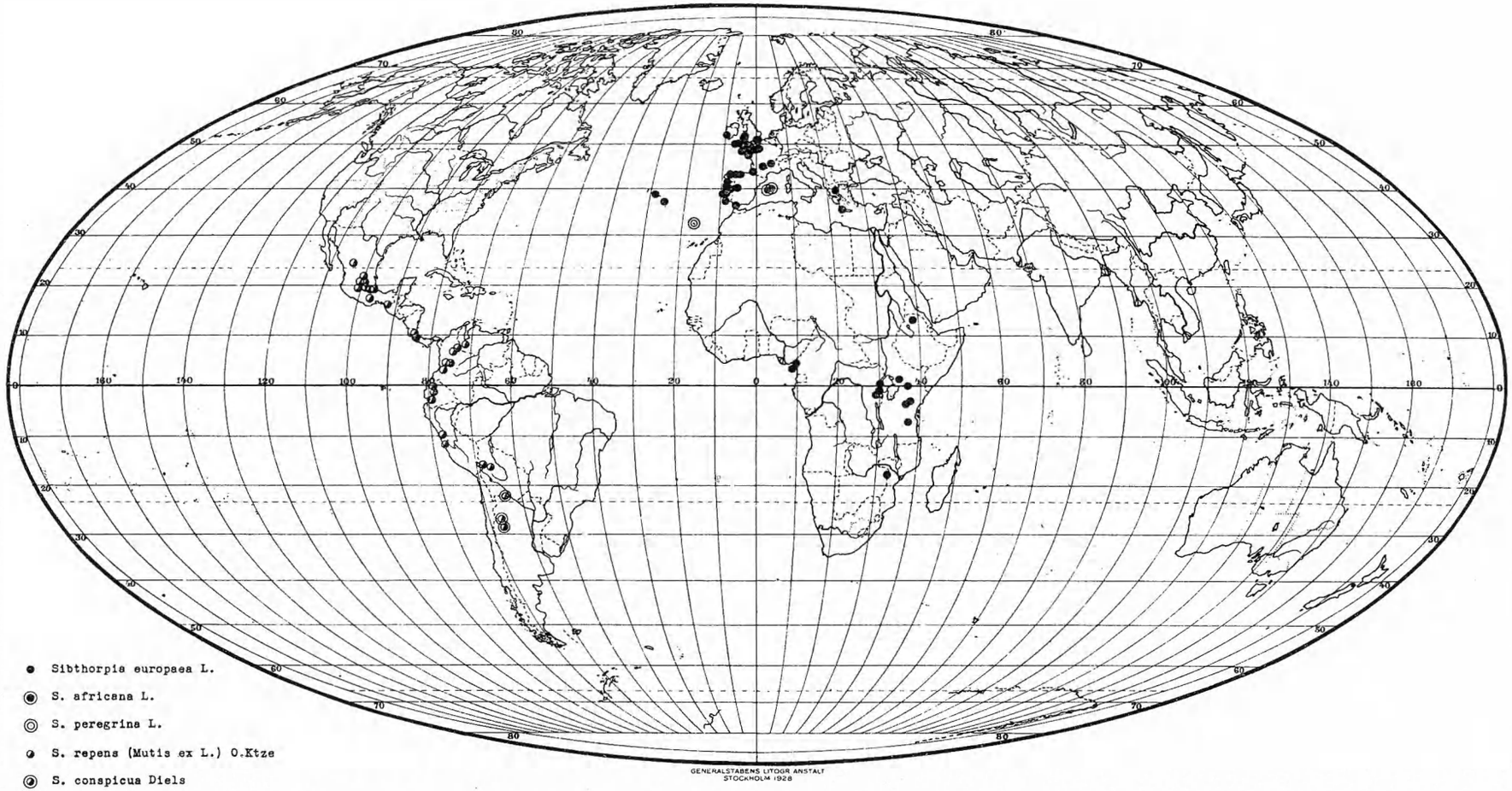

Fig. 3. World distribution of the genus *Sibthorpia* L., according to herbarium material seen by the author (from the following herbaria: BM, BR, BRLU, G, K, LD, M, NY, S, UPS). Each species is represented by a special symbol, as explained in the lower left corner. — A very primitive and partly erroneous map of the genus has been published earlier by Knoche (1923 p. 206).

moist and cool climate, since they occur in Europe only in oceanic areas and in America and Africa in mountains between about 2000 and 4000 m altitude. The only possibilities to explain this area seem to be either long distance dispersal by natural agents or the absence in the past of some of the present geographical barriers. Most modern phytogeographers seem to consider that long distance dispersal of plants is generally insufficient to account for major discontinuities of this kind (cp. e.g. Skottsberg 1928 p. 917, 1931 p. 65, etc.; van Steenis 1935, p. 412—417; Du Rietz 1940 p. 326 ff.; Cain 1944 p. 242; Wulff 1950 p. 134). And the present distribution pattern of *Sibthorpia* could not easily be explained if long distance dispersal had played a major rôle in its creation. Circumstantial evidence in favour of former ± continuous land connection between Europe—Africa and Central America has been provided by a considerable number of biologists. The geographical explanation has been sought by many authors in the theory of continental drift (cp. e.g. Good 1953 p. 350 ff.). Others believed to have found the explanation in the theory of "Atlantis" — a lost continent formerly occupying much of the central part of the Atlantic (see reviews in Högbom 1938 and Lundblad 1947). The geological evidence for and against each of these alternatives is far from conclusive (cp. e.g. Kuenen 1950 p. 125 f., 131, etc.; Malaise 1951), and apparently the time is not ripe to decide which of them comes nearest to the truth. Biologists would probably do best at present to present their biological facts without prejudice and without indulging in too much speculation. — As for the genus *Sibthorpia* we may only assume that it was developed in an area with oceanic climate bordering the middle part of the Atlantic basin, and that its dispersal across the Atlantic — and likewise across North Africa — was probably favoured in the past by geographical and climatic conditions different from the present. The evidence at hand might possibly indicate that its center of origin was located somewhere near the SW. corner of Europe, and that its amphiatlantic distribution dates from late Tertiary times.

Summary

In order to disentangle the nomenclature and taxonomy of some *Sibthorpia* material from Tropical Africa the author found it advisable to make a revision of the whole genus. Examination of the taxonomic features used in the past to separate the species in this group revealed that several of them display a large and ± continuous variation, making them unsuitable for taxonomic distinction (e.g. number of stamens, texture of seed surface, size and shape of leaves, etc.). Thus several of the 14 species described had to be relegated to

synonymy. Only 5 species are retained: *Sibthorpia europaea* L., *S. peregrina* L., *S. africana* L., *S. repens* (Mutis ex L.) O. Ktze, and *S. conspicua* Diels. The main differences between these are given in a key (p. 168), and their distribution areas are illustrated on the map Fig. 3.

The genus is considered to be a monophyletic group and may thus be treated as a phytogeographical unit. The American material displays a more continuous variation in most respects than that from the Old World; the two American species are less well demarcated from each other than are the three species from Europe+Africa. The genus is assumed to have originated in an area with oceanic climate bordering the Middle Atlantic — perhaps not far from the SW corner of Europe. Its dispersal across the Atlantic and across North Africa was probably favoured in the past (perhaps in the late Tertiary) by geographical and climatic conditions different from the present.

Acknowledgements

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References

Beauverd, G. 1937. Plantae Novae Graecae. — Candollea 7: 255—278. Genève.

Bentham, G. 1846. Scrophulariaceae. — De Candolle, Prodromus regni vegetabilis 10: 186—586. Parisiis.

Bonpland, A., von Humboldt, A., et Kunth, C. S. 1817. Nova genera et species plantarum, T. 2. — Lutetiae Parisiorum.

Brand, A. 1913. Hydrophyllaceae. — A. Engler, Das Pflanzenreich, IV. 251. Leipzig.

Cain, S. A. 1944. Foundations of Plant Geography. — New York & London.

Cambessedes, J. 1827. Enumeratio plantarum quas in insulis balearibus collegit J. Cambessedes. — Mém. Mus. Hist. nat. 14: 173—335. Paris.

Curtis, W. 1794. Disandra Prostata. Trailing Disandra. — The Botanical Magazine 7: 218. London.

Diels, L. 1906. Scrophulariaceae andinae (Calceolariis exceptis), in I. Urban, Plantae novae andinae imprimis Weberbauerianae. I. — Bot. Jahrb. 37: 427—433. Leipzig.

Du Rietz, G. E. 1940. Problems of Bipolar Plant Distribution. — Acta Phytogeogr. Suecica 13: 215—282. Uppsala.

Engler, A. 1892. Über die Hochgebirgsflora des tropischen Afrika. — Abh. königl. preuss. Akad. Wiss. Berlin (1891).

Fries, R. E. 1916. Wissenschaftliche Ergebnisse der schwedischen Rhodesia-Kongo-Expedition 1911—1912 unter Leitung von Eric Graf von Rosen. Bd I. Botanische Untersuchungen. H. 2. Monocotyledones und Sympetalae. Stockholm.

Fries, R. E. and Fries, Th. C. E. (†) 1948. Phytogeographical Researches on Mt. Kenya and Mt. Aberdare, British East Africa. — K. Sv. Vet.-Akad. Handl. ser. 3, Bd 25, 5. Stockholm.

Good, R. 1953. The Geography of the Flowering Plants, ed. 2. — London, New York and Toronto.

Harvey, W. H. 1838. The Genera of South African Plants. — Cape Town.

Hayek, A. 1929. Prodromus Florae peninsulae Balcaniae, II: 2. — Fedde, Rep. spec. nov. r. veg., Beih. 30, 2. Dahlem bei Berlin.

Hedberg, O. 1952. Cytological studies in East African mountain grasses. — Hereditas 38: 256—266. Lund.

Hemsley, W. B. and Skan, S. A. 1906. Scrophulariaceae. — Fl. Trop. Afr. IV, 2: 261—462. London.

Hiern, W. P. 1904. Scrophulariaceae. — Flora capensis IV, 2: 121—420. London.

Högbom, A. G. 1938. Die Atlantislitteratur unserer Zeit. Beachtungen eines Geologen. — Bull. Geol. Inst. Uppsala 28: 17—78.

Hooker, J. D. 1864. On the Plants of the Temperate Regions of the Cameroons Mountains and Islands in the Bight of Benin; collected by Mr. Gustav Mann, Government Botanist. — Journ. Linn. Soc. (Bot.) 7: 171—240. London.

Hutchinson, J. and Dalziel, J. M. 1931. Flora of West Tropical Africa, 2. — London.

Knoche, H. 1922. Flora Balearica, 2. — Montpellier.

— 1923. Flora Balearica, 3. — Montpellier.

Kuenen, Ph. K. 1950. Marine Geology. — New York & London.

Kuntze, O. 1898. Revisio Generum Plantarum 3, 2. — Würzburg.

Lanjouw, J. and Stafleu, F. A. 1954. Index Herbariorum, I. The herbaria of the world. — Regnum Vegetabile 2, ed. 2. Utrecht.

Linnaeus, C. 1753. Species plantarum. — Holmiae.

Linné, C. a. 1771. Mantissa plantarum altera. — Holmiae.

Linné, C. a. (fil.). 1781. Supplementum plantarum. — Brunsvigae.

Lundblad, O. 1947. Makaronesien und Atlantis. — Zool. Bidrag fr. Uppsala 25: 201—323. Uppsala.

Makino, T. 1906. Observations on the flora of Japan. — The Botanical Magazine 20 (1906): 91—94. Tokyo.

Malaise, R. 1951. Atlantis. En geologisk verklighet. — Kalmar.

Martens, M. et Galeotti, H. 1845. Enumeratio synoptica plantarum phanerogamicarum ab Henrico Galeotti in regionibus Mexicanis collectarum, Scrophularineae. — Bull. Acad. Roy. de Bruxelles 12, 7: 1—21. Bruxelles.

Maximowicz, C. J. 1871. Diagnoses breves plantarum novarum Japoniae et Mandshuriae. — Bull. Acad. Imper. Sci. St. Pétersbourg 16: 212—226. St. Pétersbourg.

Mildbraed, J. et al. 1914. Wissenschaftliche Ergebnisse der deutschen Zentral-Afrika-Expedition 1907—1908. Bd 2. Botanik. — Leipzig.

NILSSON, E. 1932. Quaternary glaciations and pluvial lakes in British East Africa. — — Geogr. Ann. 13 (1931): 241—348. Stockholm.

— 1940. Ancient changes of climate in British East Africa and Abyssinia. — Geogr. Ann. 22: 1—79. Stockholm.

RICHARD, A. 1851. Tentamen Florae Abyssinicae, 2. — Parisiis.

ROBYNS, W. 1947. Flore des Spermatophytes du Parc National Albert. 2. Sympétales. — Bruxelles.

RUIZ, H. et PAVON, J. 1798. Flora peruviana, et chilensis, 1. Matritii.

SHAW, TH. 1738. Travels, or Observations relating to several parts of Barbary and the Levant. — Oxford.

SKOTTSBERG, C. 1928. Remarks on the Relative Independency of Pacific Floras. — Proceed. Third Pan-Pacific Science Congress, Tokyo 1926. Tokyo.

— 1931. Remarks on the Flora of the high Hawaiian volcanoes. — Meddel. Göteborgs Bot. Trädg. 6 (1930): 47—65. Göteborg.

STEENIS, C. G. G. J. VAN. 1935. On the Origin of the Malaysian Mountain Flora. 2. Altitudinal Zones, General Considerations and Renewed Statement of the Problem. — Bull. Jard. Bot. Buitenzorg sér. 3, 13: 289—417. Buitenzorg.

SUESSENGUTH, K. 1935. Neue und kritische Pflanzen aus Südamerika, insbesondere Amarantaceen, sowie eine neue Gattung der Podostemonaceae. — FEDDE, Rep. spec. nov. r. veg. 39: 1—20. Dahlem bei Berlin.

SVENSSON, H. G. 1938. Zur Entwicklungsgeschichte der Blüten und Samen von Limosella aquatica L. — Svensk Bot. Tidskr. 22: 465—476. Uppsala.

THUNBERG, C. P. 1800. Prodromus plantarum capensium. Pars posterior. — Upsaliae.

— 1823. Flora capensis. Ed. I. A. Schultes. — Stuttgardtiae.

WEDDELL, H. A. 1858—1862. Chloris Andina. (Essai d'une flore de la région alpine des Cordillères de l'Amerique du sud.) T. 2. — Paris.

WETTSTEIN, R. v. 1891. Scrophulariaceae. — ENGLER und PRANTL, Die natürlichen Pflanzenfam. IV, 3 b: 39—107. Leipzig.

WULFF, E. V. 1950. Historical Plant Geography. Authorized translation by ELIZABETH BRISSENDEN. — A new series of plant science books, 10. Waltham, Mass., U.S.A.

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The Radiation Induced Growth Inhibition in Seedlings

By LARS EHRENBERG

Institute of Organic Chemistry and Biochemistry, University of Stockholm

Contents

I. Introduction

In several years' experimentation with barley seeds treated with ionizing radiations, considerable variation in induced changes were observed, both between individual seeds and between experimental series (Ehrenberg and Nybom 1954; *cf.* Mac Key 1951; Caldetcott *et al.*

1952). This variation was consistently greater after treatment with sparsely ionizing radiations, *i.e.,* radiations with a low linear energy transfer (γ-rays, X-rays), than after exposure to densely ionizing radiations (neutrons, α-rays). Attempts to elucidate the factors responsible for this variation demonstrated an influence of the moisture of the seeds at the moment of irradiation (Lefort and Ehrenberg 1955, Ehrenberg and Nybom 1954, *cf.* Caldecott 1954), the radiosensitivity of the seeds decreasing with increasing water content in the range of 7—20 per cent water. The growth retardation was further found, in accordance with Gelin's observations for X-ray induced chromosome disturbances (1953), to be greater at a lower temperature during germination and growth (*cf.* Ehrenberg 1954). The temperature effect on growth inhibition was already observed by Ancel (1925).

The aims of the present investigation were to elucidate (a) in what degree the factors mentioned, seed moisture and germination temperature, and others were responsible for the experimental variation, and (b) the mode of action of these factors insofar as to provide sufficient data on the mechanism of action of the radiations or points of attack for further treatment of the problem on a chemico-biochemical level.

In addition to detailed investigation of the influence of *seed moisture* and *temperature during germination and growth,* the effect of *storage* at different temperatures was studied. Where data were not available from earlier investigations, the influence of the *oxygen tension* during irradiation and germination, and of the *irradiation temperature,* was determined.

Seeds in three basic physiological states were exposed to irradiation under varying conditions: *viz., resting* seeds, *i.e.,* "dry" after-ripened seeds capable of germination; *dormant* seeds, *i.e.,* seeds in that post-harvest condition, unripeness, which for a time prevents them from germination when they are placed under otherwise suitable conditions;[1] and soaked (in the following also called *pre-germinated*) seeds, *i.e.* seeds which, under treatment with water, have started their germination process.

The relative effectiveness of the various factors was determined at different ion densities of the radiations. The irradiation was done with γ-rays, X-rays, fast neutrons and, in one experiment, fast protons.

[1] The terminology as to the states of seeds is not yet settled. The present distinction between "dormancy" and "rest" has been found most appropriate, although the words have sometimes been used in the reverse sense (*cf.* Curtis and Clark 1950). The relativity of the dormancy condition should be remembered (p. 186).

II. Material and Methods

1. *Material.* — Seeds of a pure strain of the commercial variety, Bonus, of barley (*Hordeum distichum*) were used, except in experiments involving the dormancy factor, where strains, chiefly Herta and Rika, with a slower after-ripening, were studied.

2. *Gas Treatment before Irradiation.* — Seeds were equilibrated[1] for varying times (in most experiments six days) by streams of air of relative humidities between 0 and 100 per cent, and at 20° C.; in the case of dormant seeds equilibration occurred at 5° C. Compressed air or room air, the latter pumped with the aid of a vibration pump of the type used for aeration of aquaria was directed through systems of wash-bottles containing KOH solutions of the required vapour pressure (Kobayashi 1932) before passing it through the vessels containing the seeds. Zero per cent humidity was obtained by passing the air through a wash-bottle with sulfuric acid and then through a U-tube with silica gel; 100 per cent humidity by passing the air through two wash-bottles with distilled water.

Immediately before irradiation, the seeds were transferred to stoppered thin-walled test-tubes or, in a few cases, stoppered and sealed plastic or paper containers, used as irradiation vessels.

Using a similar procedure, oxygen and nitrogen (oxygen-free through treatment with alkaline hydroquinone) of different relative humidities were produced. In the experiments involving a variation of the oxygen tension during irradiation, the gas treatment was done (for six days at 20° C.) in the irradiation vessels, the water content being determined in a part of each sample after the irradiation. It was found to be immaterial, as regards the influence of the oxygen tension, whether the containers were closed before, or whether the gas treatment continued during, the irradiation.

3. *Treatment of the Dormant Material.* — Shortly after harvest barley and other seeds are, as a rule, incapable of germination. After a time, which, depending on genotype, meteorological factors during maturation, and conditions of storage after harvest, may vary from 1—2 weeks to several months, the barley seeds gradually become germinable, first at low germination temperatures, then progressively and with great individual variations at increasing temperatures.

Due to the damp weather in large parts of Sweden during the latter parts of the summers of 1952 and 1954, it was possible to obtain, through the courtesy of *Statens Centrala Frökontrollanstalt,* Stockholm, and of Dr. O. Gelin, Weibullsholm, Landskrona, samples, especially of the barley strains Herta and Rika, which exhibited a pronounced dormancy but which were otherwise viable.

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[1] The term "equilibration" has been used in spite of the fact that, after about 6 days treatment, equilibrium is only attained at medium humidities. At 100 % the water uptake continues until germination starts or the seeds become infected by molds, and at 0 % the grains continue to lose water slowly. In the short-term treatments the purpose was to induce a certain water content, which was determined at the moment of irradiation. In prolonged storage at different humidities, 90 % or 5 % was preferred.

The influence of the dormancy factor had to be investigated independently of the seed moisture. In order to maintain the state of dormancy, the dormant seeds were equilibrated to air of different humidities at 5° C., but other samples, the ripeness of which had been induced by treatment for 8 days with streaming dry air of 40° C. (Atterberg 1899, *cf.* Harrington 1923), were equilibrated at room temperature. After correction of the moisture all samples, *i.e.,* dormant and resting (=ripe) seeds of different water contents, were divided into smaller portions used for:

(a) irradiation with different doses;
(b) determination of water content; and
(c) determination of germinability.

The last-named test was kindly done by Dr. A. Gadd, of *Statens Centrala Frökontrollanstalt,* with the standard methods of that institute, involving germination in moist sand. In order to accentuate the dormancy condition, this test was made at a fairly high temperature, 20° C. Counts were made after 3 and 5 days, the latter values being used in the text.

After irradiation, all seed portions were divided into two parts, one being sown immediately, the other after treatment (for the sake of conformity, dormant as well as resting samples) for a further 8 days with streaming air of 40° C. In one case, sowing was done at a temperature sufficiently low to permit germination also of seeds ingerminable at 20° C.

4. *Pre-germination Treatment.* — Two soaking methods were applied:

A: A limited number of seeds (< 200) were soaked on double filter papers in 200×30 mm Petri dishes containing 30 ml of tap water; *i.e.,* one side of the seeds was in contact with a thin layer of water.

B: Where a large number of samples had to be treated identically the seeds were laid on glass plates enclosed in filter paper, which along one edge was joined to wicks by which water was absorbed. The glass plates were placed in big enamelled cauldrons with a little water at the bottom.

Soaking was done for varying periods and at different temperatures. In investigations of changes in sensitivity conditioned by the start of germination processes the seeds were, in some series, re-desiccated to different water contents (point 2 above).

5. *The water contents of seeds* were determined by drying to constant weight, samples of 50 seeds at 105° C. Although very slow, this method was preferred to a determination on ground material, since the water content is changed in the milling process, especially at high moisture contents.

6. *Irradiations.* — The following radiation types were applied:

X-rays. In most experiments the therapy units of the Royal Veterinary College, Stockholm, and of the Institutes of Genetics of Stockholm and Lund Universities were used. They were run at 175 (± 5) kV and without filtration, the intensities at the focal distance used, 21 cm, being 300, 500, and 1,000 r min^{-1}, respectively. Within this range no influence of the intensity on the results could be observed. Since X-rays were used as a common link in all the experimental series, other units had to be employed (at the hospitals of Uppsala and Kristianstad) in order to obtain a fully parallel X-ray series, when

the effects of other types of radiation were studied. The latter machines were operated under the same conditions as those ordinarily used.

The dose rates were determined, inside the irradiation vessels, with Victoreen type ionization chambers, constructed by Dr. Moxnes, Oslo. From a chemical analysis of the seed embryos (Ehrenberg and Nybom 1952) it follows that, within 3 per cent, 1 r corresponds to 1 rep, *i.e.,* an absorption of 93 ergs/g tissue (*cf.* National Bureau of Standards, Handbook No. 42, 1949).

Fast neutrons, produced by the reactions with copper or beryllium targets of 25 MeV deuterons, accelerated in the 225 cm cyclotron at the Nobel Institute for Physics, Stockholm. Dose rates of the order of 10—100 rep/min could be obtained, the doses being determined by the oxidation of ferrous sulphate in sulphuric acid solution. The irradiations had to be delivered at different angles (0—15°) from the forward beam direction, *i.e.,* with a varying neutron energy, regarded from the variation of the ratios between the actinometrically determined doses and the yields of radio-silicon and radio-sodium induced in (np) and (nα) reactions with phosphorus and aluminium, respectively. The seedling reaction was found to be proportional to the Fe^{3+} yield; and in spite of a systematic error of some ten per cent, still adhering to the method (*cf.* Ehrenberg and Saeland 1954 a), the neutron doses are, relatively speaking, correct. With the procedure used (cadmium and lead shielding), the contaminations of thermal neutrons and γ-rays were found to be negligible. A full account of the neutron dosimetry will be published shortly (1955 a).

In some series the Norwegian heavy water reactor (JEEP) was used as a fast neutron source, the irradiation being done at the center of the pile. The total dose of densely ionizing radiations, *i.e.,* particle radiations from thermal neutron reactions with nitrogen and boron, and nuclei from elastic collisions of resonance and fast neutrons, was calculated according to Ehrenberg and Saeland (1954 b). The pile was run at 10 kW, at which effect an intensity of about 300 rep/min was obtained. The contaminating γ-flux was estimated from the oxidation yield of $FeSO_4$ in 0.8 N H_2SO_4 (*l.c.*).

Gamma-rays. The 20 Curie ^{60}Co source at the Balsgård Fruit Breeding Institute, Fjälkestad, was used. The arrangement, which is an improvement of the preliminary 2 Curie source (Granhall *et al.* 1953) has been described briefly by Ehrenberg *et al.* (1954). The dose rate at the distance used, 11 cm from the source, was determined, with a Victoreen type ionization chamber, at 33 rep/min inside the test tubes used for irradiation, the accuracy of this determination in relation to the X-ray doses being about 5 per cent.

Fast protons, accelerated to about 160 MeV in the Uppsala synchrocyclotron, were used in one experiment. Dose rates amounting to 20—100 rep/min were obtained. A full account of the dosimetry and experimental procedure will be published shortly.

7. *Cultivation Conditions.* — In several experiments the seedling growth simply occurred as a continuation of the soaking under conditions described as *A* and *B* (point 4 above). In these cases the growth occurred in darkness and at temperatures given in connection with the experiments. In some series (method *C*) the seeds were sown in soil in wooden boxes in the greenhouses of the Forest Research Institute, Stockholm, and the Institute of Genetics, Lund. The temperature can, according to termograph curves, be expressed as

Table 1. Variability of seedling heights.

Specification of sample	Coefficient of variation, per cent	Standard error at sample size	
		50 seeds (per cent)	25 seeds (per cent)
Unirradiated (controls)	15 (±5)	2.1	3.0
25—75 % rel. seedling height after X-irradiation	35 (±10)	5.0	7.0
25—75 % rel. seedling height after neutron irradiation	20 (±5)	2.8	4.0

$(20 \pm 3)^\circ$ C. At the latter institute a couple of thermostat chambers could be utilized to obtain a better temperature control ($\pm 1^\circ$; method *D*). In methods *C* and *D* the seedlings were illuminated during the day (about 14 hours). The variations, *A*—*D*, of the cultivation conditions invariably gave, at least in principle, the same results.

8. *Measurements.* — With few exceptions the radiations, within the dose ranges applied, do not affect the germination of the seeds. The growth of the shoot is slower after irradiation.

The seedlings were mostly measured at control heights in the region of 75—175 mm, *i.e.*, 1—2 weeks after sowing (germination and growth at 20° C.). Within this region the values for seedlings with radiation-induced retardation of growth are, with sufficient accuracy, a constant fraction of the control value. In several cases the seedling heights have therefore been expressed as per cent of the corresponding controls.

Since irradiation and cultivation had to be done at different places, it was impossible to secure full parallelism between all experiments. No new condition was introduced, however, without comparison with a series whose mode of reaction was already known. The picture of the factors influencing the radiation induced growth inhibition is, therefore, qualitatively correct. As to quantitative relations, these have at present to be restricted to the individual experiments.

Statistical treatment of the data has not been thought necessary, since in all cases an introduced experimental condition caused either a clear change or no change at all. In the experiments samples of 50 or 25 seeds were used. Table 1 shows the variation within the samples, expressed as the coefficient of variation, $\frac{100}{\bar{x}} \cdot \sqrt{\frac{(x-\bar{x})^2}{n-1}}$, where x and $\bar{x}$ are the individual seedling heights and their mean value, respectively. The standard errors of the mean values of 50 and 25 seed samples are also given, in per cent of the mean values. The data in the Table are averages from several experiments.

III. Results: Water Content and Radiosensitivity of Seeds

1. *Variation of Ion Density.* — In the region of low seed moisture contents, ~7—~20 % H_2O, an increase of the water content provokes

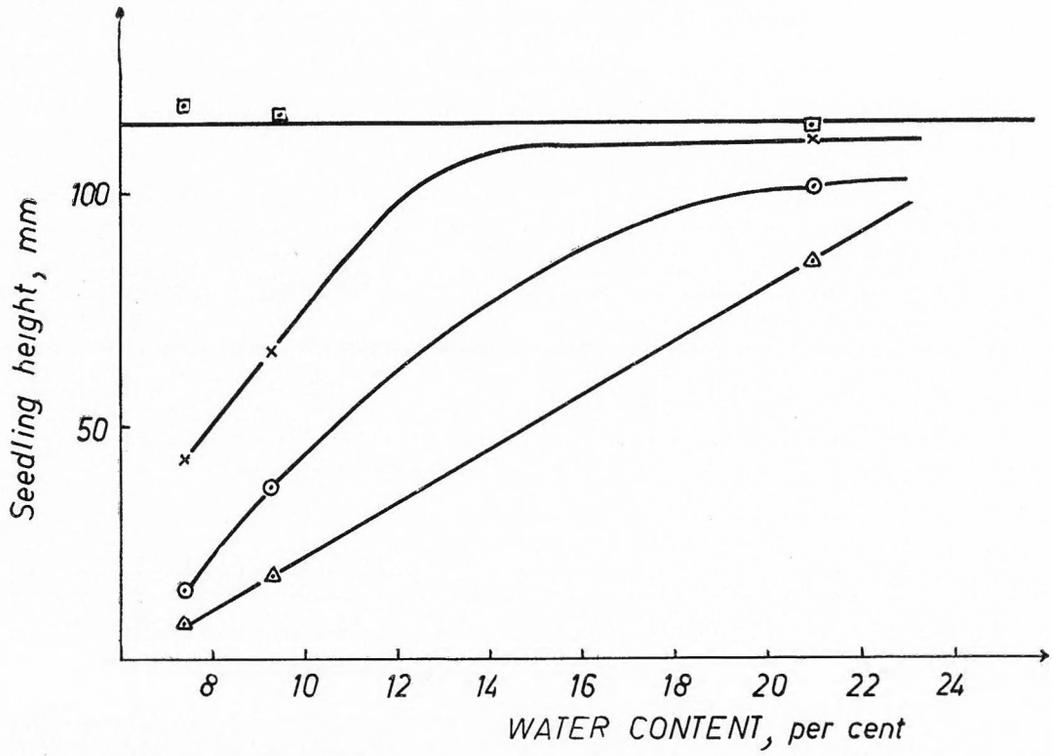

Fig. 1. Seedling heights after X-irradiation of seeds of different water content. ⊡: controls; ×: 10 kr; ⊙: 15 kr; △: 20 kr. Sample size: 50 seeds.

a decrease of the sensitivity to X-rays (Lefort and Ehrenberg 1955, *cf.* Ehrenberg and Nybom 1954). In experiments with resting seeds this reduction of the radiation effectiveness was investigated at different ion densities. After irradiation the seeds were sown in the greenhouse (cultivation method *C*, p. 188).

In a strictly parallel experiment, involving simultaneous irradiation of portions from the same equilibrated samples, the effectiveness of *X-rays* (~100 ion pairs/μ tissue) and cyclotron-produced *neutrons* (~400 ion pairs/μ) were compared; see Figs. 1 and 2. The effectiveness of the X-rays was highly dependent on the moisture content (the curves drawn from general experience of the mode of reaction of the material), whereas that of the neutrons was constant within the whole range. The latter applied also to the still more densely ionizing pile neutrons (1—3,000 ion pairs/μ, *cf.* Ehrenberg and Saeland 1954 a), in spite of the rather intense contamination of γ-rays (Fig. 3). Due to the higher biological effectiveness of the neutrons (Ehrenberg and Saeland 1954 b), their effect totally dominates over that of the γ-rays, the effectiveness of which exhibits a large dependence on the water content (*v.* below).

Due to the low dose rate obtainable with *γ-rays* (ion density about

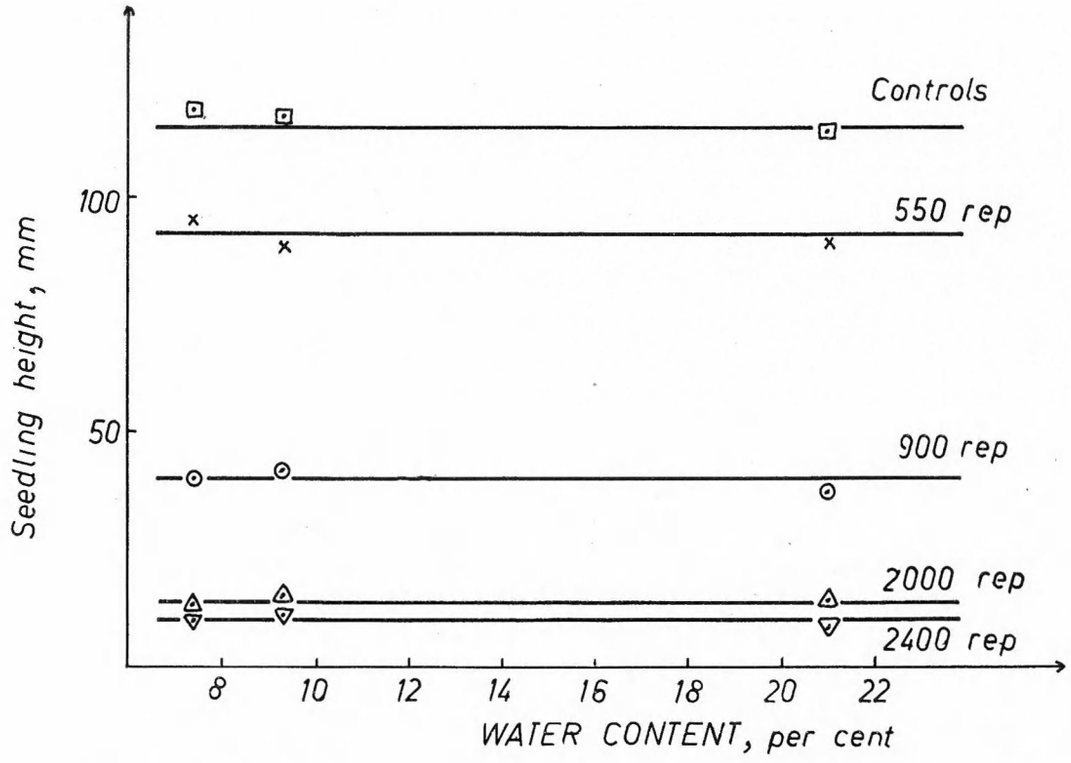

Fig. 2. Seedling heights after irradiation with cyclotron produced fast neutrons at different water content of seeds. γ-ray contamination about 1 per cent of dose. Sample size: 50 seeds.

8 ion pairs/μ) and due to the great distance between γ- and X-ray sources (10 or 80 kilometers), a fully reliable comparison of the two radiations required certain precautions. In one experiment (Fig. 4) all samples to be irradiated were placed simultaneously in test tubes, which were then sealed. One X-ray series was irradiated before the start of, and one after the end of, the γ-ray series, the highest dose of which required about 12 hours. All tubes were then opened and the seeds sown simultaneously. In a second experiment, the result of which is included in Table 2, one X-ray parallel was irradiated while the γ-irradiation was in progress. From the Figure and the Table, it will be seen that a greater effectiveness reduction was obtained in the γ-ray series. Within the errors of dose measurement the two radiations are about equally efficient when seeds treated with dry air are irradiated; but for the production of a given degree of injury by irradiating moist seeds, the X-ray dose required is about 20 per cent lower than the γ-ray dose. In the comparison an influence of the dose rate, though improbable, is not excluded. Utilizing a stronger γ-ray source, the experiment should be repeated with equal dose rates of both radiations.

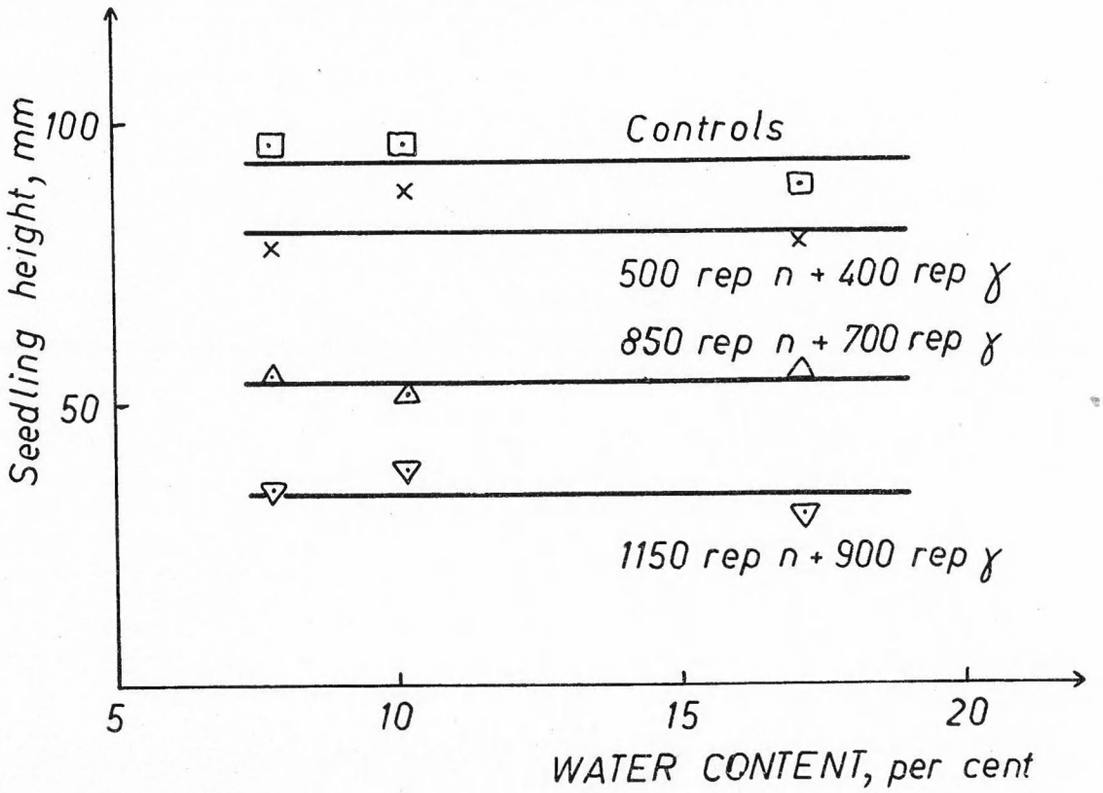

Fig. 3. Seedling heights after irradiation in pile center at different water content of seeds. 1 cm Pb shielding reduces γ-ray contamination to about 45 per cent of total dose. Sample size: 25 seeds.

Conclusion: The effectiveness-reducing influence of increasing water content is a sparse-ionization effect, being greater for γ-rays than for X-rays, and zero for neutrons giving > 400 ion pairs/μ.

In treatments with high energy protons (~ 20 ion pairs/μ) the influence of seed moisture was found to be only about one-third of that obtained in the X-ray parallels. Together with other discrepancies, this was taken to indicate that nuclear reactions of the protons, leading to densely ionizing particles, as well as a contamination of fast neutrons in the beam, exerted a disturbing action (Ehrenberg and Andersson 1954).

2. *Variations of Physiological State of Seeds and of Oxygen Tension.* — One typical experiment involving parallel irradiations of *dormant* and *resting* (after-ripened) seeds of Herta barley is shown in Figs. 5 a and 5 b. In 5 a only the dormant seeds, but in 5 b all samples, were treated with 40° air for 8 days after irradiation. The seeds were irradiated at a rather late stage of dormancy; the germinability test gave 60 % for the dormant seeds, as compared with 96 % for the resting ones. Especially at low water contents (at the moment of

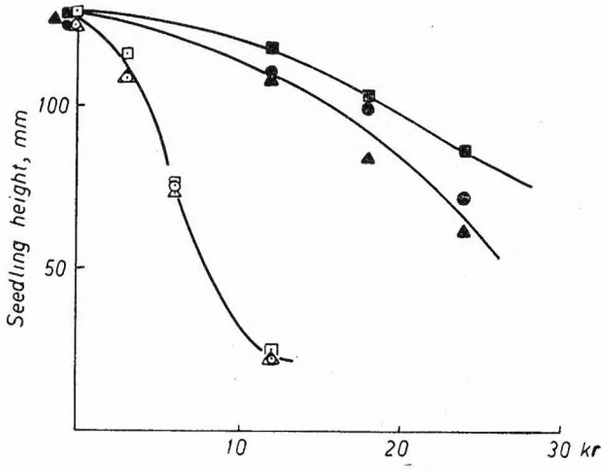

Fig. 4. Comparison between effects of X- and γ-rays. Seedling heights after irradiation, with different doses, of dry seeds (8 % H_2O; empty symbols) and moist seeds (20 % H_2O; filled symbols). ○: X-irradiation at start of γ-irradiation (□); △: X-irradiation after end of γ-ray series. Sample size: 25 seeds. Abscissa: dose.

irradiation), the dormant seeds were found to be more sensitive than the after-ripened ones. That this difference is causally related to the change in the physiological state of the seeds emerges from the fact that in parallel treated Bonus barley, which was fully ripe (germinability test: 100 %), no influence of the heat treatment before irradiation was obtained.

Other trends of this and similar experiments should be mentioned: Especially in cases of bad vitality the number of seedlings is reduced — *cf.* the numbers in Figs. 5 —, which is seldom the case with full-vitality Bonus barley. In the region of low water contents (Fig. 5 a) the dependence of growth inhibition on the moisture content of the resting seeds was repeatedly found to be less than is regularly observed in Bonus barley. The gradients of the curves are changed further by the heat treatment after irradiation, due to the fact that the injury-increasing influence of storage is greater after irradiation at high moisture contents (*cf.* p. 199).

In Table 3 data are given to show that the dormant seeds, even in the range of high moisture contents at irradiation, are more (in the

Table 2. γ- and X-ray doses (kr) giving corresponding growth inhibition in irradiation of "dry" and "moist" seeds.

(Water contents 7—8 and 15—20 per cent, respectively.)

Experiment	Growth reduction per cent	"Dry" seeds		"Moist" seeds		Efficiency reduction (moist/dry)	
		γ-dose	X-ray dose	γ-dose	X-ray dose	γ-rays	X-rays
Data of Fig. 4	36 (*i. e.*, 85 mm seedlings)	5.5	5.5	24	19.5 ± 1.5	4.4	3.5 ± 0.3
	50	7	7	~ 30	25	4.3	3.6
Expt. with one X-irradiation during the γ-ray exposure	50	5.5	5.5	17.5	14.5	3.2	2.6

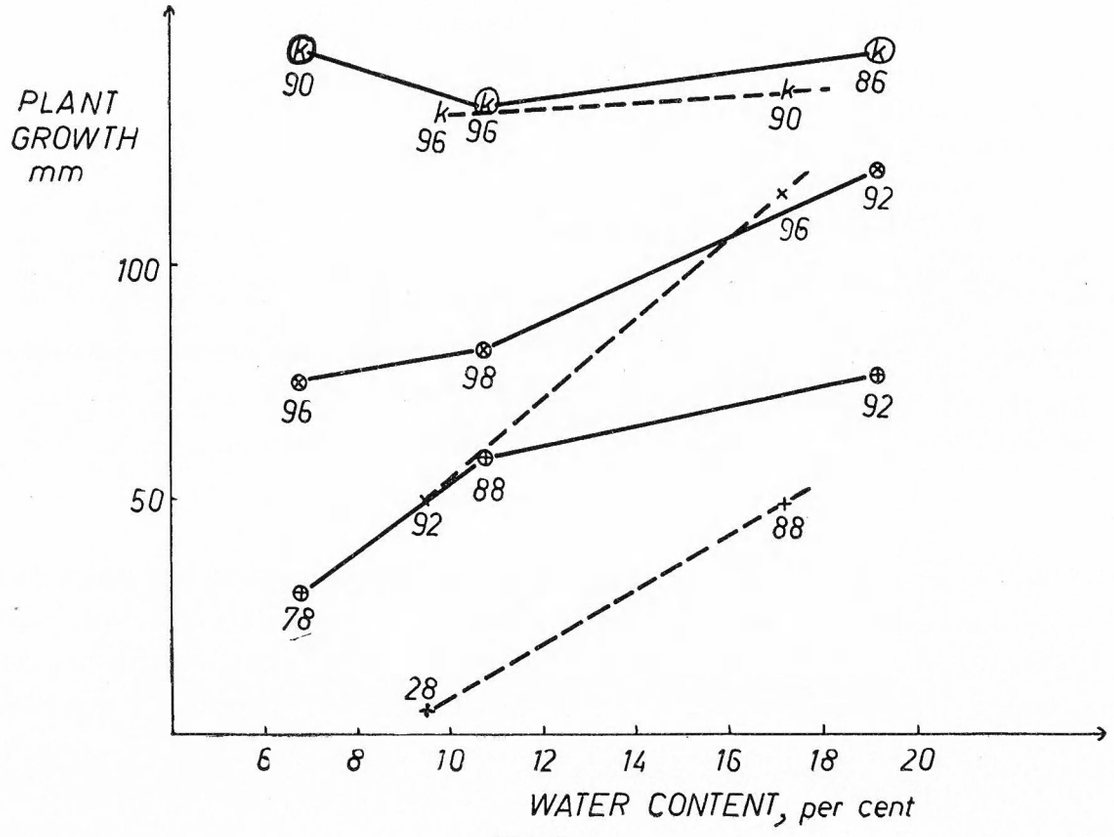

Fig. 5 a.

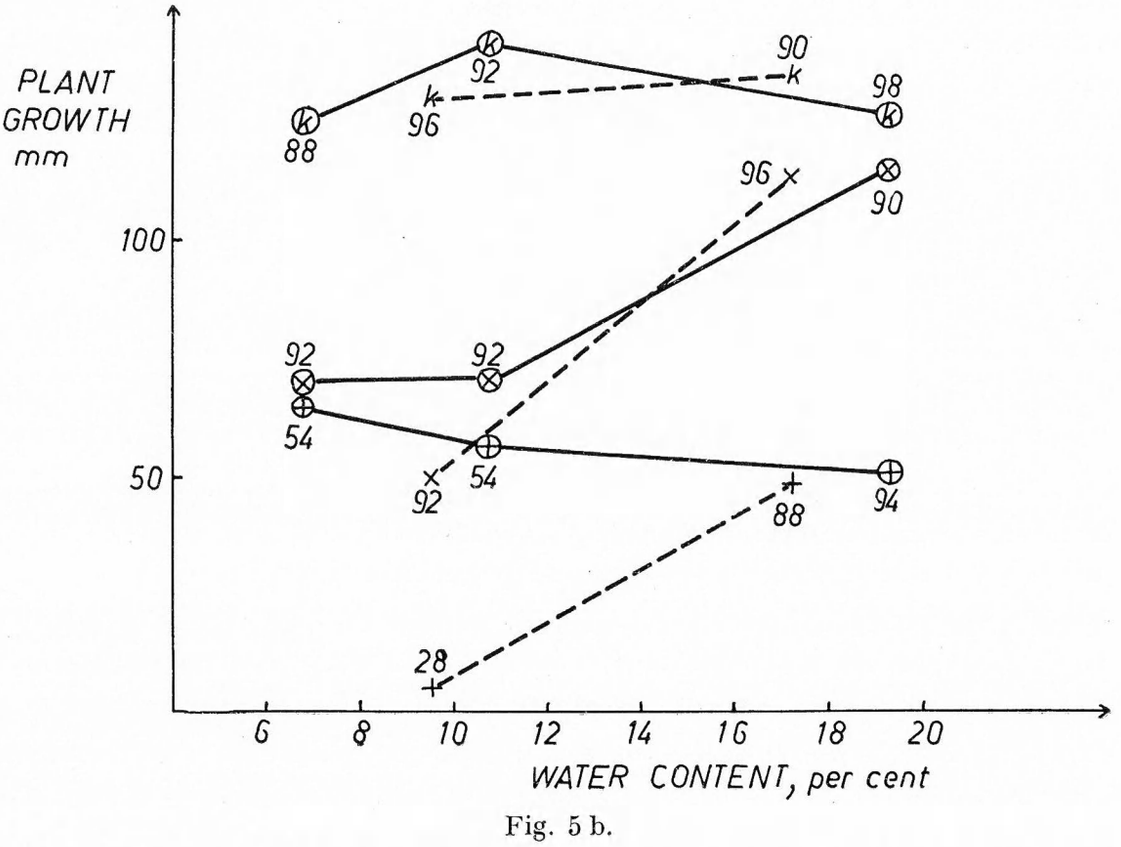

Fig. 5 b.

Fig. 5. Seedling heights after X-irradiation of resting (with ○) and dormant without ○) seeds of different water content. K: controls; ×: 10 kr; +: 20 kr. a) no heat treatment of resting seeds after irradiation; b) resting and dormant seeds treated with 40° air for 8 days after irradiation. The per cent surviving seedlings of each sample (size: 50 seeds) is indicated.

Table 3. Influence of the dormancy state on the sensitivity to X-rays.
All seeds irradiated at the same moisture content, 15.1 %. All seeds sown at 12° C., where they show full (90—100 %) germinability.

State of seeds at irradiation	Treatment after irradiation	Relative seedling height, per cent, after irradiation with, kr:			
		0 (control)	6	12	18
Dormant	none, *i. e.*,	100	95.8	74.5	44.6
Resting	4° C. 8 days	100	100.7	93.7	87.1
Dormant	40° C. dry air	100	89.9	61.3	34.4
Resting	8 days	100	93.0	87.3	77.5

present case about twice) sensitive than the resting ones. The experiment was performed with a Herta barley which was fully vital but in an extremely deep dormancy (germinability test, readings after 3 and 5 days, gave for the dormant seeds 0 and 4.5 per cent, for the resting ones 96.5 and 99.5 per cent, respectively). All seeds were irradiated at the same water content and irrespective of whether they had been heat treated after irradiation, they were sown at 12° C., where the dormant seeds, too, germinated to 100 per cent.

The influence of *incipient germinitive processes* was studied by soaking seeds (method *A*) for 8 and 24 hours at 20° C. and re-desiccating them to different water contents (in a similar treatment of *Antirrhinum* seeds, Knapp and Kaplan 1942, found part of sensitivity increase retained after desiccation). In Fig. 6, interpolated doses causing 50 % decrease of the seedling height are given. In the range of low water contents the dependence of the sensitivity on the moisture is evident in all pre-treatments, at the same time as the sensitivity increases with the soaking time. At high water contents (> 20 % H_2O) the sensitivity is again higher, in accordance with general experience of the effect of soaking (*cf.* Ehrenberg *et al.* 1953). This is also the case in the unsoaked series, where the germinative processes were obviously initiated by treatment with moist air (*cf.* Machalica, 1926).

In a similar experiment seeds were soaked for 0, 8, and 24 hours and re-desiccated in equilibrium with air of 0 and 30 % relative humidity, and then irradiated simultaneously and under identical conditions with X-rays and fast (cyclotron produced) neutrons. The seeds were sown in two replications in the greenhouses in Stockholm and Lund. In Table 4 the doses causing 50 per cent decrease of the seedling heights are calculated. The X-ray data confirm the conclusions drawn from Fig. 6. They further demonstrate, as was already indicated in that

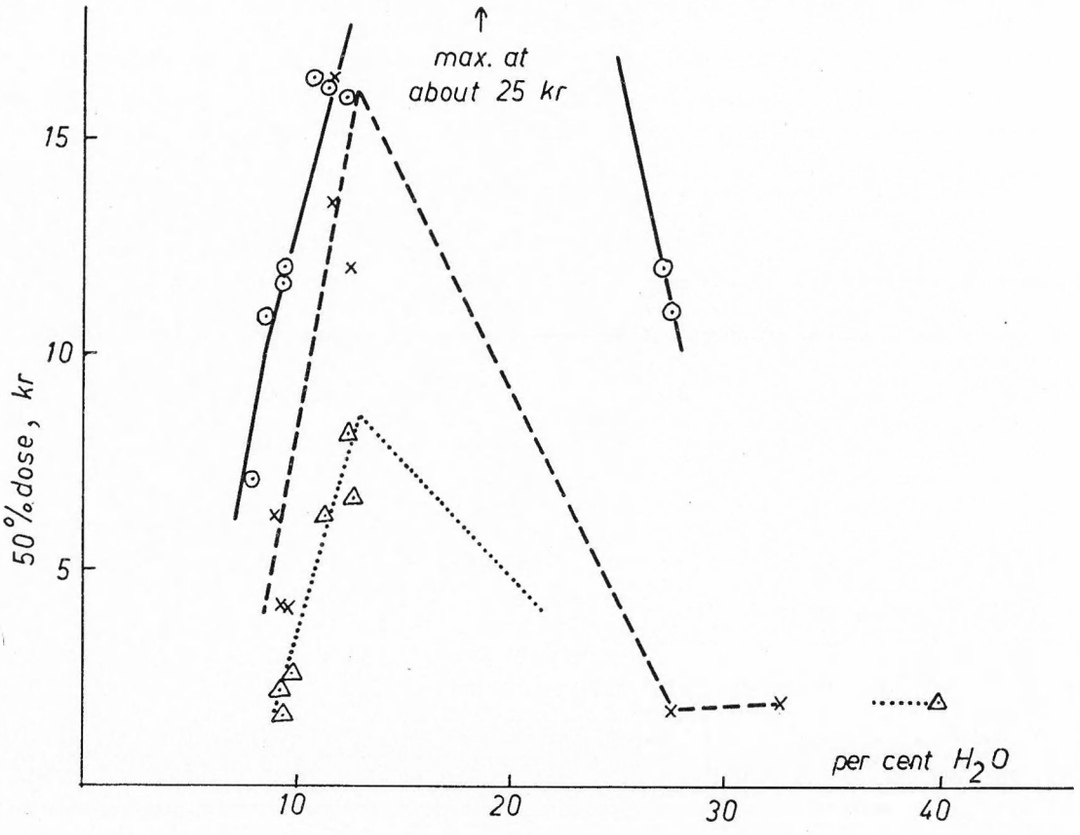

Fig. 6. X-ray doses causing 50 per cent reduction of seedling height at 20° C., seeds of different water content being irradiated. ⊙: resting seeds; ×: seeds soaked 8 hr; △: seeds soaked 24 hr prior to desiccation. (The course of the curves is indicated roughly, as well as the maximum for resting seeds, which was obtained in another, about simultaneous experiment.)

Figure, that the relative influence of the water content is greater in the pre-germinated series. With increasing soaking time the material becomes more sensitive to neutrons, the value at 24 hours' soaking being close to that obtained after soaking without re-desiccation. At this soaking time a slight influence of the water content present at irradiation is significant in the neutron series, too. The last column of Table 4 shows how greatly the relative biological effectiveness of neutrons varies with the state of the material (*cf.* Ehrenberg and Nybom 1954).

In Fig. 7, interpolated doses causing 50 per cent growth reduction are given, from experiments involving X-ray irradiation of seeds equilibrated for six days with *oxygen, air,* or (oxygen-free) *nitrogen* of different humidities. At low water contents, the sensitivity dependence on the seed moisture is present at all oxygen tensions, but seems to be greatest at 0 mm O_2, and lowest in pure oxygen. Especially in the nitrogen series is the higher sensitivity at high water contents (> 20 %)

Table 4. Doses giving 50 per cent decrease of plant height.
Germination temperature about 20° C., seedlings measured at about 100 mm height of unirradiated controls.

Soaking time hrs	Water content at the moment of irradiation %	diff.	X-ray dose kr	Neutron dose rep	X-ray dose / neutron dose
0	9.4	2.0	11.7	850	13.8
	11.4		16.2	850	19.0
8	9.4	2.3	4.2	730	5.8
	11.7		13.5	730	18.5
24	9.5	2.7	1.6	300	5.3
	12.2		8.2	400	20.5
8	seeds not dried		~ 4[1]	250[2]	
24	before irradiation		~ 2[1]		

[1] From Nybom, Gustafsson and Ehrenberg (1952).

[2] From Ehrenberg and Nybom (1954). The value not quite comparable since neutrons of different energies were used. With the established relation: 2—3 times higher efficiency than in resting seeds (*l.c.*: Table 5), a more correct value would be 280—425 rep.

evident; *i.e.*, those germinative processes which make the material more radiosensitive occur independently of the presence of oxygen.

When compared at one and the same water content the radiation effectiveness increases with increasing oxygen tension, as is found in most irradiations of biological or chemical material. That the influence of the oxygen tension was not detected in a previous study (Nybom

Table 5. Reversibility of the influence of the moisture of seeds on their radiation sensitivity.
Sample size: 50 seeds.

Pretreatment[1] with air of rel. humidity (5 days)	Later treatment with air of rel. humidity (5 days)	Water content of seeds at irradiation %	Rel. seedling height[2] % of control, after 0 kiloroentgens	8 kiloroentgens	16 kiloroentgens
0 %	None (irr. before later treatment)	8.9	100.0	48.2	6.7
	0 %	9.2	100.0	54.6	10.2
	100 %	18.8	100.0	97.6	75.7
100 %	None (irr. before later treatment)	18.7	100.0	96.5	77.2
	0 %	10.1	100.0	72.5	10.1
	100 %	18.8	100.0	98.5	84.0

[1] Original water content of sample: 11.5 %.

[2] The seedlings were measured at a control seedling height of 125 mm.

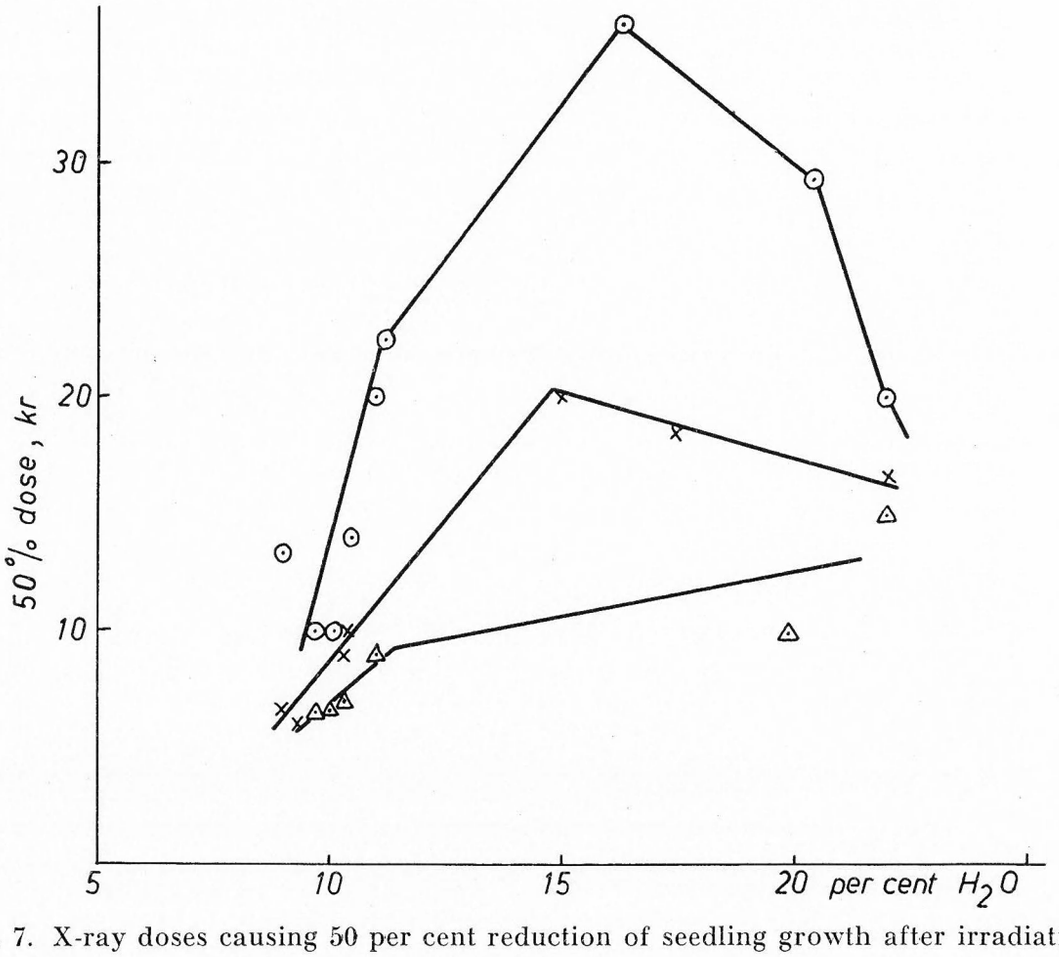

Fig. 7. X-ray doses causing 50 per cent reduction of seedling growth after irradiation of seeds treated for 6 days with nitrogen (⊙), air (×), or oxygen (△) of different rel. humidity. Abscissa: water content of seeds.

et al. 1952, Fig. 13) has to be ascribed to the short duration of gas treatment — only two hours — as compared to the low permeability of seed coats, and to the fact that the seed moisture was not controlled.

Conclusion: The water content exerts, in principle, the same influence on the X-ray sensitivity of dormant, resting, and pre-germinated seeds, and at all oxygen tensions between 0 and 760 mm. Dormant and pre-germinated seeds are more sensitive than the resting ones; the effect of pre-germination is also demonstrated by the increasing sensitivity with increasing water content around 20 %. The sensitivity increases with the oxygen tension. The pre-germination treatment makes the material also somewhat more sensitive to neutrons; at the longest soaking time, 24 hours, a slight influence of the water content on the sensitivity to neutrons is indicated.

3. *Influence of Condition of Seeds before and after Irradiation.* — In Table 5 data are shown to illustrate that the influence of the water

Table 6.

Seeds of 15.7 % moisture were irradiated and afterwards treated for five days with air of different humidity. They gave the following relative seedling heights (sample size: 50 seeds):

Moisture at sowing per cent	Rel. seedling height (per cent of control) after irradiation with	
	8 kr	16 kr
10.4	91	64
15.3	96	60
18.5	96	62

content on the radiosensitivity of the seeds depends on a fully *reversible condition* of the latter. Seeds of moisture 8.9 and 18.7 %, the former thus being most sensitive, were treated, before irradiation, with dry and moist air. Irrespective of whether a water content is reached from a previously higher or lower value, the sensitivity is the same.

It can further be observed that the influence of the water content on the sensitivity is confined to the moment of irradiation (or a short time after it). In Table 6 are data which demonstrate that a change of the moisture content between irradiation and start of germination, *i.e.*, contact with liquid water, has no influence on the degree of growth retardation.

It is well-known that the radiation injury is increased by *storage* of irradiated seeds before sowing (Gustafsson 1947). Even a few days storage will increase the growth inhibition appreciably. The data given in Table 7 demonstrate that the storage effect is greatest at a high temperature when the irradiation is performed at a high moisture content (*cf.* also Figs. 5 a, b and Table 3). Ehrenberg (1954 a: Fig. 6) reported findings showing that the storage effect is lesser after neutron than after X-ray irradiation.

Conclusion: The influence of moisture on the sensitivity of seeds is confined to the moment of irradiation. If the physiological state of the seeds is not changed, *e.g.*, by incipient germinative processes (*cf.*

Table 7. Effect of storage temperature.

Seeds treated, before irradiation, with air of humidity, %	Dose, kr, causing 50 % growth inhibition after storage 6 weeks at		
	— 20° C.	+ 3° C.	+ 20° C.
0	5.0	5.0	5.3
100	18.2	17.0	11.3

Table 8. Doses giving corresponding growth inhibition at two temperatures.

Experiment	Radiation	Water content of seeds per cent	Dose, kr or rep, giving 50 per cent growth inhibition at temp		$\frac{D_{25°}}{D_{12°}}$
			11—12°	25—26°	
a, undulating temp.	X-rays	19.1	20 kr	25 kr	1.25
		10.3	9.5 kr	10.0 kr	1.05
b, constant temp. (*cf.* Ehrenberg 1954: Fig. 3)	X-rays	22.0	16 kr	24 kr	1.50
		9.3	4.5 kr	6 kr	1.33
c, constant temp. (Ehrenberg 1954: Fig. 4)	fast neutrons	9.0	680 rep	750 rep	1.10
	X-rays		3.5 kr	6.5 kr	1.85

preceding section), the moisture influence on the radiation sensitivity will be reversible. Storage increases the radiation injury, more at high temperatures and after irradiation at high moisture contents, not after irradiation of soaked seeds (*cf.* Table 11).

IV. Results: Influence of Germination Temperature on the Radiation Injury

The influence of cultivation temperature is demonstrated in Table 8. The seeds were cultivated in thermostat chambers (method *D*), and in experiment *a* the day and night temperatures varied:

Cold thermostat:	Day 14 hours	15° C.	mean 11° C.
	Night 10 hours	5° C.	
Warm thermostat:	Day 14 hours	30° C.	mean 26° C.
	Night 10 hours	20° C.	

In experiments *b* and *c* the temperature was kept constant, at 12° and 25° C., respectively. In all instances (*cf.* the last column) the injury was less developed at the higher temperature. Although the quotient, $D_{25°}/D_{12°}$, is somewhat irregular, it can be concluded that in one and the same experimental series, temperature exerts a lesser influence in the case of seeds irradiated at a low water content, and, further, that in a parallel experiment with X-rays and neutrons on the same seed material, the neutron injury is the one least affected.

An attempt was made to determine whether any particular stage of germination and growth was preferentially sensitive to temperature with respect to the development of radiation injury. For this purpose, the development of the seedlings was divided into periods, through which the seeds (seedlings) were allowed to pass, in different combina-

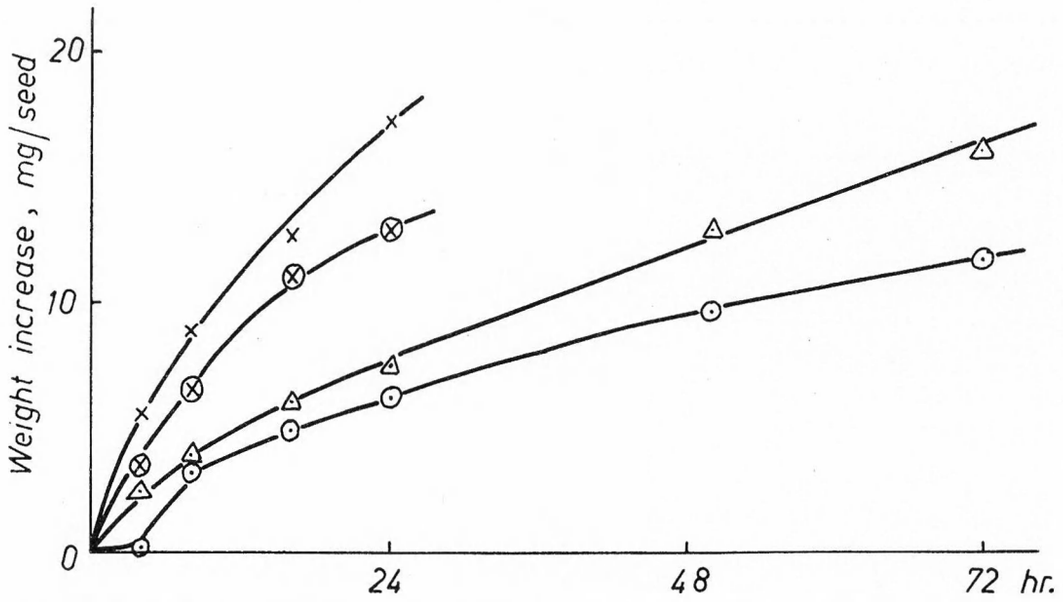

Fig. 8. Rate of water intake of seeds, containing 8 % H_2O (42.1 mg fresh weight per seed; ×, △) and 20 % H_2O (48.4 mg fresh weight per seed; ⊗, ⊙) at start of soaking, at 5° (△, ○) and 20° C. (×, ⊗). Sample size: 25 seeds. Soaking method *B*. Abscissa: soaking time.

tions, at two different temperatures, 5° and 20° C. For the sake of simplicity, seeds with corresponding total fresh weights were regarded as equally developed, although the chiefly physical water uptake probably has a different temperature dependence than several chemical and biochemical reactions (*e.g.,* the activation of α-amylase, *cf.* Ehrenberg 1955 c).

The interval between sowing and measurement was subdivided into four periods, A—D, corresponding to the first four days at 20° C., and a fifth period, E, lasting to measurement of the seedling heights. The subdivision was made with due respect to the fact that during period D the first macroscopic effects of irradiation can be detected, *e.g.*, a slower increase in respiration rate (Mikaelsen and Halvorsen 1953) and fresh weight (unpublished). At the termination of period C most seeds have developed roots 1 cm long and coleoptiles of a few millimeters. At 5° the water uptake is about three times slower than at 20° (Fig. 8, *cf.* Brown and Worley 1912), and periods A—D were therefore given a duration of three days each at the lower temperature. Since the continued growth of the plant exhibits a greater temperature dependence, one day at 20°, in period E, corresponds to about ten days at 5°.

Seeds of 20 % water content were irradiated with 22.5 kr and then sown on glass plates (method *B,* p. 187), one control and one irradiated

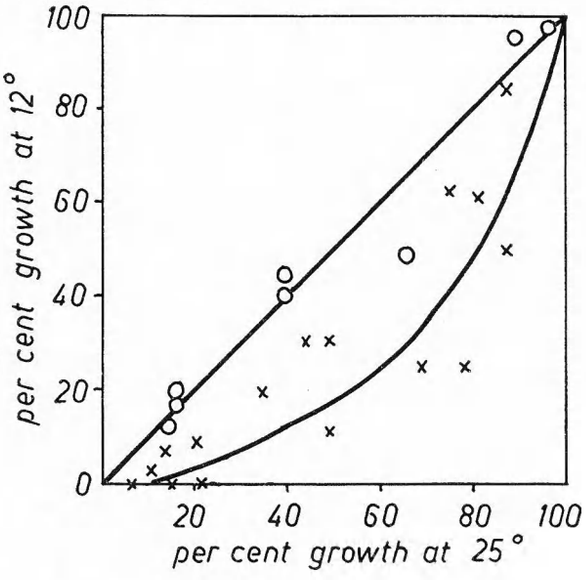

Fig. 9. Corresponding values of relative seedling height (per cent of control), irradiated samples divided into two parts sown at 12° and 25° C., respectively. ×: resting seeds (of different water contents); ⊙: seeds soaked 24 hr before X-irradiation. Sample size: 25 seeds

sample together. The plates were then moved between the two temperatures according to the plan in Table 9. It was found that in all cases where the seeds passed period A at the higher temperature (*i.e.*, samples *a, c, d, e, g, i*), the relative height of the irradiated sample was about 50 per cent. If this period was passed at the lower temperature (samples *b, f, h*), further growth of the irradiated sample was blocked effectively; as regards the apparent exception, sample *fc*, see below. The differences within these two groups are not greater than might be ascribed to a random variation, including differences in the time of measurement (since in this experiment the shoots were measured at a relatively early stage) and any shocks due to the temperature changes. An influence of temperature from period B and further on is, accordingly, appreciably less evident.

In the discussion of data like those presented in Table 9, it should be remembered that due to the complexity of the germinative process the subdivision made involves extremely simplified modes of consideration. Although the irradiated seeds exhibit the slowest growth, both absolute and relative, a low temperature during period A involves a marked stimulation of the growth of unirradiated seeds (compare the control heights in *bw* with the parallel *cw, dw,* and *ew*; *bc* with *cc* and *ec*; *hw* with *gw*; and *hc* with *gc*). This stimulation effect cannot develop, however, if the cold period during A is not followed, at some period, by warmth. The leaf in the *fc* control thus showed an extremely poor development (only a few millimeters at the base of the coleoptile), which was somewhat better in *ic,* and quite normal in *gc* and *hc*. The differences of a few days in the times of measurement of these samples cannot account for the observed differences in the development of the leaf. Within the time limits of this experiment, it can therefore be concluded that if the seedling growth is continued at a low temperature, a period

Table 9. Influence of warmth and cold applied to different stages of development on the growth inhibition of seedlings caused by X-rays.

Sample size: 25 seeds. — Warmth (W) = +20° C.; cold (C) = +5° C. See further in the text.

Sample no.	Temperature in period A	B	C	D	E	Days to measurement (period E)	Control height mm	Height of irradiated sample mm	% of control
aw	W	W	W	W	W	6	94.5	59.3	62.6
ac	W	W	W	W	C	8	16.8[1]	12.0[1]	(71.3)
bw	C	W	W	W	W	4	67.1	9.8	14.4
bc	C	W	W	W	C	56	80.2	9.1	11.3
cw	W	C	W	W	W	4	48.0	23.7	51.5
cc	W	C	W	W	C	56	72.2	32.0	44.3
dw[2]	W	W	C	W	W	4	44.1	26.3	59.6
ew	W	W	W	C	W	4	47.2	24.5	51.9
ec	W	W	W	C	C	56	68.0	24.7	36.3
fw	C	C	C	C	W	5	32.2	4.5	14.0
fc	C	C	C	C	C	50	33.7[3]	14.0[3]	41.5
gw	W	W	C	C	W	4	34.0	17.6	51.8
gc	W	W	C	C	C	54	43.1	18.8	43.6
hw	C	C	W	W	W	4	47.6	5.3	11.1
hc	C	C	W	W	C	54	61.9	5.8	9.3
iw	W	C	C	C	W	5	37.8	19.3	51.0
ic	W	C	C	C	C	52	36.0	21.1	58.7

[1] For technical reasons measured at a too early stage, therefore not quite comparable.

[2] *dc* excluded for technical reasons.

[3] Very poor development of first leaf.

Table 10. Effect of oxygen tension during germination.

Seeds with 11 % water, irradiated, and then pre-germinated on moist filter paper in exsiccators, in air or streaming nitrogen, at two temperatures. Then sown at 20 or 25° C. (method *A*).

Pre-soaking in, temp., ° C. (days)	Cultivation temp. ° C.	Control height at measurement, mm (No. of seedlings per 25 germinated)	Relative growth, % (No. of seedlings per 25 sown) at a dose of 10 kr	15 kr
air 20° (2d)	20	79.5 (25)	56.7 (24)	26.2 (23)
	25	96.9 (20)	51.9 (22)	23.5 (23)
air 5° (7d)	20	97.8 (15)	15.8 (13)	11.4 (19)
	25	99.0 (10)	13.7 (13)	11.0 (8)
N_2, 20° (2d)	20	83.2 (12)	44.9 (13)	19.4 (12)
	25	84.0 (13)	49.6 (11)	14.7 (8)
N_2, 5° (7d)	20	100.4 (7)	15.8 (11)	11.5 (6)
	25	77.4 (5)	21.3 (2)	0 (0)

Table 11. Influence of post-irradiation treatments of soaked seeds.
Sample size: 50 seeds.

Treatment after irradiation	Control height mm	Relative growth, in per cent of control after irradiation with 2 kr	4 kr
No treatment	141.5	72.0	34.2
Further pregermination, 1 day in air	120.7	72.3	27.7
Further pregermination, 1 day in O_2	142.9	71.0	32.4
Further pregermination, 1 day in N_2	112.7	74.9	28.4
Drying, before sowing, to 24.6 % H_2O	175.2	63.4	29.2
Drying, before sowing, to 10.6 % H_2O	148.5	69.5	33.3

of warmth during some part of germination is necessary for normal development of the seedling. The numerically good growth obtained in sample *fc* is thus not comparable to the other values, since the control was already abnormal.

A preliminary experiment with further subdivision of the temperature-sensitive period, A, indicates that the last third, *i.e.* between 16 and 24 hours at 20°, after contact with water is the most sensitive one. These experiments were not so clear-cut, however, since differences in developmental rate between individual seeds produced an increased variation.

When *soaked seeds* are irradiated, the growth inhibition caused is quite independent of the cultivation temperature. This is demonstrated in Fig. 9, where corresponding relative seedling heights at the two temperatures, 12° and 25° C., are compared. This finding is consistent with the fact that the soaked seeds have already passed, at the moment of irradiation, the temperature sensitive period, A (*cf.* above).

Oxygen is 40 per cent more soluble (in water) at 5° than at 20° C. It might, therefore, be logical to postulate an influence of oxygen as a cause of the greater injury after low temperature germination. In one experiment (Table 10) irradiated seeds were pre-soaked in air or nitrogen atmosphere at two temperatures, 5° and 20° C., and then sown (in air) at 20° or 25° C. Although for some reason the material exhibited a decreased germinability, especially after nitrogen treatment and at the higher cultivation temperature, it suffices to demonstrate that the temperature effect is as well developed at the two oxygen tensions. The greater radiation injury observed after nitrogen treatment is not significant.

In Table 11 data are included to show that after irradiation of seeds

soaked for 24 hours, a change of oxygen tension, in this case applied within one minute after the end of irradiation, does not influence the growth inhibition induced.

Conclusion: A low temperature applied during an early stage of germination causes an increase of the radiation injury; this effect is independent of the oxygen tension. After irradiation of soaked seeds, *i.e.*, which have already passed the critical stage, the germination temperature does not affect the injury.

V. Results: Effects of Irradiation Temperature

Several investigators have, in their experiments, varied the irradiation temperature (*cf.* Nybom *et al.* 1952, 1953, and quoted papers). In resting seeds, lowering of the temperature to 0° C. causes a hardly perceptible protection (*cf.* Kempton and Maxwell 1941), which becomes more evident if the temperature is reduced further to that of liquid air (Nybom *et al., l.c.*). In seeds soaked for 24 hours at 20° C., lowering of the irradiation temperature from 20° to 0° C. causes a slight increase of the X-ray effectiveness (Nybom *et al.* 1952: Fig. 17), of a magnitude that could be explained by the greater solubility of oxygen (*cf.* Baker and Sgourakis 1950).

In the present investigation we are principally concerned with the effect of irradiation temperature at those stages of germination during which, according to the preceding section, temperature exerts a major influence on the development of radiation damage induced by irradiating resting seeds. One experiment was performed in which seeds were soaked for different times at 5° and at 20° C. (method *A*). Fifteen minutes before irradiation each sample was divided into two portions, one being transferred to a tube immersed in an ice-bath, the other to a 20° water-bath. Still in the baths, the seeds were irradiated with 3 kr (1 kr/min) and then, within one minute, sown at 20°. Controls were treated parallel therewith, and water contents were determined. From Figs. 10 a and b it will be seen that, irrespective of the soaking temperature, the seeds pass through a stage of pronounced sensitivity to the irradiation temperature. This stage coincides with that of the sensitivity increase provoked by the soaking and also with that of the temperature influence on the post-irradiation soaking. The time scale for the fresh-weight increase is somewhat displaced, as compared to the experiments shown in Fig. 8, due to the fact that in the present case the seeds were partly immersed in water in Petri dishes. Water was

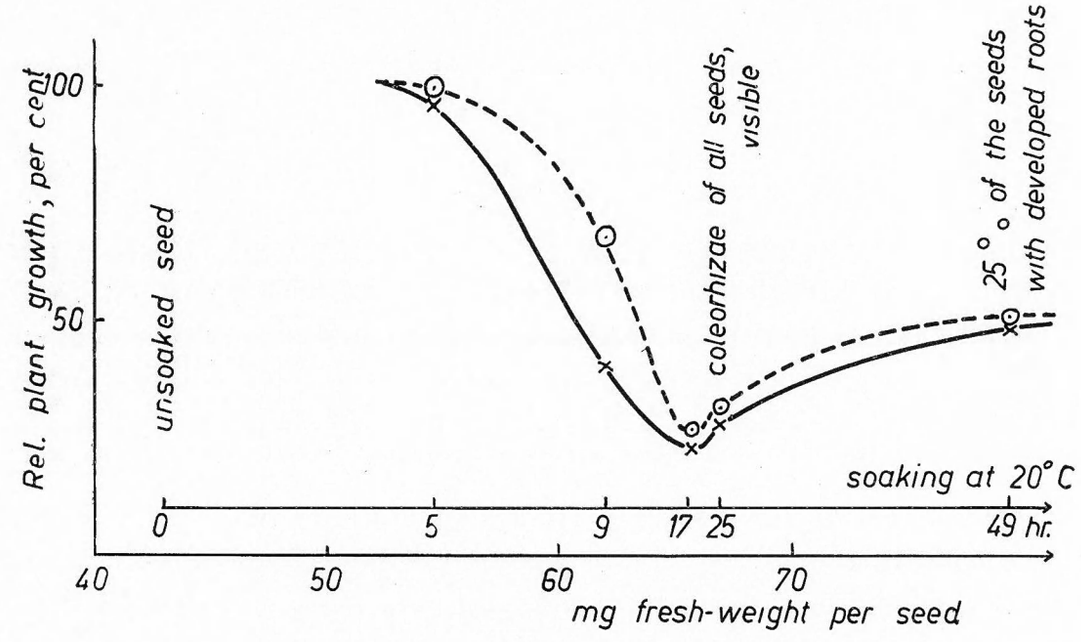

Fig. 10 a.

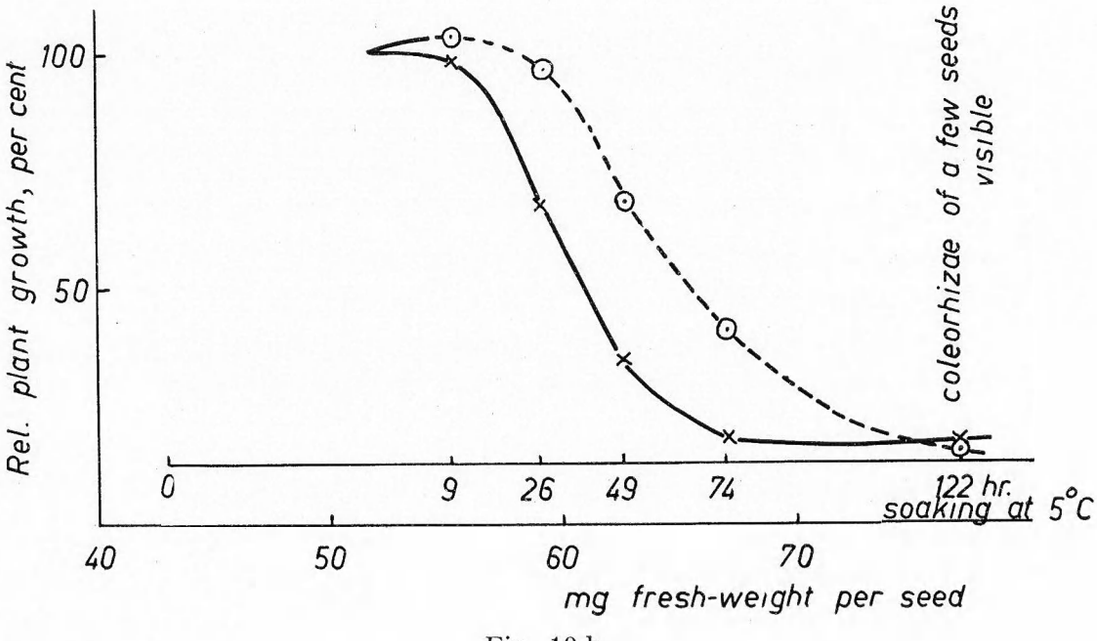

Fig. 10 b.

Fig. 10. Seedling heights (per cent of control) after X-irradiation, with 3 kr, of seeds soaked to different fresh weights at 20° (a) or 5° C. (b). Irradiation at 20° (⊙) and 0° (×). Sample size: 25 seeds.

taken up about five times more slowly at the lower temperature. At least from 55 mg up to 63 mg fresh weight, there is no significant influence of the soaking temperature, but only of the irradiation temperature. In the procedure used for the localization-in-time of the temperature effect on the post-irradiation soaking (p. 201, Fig. 8), this

range of fresh weights corresponds to the last third of sensitive period A. A causal relation between the phenomena is therefore not excluded. — At higher fresh weights a strong influence of soaking temperature becomes evident, probably due to the start, at the higher temperature, of such germinative processes, *e.g.*, connected with sprouting, as show a different temperature dependence than the water uptake. After about 24 hours soaking at 20° the seeds are at a sensitivity maximum; a similar effect has been reported in lentil (Ancel 1927) and wheat (Henshaw and Francis 1935).

Conclusion: When seeds are soaked to different water contents, they pass through a stage of high sensitivity to irradiation temperature. This stage coincides with that during which temperature exerts an influence on the injury caused by irradiating seeds before soaking.

VI. Significance of Data for the Interpretation of Variability

The moisture of seeds stored in open vessels changes rapidly with the humidity of the air. Consequently, the water content is subjected to a seasonal variation, being highest in summer, lowest in winter (Barton 1941). Due to the great dependence of the radiation sensitivity of seeds on the water content, it is logical to assume this factor to be responsible for most of the variations between different experiments performed at different times. Seed dormancy (*cf.* pp. 186 and 192 ff.) might also be a factor causing a seasonal variation in the radiation sensitivity. It is important to recognize this, especially since the condition is relative and therefore not detected if the material is cultivated at a sufficiently low temperature. Another factor to be considered, but which was not included in the present study, is the age of the material: old seeds are more sensitive than young ones (Gustafsson 1947).

The necessity of controlling the germination temperature, in order to get reproducible results, has also been demonstrated. The latter factor is of special importance in field experiments, *e.g.*, for the purpose of mutation production, where the material is exposed to variations of both the mean temperature and the day and night temperatures. Due to the shortness of the period of temperature sensitivity, two samples might be sown at nearly the same time and germinate at the same average temperature, but pass the sensitive stage at very different temperatures, thus developing unequal radiation effects (*cf.* Ehrenberg 1955 b). Experience shows that all the factors mentioned exert a smaller influence on the effects produced by neutron irradiation.

The data also suffice to explain the variation between the individuals of the same irradiated sample, and why this variation is regularly greater in X-ray than in neutron experiments (*cf.* Table 1).

The water contents of twenty individual seeds, taken at random from the big sample used for most of the present experiments, were determined. From the values the mean and the standard deviation were estimated at 11.8 and 1.6 % H_2O, respectively. In a simultaneous experiment (*cf.* Figs. 1, 2) it was found that at about 50 per cent growth inhibition induced by X-rays, a change of the water content in the region of the average, 11.8 % H_2O, by 1.6 % H_2O, corresponds to a change of the plant height by about 24 per cent. The latter value means that part of the coefficient of variation, which at about 50 per cent growth inhibition obtained in X-ray experiments, is due to a correlation with water content. In a control sample (and a neutron irradiated sample) the coefficient of variation amounts to about 15 % (Table 1); this value will, in an X-ray experiment, correspond to the variation of seedling height around the regression line. The variances — in the present case squares of coefficients of variation — being additive, the expected total coefficient of variation in a sample irradiated with X-rays to 50 per cent growth inhibition will be $\sqrt{24^2+15^2}$ %=28 %. The agreement of this value with that found in the experiments, 35 ($\pm$10) %, indicates that the chief reason for the greater variation in X-ray experiments is the variation of the water contents of individual seeds.

VII. Data Relating to the Mechanism of Action of Radiations

1. *Earlier Observations.* — When the water content of seeds is increased, the radiosensitivity of the latter first decreases, to reach a minimum, in the present material, with some variation, near 20 % H_2O; at higher water contents it increases again, eventually to pass a (flat) maximum (*cf.* Fig. 10). In discussions of the importance of reactions of intermediates from water, the concensus of opinion has been that an increase of the water concentration leads to greater radiosensitivity. In the present material obviously two factors are at work, at moisture contents higher than about 20 per cent: an increase of the water content as well as the start of germinative processes provoke greater sensitivity.

The sensitivity minimum near 20 % H_2O is no doubt a general phenomenon, since it has been found, except in barley, in seeds of such different structure and radiosensitivity as those of tomato (Lefort and Ehrenberg 1955), mustard, and maize (unpublished investigations in cooperation with Nybom and Nelson). The radiosensitivity minima observed after short-time soaking of barley seeds (*vide* Fig. 5 of Nybom *et al.* 1952) and peas (Lambert 1933) are undoubtedly related to that

obtained when seeds are treated with moist air. Also in pollen grains a similar phenomenon has been revealed (Kaplan 1940). In most earlier investigations, however, the sensitivity minimum seems to have been overlooked — due to too long soaking times or too low doses; *cf.* the resumé given by Hayden and Smith (1949).

Gustafsson (1940, 1947) and Gelin (1941) found barley seeds containing 10 per cent water to be less sensitive than those containing 15 per cent, for the production of sterility, and chromosomal disturbances, respectively. In a later paper (1955 b) it will be shown that, within the relevant moisture range, an increased water content involves a protection of these effects, too. The contradictory findings indicate that the whole question is not yet elucidated. In the material of the authors mentioned the seeds had been stored for some time at the respective water contents, the dry ones at room temperature, the moist ones at a somewhat lower temperature. In order to solve the problem, the influence of pre-irradiation storage temperature should, therefore, be investigated further. When drying seeds at room temperature over H_2SO_4 or P_2O_5, Gustafsson, too, got indications of an increased radiosensitivity (*l.c.*). It seems possible that the protective effect of desiccation at 80° C. (Gustafsson 1947) is a consequence of changes in the material produced at the high temperature. Smith demonstrated that heat treatment (75—85° C.) prior to X-irradiation may make the seeds less sensitive, at least to the production of growth inhibition (1946, *cf.* Caldecott and Smith 1951). On this point, too, opinions diverge: Personally, in spite of point by point duplication of Smith's experiments, even as to the barley strain, I have failed to verify his results. The situation bears what might be more than a superficial resemblance to the heat-desensitization of infrared sensitized *Tradescantia* microspores (Swanson and Yost 1951): in this case the heat treatment before irradiation has a protective effect, but only if the material has previously been treated by infrared radiation. As a parallel it might recalled that the heat treatment — +40° C. for 8 days — which in the present investigation was used to afterripen dormant seeds, in fact involved a protection, which was totally absent in parallel treatment of fully ripe kernels. A more or less deep dormancy (or a similar state, induced under certain storage conditions) might be a conceivable explanation of the protective effect of heat, quoted above.

2. *Effect of Moisture on Radiosensitivity.* — Possible explanations of the effect, in experiments with sparsely ionizing radiation, would lie in some kind of protection or some kind of repair becoming more

active with increasing water content (below that, about 20 % H_2O, giving the sensitivity minimum). The injury increasing effect of storage suggests that more happens after the irradiation at a high water content, thus contradicting the assumption of repair due to the increased metabolic activity. This increased activity is clearly shown by the several-hundredfold increase of respiration rate, with increasing moisture content within the actual range (Bailey 1940). Since the permeability of seed coats to oxygen is low, the more intense respiration could, it might be logical to conclude, provoke an oxygen depletion causing a lowered sensitivity. This is certainly not the case, however, since the moisture influence was found at all oxygen tensions, even most pronounced in pure nitrogen (Fig. 7). From similar (unpublished) experiments an action of CO_2, the concentration of which inside the seeds is high at intense respiration, can be excluded as an agent in the protection mechanism of the moisture.

A search for a variation of the concentration of chemical protectors of the conventional type has also given negative results: In contrast to earlier estimates from the catalase activity (Ehrenberg and Nybom 1954) a direct titration — amperometrically, with silver nitrate — of free —SH groups showed the latter to be independent of the moisture (Ehrenberg 1955 c). The concentration of reducing sugars was also found to be constant (Ehrenberg and Jaarma, unpublished), in contrast to the data of Kiesel and Gordienko (1937). If some protector is formed when the moisture is raised, it must be destroyed rapidly upon a reversal of the water content (*cf.* the reversibility experiment, Table 5).

When cells are irradiated with the same X-ray dose, at 7 and 20 per cent moisture [1] approximately equal amounts of energy are dissipated, per cell, in both cases (or a somewhat greater amount at 20 per cent). The radiation injury is, however, about four times greater in the former case. The fact that the influence of germination temperature on the development of the injury is localized to a short period of the early development (or to a certain range of water contents) indicates that the extent of the injury becomes fixed during this period.

It seems then plausible to assume that, at the moment of irradiation and until the temperature sensitive stage is reached, a fraction of the radiation energy, increasing with the water content, is dissipated into stabilized end products. This is indicated by the storage effect being greater after irradiation at a high moisture content, and explains the

[1] Within this range of moisture the embryo, which is the radiosensitive part of the seed, has about the same water content as the total seed.

protective effect of water. If the assumption is correct, the seeds *are* more radiosensitive at higher moisture contents, in the sense that greater chemical change is produced. This occurs, however, when the seeds are in a physiologically less sensitive state. The fraction of energy not stabilized chemically is probably present as the energy of some kind of radicals, which become stabilized at a suitable water content during germination. Now, a greater amount of chemical change is produced, and at a physiologically more sensitive state, if dry seeds are irradiated.

The temperature effect might be due to a greater stability of radicalized molecules at a lower temperature.[1] Similar explanations have been used to interpret the higher frequency of chromosomal aberrations at the low temperature as an effect of a slower reunion of broken ends (Sax and Enzmann 1939). Swanson (1954) showed that chromosomal breaks are latent for some time before they get repaired, or stabilized as aberrations. Such a discussion need not, however, be limited to the genic material. Consider the results of Hannan and Shepherd (1954), who irradiated fats and found the decomposition, due to increased radical stability, to be greater at low post-irradiation temperatures. — In this connection the results of Hollaender and Stapleton (1954) should be recalled; they found, in *Escherichia coli,* a maximum survival at a suboptimum temperature around 18° C. applied after X-irradiation, and which they ascribed to a recovery process, for which some compound in the substrate was necessary. The present results bear at least a superficial resemblance to the low-temperature limbs of the survival/temperature curves given by these authors.

All the factors studied have little or no influence on the sensitivity to neutrons. Several findings, including this indepedence of physiological factors, were gathered by Ehrenberg and Nybom (1954) to indicate that due to the marked localization of the energy absorbed, neutrons should produce effects in macromolecules, *e.g.* genes, much more readily than X-rays (γ-rays, *etc.*). The greater effectiveness of X-rays as compared with γ-rays, in moist seeds, as well as the different dependence of the effects of the two radiations on the water content (Table 2), might be explained on a similar basis: A small frac-

[1] If irradiated seeds are soaked at different temperatures, and then re-desiccated to a low moisture content, they retain, when sown, the injury developed during the first period of soaking. It seems, therefore, not possible to explain the temperature effect on the basis of a more effective recovery due to the more intense metabolic rate at the higher temperature.

tion of the X-ray energy is absorbed at high ion densities (~200 ion pairs/μ, *cf.* Spiers 1952), and can be expected, analogously with neutron energy, to be equally effective at all water contents. This fraction of the X-ray energy will therefore produce detectable effects around 20 % H_2O, where the protection against sparsely ionizing energy (*e.g.* all that of γ-radiation) is most effective, thus increasing the effectiveness of X-rays in comparison with that of γ-rays. (A similar interpretation holds for the greater effectiveness of X-rays in relation to those of γ-rays, fast electrons, *etc.,* in experiments with wet tissue in general, *cf.* Ehrenberg and Nybom 1954, and also the resumé given by Zircle 1954.)

The fact that the greater sensitivity of pregerminated material to fast neutrons is retained after re-desiccation (Table 4) — pre-germination being the only factor which in the present material changes the sensitivity to neutrons — indicates that some fundamental change of the properties of macromolecules occurs in germination. In point of fact, seeds in all those states — dormant, pre-germinated, and aged — where they are more sensitive than young, resting seeds, have been found to containt a higher concentration of readily titratable sulfhydryl in the embryos (Ehrenberg 1955 c). Although the significance of this fact has not yet been investigated further, it is plausible to assume a change in the state of proteins in the direction of denaturation, at high sulfhydryl contents.

Summary

Barley seeds were irradiated and germinated under different conditions, and the retardation of seedling growth was determined. The effectiveness of sparsely ionizing radiations (γ-rays > X-rays; that of neutrons not influenced) decreases with increasing water content of seeds, in the region of 7—20 % H_2O. The effect is found at different oxygen tensions and physiological states, which, *per se,* affect the radiosensitivity. Injury increases during storage, especially after irradiation of moist seeds. During an early stage of germination of irradiated seeds, temperature determines the extent of lesions, greatest retardation of growth being obtained at low temperatures; if seeds are irradiated during this stage, irradiation temperature exerts a corresponding influence.

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References

ANCEL, S. 1925. Sur les variations dans la manifestation de la lésion produite par les rayons X dans les graines, en fonction de la température a laquelle elles se développent après l'irradiation. — Compt. rend. soc. biol. 93: 1671—1672.

— 1927. Sur les variations de sensibilité aux rayons X de graines germées suivant le stade du développement. — Compt. rend. soc. biol. 96: 986—989.

ATTERBERG, A. 1899. Om sädesvarornas eftermognad. — Kgl. Landtbruks-Akad. Handl. Tid. 38: 227—250.

BAILEY, C. N. 1940. Respiration of cereal grains and flax seed. — Plant Physiol. 15: 257—274.

BAKER, K. W. and SGOURAKIS, E. 1950. The effect of oxygen concentration on the rate of X-ray induced mutations in Drosophila. — Proc. Nat. Acad. Sci. U.S. 36: 176—184.

BARTON, L. V. 1941. Relation of certain air temperatures and humidities to viability of seeds. — Contribs. Boyce Thompson Inst. 12: 85—102.

BROWN, A. J. and WORLEY, F. P. 1912. The influence of temperature on the absorption of water by seeds of Hordeum vulgare in relation to the temperature coefficient of chemical change. — Proc. Roy. Soc. London B 85: 546—553.

CALDECOTT, R. S. 1954. Inverse relationship between the water content of seeds and their sensitivity to X-rays. — Science 120: 809—810.

— FROLIK, E. F. and MORRIS, R. 1952. A comparison of the effects of X-rays and thermal neutrons on dormant seeds of barley. — Proc. Nat. Acad. Sci. U.S. 38: 804—809.

— and SMITH, L. 1951. The influence of heat treatments on the injury and cytogenetic effects of X-rays on barley. — Genetics 36: 546.

CURTIS, O. F. and CLARK, D. G. 1950. An Introduction to Plant Physiology. — New York, Toronto, and London. *Vide* p. 571.

EHRENBERG, L. 1954. The influence of post-radiation factors on effects produced in barley. — Radiobiology Symposium Liège. London. Pp. 285—289.

— 1955 a. Biological effectiveness of fast neutrons. (In preparation.)

— 1955 b. Factors influencing radiation induced lethality, sterility, and mutations in barley. — Hereditas 41: 123—146.

— 1955 c. Studies on the mechanism of action of ionizing radiations in plant seeds. — Svensk Kem. Tid. 67 (in press).

— and ANDERSSON, G. 1954. Probable side-effect of nuclear reactions in the biological action of fast protons. — Nature 173: 1086.

— GRANHALL, I., GUSTAFSSON, Å and NYBOM, N. 1954. Acute and chronic ^{60}Co gamma irradiation of plants. — Proc. 2nd Radioisotope Conf. Oxford: 391—395.

— GUSTAFSSON, Å., LUNDQVIST, U. and NYBOM, N. 1953. Irradiation effects, seed soaking and oxygen pressure in barley. — Hereditas 39: 493—504.

— and NYBOM, N. 1952. Chemical and biological effects of neutrons and X-rays. — Hereditas 38: 481—501.

— and — 1954. Ion density and biological effectiveness of radiations. — Acta Agr. Scand 4: 396—418.

— and SAELAND, E. 1954 a. Chemical dosimetry of radiations giving different ion densities. — JENER Publ. No. 8: 1—25.

— and — 1954 b. Effects of pile radiation on barley seeds. — J. Nuclear Energy 1: 150—169.

GELIN, O. E. V. 1941. The cytological effect of different seed-treatments in X-rayed barley. — Hereditas 27: 209—219.

— 1953. Mitotische Störungsfrequenzen in röntgenbestrahlter Gerste. — Agri Hort. Genet. 11: 66—81.

GRANHALL, I., EHRENBERG, L. and BORENIUS, S. 1953. Experiments with chronic gamma irradiation on growing plants. — Bot. Notiser: 155—162.

GUSTAFSSON, Å. 1940. The mutation system of the chlorophyll apparatus. Lunds Univ. Årsskr. N.F. Avd. 2, 36: 1—40.

— 1947. Mutations in agricultural plants. — Hereditas 33: 1—100.

HANNAN, R. S. and SHEPHERD, H. J. 1954. Some after-effects in fats irradiated with high-energy electrons and X rays. — Brit. J. Radiol. 27: 36—42.

HARRINGTON, G. T. 1923. Forcing the germination of freshly harvested wheat and other cereals. — J. Agr. Research 23: 79—100.

HAYDEN, B. and SMITH, L. 1949. The relation of atmosphere to biological effects of X-rays. — Genetics 34: 26—43.

HENSHAW, P. S. and FRANCIS, D. S. 1935. A consideration of the biological factors influencing the radiosensitivity of cells. — J. Cellular Comp. Physiol. 7: 173—195.

HOLLAENDER, A. and STAPLETON, G. E. 1954. Modification of radiation damage after exposure to X rays. — Brit. J. Radiol. 27: 117—121.

KAPLAN, R. 1940. Experimentelle und theoretische Untersuchungen über den Mechanismus der Keimungsschädigung durch Röntgenstrahlen beim Pollen von Antirrhinum majus L. — Biol. Zentr. 60: 298—318.

KEMPTON, J. H. and MAXWELL, L. R. 1941. Effect of temperature during irradiation on the X-ray sensitivity of maize seed. — J. Agr. Research 62: 603—618.

KIESEL, A. and GORDIENKO, K. 1937. Über die Tätigkeit der Fermente im Weizenkorn von verschiedenem Wassergehalt während der Lagerung. — Bull. soc. naturalistes Moscou Sect. biol. 46: 339—350. (In Russian, with German summary.)

KNAPP, E. and KAPLAN, R. 1942. Beeinflussung der Mutationsauslösung und anderer Wirkungen der Röntgenstrahlen bei Antirrhinum majus durch Veränderung des Quellungszustandes der zu bestrahlenden Samen. — Z. ind. Abstamm.- u. Vererb.-Lehre 80: 501—550.

KOBAYASHI, Y. 1932. Wasserdampfspannung über wässerigen Lösungen von Kaliumhydroxid. — J. Sci. Hiroshima Univ. A 2: 269—274.

LAMBERT, J. 1933. Recherches sur les facteurs de la radiosensibilité tissulaire en dehors des phénomènes morphologiques. Les propriétés biologiques des tissus latents. — Arch. biol. Liège 44: 621—739.

LEFORT, M. and EHRENBERG, L. 1955. L'influence de la teneur en eau des graines sur leur sensibilité aux rayons X. — Arkiv Botan. 3. No. 7: 121—124.

MACHALICA, J. J. 1926. Przyczynek do badań nad zdolnością pobierania i wykorzistania przy kiełkowaniu hygroskopowej wilgoci z atmosfery przez ziarna żyta, pszenicy, jęczmienia i owsa. — Roczniki Nauk Rolniczych i Leśnych 15: 407—423. (With German summary, p. 420.)

MAC KEY, J. 1951. Neutron and X-ray experiments in barley. — Hereditas 37: 421—484.

MIKAELSEN, K. and HALVORSEN, H. 1953. Experiments on the respiration of X-irradiated barley seeds. — Physiol. Plant. 6: 873—879.

NYBOM, N., GUSTAFSSON, Å. and EHRENBERG, L. 1952. On the injurious action of ionizing radiations in plants. — Bot. Notiser: 343—365.

— LUNDQVIST, U., GUSTAFSSON, Å. and EHRENBERG, L. 1943. Biological effects of X-irradiation at low temperatures. — Hereditas 39: 445—457.

SAX, K. and ENZMANN, E. V. 1939. The effect of temperature on X-ray induced chromosome aberrations. — Proc. Nat. Acad. Sci. U.S. 25: 397—405.

SMITH, L. 1946. A comparison of the effects of heat and X-rays on dormant seeds of cereals, with special reference to polyploidy. — J. Agr. Research 73: 137—158.

SPIERS, F. W. 1952. Radiation absorption and energy loss by primary and secondary particles. — Discussions Faraday Soc. 12: 13—24.

SWANSON, C. P. 1954. Effect of oxygen tension on the production of chromosome breakage by ionizing radiations: An interpretation. — Radiobiology Symposium Liège. London.

— and YOST, H. T., JR. 1951. The action of infrared radiation on the chromosomes of Tradescantia. — Genetics 36: 579.

ZIRCLE, R. E. 1954. The radiobiological importance of linear energy transfer. — In HOLLAENDER, R.: Radiation Biology, Vol. I: High Energy Radiation. New York, Toronto, and London. Pp. 315—350.

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Radiation Effects on the Dry Matter Content in Barley

By LARS EHRENBERG and DIETRICH VON WETTSTEIN

Institute of Organic Chemistry and Biochemistry, University and Forest Research Institute, Stockholm

Comparative experimental investigations into the effects of various ionizing radiations on plants, have revealed several facts which indicate that fundamentally different mechanisms are at work, depending on the quality of the radiation used. Thus the primary effects of densely ionizing radiations, *e.g.*, neutrons, seem to be localized chiefly to the cell nuclei, whereas sparsely ionizing radiations such as γ- and X-rays produce their effects, at least partially, via an action on the cytoplasm. This was concluded from the high efficiency of neutrons in the production of chromosome injury (estimated as rearrangements, sterility, or mutations) and from the absence of influence of physiological and chemical factors on the development of neutron lesions. The sparsely ionizing radiations, however, act conversely in the above-mentioned respects (Ehrenberg and Nybom 1954, Ehrenberg and Saeland 1954 a). The aim of the present investigation is to elucidate, from radiobiological points of view, certain aspects of the germination and seedling growth of barley seeds irradiated with fast neutrons and X-rays.

When growing seedlings from seeds irradiated with α-rays or neutrons are compared with those subjected to X-ray treatment, the former exhibit, apart from the small variability in height (Ehrenberg and Nybom, *l.c.*), a conspicuously robust habitus with thick stems and leaves. This can be seen, for instance, in Fig. 4: the leaves of plants after heavy X-ray treatments are thinner and more elongated than those after corresponding neutron treatments. This difference is very appreciable in the flowering plants of the first field generation after irradiation. Neutron plants are, in comparison with X-ray plants, stunted and their stems often twice as thick. In woody plants this mode

of reaction corresponds to a xeromorph leaf type observed after irradiation of twigs or branches. A similar case following β-irradiation of rose bushes was described by Ehrenberg and Granhall (1952). This morphological appearence is obviously related to an *increase of dry matter content* found in seedlings from irradiated seeds (*vide* Benedict and Kersten 1934), this increase being greatest after neutron irradiation. The effect may be so marked that at low neutron doses, producing about 20 per cent growth inhibition (measured as decreased seedling height), no significant change in the total dry weight of the shoot will be found.

Since it is plausible to attribute this radiation effect on dry matter content to an inhibition of water uptake — as Benedict and Kersten did — we approached the problem of this deficiency of water by first studying the *development of the roots and the uptake of the phosphate ion at varying degrees of inhibition of the shoot growth.*

Experimental

Portions of a sifted sample of seeds of the market variety Bonus barley (*Hordeum distichum*) were irradiated, after equilibration with air of 30 per cent humidity, with X-rays and fast neutrons (with regard to the necessity of equilibration, *vide* Lefort and Ehrenberg 1955). The *X-rays* were produced with the equipment of the Institute of Genetics, Stockholm; the machine was run at 170 kV without filtration and the dose rate amounted to 500 r/min. The *neutrons* were produced by bombarding a beryllium target with 25 MeV deuterons, accelerated in the 225-cm cyclotron of the Nobel Institute for Physics, Stockholm. The neutron doses were determined by the oxidation of ferrous iron in sulfuric acid solution (Ehrenberg and Saeland 1954 b, *cf.* Ehrenberg 1955).

In some series the seeds were sown in wooden boxes, filled with soil, in a greenhouse at 17—20° C. In order to facilitate the collection of intact root systems, single seeds were sown in small carton frames according to Berner's method (1923).

In one series the seeds were pre-germinated in the dark at 22° C. on moist filter paper to a root length of a few centimeters and the seedlings afterwards grown in a nutrient solution of the following composition:

$Ca(NO_3)_2$	0.25×10^{-3} mols/l	KH_2PO_4	0.8×10^{-3} mols/l
$MgSO_4$	0.5×10^{-3} mols/l	Na_2HPO_4	1.2×10^{-3} mols/l
H_3BO_3	0.1×10^{-3} mols/l		

The pH was adjusted with NaOH to 6.7. — These salt concentrations and this pH have been found to be optimal for the root and shoot growth of the barley variety used. — The seedlings were placed in holes bored through cork floats, so that the roots were immersed in the solution with the seeds and

shoots in the air. The cultures were illuminated by daylight lamps with a total intensity of about 3,000 lux, and were kept at room temperature ($22 \pm 2°$ C.). The solutions were adequately aerated and renewed completely every 24 hours.

With this arrangement the uptake of ^{32}P labelled phosphate was studied. Seedlings one week old — the controls having gained a shoot length of about 10 cm — were transferred, still on the floats, to a large vessel containing 5 l of solution with phosphate marked to a specific activity of 13 μC/mmol. After 24 hours in the active solution the plants were removed for analysis of ^{32}P, which was performed according to methods applied by Ehrenberg *et al.* 1949. The use of a single large vessel secured a constant and identical milieu for all seedlings during the period of absorption, and at the same time the aeration ensured sufficient stirring, whereby concentration gradients were avoided.

At the low activity used — 26 μC ^{32}P/l, that is, 0.6 μC per seedling — no biological effects of the β-radiation can be expected (*cf.* Ehrenberg *et al.* 1949, Virgin and Ehrenberg 1953). The activity of the nutrient solution corresponds to a dose of 1 rep ($=93$ erg g^{-1}) per 24 hours, and in those plant organs which show the highest uptake, *i.e.,* roots of seedlings after strong neutron irradiation, the dose rate amounts to about 3 rep per 24 hours.

For fresh-weight determinations, samples were harvested after 8, 10, or 12 days, and weighed at identical times, mostly one minute, after cutting. Drying was done at 105° C.

Results

Before proceeding to the irradiation effects, a few words may be said about the normal developmental processes occurring during germination and initial seedling growth up to the twelfth day. Considering the changes in dry weight accompanying germination and growth, the initial phase of development is clearly dominated by a redistribution of dry matter. This is transferred from the seed endosperm to stem and roots. During this process a small loss of dry matter due to respiration occurs, but gradually it will be compensated by increasing assimilation as soon as the green leaves unfold. After this period of redistribution comes a period of growth characterized by the substantial increase of *total dry matter.* In the case of barley this development may be illustrated by the following data. The dry weight of a single grain is about 35 mg. During the first few days after the onset of germination it is reduced by maximally 5 mg, the reduction reaching a minimum after four to five days — here regarded as the end of germination (Thomas 1947: *cf.* Fig. 56). Due to the incipient assimilation the dry matter rises slightly and reaches the original dry weight of the seed on the eighth to tenth day, *i.e.,* at a time when the primary leaf is already about 10 cm in height. A rapid increase of dry matter content

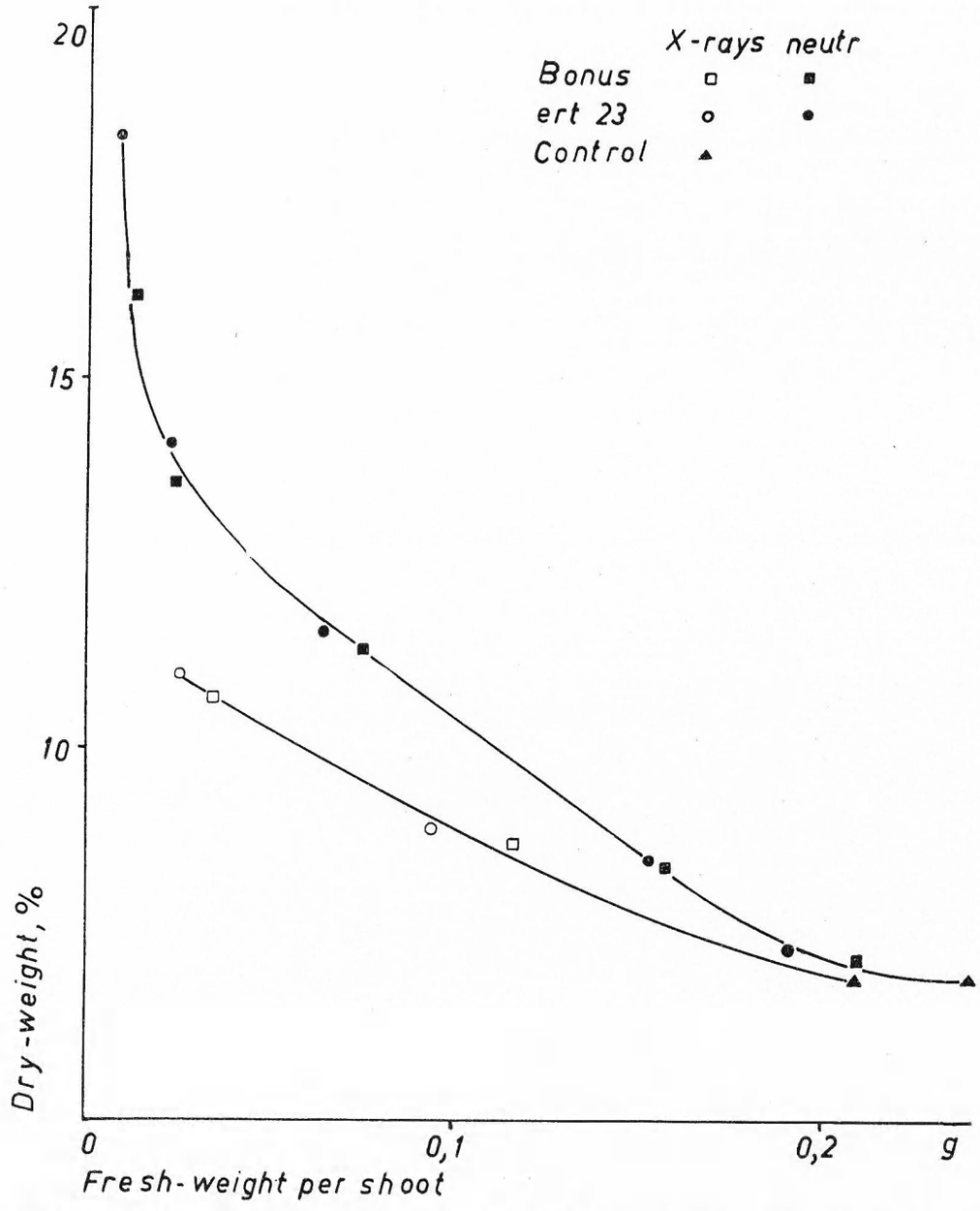

Fig. 1. Dry matter content, in per cent of fresh weight, of shoots after irradiation of seeds with neutrons and X-rays. Bonus barley and the mutant, *erectoides* 23. Seeds sown in soil. Each point a sample of 25 seedlings. Abscissa: shoot development.

then takes place. The development outlined here is valid under the experimental conditions applied in the present investigation.

Turning to the shoot, it may be stated that its *relative dry weight* — *i.e.*, the dry matter content expressed as per cent of the fresh weight — has been found to be practically constant up to the twelfth day. It amounts to about 8 per cent under the conditions applied.

Dry Weight of Shoots after Irradiation. — On analyzing the relative dry weights at different degrees of growth inhibition after irradiation

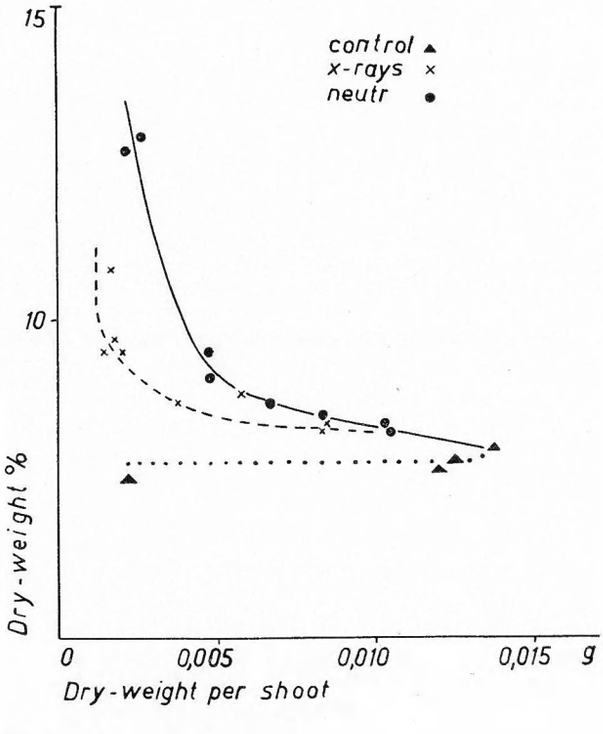

Fig. 2. Dry matter content, in per cent of fresh weight, of shoots. Seedlings cultivated in nutrient solution. Sample size: 3—5 seedlings. Abscissa: shoot development.

we generally obtain curves of the type shown in Figs. 1—3. The applied doses ranged from 10 to 20 kr of X-rays and 350 to 1200 rep of neutrons. If the growth inhibition is expressed as decrease of dry weight or fresh weight, the relative dry weight increases with increasing retardation of the shoot growth. The neutron-treated seedlings regularly showed a more rapid increase of dry weight than did the X-irradiated ones, and this difference was manifested irrespective of whether the culture medium was soil (Figs. 1, 3) or nutrient solution (Fig. 2). The appreciable constancy of the unirradiated plants with respect to their relative dry weights during development, has already been mentioned and can be found in plants of varying age (*cf.* Fig. 2) or in seedlings which, within the normal range of variation, grow extremely slowly (*cf.* Fig. 3). *It can therefore be stated that the dry weight increase in the irradiated samples was in some way caused by the radiation.*

The experiment in Fig. 1 includes a mutant, *erectoides* 23, which is of special interest by virtue of its changed mode of growth, its anatomical and vascular organization, and its changed physiology of root growth (*cf.* von Wettstein 1954). The mutant data closely accord with those of the mother variety, no difference being observed either between the controls or within the irradiation series.

In order to study the influence of the degree of development in shoots which received the same irradiation dose, individual plants were com-

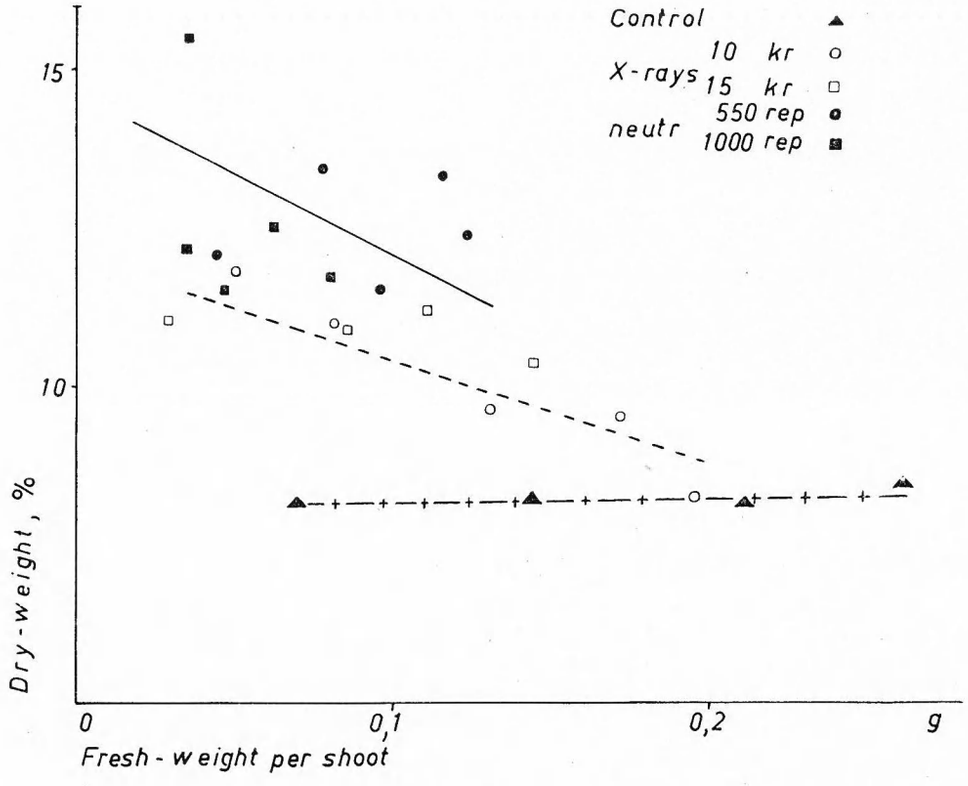

Fig. 3. Dry matter content, in per cent of fresh weight, of individual shoots at different degrees of inhibition. Abscissa: shoot development.

pared (Fig. 3). In the X-irradiated samples there was still a fairly close correlation between the shoot development and the relative dry weight. In the neutron treated samples, however, where the degree of growth inhibition was less variable, there was no clear relationship, and other factors influencing the relative dry weights have to be sought.

Root Growth of Irradiated Seedlings. — The growth of the root systems was greatly inhibited by radiation, the effect being observable whether the plants were grown in soil or nutrient solution. The root retardation was most accentuated after neutron irradiation, and is illustrated in Fig. 4. Here "X-ray" and "neutron" plants with about the same degree of shoot inhibition are compared. The difference between the two groups of irradiated seedlings is present throughout the range of doses applied, but becomes quite appreciable at higher doses.

The different effects of the two types of radiation on root development may also be expressed in terms of the root-shoot ratio, using for instance the ratio between the absolute dry weights. In several series the root-shoot dry weight ratio for unirradiated seedlings after 10 days was determined as 0.82 ± 0.06. Fig. 5 shows the ratios for plants after

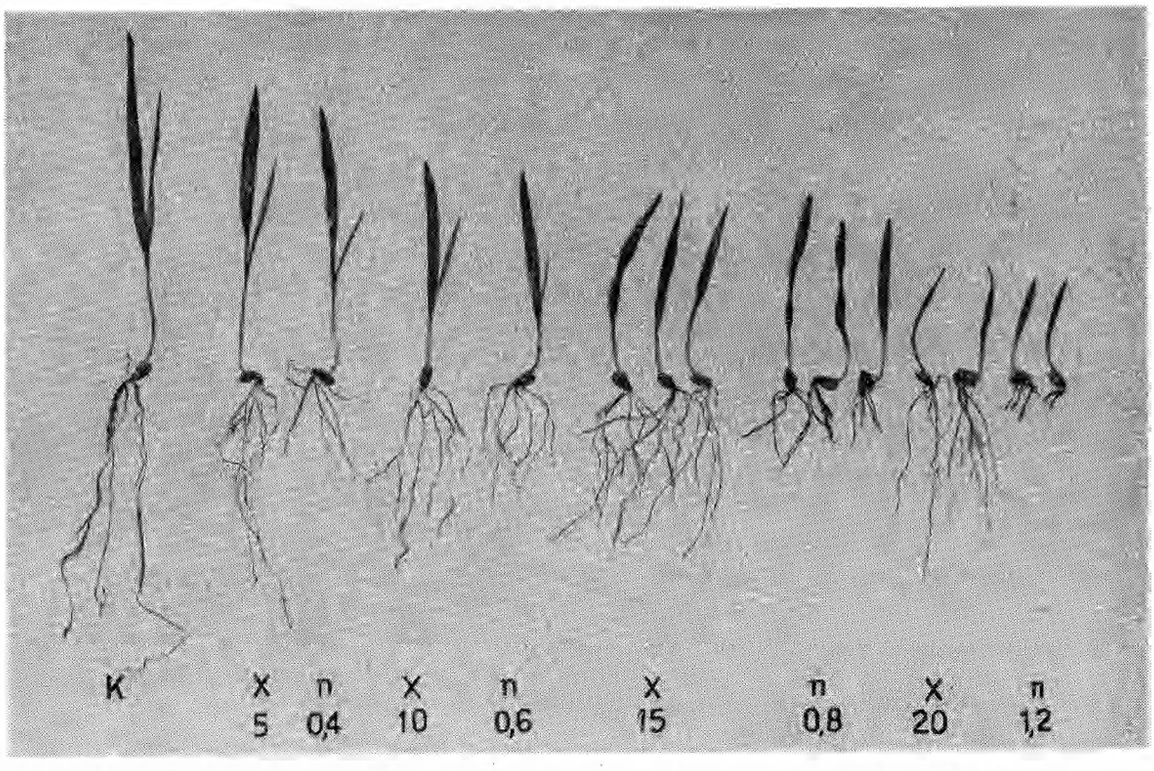

Fig. 4. Photographs of plants, showing shoot and root inhibition after irradiation of seeds with different doses of X-rays (X) and neutrons (n), expressed in krep. K=control. Observe the different root development at corresponding inhibition of shoots by neutrons and X-rays. — ×0.3.

treatment with different doses of X-rays and neutrons. Each point on the curves represents the mean of five separate experiments, with ten individuals analyzed in each experiment; their standard deviations are less than those in the control material. The experiments included different treatments, such as irradiation of resting (*i.e.,* ripe) seeds as well as seeds pre-soaked for 8 or 24 hours in water. Typical curves are also given for shoot inhibition, presented in terms of plant heights relative to those of the unirradiated controls.

Up to 25 per cent growth inhibition, the "*X-ray*" *seedlings* showed an approximately normal constant ratio and revealed a similar growth inhibition in shoots and roots. A slight decrease in the root-shoot ratio was observed in some experiments but not in others. With a growth inhibition exceeding 50 per cent, the ratio rose considerably above 1.0, and hence above that of the control. Here, more dry matter was evidently built up in the roots than in the shoot, and this resulted in the development of remarkably long roots (*cf.* Fig. 4). But after *neutron irradiation* the situation was different. The root-shoot ratio declined markedly to 0.4 or less at 50 per cent growth inhibition of the shoot.

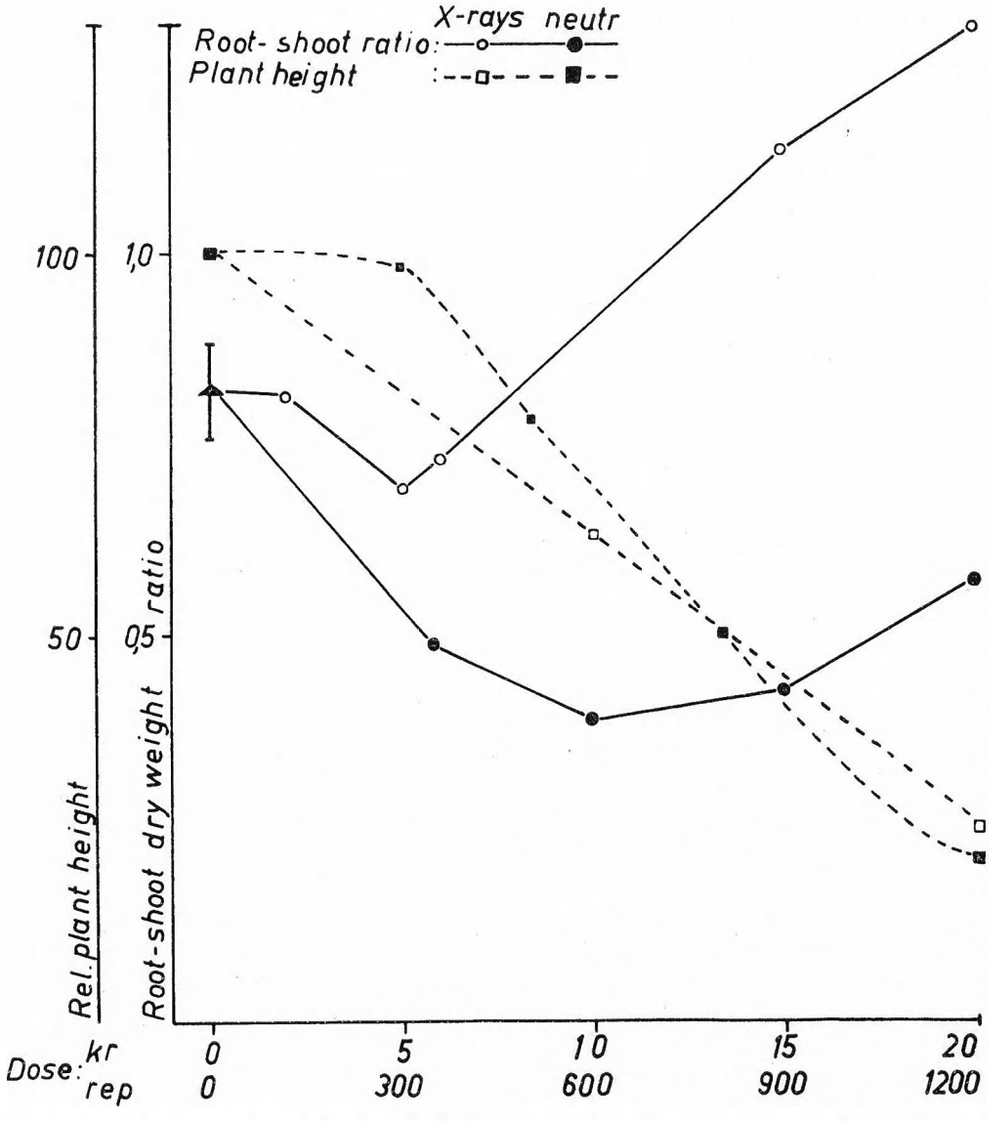

Fig. 5. Root-shoot ratio (dry weights) after irradiation with different doses of neutrons and X-rays. Seedlings cultivated in soil. Points represent averages of 5 experiments with 10 seedlings per sample. Broken lines: relative plant heights (per cent of control).

At higher degrees of inhibition the ratio rose, sometimes to a normal value. This was not surprising, as a maximal root reduction was reached with 50 per cent shoot retardation, the secondary roots having the length at which, under normal conditions, the first mitoses appear. Progressively higher doses chiefly affected the shoot growth to an increasing degree.

The curves express the redistribution processes taking place when the dry matter of the seed (endosperm) is transferred to the shoot and the roots during the initial phase of development. Fig. 5 illustrates the difference in utilization of the dry matter after X-ray and neutron

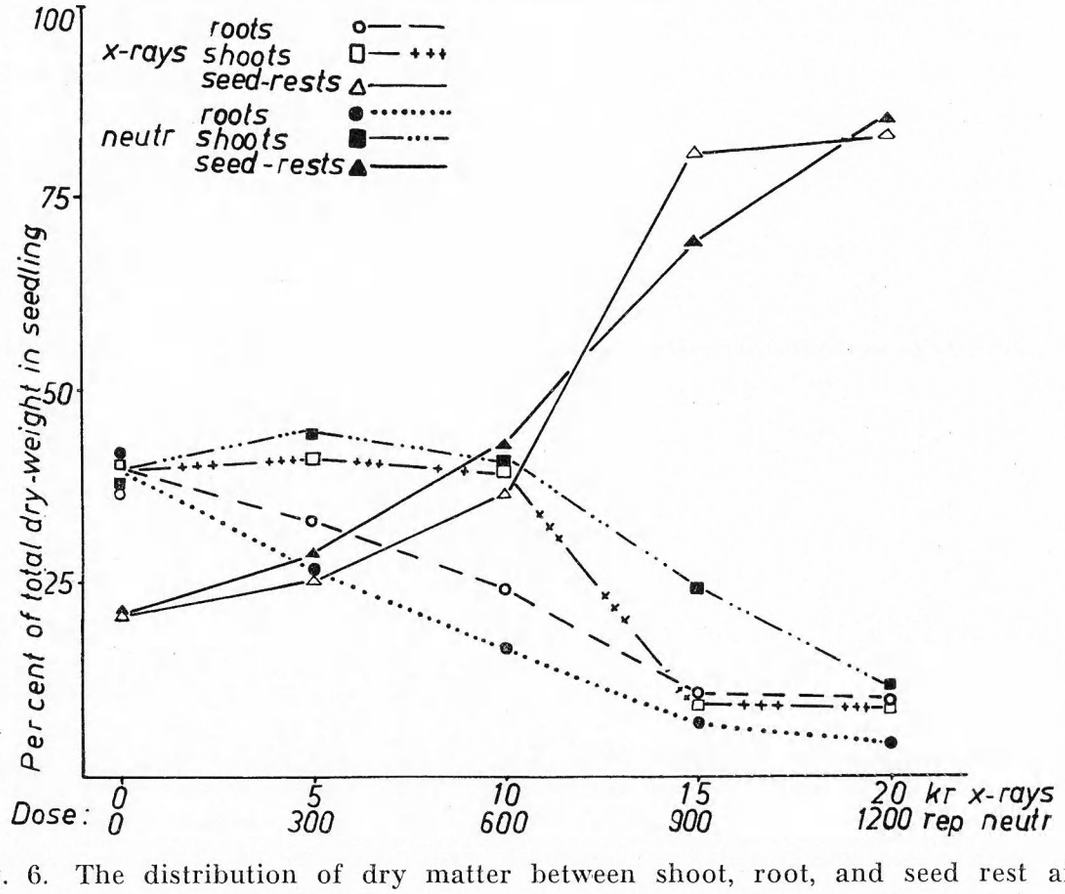

Fig. 6. The distribution of dry matter between shoot, root, and seed rest after irradiation with different doses of X-rays and neutrons. Seedlings cultivated in soil. Sample size: 10 seedlings.

irradiation. For a more detailed analysis, Fig. 6 is given too, and shows the distribution of dry matter, in per cent of the total dry weight, within different parts of the seedlings. Even at low doses the relative dry weight of the seed-rest increased, indicating decreased utilization of the reserve foods. This is equivalent in both types of radiation but especially the neutron type, to a decreased accumulation of dry matter in the roots but only at higher doses in the shoot.

Summing up, the following holds good for root and shoot growth after irradiation, as related to the redistribution of dry matter:

At low X-ray doses: Inhibition of shoot and root growth in the ratio of 1 : 1. Redistribution of dry matter from seed to shoot: normal. Redistribution of dry matter from seed to roots: slightly reduced or normal.

At low neutron doses: Inhibition of shoot and root growth in the ratio of 1: 2. Redistribution of dry matter from seed to shoot: normal. Redistribution of dry matter from seed to roots: reduced.

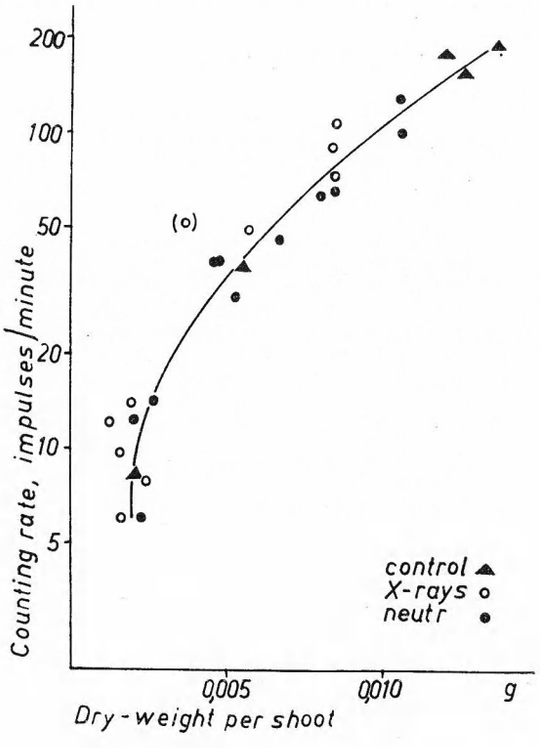

Fig. 7. Rates of phosphate uptake (log scale), as determined from ^{32}P analyses, in shoots of different degree of development. Unirradiated seedlings of different age (4—8 days) compared with 8 day seedlings from X-ray and neutron irradiated seeds. Each point represents a sample of 3—5 seedlings. Standard error of countings 3 %; for the group of low values 5 %. — Point (o): contamination of active solution not excluded. (One impulse per min. corresponds to $0.4 \cdot 10^{-6}$ mmols phosphate per 24 hours per shoot.)

At high X-ray doses: Inhibition of shoot and root growth in the ratio of 1 : 0.5. Redistribution of dry matter from seed to shoot and roots reduced, but *more* material transferred to roots than to shoot.

At high neutron doses: Inhibition of shoot and root growth in the ratio of 1 : 1.3. Redistribution of dry matter from seed to shoot and roots reduced, but *less* material transferred to roots than to shoot.

Phosphate Uptake. — In Fig. 7 the rate of phosphate uptake in seedling shoots is presented as a function of the degree of shoot development (shoot dry weight). In order to vary the degree of development in the control material too, seedlings of different age were used. The curve plotted in Fig. 7 connects the control values, and it may be noted that, within the limits of error, this curve also represents the irradiated samples. There is certainly a slight, though negligible, tendency to higher values in the X-irradiated seedlings as compared to those irradiated with neutrons — a circumstance which, if verified, may be related to the better root growth. Since, within a great part of the range of shoot weights, the root-shoot ratios of the neutron-irradiated samples are less than half of those in the X-irradiated ones (Fig. 5), it may be concluded that the predominant factor determining the phosphate supply of the shoots is the development of the shoots themselves. This is true, at all events, when phosphate ions are abundantly present

in the culture medium. A possible influence of the root systems might amount to about 10 per cent, but due to the great individual variations more extensive experiments would be required to prove whether it exists at all.

Discussion

The developmental inhibition of seedlings caused by ionizing radiations implies a complex disturbance of growth and water balance. Several part reactions can be identified by the application of different sorts of radiation. In the experiments described above, effects concerning the following properties were analyzed: (1) The water content of the shoot; (2) the shoot and root growth; and (3) the dry matter distribution. We can now discuss the possible significance of these properties in X-ray and neutron lesions.

The fact that the habitus of the seedlings seems more "robust" (*cf.* p. 216) after neutron irradiation than after roentgen treatment is evidently attributable to the higher dry matter content or, in other words, to a reduced water content in the neutron shoots.

The simplest explanation of the data presented seems to be that the radicles of the embryo are especially sensitive to densely ionizing radiation, and hence that the low root-shoot ratio after neutron irradiation is directly associated with a selective inhibition of the root growth. This is consistent, moreover, with the observations that neutrons chiefly injure the nuclear material. The first mitoses after the start of germination occur in the roots (*cf.* Wertz 1940) within a concentrated meristematic zone near the root tip. It is readily understandable that destruction of the majority of cell divisions in such a meristem would lead to necrosis of the whole root tip. After X-irradiation, such an effect on the root development is not obtained until very high doses have been given.

There are three plausible explanations of the increased relative dry matter content in the shoot, observed to follow irradiation: (1) The inhibition of the root development after irradiation limits the water supply of the shoot. (2) The processes leading to an increase of the amount of dry matter are less affected by the radiation than is the growth, here defined as change in volume. (3) The water supply of the shoot is indirectly disturbed by radiation effects on the respiration or on auxins:

1. It was found that the roots of seedlings from X-irradiated and neutron-irradiated seeds were able to supply the shoots with a normal

Table 1. Amounts of reducing sugars in 10-day-old shoots from irradiated barley seeds.

Determinations on samples of 10 seedlings. (For analysis, the shoots were cut at the soil surface, *i.e.*, about 1 cm from the seed rests. Especially at the highest doses, a relatively large part of the shoot was therefore left unanalyzed.)

Radiation	Dose	Fresh weight per shoot, mg	Reducing sugars per shoot, mg	% reducing sugars
X-rays	control	127.7	0.50	0.39
	5 kr	121.7	0.41	0.34
	10 kr	91.2	0.82	0.90
	15 kr	55.4	0.56	1.01
	20 kr	50.0	0.30	0.60
Fast neutrons	control	135.5	0.74	0.55
	300 rep	108.9	0.93	0.85
	600 rep	75.7	0.64	0.85
	900 rep	47.7	0.50	1.04
	1200 rep	22.8	0.22	0.97

amount of phosphate, irrespective of the severe injury of the roots after neutron treatment. It is thus indicated that the roots are not out of function. A disturbance of water uptake is nevertheless possible, however, since according to Hanson and Bonner (1954) salt and water absorption are related in such a manner that they may compete for a common energy supply.

2. A preliminary analysis [1] (Table 1) demonstrated that the total amount of reducing sugars per shoot is practically independent of the growth inhibition, at least in the range of moderate doses. These data, as well as the analysis of the distribution of dry matter in different parts of the plant (p. 224), indicate that the increase of dry matter (in the shoot) is not checked simultaneously with the growth. This will, therefore, explain the high dry matter content in shoots of "X-ray" as well as "neutron" plants. The fact that the dry matter content is higher after neutron than after X-ray irradiation seems to be connected with the difference between root-shoot ratios: The relatively strong inhibition of roots, after neutron irradiation, directs the transport of the mobilized reserve foods preferably to the shoot part of the plants.

X-rays might inhibit the growth by nuclear disturbances as well as destruction of enzymes and hormones (*e.g.*, radiosensitive auxins and calines, *cf.* Smith and Kersten 1942). The low doses of neutrons, suf-

[1] After extraction with boiling 95 % ethanol the sugars were titrated *ad modum* Somogyi (1945).

ficient to check growth, and their low chemical efficiency (*cf.* Ehrenberg and Saeland 1954 b, and cited papers), indicate that nuclear disturbances are chiefly responsible for the growth inhibition caused by this radiation.

3. Radiation affects respiration (*cf.* Mikaelsen and Halvorsen 1953, Benedict and Kersten, *l.c.*) and auxins (Smith and Kersten, *l.c.*), which factors are known to influence water uptake (Reinders 1942, Hanson and Bonner 1954). They may, therefore, in part account for the disturbed water supply of the shoot, especially in the case of X-irradiation.

There are, of course, other possible explanations, but those given here have the advantage of lending themselves to immediate experimental verification. Let us state at once, however, that the radiation effects on the water content are not manifested until the fourth day after the start of soaking. Thus they appear during the seedling growth, since the germination ends with the third or fourth day. Seeds irradiated with half a million r-units absorb, during the first three days of germination, the same quantity of water as do the unirradiated seeds. They form roots and coleoptiles. Hence not even the divisions of the first mitotic cycle in the coleorhiza and the coleoptile, which take place within three days of germination (*cf.* Wertz, *l.c.*), are inhibited by the irradiation. Nor is the effect on respiration manifested before the fourth day. Hence the radiation effects described in this paper do not appear before the start of shoot growth.

Field Experiments. — The experience gained demonstrates the mechanism of plant elimination in field experiments conducted with the aim of producing mutations. It has been repeatedly observed that after X-irradiation nearly all plants that have developed their first foliage leaves are able to recover from their injury and continue their growth to maturity, whereas after neutron irradiation many seeds produce normal seedlings, which then suddenly die (*cf.* Nybom *et al.* 1952, Ehrenberg and Anderson 1954, Ehrenberg and Saeland 1954 a). This phenomenon has been interpreted as indicating a predominance of nuclear damage in the neutron treatment. We understand now that the roots of neutron-treated seeds die as soon as cell divisions become of critical importance to the further growth. The poor development of the roots causes the death of the seedlings, probably due to a deficiency of water making the further growth impossible. For the production of mature plants after X-irradiation the limiting factor is, in part, a different one: The seedlings tend to die before they have developed their first foliage leaves. The relatively well developed root

systems allow the surviving seedlings to reach maturity in spite of the injury in the shoot part.

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Zusammenfassung

1. Die Sprosse von 10 Tage alten Gerstenkeimlingen, deren Samen wachstumshemmende Dosen von Röntgenstrahlen und Neutronen erhalten haben, zeigen einen höheren Gehalt an Trockensubstanz als unbestrahlte gleichalte, jüngere oder in der Entwicklung gehemmte Kontrollen. Der Effekt ist nach Bestrahlung mit Neutronen wesentlich stärker ausgeprägt.

2. Das Wurzelwachstum ist bei gleicher Sprosshemmung nach Neutronenbestrahlung stärker als nach Röntgenbestrahlung gehemmt. Das bedeutet eine Senkung des Wurzel-Spross-Verhältnisses auf 0.4 gegenüber dem normalen (0.8). Das nach Röntgenbestrahlung erhaltene Verhältnis schwankt zwischen 0.7 und 1.4.

3. Die Phosphat-Aufnahme der Sprosse ist von der Wurzelschädigung unabhängig und wird allein von der Sprossentwicklung festgelegt.

4. Der elektive Hemmungseffekt von Neutronen auf das Wurzelwachstum wird auf eine spezielle Empfindlichkeit der Wurzelinitialen gegenüber Neutronen zurückgeführt.

5. Die Wurzelschädigung nach Neutronenbestrahlung erklärt das Keimlingssterben in Feldversuchen, das nach parallelen Röntgenbestrahlungen nicht auftritt.

References

BENEDICT, H. M. and KERSTEN, H. 1934. Effects of soft X-rays on germination of wheat seeds. — Plant Physiol. 9: 173—178.

BERNER, N. 1923. Berners planteringsmetod. — Skogen 10: 301—314.

EHRENBERG, L. 1955. The radiation induced growth inhibition in seedlings. — Botan. Notiser 108: 184—215.

— and ANDERSSON, G. 1954. Probable side-effect of nuclear reactions in the biological action of fast protons. — Nature 173: 1086.

— and GRANHALL, I. 1952. Effects of *beta*-radiating isotopes in fruit trees. — Hereditas 38: 385—419.

— GUSTAFSSON, Å., LEVAN, A. and v. WETTSTEIN, U. 1949. Radiophosphorus, seedling lethality and chromosome disturbances. — Hereditas 35: 469—489.

— and NYBOM, N. 1954. Ion density and biological effectiveness of radiations. — Acta Agr. Scand. 4: 396—418.

— and SAELAND, E. 1954 a. Effects of pile radiation on barley seeds. — J. Nuclear Energy 1: 150—169.

EHRENBERG, L. and SAELAND, E. 1954 b. Chemical dosimetry of radiations giving different ion densities. — JENER Jubl. No. 8: 1—25.

HANSON, J. B. and BONNER, J. 1954. The relationship between salt and water uptake in Jerusalem artichoke tuber tissue. — Am. J. Bot. 41: 702—710.

LEFORT, M. and EHRENBERG, L. 1955. L'influence de la teneur en eau des graines sur leur sensibilité aux rayons X. — Arkiv Botan. 3 No. 7: 121—124.

MIKAELSEN, K. and HALVORSEN, H. 1953. Experiments on the respiration of X-irradiated barley seds. — Physiol. Plant. 6: 873—879.

NYBOM, N., GUSTAFSSON, Å. and EHRENBERG, L. 1952. On the injurious action of ionizing radiations in plants. — Botan. Notiser: 343—365.

REINDERS, D. E. 1942. Intake of water by parenchymatic tissue. — Rec. trav. bot. néerl. 39: 1—140.

SMITH, G. F. and KERSTEN, H. 1942. Auxin and calines in seedlings from X-rayed seeds. — Am. J. Bot. 29: 785—791.

SOMOGYI, M. 1945. A new reagent for the determination of sugars. — J. Biol. Chem. 160: 61—68.

THOMAS, M. 1947. Plant Physiology. 3rd ed. — London.

VIRGIN, H. I. and EHRENBERG, L. 1953. Effects of β- and γ-rays on the protoplasmic viscosity of *Helodea* cells. — Physiol. Plant. 6: 159—165.

WERTZ, E. 1940. Ueber die Abhängigkeit der Röntgenstrahlenwirkung vom Quellungszustand der Gewebe, nach Untersuchungen an Gerstenkörnern. I. — Strahlentherapie 67: 307—321.

WETTSTEIN, D. VON 1954. The pleiotropic effects of erectoides factors and their bearing on the property of straw-stiffness. — Acta Agr. Scand. 4: 491—506.

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The Development of Endosperm and Embryo in Cistanche tinctoria (Forssk.) G. Beck

By ABD EL RAHMAN KADRY

Faculty of Agriculture, Ein Shams University, Quobbah Palace, Egypt

The material and method employed have been described in earlier papers (Kadry 1952 and 1953) of which the present paper is a continuation.

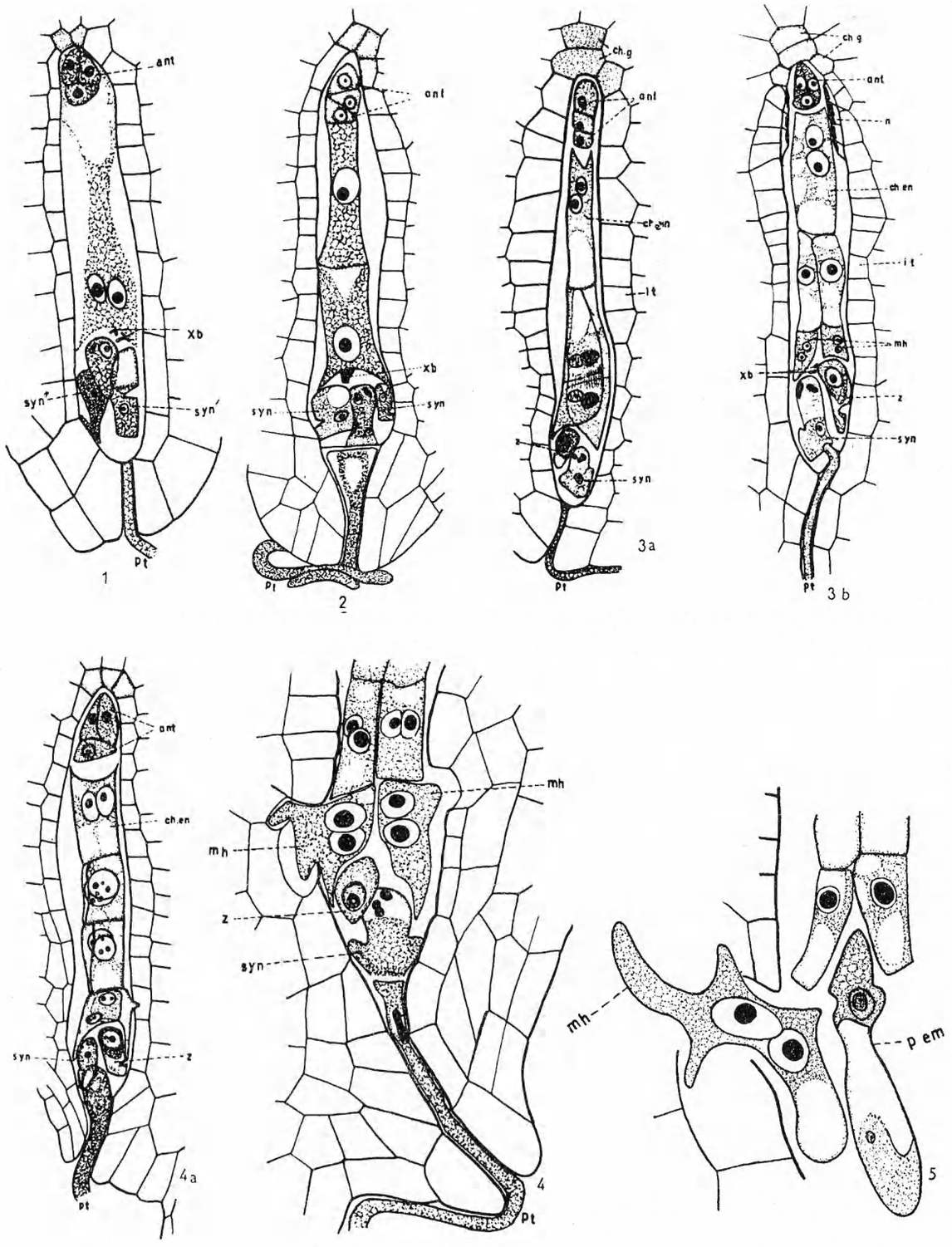
Development of the Endosperm

The endosperm development in *Cistanche tinctoria* is of the cellular type, the same as in the other members of *Orobanchaceae*. The first and the subsequent divisions are usually accomplished by wall formation. The nucleus of the primary endosperm divides very early after its fusion with its male nucleus to form two nuclei (Fig. 1). Cooke and Schively (1904) stated that in *Epiphagus virginiana* the division of the endosperm nucleus begins before fertilization. A transverse wall is formed between the two nuclei, dividing the embryo-sac into two chambers of nearly the same size (Fig. 2). A vacuole begins to appear at the chalazal end of the primary micropylar endosperm cell. The nucleus of each cell divides and then each endosperm cell becomes elongated and binucleated (Fig. 14). The chalazal endosperm cell does not divide further and a large vacuole appears at its micropylar side. Further divisions take place in the micropylar binucleated endosperm cell. A longitudinal wall is formed between the two nuclei, then both nuclei divide simultaneously and transverse walls are formed between the daughter nuclei, separating them into four uninucleate cells (Fig. 3). At this stage the embryo-sac contains five endosperm cells in three tiers. The micropylar tier consists of two haustorial mother cells, the chalazal tier of a binucleate cell and the middle tier of two uninucleate cells which are responsible for the origin of the main body of the endosperm.

Schlotterbeck (1896) believed that in *Orobanchaceae* the micropylar haustoria arise from the synergids. Cassera (1935) and Srivastava (1939) noted that the endosperm in *Orobanchaceae* may develop in one of the two ways designated as type A and type B. In the former, which is the more common, the first division in the micropylar chamber is longitudinal, followed by transverse divisions separating off the micropylar haustorial mother cells from the middle ones which give rise to the endosperm tissue. In type B the micropylar chamber divides transversely, cutting off a micropylar cell and a middle cell. The latter undergoes some further transverse divisions, followed by longitudinal ones giving rise to the body of the endosperm. Koch (1887), Worsdell (1896) and Bernard (1903) observed type B of endosperm development in *Orobanchaceae*. Glisic (1929) and Juliano (1935) have reported that type A of endosperm development is the only method of development in *Orobanchaceae*. Glisic doubts the observations made on type B in this family. Tiagi (1951) supports Glisic's view. The writer has observed in *Cistanche tinctoria* a single type of endosperm development which is the type A recorded by Glisic and Juliano. He has found in a few sections that the endosperm appears at first sight similar to type B; after more careful investigation of these sections and examination of the cell walls of the endospermal cells and their planes of cutting he points out that the cells are very close together. Each tier that appears as a single cell is actually two cells (Figs. 3 a and 4 a). This leaves no doubt that type B is not found in *Cistanche tinctoria*.

Each nucleus of the middle and micropylar tiers of the endosperm cells divides and hence all the cells of the endosperm in the embryo-sac are binucleated. The micropylar haustorial mother cells divide further by transverse walls, giving rise to a number of small cells surrounding the proembryo to form a narrow isthmus (Figs. 6 and 8). Their cytoplasm is densely stained with distinct nuclei. The two terminal micropylar endosperm cells extend further around the suspensor and play an

Figs. 1—5. *Cistanche tinctoria*. — 1: Embryo-sac after fertilization and first division of the primary endosperm nucleus; antipodal cells (ant), pollen tube (pt), living synergid (syn′), degenerating synergid (syn″), bodies (xb). ×250. — 2: Embryo-sac with two primary endosperm chambers. × 250. — 3: Embryo-sac with micropylar endosperm cell showing first longitudinal and then transverse walls. ×200. — a: during mitosis in side view. — b: after the formation of three tiers of endosperm cells; the chalazal tier of a binucleate cell (ch en), the middle tier of two uninucleate cells, the micropylar tier of two binucleate haustorial cells (mh). — 4 a—4: Embryo-sac with four tiers of endosperm cells. ×200. — 4 a: later stage in side view. — 4: the micropylar region of a, showing the aggressive micropylar haustoria growing



Figs. 1—5.

in amoeboid form (mh), the remaining synergid (syn) containing two male nuclei of a second pollen tube (pt), the zygote in a resting state after syngamy (z). — 5: One of the two aggressive micropylar haustorial cells in amoeboid form (mh), the two-celled proembryo (p em) pushing its apical cell in between the isthmus cells of endosperm. ×450.

important part in the formation of the haustoria. Cooke and Schively (1904) stated in *Epiphagus virginiana* that the endosperm cells have grown up around and above the egg cell and form a structure resembling an archegonial neck below the micropyle, having pushed apart the seed coats. Netolitzky (1926) stated in his book on *Orobanchaceae* that the two micropylar haustoria die rapidly and that their remains persist for a long time as a dead mass. Glisic (1929) observed in *Orobanche hederae* that the two micropylar haustoria are strongly hypertrophied, one of them enters the micropyle and the other passes through the integument. Koch (1878) and Srivastava (1939) observed in *Orobanche hederae* and *O. aegyptiaca* respectively that the two micropylar haustoria are prominent only during the early stages of embryonal development. These two latter authors have not demonstrated in their figures the growth of the micropylar haustoria through the integument. Srivastava (1939) established that these cells are formed of a part which is active and consists of two longitudinal rows of cells passing into regular endosperm tissue. Tiagi (1951) stated that in *O. cernua* the two micropylar haustorial cells show vigorous growth and become vesicular, vacuolate and give out intercellular branches ramifying into the integument. Moreover each cell shows an amoeboid hypertrophied nucleus which usually migrates into one of the processes. The writer has observed in *Cistanche tinctoria* that the two micropylar haustoria grow in an amoeboid form and branch with hyphae-like structure, passing through the integumental tissue and becoming very aggressive. Each micropylar haustorial cell has two distinct nuclei and dense cytoplasm (Figs. 4 and 5). They remain in a good state and are active for a long time. Their remains, which are observed inside the embryo-sac close to the suspensor, are their basal parts filled of large vacuoles (Figs. 7 and 8).

Divisions continue in the middle endosperm cells followed by transverse and longitudinal walls, giving rise to the body of the endosperm. On maturation, the embryo-sac increases in length and width and becomes more or less a spherical structure full of a mass of endospermal tissue which becomes filled with starch grains (Figs. 9 and 10). This nutritive material acts as a permanent store until the germination of the seed. The primary chalazal endosperm cell formed after the division of the primary endosperm nucleus becomes separated from the endosperm tissue at the time of the first division of the zygote. Glisic (1929) found in *Orobanche hederae* that a chalazal endosperm haustorium is a single binucleate cell which does not divide any more. Persidsky

(1926) recorded in *Orobanche cumana* and *O. ramosa* that the chalazal haustorium is a large cell which develops with three to four nuclei. It forces the antipodals against the chalaza and then rapidly degenerates. Cassera (1935) observed in *Orobanche uniflora* that the chalazal chamber of the primary endosperm becomes binucleate, elongates and functions as a chalazal haustorium without any more longitudinal or transverse divisions. He described it as an organ representing a stunted haustorium. Srivastava (1939) stated that in *Orobanche aegyptiaca* the chalazal cell is binucleate or sometimes with three to four nuclei and becomes divided by an oblique wall. He described it as an active organ reduced to a small pouch-like structure which soon shows signs of degeneration. Tiagi (1951) stated in *Orobanche cernua* that the nucleus of the primary chalazal chamber divides without wall formation to form a weak two-nucleate haustorium which is long and that a wall is rarely formed between them. The writer has found in *Cistanche tinctoria* that the chalazal endosperm cell is always a binucleate cell without any further division or any more nuclei or walls. It remains in a good state in the early stages of endosperm development.

Glisic (1929) and Cassera (1935) held the same views in respect to the chalazal endosperm. It never becomes as highly developed as the micropylar haustoria, in contradistinction to the conditions found in *Scrophulariaceae* and other *Sympetalae*. This agrees with the observations made by Cassera (1935), Srivastava (1939) and Tiagi (1951, 1952). Denominating this chalazal cell "a haustorium" is wrong, as it never becomes aggressive or grows out of the embryo-sac. The other authors who have dealt with *Orobanchaceae*; Cooke and Schively (1904), Persidsky (1926), Carter (1928), Gurgenova (1928), Finn and Rudenko (1930), Cassera (1935), Juliano (1935), Srivastava (1939) and Tiagi (1951, 1952) have observed that the chalazal endosperm cell never grows or exceeds the limit of the embryo-sac wall and it is weak and less aggressive than the micropylar haustoria and that it rapidly degenerates. Nevertheless they call it "the chalazal haustorium". The writer considers the name "chalazal endosperm" to be more correct in *Orobanchaceae*. Cassera (1935) and Srivastava (1939) believed that the degeneration of the chalazal endosperm cell is due to the pressure exerted by the aggressive endosperm tissue and did not accept the view expressed by Persidsky (1926) that the whole nuclear mass in the chalazal endosperm causes its rapid degeneration. Tiagi (1951) stated that in *Orobanche cernua* the chalazal haustorium is squeezed and reduced to a narrow canal during the development of the seed due to

the enlargement of the adjacent endothecial cells, and finally the encroachment of the endosperm cells crushes it. In 1952 he stated that in *Cistanche tubulosa* in later stages of development, the chalazal endosperm haustorium becomes pressed and squeezed by the enlarging cells of the integumentary tapetum and is flattened to a narrow canal. The writer has observed in *Cistanche tinctoria* that the chalazal endosperm cell does not come so close to the rest of the endosperm cells, neither to the antipodal cells nor to the integumentary tapetum. It contains a large vacuole on both upper and lower ends. In respect to these conditions the writer is of the opinion that the degeneration of the chalazal endosperm cell does not occur by the pressure exerted from the endosperm or from the impetus of the nuclei which are not massive. As it becomes functionless, it appears as a weak cell and degenerates gradually together with the antipodal cells.

Netolitzky (1926 p. 289) stated that starch grains are absent from the endosperm of *Orobanchaceae,* and it contains aleurone grains and proteins. Tiagi (1952) has found in *Cistanche tubulosa* that large quantities of oil and starch are stored in the endosperm. The writer has found in *Cistanche tinctoria* that starch grains in big granules fill up the whole tissue of the endosperm except the outer limiting layer (of the endosperm in the mature seed) which contains aleurone grains and proteins without any starch grains (Fig. 10). The chalazal end of the embryo-sac forms a pouch-like structure which pushes slightly through the chalazal cells of the ovule. The chalazal endosperm cell and the antipodals remain in this chalazal pouch till they become completely degenerated.

Development of the Embryo

After fertilization, the male and the female nuclei remain unfused inside the egg cell for a long period during which the primary endosperm nucleus is active. The vacuole originally present in the basal part of the egg cell gradually disappears and the cytoplasm assumes a fairly homogeneous appearance (Fig. 11 b). Juliano (1935) observed in *Aeginetia indica* that the zygote remains dormant for a considerable time after the endosperm formation has commenced. Syngamy takes place in *Cistanche tinctoria* at the five- to seven-celled endosperm stage. The zygote has an oval-like structure and undergoes another period of rest. The endosperm continues in its activity and growth. The zygote begins its first division at about the fifteen-celled endosperm stage with

eighteen-nuclei. During the division of the zygote nucleus a vacuole appears again at its basal part (Fig. 11 d). According to Souéges (1939, 1941), Schnarf (1929) and Johansen's (1945, 1950) classification of the principal types of embryonal development in Angoisperms, the embryo of *Cistanche tinctoria* develops like the Caryophyllad type. The zygote divides by a transverse wall giving two unequal cells (Fig. 11 e). The basal cell *cb* enlarges and becomes vacuolated, taking the form of a large vesicle with its small degenerating nucleus. It undergoes no further division. It is surrounded by the two micropylar haustorial cells. It pushes the terminal cell in between the narrow isthmus region of the endosperm (Fig. 5). The terminal cell *ca* is exceedingly rich in cytoplasm. A vacuole appears at its micropylar end. It elongates in a tubular form (Fig. 11 f). It divides by a transverse wall during the second cell generation resulting in two cells *cc* and *cd* (Fig. 11 g). Each cell has a prominent nucleus and is rich in cytoplasm. The embryo at this stage comprises three tiers namely *cb, cd,* and *cc*; each tier consists of one cell. The middle cell *cd* becomes more elongated and slender in a filamentous form. A large vacuole fills up the majority of its basal and distal parts. It pushes up the apical cell *cc* into the endosperm.

Koch (1878) described in *Orobanche hederae* that the suspensor is a single filamentous cell. Worsdell (1896) stated that in *Christisonia subacaulis* the suspensor is a single empty cell developed from the basal cell of the two-celled proembryo. Cooke and Schively (1904) established in *Orobanche virginiana* that the suspensor is of four or five cells. Persidsky (1926) reported in *Orobanche cumana* that the embryo develops a long suspensor consisting of a row of cells. Cassera (1935) mentioned that in *Orobanche uniflora* the suspensor is always unicelled and is soon resorbed by the embryo. Juliano (1935) stated that in *Aeginetia indica* the suspensor is a single cell and soon degenerates. Srivastava (1939) mentioned that in *Orobanche aegyptiaca* the suspensor is an elongated structure and sometimes consists of a number of cells. Tiagi (1951, 1952) stated that in *Orobanche cernua* and in *O. aegyptiaca* the suspensor consists of three cells derived from the basal cell, and that in *Cistanche tubulosa* the suspensor is a single, long, tapering cell situated between the cells of the narrow isthmus region of the endosperm. The writer has found in *Cistanche tinctoria* that the suspensor consists of two cells: one is derived from the basal cell as a large vesicle *cb* and the other *cd* develops from the terminal cell *ca* and elongates in a filamentous tube. These two cells of the suspensor degenerate and disappear at about the twelve-celled proembryo. The

terminal cell *cc* of the three-celled proembryo divides by a transverse wall giving two cells *m* and *c* (Fig. 8). The apical cell *c* undergoes two longitudinal divisions to form four cells in one tier. The subterminal cell *m* divides by a transverse wall, forming two cells in two tiers (Fig. 11 h, i). This is followed by another transverse division, resulting in three to four cells linearally arranged (Fig. 11 j). Transverse and longitudinal walls appear in the terminal tier forming an oval body which is the embryo proper (Fig. 11 k). It is entirely devoid of even the rudiments of cotyledons, root tip, stem tip or other customary embryonal region.

Koch (1878) observed in *Orobanche hederae* the radicle and the plumule in the old embryo. Johansen (1950) has mentioned that the embryos of *Orobanche hederae, O. eryngii* and *O. cumana* develop in accordance with the Onagrad type, and *Christisonia subacaulis* and *Aeginetia indica* as belonging to the Caryophyllad type. The writer has found in *Cistanche tinctoria* that the embryo develops in accordance

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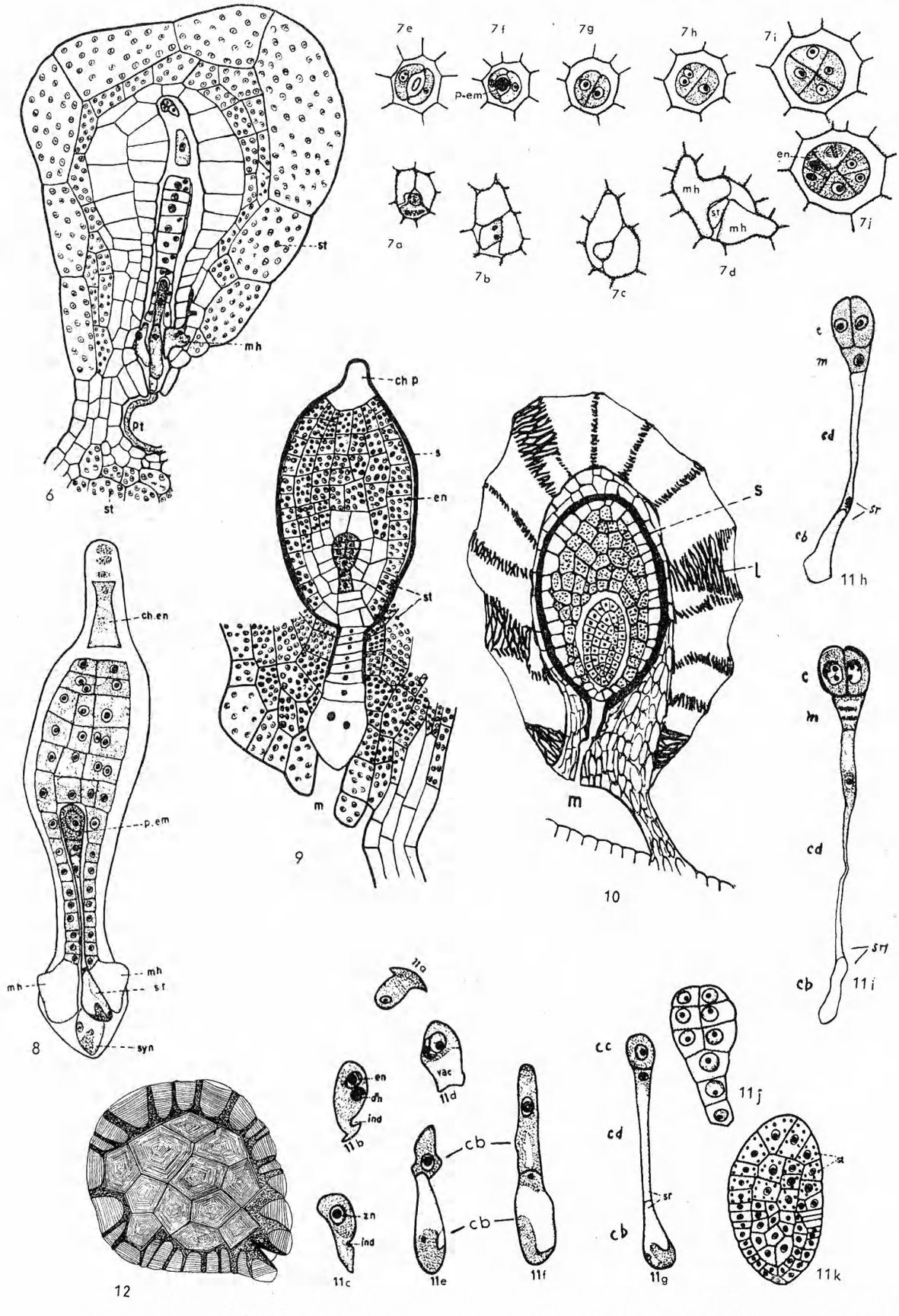
Figs. 6—12. *Cistanche tinctoria* in longitudinal section with two-celled proembryo, showing the free chalazal endosperm cell, micropylar haustorial cell (mh) penetrating the integumentary tissue, pollen tube (pt), starch grains (st). ×100. — 7 a—j: Series of transverse sections in an embryo-sac of two-celled proembryo (p.em), endosperm cells (en), micropylar haustorium (mh), the vesciular cell of the suspensor (sr). ×200. — 8: Embryo-sac showing four-celled proembryo (p.em), chalazal endosperm cell (ch.en) and antipodals degenerating, enlarged vacuolated basal parts of the micropylar haustorial cells (mh), two-celled filamentous and vesicular suspensor (sr), remains of the synergid (syn). ×200. — 9: Part of an old ovule in longitudinal section showing proembryo with degenerating suspensor, pouch-like chalazal end of the embryo-sac (ch p), endosperm (en) and integumentary tissue full of starch grains (st), micropyle (m), suberised layer of the integumentary tapetum (s). ×100. — 10: Longitudinal section in a mature ovule showing the lignified pitted and reticulate outer layers of the integument (l), the micropyle (m), the suberised inner layer of the integumentary tapetum (s), the outer layer of the endosperm free of starch grains, the oval mature embryo. ×50. — 11: Different stages of syngamy, proembryo and embryo development. — a: egg cell before fertilization. — b: after the entrance of the male nucleus; egg nucleus (en), indentation (ind), male nucleus ♂n). — c: after syngamy; zygote nucleus (zn). — d: the first division of the zygote nucleus; vacuole (vac). — e: two-celled proembryo. — f: the same as d showing the elongated terminal cell (by error called cb instead of ca) and the basal vesicular cell (cb). — g: three-celled proembryo. — a—g ×250. — h: five-celled proembryo. — i: more advanced stage of proembryo. — h—i ×300. — k: mature embryo with small starch grains filling its upper region. ×100. — 12: Surface view of a mature seed with small depressions in the reticulate lignified testa, beakshaped micropyle (m). ×150.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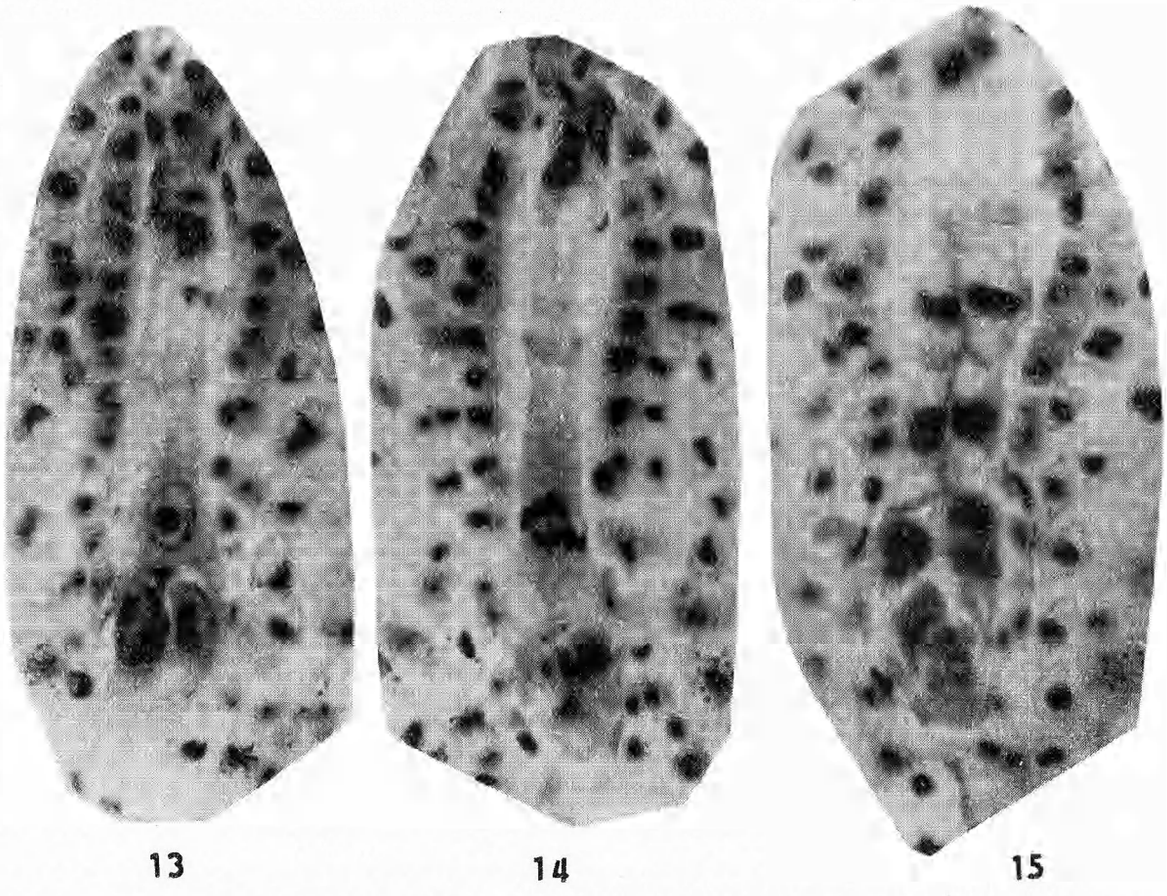
Figs. 6—12.



Figs. 13—15. *Cistanche tinctoria.* — 13: Embryo-sac with two primary endosperm chambers, photomicrograph of Fig. 2. — 14: Photomicrograph of an embryo-sac showing mitosis in the micropylar chamber (in longitudinal division) and a binucleate endosperm cell. — 15: Embryo-sac with four tiers of endosperm cells, photomicrograph of Fig. 4.

with the Caryophyllad type. He has observed starch grains of small granules fill up nearly half the embryo cells which are towards the chalazal side. This is not reported earlier in any member of *Orobanchaceae.*

Development of the Seed

The outermost cells of the integumentary tapetum become enlarged and lignified with reticulate and pitted thickenings (Fig. 10). They give rise to a hard testa of dark brown colour (Fig. 12). A narrow canal is left at the micropylar end in a beak-shaped micropyle (Figs. 10 and 12). The middle layer of the integument degenerates. Netolitzky (1926) and Tiagi (1951) stated that a cutinised layer is formed both from the outer layer of the endosperm and the inner layer of the integument. The writer has found in *Cistanche tinctoria* that this layer surrounding the

endosperm is formed only from the inner layer of the integument without any interference of the endosperm cells and that it is suberised. The seed is minute of globose structure. The fruit is a capsule of two valves. It dehisces in the anteroposterior plane along two furrows found on the pericarp.

The Nutritive Mechanism

The nutritive mechanism in *Cistanche tinctoria* is very complicated and efficient. Starch grains are very common and stored in the following tissues: in the epidermis and in the endothecium of the anthers (Kadry 1952); in the stylar tissues; in the placentae of the ovaries; in the epidermis of the ovules; in most of the integumentary tissues surrounding the embryo-sac (Kadry 1953); in the mature endosperm cells of the seed; and in the cells of the embryo proper which are towards the chalazal side.

The nutritive substances are absorbed by the embryo-sac during its development in different ways: a) From the nucellus by the growing embryo-sac. b) From the group of the chalazal cells of the ovule by the antipodals. c) From the integumentary tapetum by the developed embryo-sac. d) Possibly from the placentae by the pollen tubes. e) From the integumentary tissue by the amoeboid hyphae-like micropylar haustoria which are very aggressive and branched.

Summary

1. The endosperm is cellular. The first division is transverse resulting in two chambers, the primary micropylar and the primary chalazal endosperm cell.

2. The chalazal endosperm cell is a weak binucleate cell and does not act as a haustorium.

3. The primary micropylar cell of the endosperm divides first by a longitudinal wall, then by transverse walls resulting in four cells arranged in two tiers; the lower tier is the two micropylar haustorial mother cells, the upper tier is two cells which divide by transverse and longitudinal walls to form the spherical body of the endosperm.

4. The micropylar haustorial cells are very active. They grow aggressively in the integumentary tissue in an amoeboid form.

5. The chalazal endosperm cell together with the antipodals degenerate after the two-celled proembryo.

6. The mature endosperm becomes full of starch grains except in its outer layer close to the inner integumentary layer.

7. The first division of the zygote usually occurs at the fifteen-celled endosperm stage.

8. The embryo develops according to the Caryophyllad type.

9. The suspensor is two-celled. The micropylar cell of the suspensor becomes enlarged and vesicular; the terminal cell becomes elongated in a tubular and filamentous form.

10. The embryo is undifferentiated and devoid of cotyledons, radicle and plumule. The chalazal half of the embryo body is full of small starch grains.

11. The endosperm is surrounded by a thin layer of suberin originating from the integumentary tapetum. The outer layers of the integuments become lignified in reticulate and pitted thickenings.

12. The seed coat is hard and reticulate with small depressions.

13. The seeds are minute and numerous.

14. The fruit capsule dehisces in the antero-posterior plane.

Acknowledgments

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References

BERNARD, CH. 1903. Sur l'embryogénie de quelques plantes parasites. — Journ. de Bot. 17.

CARTER, K. M. 1928. A contribution to the cytology of the ovule of Orobanche minor. — Jour. Roy. Micro. Soc. 48: 389—403.

CASSERA, J. D. 1935. Origin and development of the female gametophyte, endosperm and embryo in Orobanche uniflora. — Bull. Torrey Bot. Club. 62: 455—466.

COOKE, E. & SCHIVELY, A. F. 1904. Observations on the structure and development of Epiphagus Virginiana. — Cont. Bot. Lab. Univ. Penn. 2: 252—398.

FINN, W. W., & RUDENKO, T. 1930. Spermatogenesis und Befruchtung bei einigen Orobanchaceae. — Bull. Jard. Bot. de Kieff. 11: 69—82.

GLIŠIC, L. M. 1929. Über die Endosperm- und Haustorienbildung bei Orobanche hederae duby und Orobanche gracilis. — Bull. Inst. Jard. Bot. Univ. Belgrade. 2: 106—141.

GURGENOVA, M. 1928. Fertilization in Phelipaea ramosa. — Nawashin Festschr. 157—168.

JOHANSEN, D. A. 1945. A critical survey of the present status of plant embryology. — Bot. Rev. 11: 87—107.

— 1950. Plant embryology. A new series of plant Science Books. 24. New York.

JULIANO, J. B. 1935. Anatomy and morphology of the Bunga, Aeginetia indica L. — Philippine Jour. Sci. 56: 405—451.

KADRY, A. 1952. The development of microsporangium and pollen grains in Cistanche tinctoria (Forssk.) G. Beck. — Bot. Not. 1952: 46—57.

— 1953. The development of the female gametophyte in Cistanche tinctoria (Forssk.) G. Beck. — Svensk Bot. Tidskr. 47: 488—508.

KOCH, L. 1875. Ueber die Entwicklung des Samens der Orobanchen. — Jahrb. Wiss. Bot. 11: 218—261.

KOCH, L. 1878. Ueber die Entwicklungsgeschichte des Samens der Orobanchen. — Jahrb. Wiss. Bot. 11: 218—261.

— 1887. Entwicklungsgeschichte der Orobanchen. — Heidelberg.

NETOLITZKY, F. 1926. Anatomie der Angiospermen — Samen. — Linsbauer Handbuch der Pflanzenanatomie. X, Berlin 1926.

PERSIDSKY, D. 1926. Zur Embryologie der Orobanche cumana Wall. und der Orobanche ramosa L. — Bull. Jard. Bot. de Kieff. 4.

SCHLOTTERBECK, 1896. Beitrage zur Entwicklungsgeschichte pharmakognotisch wichtiger Samen. — Bern.

SCHNARF, K. 1929. "Embryologie der Angiospermen." Berlin.

SRIVASTAVA, G. D. 1939. Contribution to the morphology of Orobanche aegyptiaca Pers. — Proceeding of the National Academy of Sciences, India, 9: 58—68.

SOUÈGES, R. 1939. Embryogénie et classification. Deuxième fascicule. Essai d'un système embryogenique. — Actualités Sci. et Indust. 781: Paris, Hermann et Cie.

— 1941. Variantes dans les deux premiers groupes des périodes de in classification embryogénique. — Bull. Soc. Bot. France. 88: 602—608.

TIAGI, B. 1951. Studies in the family Orobanchaceae. 111. A contribution to the embryology of Orobanche cernua Loeffl. and O. aegyptiaca Pers. — Phytomorphology, 1: 158—169.

— 1952. Studies in the family Orobanchaceae. I. A contribution to the embryology of Cistanche tubulosa Wight. — Lloydia. 15: 129—148.

WORSDELL, W. C. 1896. On the development of the ovule of Christisonia. — Jour. Linn. Soc. Bot. 31. London: 576—584.

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On some Fructifications borne on Glossopteris Leaves

By J. SEN

Botanical Laboratory, University College of Science, Calcutta

Introduction

The outstanding discovery of the ovulate organs borne on *Glossopteris* leaves [1] in the Middle Ecca (Lower Permian) beds of South Africa (Plumstead 1952) opens the possibility of the occurrence of similar fertile materials from other parts of the Gondwanaland. Since then the present author has collected several types of such fructification from Murulidih Collieries of the Ranigunj stage (Upper Permian, India). This brief paper may, therefore, be considered as a subsequent development of Plumstead's (1952) excellent contribution to our knowledge of the enigmatic *Glossopteris*. It is hoped that some of the questions raised by different authorities (Edwards, Harris, Thomas, and Walton — see Plumstead 1952) regarding the nature of the fructifications and the systematic position of *Glossopteris* as envisaged by Plumstead (1952) may now be partly answered here. In another paper the present author has also described the probable pollen bearing organs of *Glossopteris* with a view to further elucidate the confusing situation (Sen, unpub.).

The shaly roof of the thick bituminous Mohuda coal seam at Murulidih Collieries is astonishingly rich in plant fossils. The fertile materials are plenty. In most of the cases the fructifications are in detached condition, but at least in some they are convincingly attached to two species of *Glossopteris* fronds. The fossils are generally in the form of compression in which occasionally thin carbonised patches are present. The maceration ($KCLO_3$ in HNO_3) and transfer techniques have been employed in some cases, the latter method without any success, for ascertaining the nature of such fructifications.

[1] Organic connection between a reproductive structure of the type described by Plumstead (1952) (i.e., *Scutum*) and *Glossopteris* has first been clearly figured by Zeiller (1902) as *Ottokaria bengalensis*.

Description and Interpretation of Fructifications borne on Glossopteris Leaves

The types of fructification borne on two species of *Glossopteris* are not at all in agreement with the structure of the genus *Scutum* proposed by Plumstead (1952) or any of the known species of *Ottokaria* (Zeiller 1902, Seward and Sahni 1920, Thomas 1921) and other supposedly fertile organs assigned to *Glossopteris* (Arber 1905). However, they resemble Plumstead's (1952) genus *Lanceolatus* fairly well.

The fructifications are associated with large leaves of *Glossopteris communis* (Fig. 1) and a species of *Glossopteris* (Fig. 2) which is not properly determinable because of broken specimens. This species is closely comparable to *Glossopteris browniana.* But unfortunately the fructification of *G. browniana,* i.e., *Scutum leslium,* as described by Plumstead (1952), is characteristically different from the one referred to here. So this leaf is obviously not *G. browniana.* To avoid nomenclatorial difficulties no names have been proposed by the present author for these two types of fructification. They should for the present be known as ovulate organs of *Glossopteris communis* and *Glossopteris* sp. (Figs. 1—2) respectively.

In both the cases the fructification is protected by a broadly lanceolate boat-shaped covering bract-like appendage (or cupule as Plumstead, 1952, calls it) (Figs. 1—2). It is sessile and grows from the midrib of a leaf, about one-third of its length from the base. There is practically no difference between a fertile leaf and a vegetative one. The so-called cupule is distinctly veined, and larger than the fertile surface which is covered by it. The two types of fructification are distinguishable by their sizes. They are also borne by different species. In *G. communis* it is about 43×14 mm, whereas it is about 18×8 mm in *Glossopteris* sp.

The fertile cushioned surface, which has been observed only in the case of *Glossopteris* sp., is borne directly on the leaf surface itself. It exhibits in surface view many embedded small apparently (at least) oval sacs measuring about 1 to 2 mm (Fig. 3).

It is difficult to determine whether the fructification is foliar as suspected by Plumstead (1952) or axillary to the leaf bearing it (Edwards 1952, Walton 1952). Plumstead (1952) has, however, later pointed out that the possibility of the axillary nature of the fructification is apparent in some *Lanceolatus* where its base has fused to the leaf petiole and midrib. The development process may be similar to that exists in *Helwingia* or *Tilia* as described in Rendle's (1952) text book.

The axillary nature is specially evident in *Lanceolatus* where the 'midrib of the leaf is noticeably hollowed below the head, presumably because the stalk of the fructification has disappeared and left its mould'. A specimen of *Scutum* also 'presents a profile view of the junction of the two stalks'.

A vertical compression of young fertile region, occurring in close proximity to *Glossopteris* leaves, necessitates reinterpretation of the morphological nature of the fructification as described by Plumstead (1952). It follows from the Fig. 5 that there is a thick central cylindrical axis (the apparent thickness is possibly partly due to slight oblique flattening) directly bearing (?possibly spirally arranged) oval embedded sacs, without megasporophylls or ovuliferous scales, about 1.6×0.5 mm in size. Such a possibility has earlier been theoretically envisaged and figured by Walton (1952) and also presumed by Edwards (1952). Since the specimens examined by the present author lack characteristic wing, almost as in *Lanceolatus,* the tubular appendages as shown by Walton (1952) are missing in the fossil in question. In view that the fructification types described by the present author and those by Plumstead (1952) are all Glossopterid and that they are basically of similar nature, it is difficult to accept Plumstead's (1952) interpretation of their morphology. The fructification is, therefore, a strobilus or cone-like body, and at least in some cases remains under the protection of a large bract-like structure.

Plumstead (1952) has most logically established the ovulate nature of the reproductive genera she described. The present author has since variously attempted to recover plant tissues from some specimens wherein occasionally very thin and small carbonised flakes are present. Unfortunately the carbonised substances do not yield anything of significance. But macerated rock matrix adhering to the fructifications often leaves interesting plant structures consisting of cutinised nucellus (1.05—1.5×0.5—0.72 mm) with or without remnants of integumental(?) tissues (Figs. 6—7), thick brownish seed-like structures without any

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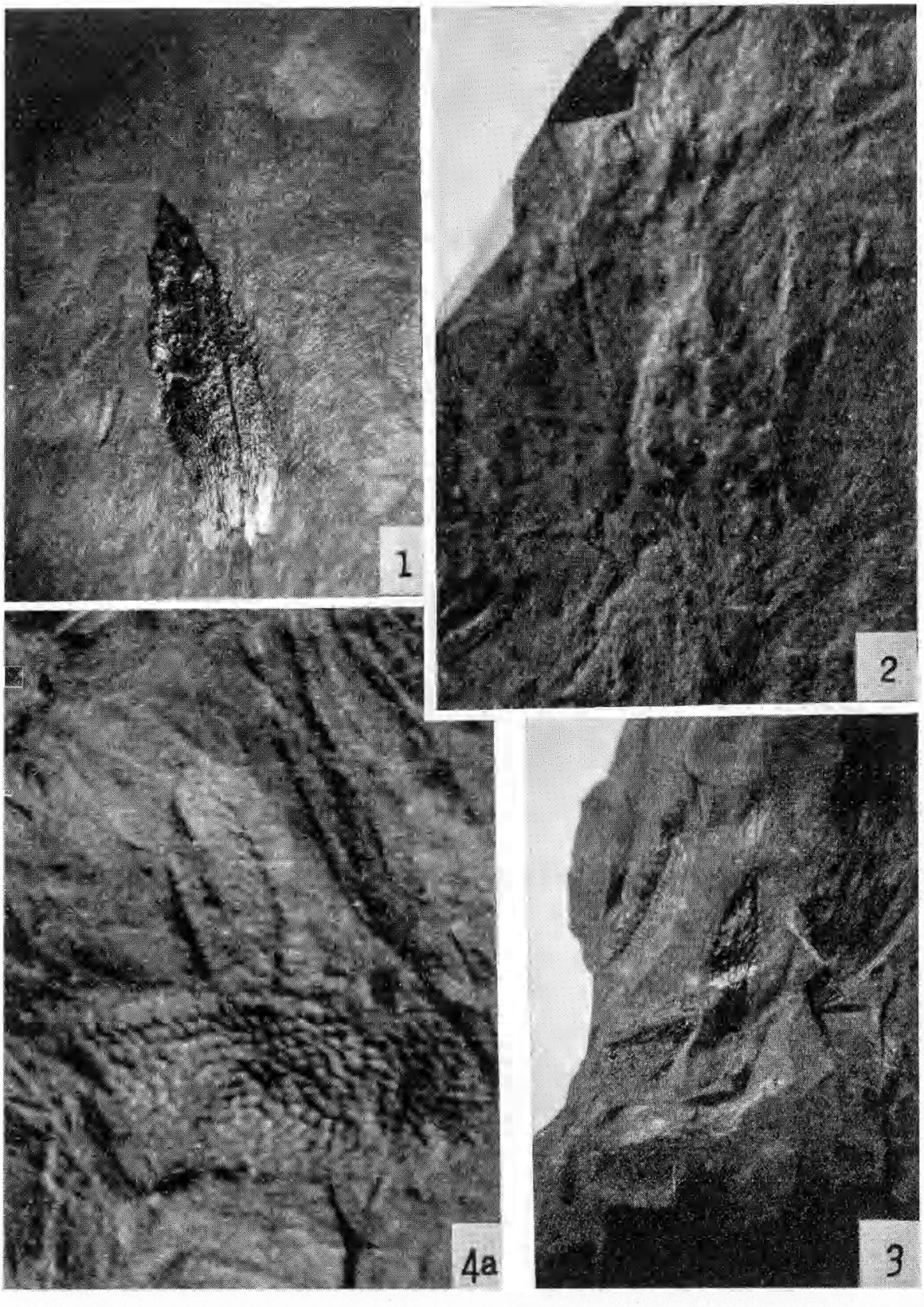
Fig. 1. *Glossopteris communis* showing the protective bract-like covering of the fructification borne on the midrib. — Nat. size.

Fig. 2. *Glossopteris* sp. in association with a fructification. — $\times 2\,1/2$

Fig. 3. *Glossopteris* sp. showing broken margins and a characteristic fructification with a few raised sac-like ovules or seeds. — Nat. size. The leaf surface immediately below the fructification has been rubbed.

Fig. 4 a. Detached fructifications with narrow wing and characteristic sac-like ovules. — a $\times 2\,1/2$.



Figs. 1—4 a.

definite embryo and variously decomposed amorphous substances. The probable micropylar region of the nucellar structures is often associated with adhering pollen of *Pityosporites* type (Fig. 7) (assigned to *Glossopteris* by Virkki 1945, Ghosh and Sen 1948, Sen 1948, 1953). The size and shape of these isolated nucellus with disintegrated integumental(?) tissues are generally more or less similar to or slightly less than those of the ovular sacs in the compressions, specially in the vertically compressed fructification. Naturally, therefore, it may not be difficult to assume that the ovulate structures in the rock matrix adhering to the compression fossils are of the same types which actually belong to the fossils themselves. The ovulate nature of the fructifications is thus more firmly established.

The *Scutum* type of compression fossils with radiating wing-like appendages (of the fertile cupule as Plumstead, 1952, says) are also plenty in detached condition (Figs. 4 a, b). They are measured as 14—28×7—15 mm including the wing expansion of 1.5—2 mm only. The wing is, therefore, relatively narrow in the Indian fructifications as compared to the species of *Scutum* described by Plumstead (1952). Whether this wing is formed by a number of minute cupules or sheaths, as suggested by Walton (1952), is difficult to determine.

In one case a *Scutum* type of fructification, as described in the foregoing paragraphs, appears to be attached to the transverse groove of a *Vertebraria* axis (Fig. 4 b). Since the present author has observed only a single specimen, he does not intend to indulge in speculating about the previously held relationship between *Vertebraria* and *Glossopteris,* which view has now been virtually discarded (Thomas 1952 b). Only additional findings of similar nature may reopen the consideration of the old idea that *Vertebraria* is related to *Glossopteris.*

It may also be mentioned that all types of well developed detached and a few attached (at least apparently mature) fructifications are not

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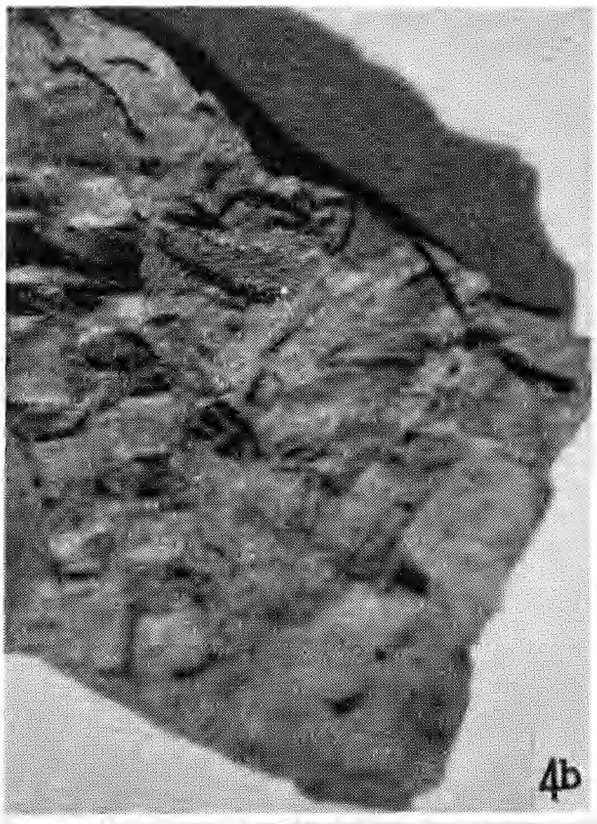
Fig. 4 b. One of the fructifications is attached to the transverse groove of the axis of *Vertebraria.* — Nat. size.

Fig. 5. Vertical compression of a fructification showing a thick cylindrical axis directly bearing oval embedded sacs without megasporophylls or ovuliferous scales. — ×4 1/2.

Fig. 6. Cutinised nucellus (in association with a few *Pityosporites* type of pollen) partially within disintegrating integument-like(?) tissues. — ×50. Recovered from the rock matrix immediately below a Glossopterid fructification following oxidative maceration and subsequent alkali treatment.

Fig. 7. Cutinised nucellus with adhering *Pityosporites* type of pollen on both sides of the probable micropylar region. — ×50. Recovered as in the previous case.



Figs. 4 b—7.

associated with the characteristic bract-like covering. This means that the protective cover falls off after a fructification matures possibly to facilitate pollination by wind. Since the characteristic double winged *Pityosporites* type of pollen has been assigned to *Glossopteris* (Virkki 1945, Ghosh and Sen 1948, Sen 1948, 1953) there is no difficulty in assuming, in conformity with Plumstead (1952), that *Glossopteris* is anemophilous rather than entomophilous as suggested by Edwards (1952).

Systematic Position of Glossopteris

It is probable that the so-called *Glossopteris* 'fruit' is a strobilus or cone-like body axillary to the leaf bearing it, and that the oval sacs are naked ovules or seeds. If this morphological interpretation as described in the foregoing paragraphs is accepted, which is in general agreement with the suggestions of Walton (1952) and Edwards (1952), the old intriguing question as to the systematic position of *Glossopteris* reopens.

Plumstead (1952) has placed the genus under the Pteridosperms (in an extended sense than hitherto known), which has been variously accepted by Thomas (1952) and Harris (1952). Thomas (1952) is, however, more inclined to profess the unique nature of the vegetative and reproductive organs as unknown among the known plants. Even angiospermous nature has been suggested for *Lanceolatus* by Harris (1952). Indeed the general architectural plan of the foliage and the cuticular structure of at least *G. angustifolia* (Sahni 1923) are angiospermous, and together with the nature and organisation of the ovulate organs (specially of *Lanceolatus* type) suggest the unique possibility of the occurrence of modified angiosperms in the Palaeozoic. Possibly the evolution of closed ovary among the Mesozoic Caytoniales with foliage of *Glossopteris* type (*Sagenopteris*) link up the Palaeozoic *Glossopteris* with the later dicotyledons. Such a possibility has already been discussed by Sahni (1938).

The present author is inclined to follow the suggestions forwarded by Edwards (1952) that the genus belongs to some unknown or imperfectly known group of gymnosperms. Undoubtedly the genus now includes characters of the Pteridosperms, stachyosporae (as redefined by Lam 1948) and dicotyledons. The supposedly male fructifications of *Glossopteris* (Sen, unpub.) and their pollen of *Pityosporites* type (assigned to *Glossopteris* by Virkki 1945, Ghosh and Sen 1948, Sen 1948, 1953), however, do not significantly help in solving the present problem.

The well knit southern genus *Glossopteris* thus occupies an unique position among the naked-seeded plants, and most probably it is in some ways related to the origin of angiosperms. The origin of flowering plants in some regions of the late Palaeozoic and Mesozoic southern Gondwanaland is indeed a possibility which may explain the problem of their sudden arrival in the north at a later date (Thomas 1947).

Summary

Two new types of fructification borne on the midrib of *Glossopteris* leaves collected from the Ranigunj stage (Upper Permian) of the Indian Lower Gondwana have been described in this paper following the discovery of related types from the Lower Permian of the South African Gondwanas. Several types of detached fructification, closely resembling the South African forms, have also been noted. The fossils are in the form of compression.

The materials from the two countries are compared, and reinterpretation of their morphology has been found necessary in the light of the fossils described here and the suggestions of some authorities. In contrast to the original conclusion of Plumstead (1952) it is believed that the fructification is a strobilus or cone-like body possibly axillary to the leaf bearing it. The ovules are directly borne by a thick cylindrical central axis without any appended ovuliferous scale or megasporophyll. The whole fertile surface develops under the protection of a bract-like covering which possibly falls off after the fructification matures.

The new interpretation, as above, reopens the intriguing question of the systematic position of the *Glossopteris*. It has been suggested that the genus belongs to some unknown or imperfectly known gymnosperms rather than Pteridosperms as believed by Plumstead (1952), with widely diffused characters of several phyla of gymnosperms (and possibly also of dicotyledons).

I gratefully acknowledge my indebtedness to Mr. K. Rawal, Assistant Manager, Murulidih Collieries, Mohuda, for extending to me all facilities to collect the materials, and to Mr. S. K. Bhattacharya for photographing some of the specimens.

Literature cited

ARBER, E. A. N., 1905: Catalogue of the fossil plants of the Glossopteris flora in the British Museum. — London.

EDWARDS, W. N., 1952: Discussion on the "Description of two new genera and six new species of fructifications borne on Glossopteris leaves". — Trans. Geol. Soc. South Afr., 55, 321—322.

GHOSH, A. K., and SEN, J., 1948: A study of the microfossils and the correlation of some productive coal seams of the Ranigunj coalfield, Bengal, India. — Trans. Min. Geol. Met. Inst. Ind., 43, No. 2, 67—95.

HARRIS, TOM M., 1952: Discussion on the "Description of two new genera and six new species of fructifications borne on Glossopteris leaves". — Trans. Geol. Soc. South Afr., 55, 322.

LAM, H. J., 1948: Classification and the new morphology. — Acta Biotheoretica, 8, 107.

PLUMSTEAD, EDNA P., 1952: Description of two new genera and six new species of fructifications borne on Glossopteris leaves. — Trans. Geol. Soc. South Afr., 55, 281—328.

RENDLE, A. B., 1952: The classification of flowering plants. — Cambridge University Press.

SAHNI, B., 1938: Recent advances in Indian Palaeobotany. — Presid. Addr., Bot. Sec., Proc. 25th Ind. Sci. Congr., 137.

— 1923: On the structure of the cuticle in *Glossopteris angustifolia* Brongn. — Rec. Geol. Surv. Ind., 34 (3), 277—280.

SEN, J., 1948: Microfossils and nature of coal in some Indian coal seams. — Proc. Ind. Sci. Congr., Geol. & Geogr., Pt. 3 (Abstract), 113.

— 1953: Principles and problems of microfloral correlations of Indian coal seams with special reference to Karharbari coalfield. — Bull. Nat. Inst. Sci. India, No. 2, 139.

— Unpub.: On the male fructifications assigned to *Glossopteris*.

SEWARD, A. C., and SAHNI, B., 1920: Indian Gondwana plants: A revision. — Pal. Indica, 7 (1), 12.

THOMAS H. HAMSHAW., 1921: An Ottokaria-like plant from South Africa. — Q.J.G.S., 77 (4), 285—288.

— 1947: The history of plant form. — Advancement of Sci., 4, 243—254.

— 1952: Discussion on the "Description of two new genera and six new species of fructifications borne on Glossopteris leaves". — Trans. Geol. Soc. South Afr., 55, 321.

— 1952 b: A Glossopteris with whorled leaves: — The Palaeobotanist, 1, 435—438.

VIRKKI, C., 1945: Spores from the Lower Gondwanas of India and Australia. — Proc. Nat. Acad. Sci. Ind., 15, Pts. 4—5, 93—176.

WALTON, J., 1952: Discussion on the "Description of two new genera and six new species of fructifications borne on Glossopteris leaves". — Trans. Geol. Soc. South Afr., 55, 322—323.

ZEILLER, R., 1902: Observations sur quelques plantes fossiles des Lower Gondwanas. — Pal. Indica, N.S., 2 (1), 34—35.

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Enteromorpha intermedia

A new Species from the Coasts of Sweden, England and Wales

By CARL BLIDING

Borås, Sweden

Already in 1943 I collected at Stockevik in the vicinity of the marine zool. station Kristineberg on the west coast of Sweden an *Enteromorpha*-species, which in its anatomical characters showed an intermediate position between *E. prolifera* and *E. ahlneriana* on one side and *E. clathrata* on the other. By means of cross-breeding experiments it was established that the new type did not conjugate neither with *prolifera* nor with *clathrata* (*ahlneriana* has only asexual reproduction). However, my material was only about 20 specimens and from the same habitat, too, and therefore I put off publishing it as a new species.

In the summer of 1953 I found the same alga on the coast of Anglesey, North-Wales. Also in Plymouth I got living material of the species in question, collected by Miss D. Ballantine. The material from Great Britain was brought alive to Sweden, was held in culture medium during the winter and then in the summer of 1954 it was compared with living Swedish material, found that summer in a great number of specimens in waters of very different salinity.

The experimental work was for the most part carried out at Kristineberg, where the Swedish Academy of Science has given me room for my work during many summers.

I also wish to express my deep gratitude to Dr D. J. Crisp, Bangor marine biolog. laboratory, North-Wales, to Mr F. S. Russel, F.R.S., and to Dr M. Parke, Plymouth, who received me with the greatest kindness and granted me room for my laboratory experiments.

Further I wish to thank the algologists Dr Parke, Plymouth, Dr Martin, Bangor, and Miss Davey, Bangor, for valuable information.

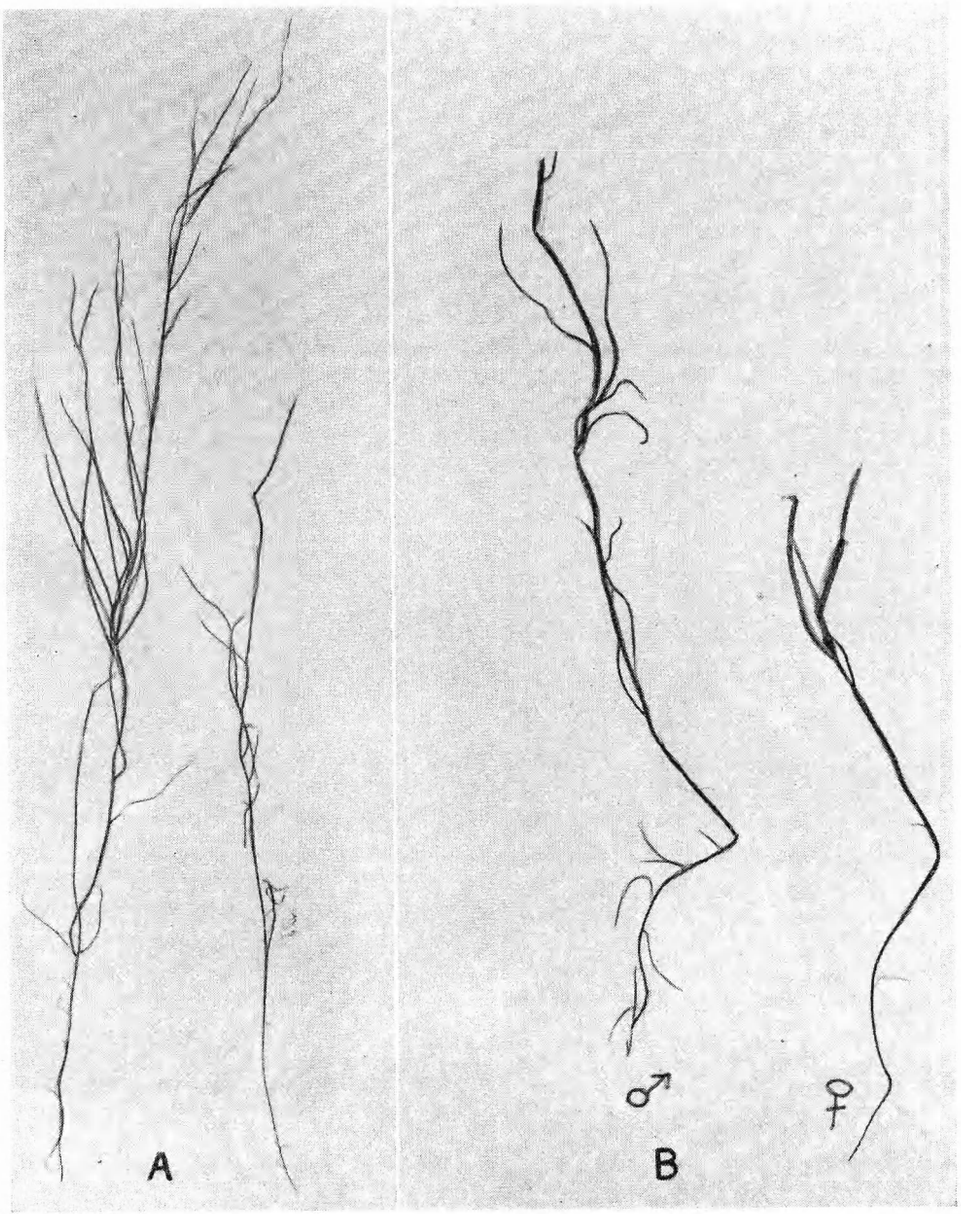

Fig. 1. *Enteromorpha intermedia.* A: from Rhosneigr, North-Wales. — B: from Teignmouth, Devonshire. — Nat. size.

Occurrence

Enteromorpha intermedia grows in the littoral zone, attached to rocks, stones, shells etc., mostly in quiet water, but also in moderately exposed shores. My Swedish material is partly from Bohuslän: Stockevik (June—August 1943 and 1954), Kristineberg (July—August 1954), Källviken (a rich occurrence in the ferry-harbour together with *Enteromorpha prolifera, ahlneriana, clathrata* and *compressa,* June—August 1954), Uddevalla (in the brackish water of shallow bays July—August 1954) and partly from Halland: Varberg (western side of

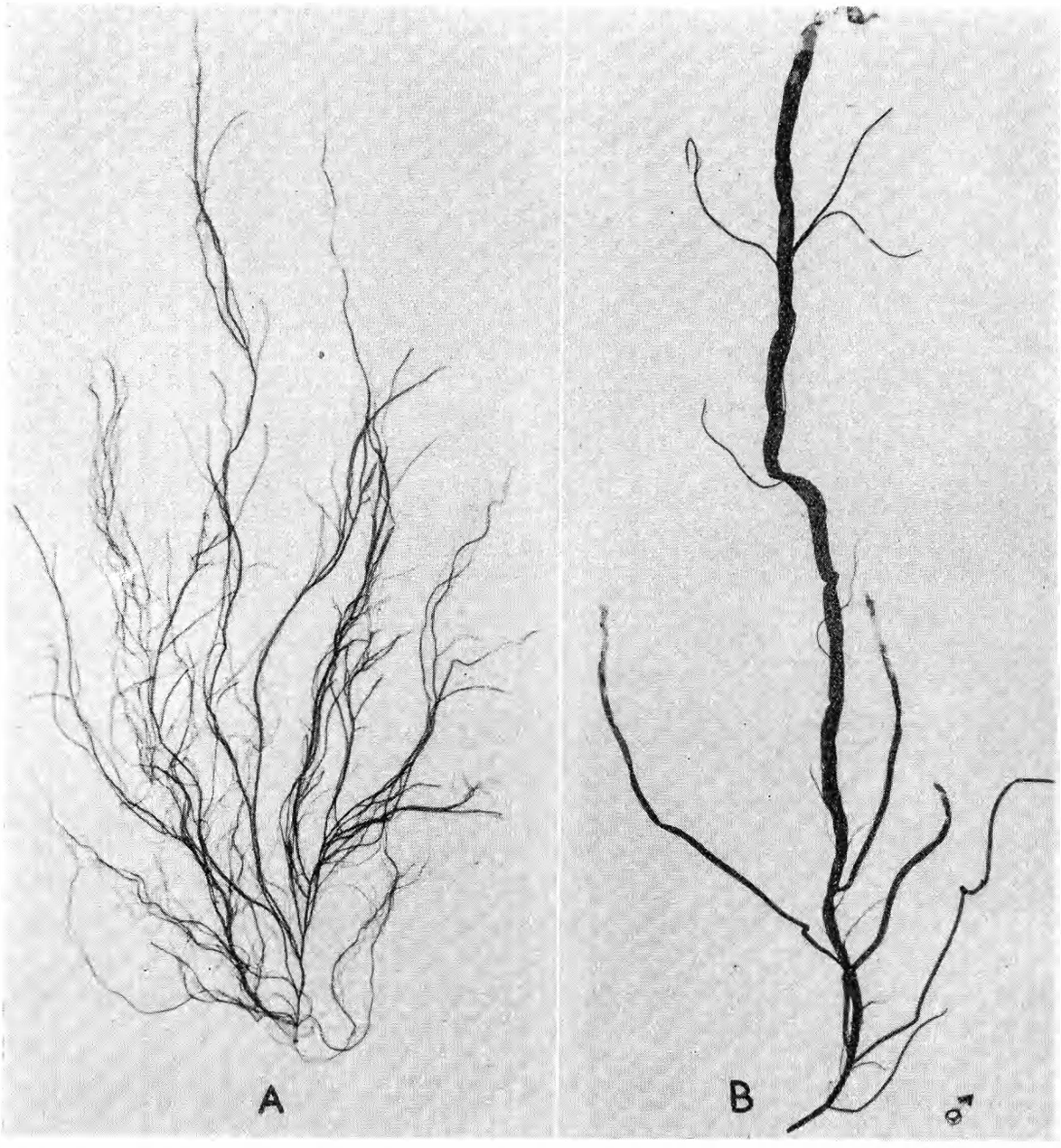

Fig. 2. *Enteromorpha intermedia.* A: from Källviken. — B: from Uddevalla. — Nat. size.

Getterön August—September 1954). The living material from Great Britain was collected in North-Wales, Anglesey, Rhosneigr, June 1953 and in Devonshire, Teignmouth, July 1953.

The investigated material has in all amounted to about 400 living plants.

Habitus

The plants (Fig. 1—2) were always branched, either with slight to fairly close typical ramification (Fig. 2 A) or with sparse prolification-

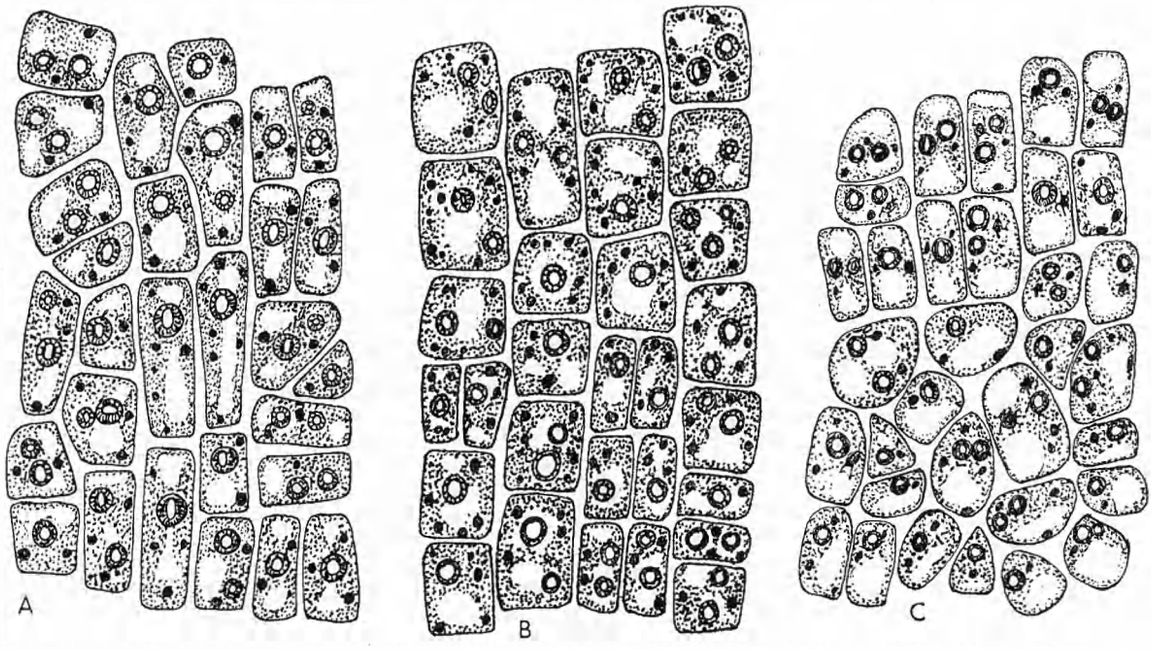

Fig. 3. *Enteromorpha.* Cells from the main stem in material from A: Teignmouth. — B: Kristineberg. — C: Kristineberg, below showing rounded, almost unordered cells (see the text). — ×600.

like branches (Fig. 2 B). Especially the plants in the normally salt water at Rhosneigr (Fig. 1 A) were very soft with slender stem, repeatedly branched or proliferous, as a rule only 0.2—0.5 mm broad. In the brackish water of Uddevalla the plants were mostly proliferously branched and the main stem was sometimes up to 5 mm broad.

Anatomy

As the name will allude to, *E. intermedia* in its anatomy holds a noticeable intermediate position between the *clathrata*-group and the *prolifera—ahlneriana*-group.

The cells are, compared with those of other *Enteromorphae,* of medium size to rather large, taken as an average they are larger than in *prolifera* but smaller than in *clathrata.* However, the dimensions of the cells are very varying as appears in the Figures 3—4, showing the lower and middle part of the main stem. The full-grown cells in the stem reach a maximal length of c. 28 μ and a breadth of c. 13 μ. Seen in surface view they are rectangular or square, characteristically angular with a medium size of about 18 μ×10 μ. These cells show a striking resemblance to the cells of *Enteromorpha biflagellata* (Bliding 1944

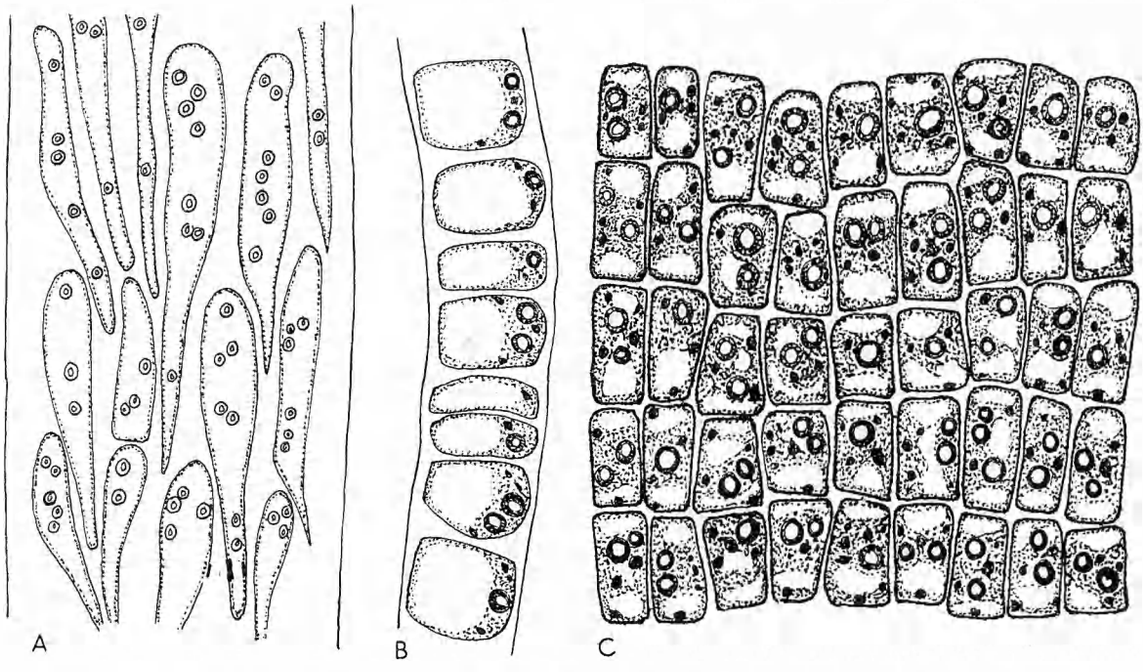

Fig. 4. *Enteromorpha intermedia.* A: cells from the main stem, 0.5 mm from the base-disc. — B: cross-section. — C: main stem with cells in longitudinal and transverse rows. — ×600.

p. 347, Fig. 20). In plants with somewhat broader main stem (Fig. 2 B) the cells are smaller, 10—18 μ×7—10 μ.

In the Swedish as well as in the Welsh material there were plants, which besides such typical, angular cells had shorter and more rounded cells, c. 13 μ×12 μ or smaller (Fig. 3 C, lower part).

The pyrenoids of the cells are 1—2, rarely 3(—4), often very large. Only in the lowest part of the main stem up to c. 1 mm from the basal disc, where the cells are sometimes especially elongated (Fig. 4 A) there occur a greater number of pyrenoids in each cell.

Table 1 shows that practically all the cells of the main stem have 1 or 2 pyrenoids (cf. *clathrata* Bliding 1944, Tables 1—3, *kylinii* 1948 p. 2 and *biflagellata* 1944 p. 347, Table 6), and that the percentage of the 1-pyrenoidal cells varies within wide limits in different populations and in different plants of the same population. Even in the same plant there occurs such a variation in various parts of the main stem.

The arched, sometimes almost cuff-shaped chloroplast occupies the larger part or only the apical part of the exterior wall of the cell.

As a rule the cells are arranged in distinct longitudinal rows, even in the lowest part of the main stem (cf. *clathrata* Fig. 6 C and 1944 p. 333, Fig. 2). Here and there in the main stem as well as in the branches

Table 1. Enteromorpha intermedia. Pyrenoids in medium part of the main stem.

Localities	Number of counted cells with			
	1 pyrenoid	2 pyren.	3 pyren.	4 pyren.
North-Wales, Rhosneigr I ...	340 (= 65 %)	174	6	1
» , » II ...	203 (= 59 %)	142	2	0
Devonsh., Teignmouth I	288 (= 58 %)	208	4	0
» , » II.....	255 (= 44 %)	315	8	1
Kristineberg I.....	243 (= 39 %)	366	11	0
» II	294 (= 41 %)	402	16	1
Källviken I	405 (= 67 %)	164	14	3
» II.....	390 (= 51 %)	345	20	5
» III	134 (= 27 %)	310	41	3
Uddevalla	160 (= 37 %)	240	25	4
Sum total	2712 (= 49 %)	2666 (= 48 %)	147	18

the cells are ordered in transverse rows (Fig. 4 C), which give the thallus a characteristically striated appearance. When a part of the stem has more rounded cells (above p. 257), new cells are often formed by oblique walls, through which the arrangement in longitudinal rows becomes more vague. This is seen in the Fig. 3 C, where a zone of cells similar to the cells of *E. intestinalis* and *compressa* meets a zone of angular, longitudinally well-ordered cells, typical of *E. intermedia*.

The Life-history

E. intermedia has a dioecious gametophyte-generation of female and male plants and a sporophyte-generation of the same morphology and anatomy as the sexual plants. Culture experiments, starting from zygotes resp. zoospores have given evidence of the alternation of generations.

E. intermedia is anisogamous in conformity to other sexual *Enteromorpha*-species except *E. kylinii* (1948 p. 3, Table 1). To establish this fact hundreds of freshly liberated male and female gametes from different localities were drawn and measured.

The male gametes (Fig. 5 B) had a mean length of 5.6 μ (varying from 4.9 to 6.1 μ) and a mean breadth of 2.2 μ (varying from 1.7 to 2.7 μ).

The female gametes (Fig. 5 A) were 6.0—7.3 μ long and 2.9—4.0 μ broad with the mean values of 6.5 μ and 3.3 μ.

These values are valid only for just liberated gametes, which round rather soon. The remarkably greter breadth (c:a 50 %) of the female

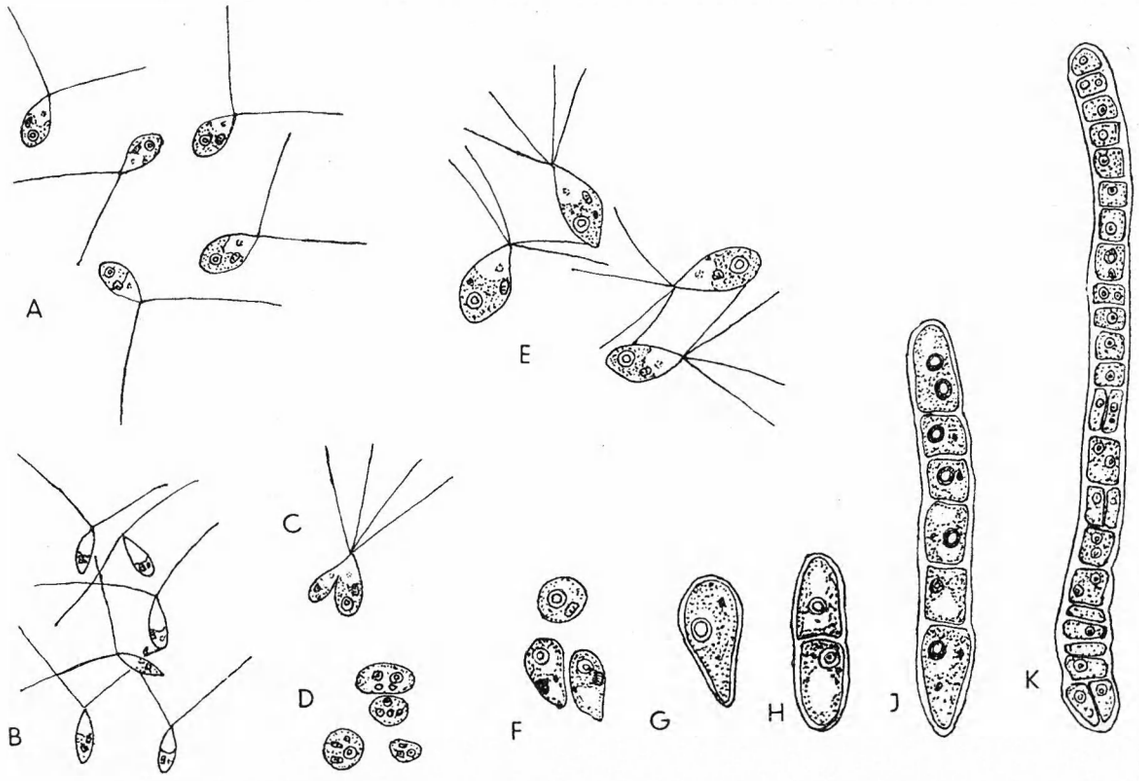

Fig. 5. *Enteromorpha.* A: female. — B: male gametes. — C: conjugation. — D: zygotes, germinating, 20 hours. — E: zoospores. — F: zoospores, germinating, 20 hours. — G—K: development of the zoospores. — A—C and E ×900, D and F—I ×600, K ×310.

gametes makes it possible to decide (after some training) the sex of a swarm of gametes direct in the microscope, with a small magnification. The gametes have the same organization as that of other *Enteromorphae* as to the eye-spot, chloroplast (smaller in the male gamete) and pyrenoid (often undistinct).

Male gametes as well as female are capable of developing parthenogenetically (Table 2).

Sexual plants from Wales and the South of England showed a clear cross-fertility between themselves and also conjugated with material from all above-mentioned localities of the west coast of Sweden.

Conjugation-experiments further proved, that *E. intermedia* does not conjugate with *E. prolifera, clathrata* and *kylinii.*

The 4-ciliate a little flattened zoospores (Fig. 5 E) are formed mostly to the number of 16 in the middle-sized, fertile cell. They have a mean

Table 2. Enteromorpha intermedia. Development of gametes, zygotes and zoospores in the material from North-Wales.

1/8—5/8	♂-gametes developed into	1—2	cells;	only c. 12 % germinate.
	♀-gametes „ „	2—4	„ ;	germinate well.
	zygotes „ „	3—6	„ ;	germinate very well.
	zoospores „ „	10—12	„ ;	„ „ „ .
31/7—8/8	♂-gametes developed into c. ..	40	cells.	
	♀-gametes „ „ „ ..	70	„ .	
	zygotes „ „ „ ..	80	„ .	
	zoospores „ „ „ ..	250	„ ;	ramification already begun.
31/7—13/8	plants from ♂-gametes	1	cm high;	few ramifications.
	„ „ ♀-gametes	1.5	„ „	more ramified.
	„ „ zygotes	1.5	„ „	more ramified.
	„ „ zoospores	3.0	„ „	more ramified.

length of 9.6 μ (varying from 9.0—10.3 μ) and a mean breadth of 5.3 μ (the broadest side).

The first germinating stages of the zoospores are shown in Fig. 5 F—K. Table 2 shows the development during the first two weeks of plants from male and female gametes, zygotes and zoospores. The young plants of *intermedia* have a remarkable slenderness compared with germinating plants of *clathrata*. The development from zoospores to fertile sexual plants and from zygotes to fertile zoospore-plants was performed in culture medium in 4—6 weeks in the summer.

Conclusions

The above described mostly proliferously ramified *Enteromorpha* with middle-sized to rather large angular cells in distinct rows in the whole thallus or parts of it, with 1 and 2 pyrenoids, alternation of generations, anisogamous gametophyte conjugating with no other *Enteromorpha* with ordered cells, must be considered as a clearly independent species, well distinguished from the more or less resembling *E. ahlneriana, prolifera, clathrata* and *kylinii*.

When parts of the thallus sometimes have rounded cells without a very plain arrangement in distinct series, these parts are similar to *E. intestinalis* and *compressa,* but naturally there need not be any confusion with these species, which have only 1 pyrenoid in their cells and no distinct cellrows.

How to distinguish *E. intermedia* anatomically from *ahlneriana, prolifera* and *clathrata* is shown in the Fig. 6, drawn from living specimens, all of them found growing together with *E. intermedia* in the ferry-harbour of Källviken.

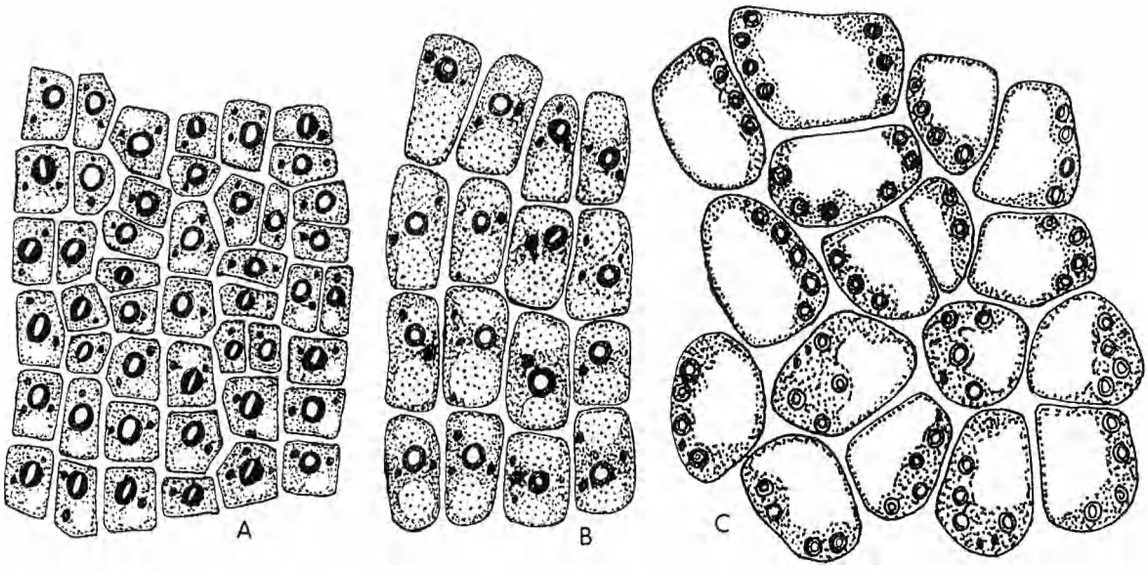

Fig. 6. Cells from the main stem of 3 *Enteromorphae,* growing together with *E. intermedia* (see the text). A: *E. prolifera.* — B: *E. ahlneriana.* — C: *E. clathrata,* from the lowest part of the main stem, where the cells are not arranged in distinct rows. — ×600.

The chief characters, separating *prolifera, ahlneriana, clathrata* and *kylinii* from *intermedia* are as follows:

E. prolifera: smaller cells with 1 pyrenoid (1939 p. 137); no conjugation with *intermedia.*

E. ahlneriana: 1 pyrenoid; no alternation of generations, only asexual reproduction with 4-ciliate zoosporoids.

E. clathrata: typical ramification; large cells with mostly 2—several small pyrenoids (1944, Table 1—3); no conjugation with *intermedia.*

E. kylinii: very long simple branches in a plaited mass; pyrenoids as in *clathrata*; isogamous, no conjugation with *intermedia.*

E. intermedia is evidently related to *E. biflagellata,* from which it is anatomically distinguished only by small differences, inter alia as to the pyrenoids (1944, Table 6). However, *biflagellata* has another life-history (only asexual reproduction with 2-ciliate, large zoosporoids), and therefore it must be interpreted as a separate type. As it is rather difficult to keep *intermedia* and *biflagellata* apart on non-living material, I think it is more practical — for the present, at any rate — to join them in the same species-name, naturally then *intermedia,* and place *biflagellata* either as a subspecies or a variety.

Under the name of *E. pilifera* Kg, Waern (1952 p. 37) has investigated an *Enteromorpha* from fresh water in Uppland, Sweden. Last autumn Dr Waern and fil. mag. T. Willén sent me living material of this alga. Hitherto it has not become fertile, but judging from its anatomy it is nearly related to *E. intermedia.*

In fresh water in the vicinity of Concarneau, Brittany, France, and in the brackish water of the canal at Velsen, Holland, I collected in the summer of 1952 an *Enteromorpha,* which will be separately described and referred to *E. intermedia.* I have also investigated a variety of *E. intermedia* from the coast of U.S.A., sent alive here by Dr Maxw. Doty.

E. intermedia evidently has a very wide distribution and occurs in waters with different degrees of salinity.

Diagnosis

Planta mollissima, gracilissima, pallide virens—virens. Caulis c:a 5—30 cm altus, 0.2—3(—5) mm latus, ramosus — ramis saepissime rare positis, inferioribus longissimis — sive parce prolificans. Cellulae caulis usque ad 28 μ×13 μ, series longitudinales et nonnumquam transversales formantes, angulares, plerumque rectangulares (c:a 18 μ×10 μ) sive passim rotundatae (c:a 13 μ×12 μ) et subseriatae.

Pyrenoides cellularum plerumque 1 et 2, raro 3(—4), saepe majusculi. Anisogameta: ♂-gametum c:a 5.6 μ×2.2 μ, ♀-gametum c:a 6.5 μ×3.3 μ, quorum utrumque parthenogenetice germinat. Zoosporae, depressae, c:a 9.6 μ×5.6 μ.

Literature cited

BLIDING, C., 1933: Über Sexual. und Entwicklung bei der Gattung *Enteromorpha.* — Sv. Bot. Tidskr. 27. Uppsala.

— 1939: Stud. über Entwickl. und Systematik in der Gattung *Enteromorpha* II. — Bot. Not. Lund.

— 1944: Zur Systematik der schwedischen Enteromorphen. — Bot. Not. Lund.

— 1948: *Enteromorpha Kylini,* eine neue Art aus der schwedischen Westküste. — Kungl. Fysiogr. Sällskapets förhandl. 18. Lund.

KYLIN, H., 1949: Die Chlorophyceen der schwed. Westküste. — Lunds Univ. Årsskr. N.F. Avd. 2, 45. Lund.

WAERN, M., 1952: Rocky-shore algae in the Öregrund Archipelago. — Acta Phytogeogr. Suecica 30. Uppsala.

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Cytotaxonomical Studies on the Mediterranean Flora

By KAI LARSEN

Plant Anatomical Institute, University of Copenhagen

I. Introduction

While the North European phanerogamous flora has been rather thoroughly studied cytologically, the rich Mediterranean flora is still very unsatisfactorily investigated in spite of the publication of several works on this subject especially during recent years.

In June 1954 the present author stayed in southern Italy at the Danish institution San Cataldo, situated in the mountains above Amalfi on the South side of the Sorrento Peninsula. I wish to express my best thanks to the Board of Directors of this institution for the stay, and to Frederichsens Legat, whose grant made this journey possible.

During the stay some fixations of flower buds, and a number of collections of seeds were made in the environs of San Cataldo in order to provide material for the counting of chromosomes, and for cultivation experiments. This material was later supplemented by some fixations made in the Botanical Gardens of Copenhagen. Some few results concerning the genus *Lotus* have already been published (Larsen 1955).

The flower buds have been fixed in Nawashin-Karpechenko's fluid, with a short pretreatment with Carnoy, and stained after Feulgen. The root-tips were fixed in Nawashin-Karpechenko's fluid after being germinated on filter paper in Petri-dishes, and were stained with gentian-violet.

All the species examined are treated apart. The plants which have been fixed, are in all cases preserved as herbarium material and kept in the Plant Anatomical Institute of the University of Copenhagen.

An asterisk in front of the name of the species indicates that the chromosome number is here reported for the first time, or that it deviates from the one previously counted.

II. Species Studied

Ranunculaceae

Ranunculus cortusaefolius Webb et Berth. — This species is endemic to the Canary Islands and Madeira. The material studied originates from the Botanical Gardens of Trinity College, Dublin, Eire, from where it was received as seeds, and now cultivated in the Botanical Gardens of the University of Copenhagen (H. B. H.). The chromosome number was determined at n=8 in PMC and 2n=16 in RT. The meiosis was normal with 8 bivalents. These results are in accordance with those of Langlet (1936).

Cruciferae

Aethionema saxatile R. Br. — This calciphilous species, which is distributed all over the Mediterranean region, has been studied in material from Italy: plant growing on dry chalk rooks above Minute, alt. 550 m (No.: S.C. 13). The chromosomes of the meiotic complement are rather uniform, 24 bivalents were observed in all the metaphase plates. The same number was found by Jaretzky (1930 b).

Lobularia maritima Desv. — A common Mediterranean species the chromosome number of which has been determined by Jaretzky (1928) at 2n=24. The same number was counted by me in a fixation from Italy: dry grassland vegetation in scree in Valle d. Ferriera opposite to Pogerola, alt. 550 m (No.: S.C. 20).

Rosaceae

**Poterium spinosum* L. — An East Mediterranean species distributed from Sardinia and Djamur (at Cape Bona) in the West, to the Amanus Mts., Antilebanon and Transjordania in the East, in Africa it is found in Northern Cyrenaica. The chromosome number of this species was counted at 2n=28 (Fig. 1 a), the same number has been found in many other species of *Poterium*. The material studied was fixed in November 1954 in H. B. H. (No.: 6374/8) from a plant originating from the Botanical Gardens in Paris.

Crassulaceae

Sedum dasyphyllum L. — A polymorphous Central European-Mediterranean species. Baldwin (1939) counted the number 2n=28, 42, and

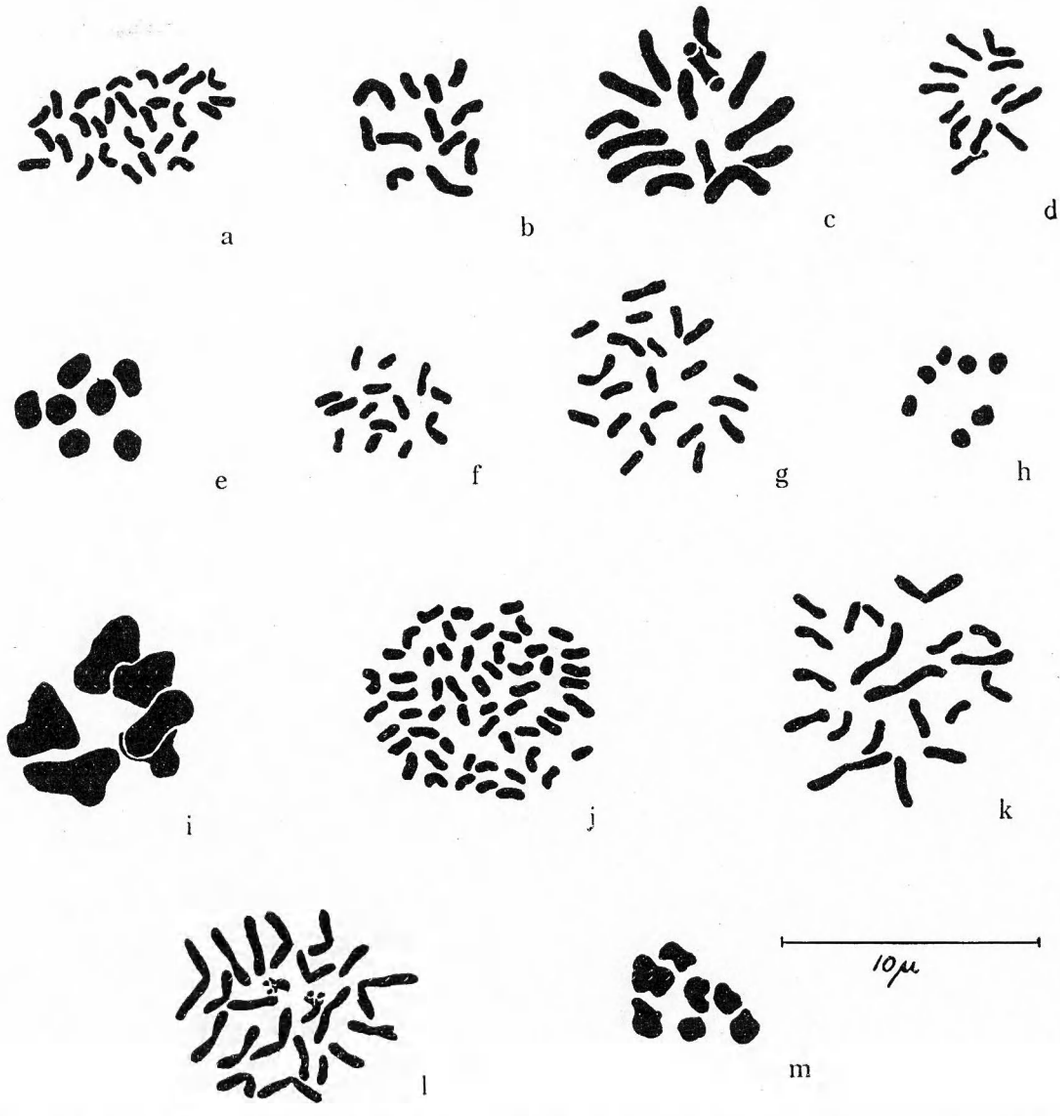

Fig. 1. — a—d: Metaphase plates from mitosis. a: *Poterium spinosum*; b: *Anthyllis polyphylla*; c: *Coronilla emerus*; d: *Coronilla scorpioides*; e: I. metaphase in PMC of *Hedysarum sibiricum*; f—g: Mitosis of *Onobrychis caput-gallae.* f: diploid; g: triploid; h: II. metaphase in PMC of *Onobrychis tommasinii*; i: I. metaphase in PMC of *Vicia ochroleuca*; j—l: metaphase plates from mitosis. j: *Digitalis micrantha*; k: *Cleonia lusitanica;* l: *Galactites tomentosa*; m: I. metaphase in PMC of *Reichardia picrioides.*

56. I counted n=28 in material fixed in Italy: San Cataldo, growing on a wall (No.: S.C. 18). This number must be regarded as octoploid. A thorough investigation of the species is needed in order to decide whether the three chromosome numbers found represent three morphologically distinct units, and whether these three chromosome races are geographically separate.

Papilionaceae

**Anthyllis vulneraria* L. var. *polyphylla* (Kit.) Ser. — This variety, often regarded as a separate species, *A. polyphylla* Kit., has not previously been studied cytologically. It is distributed over Eastern and Southern Europe. The chromosome number 2n=12 (Fig. 1 b) found in a culture from Hungary: Budapest ⊙ (No.: 3569)[1] is the same as that counted by several authors in *A. vulneraria.*

The present author has counted several strains of the collective species *A. vulneraria,* and in all cases found accordance with the results of previous authors (see Tischler 1950). The number 2n=12 was established in 22 cultures from the following stations:

Denmark: 2213. North Zealand: roadside at Hillerød, distr. 45 b. — 2279. North Zealand: dry slope at Kregme, distr. 45 b. — 2243. Zealand: Boserup near Roskilde, distr. 44. — 2685. North Jutland: Frederikshavn, distr. 1. — 2862. West Jutland: Vedersø, distr. 17, (coll. T. W. Böcher). — 3024. West Jutland: Hanklit in Mors, distr. 8, (coll. T. W. Böcher). — 3028. West Jutland: Heath South of Haderup, distr. 15, (coll. K. Rahn). — 3030. West Jutland: Hvide Sande, in the dunes, distr. 17. — Eire: 3144. Newcastle on the beach, (coll. T. W. Böcher). — Jersey: 3272. Grosnez Point, dry slope, (coll. T. W. Böcher). — France: 1318. Les Landes: St. Jean de Luz, dry slope on the Biscay. — 1543. The Pyrenees: Gavarnie, alt. 1500 m. — 1681. The Pyrenees: Val d'Eyne at Mont Louis. — 1822. Mt. Salève at Geneva, alt. 1100 m. — 2010. The Jura Mts.: Pierre Pertuis. — Portugal: 2456. Coimbra ⊙. — 2760. Coimbra ⊙. — Spain: 1409. Sierra Cantabrica in *Buxus* shrub. — 1441. Near Lumbreras in Old Castile, *Calluna* heath, alt. 1550 m. — Switzerland: 1863. Gorge du Dard, alt. 1500 m. — 1913. The Jungfrau massif: Eigergletscher, in grassland vegetation, alt. 2300 m. — 1996. Brienzer Rothorn at Brienz, in grassland vegetation, alt. 2300 m.

Astragalus glycyphyllus L. — This widely distributed species, found in almost the whole of Europe and in great parts of Asia, is rare in the Mediterranean region, it being restricted to the mountains, where it is a characteristic component of the herb-vegetation of the *Castanea* wood. The material studied by me was fixed in a *Castanea - Alnus cordata* wood at Campidoglio, Italy (No.: S.C. 4). The chromosome number n=8 was counted, which is in accordance with that found by Tschechow (1935).

**Coronilla emerus* L. — The genus *Coronilla* has not been treated by Senn (1938) in his work on the cytotaxonomy of the Leguminosae, and only a few species of this genus have been studied cytologically

[1] A bird's eye behind the locality indicates that the seeds have been obtained through botanical gardens as seeds of wild origin.

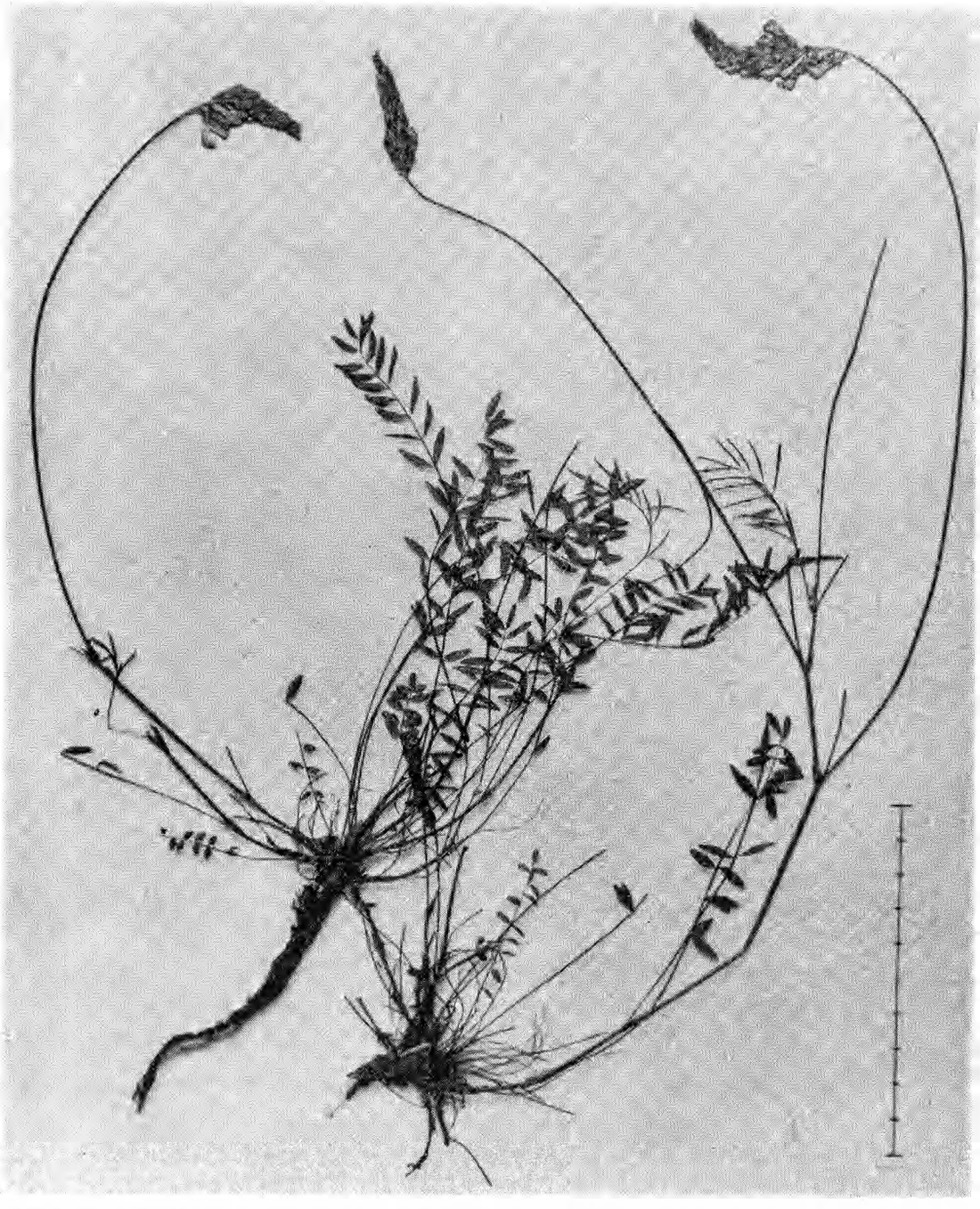

Fig. 2. *Onobrychis tommasinii* Jord. — Campidoglio, prov. Salerno, Italy. — Photo: M. Köie.

(see under the following species). Nevertheless these counts prove to be of great importance for the taxonomy of the genus. In *C. emerus* 2n=14 (Fig. 1 c) was found in a sample from Italy: dry coastal rocks West of Amalfi (No.: 54—7).

**Coronilla scorpioides* (L.) Koch. — This Mediterranean species has been studied in material from Italy: The mountain ridge above Minute,

alt. 700 m (No.: 54—6). The chromosome number was counted at 2n=12 (Fig. 1 d). There is a considerable difference in the morphology of the chromosomes of these two species of *Coronilla*. *C. emerus* has thick and rather long chromosomes, while *C. scorpioides* has short and thin ones.

In the arrangement given by Uhrová (1935) the genus *Coronilla* is divided into four sections. This view is highly supported by the cytological data:

Sect. *Emerus* Desv. Basic number 7
C. emerus L. 2n=14
Sect. *Scorpioides* Benth. Basic number 6
C. scorpioides (L.) Koch 2n=12
Sect. *Ballia* Uhrová. Basic number 6
C. viminalis Salisb. 2n=12 (Delay 1939)
Sect. *Eucoronilla* Benth. Basic number 6
C. varia L. 2n=24 (Romanenko 1937)
C. glauca L. 2n=24 (Atchison 1949)

The evolutionary trend in many leguminous genera is towards diminishing the basic number. In the present genus the section *Emerus* must be regarded as the oldest one, having the basic number 7. From this the three other sections have developed through reduction of the basic number to 6. The section *Scorpioides* includes two species of which one, *C. scorpioides,* is diploid, the other species, *C. repanda* Guss., has not been studied cytologically. The section *Ballia* includes only one diploid species, while in *Eucoronilla* polyploidy has been realized. Delay (1939) gives the name *C. viminalis* L. to the plant studied by her; as Salisbury, however, is the author of *C. viminalis,* I have regarded this species as identical with Delay's plant.

Hedysarum coronarium L. — Few species of the genus *Hedysarum* have been studied cytologically. Senn (1938) only mentions one species (*H. elongatum* Fisch.=*H. alpinum* L. (see Fedtschenko 1902)) and does not discuss the position of the genus, which includes about 60 species. *H. coronarium* has previously been studied by Lewitzky (in Tischler 1936), who counted 2n=16. The same number was found by the present author in material from H. B. H.

**Hedysarum sibiricum* Poir. — This species, belonging to the section *Obscura,* is distributed from Kola through Siberia to the Altai Mts., the Baikal district, and Dahuria. It has by several authors been regarded

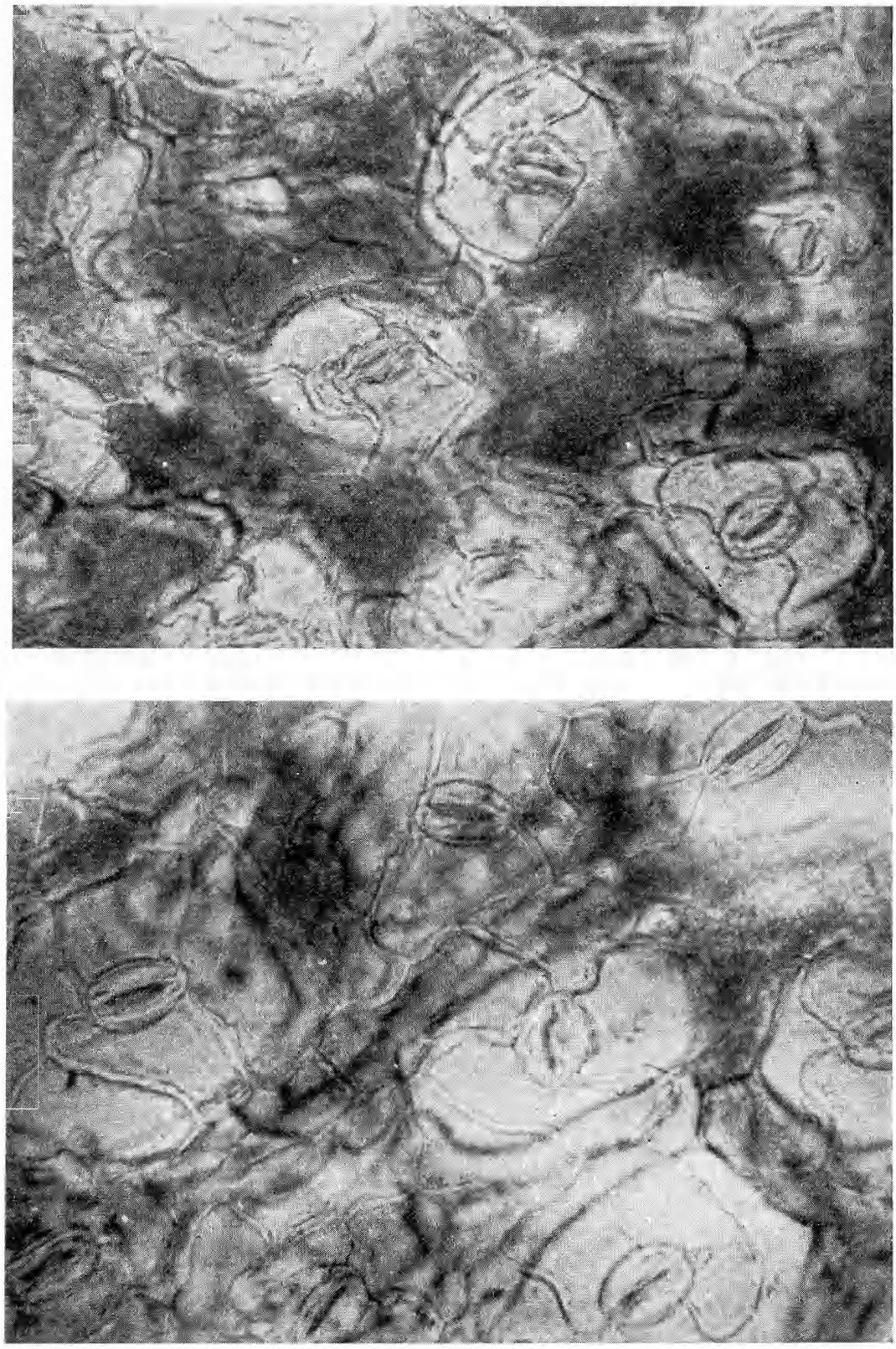

Fig. 3. Leaf epidermis with stomata and air-chambers situated below. — Above: *Onobrychis tommasinii*; below: *Onobrychis viciaefolia*. — Approx. 850/1.

as a variety, var. *sibiricum* Fedtsch. of *H. obscurum,* in which species 2n=14 has been counted. *H. sibiricum* has been studied in material from H. B. H., and proved to have the same chromosome number (Fig. 1 e).

Two of the seven sections published by Fedtschenko (1902), thus have been studied cytologically:

Sect. *Spinosissima* Fedtsch. Basic number 8
H. coronarium L. 2n=16 (Lewitsky 1936)
Sect. *Obscura* Fedtsch. Basic number 7
H. obscurum L. 2n=14 (Reese 1953, Favarger 1953, Larsen 1954)
H. sibiricum Poir. 2n=14
H. alpinum L. 2n=14 (Sakai 1934)

Medicago orbicularis Bart. — A widely distributed species found all over the Mediterranean zone, in South-West Asia, and in Africa as far South as Ethiopia. 2n=16 was counted in material from Italy, collected on a wall at San Cataldo (No.: 54—14). This is in accordance with the chromosome number found by Fryer (1930).

Melilotus neapolitanus Ten. — Distributed over the Mediterranean region from Spain to Persia. The chromosome number has been determined in a seed lot collected on the walls of San Cataldo (No.: 54—10), 2n=16. The same number was counted by Tschechov (1933).

**Onobrychis caput-galli* Lam. — A Mediterranean species of which two samples from Italy have been investigated. One originated from dry calciphilous *Cistus villosus - Euphorbia spinosa* vegetation above San Cataldo, alt. 550 m (No.: S.C. 14). In this fixation 2n=14 was counted (Fig. 1 f), which is the same number as that established by Senn (1938) in material from H. B. H. The other sample was a seed lot collected on the mountain ridge above Minute, alt. 700 m (No.: 54—4), RT-mitoses were studied and showed the triploid chromosome number 2n=21 (Fig. 1 g). The fruits look normal, but nothing can be stated about the plant from which they were collected. A closer study of the triploid will be made. Širjaev (1925) points out that this species varies considerably with regard to the dimensions of the stem and the leaves, and the degree of hairiness. The find of a tetraploid type might perhaps solve some of these problems.

**Onobrychis tommasinii* Jord. — A calciphilous species distributed in Dalmatia, and in the environs of Trieste. The localities in Southern

Italy are restricted to the mountains on the Sorrento Peninsula. The material studied by the present author (Fig. 2) was fixed in a *Castanea* wood at Campidoglio, alt. 550 m (No.: S.C. 7). Meiosis was found to be normal with 7 bivalents (Fig. 1 h). It was not possible to find any difference in size between the pollen of the diploid *O. tommasinii,* and that of the tetraploid *O. viciaefolia* (material from Denmark: Møn, Høvblege). A study of the stomata, however, showed correlation between chromosome number and size of cell, as appears from the photos (Fig. 3). Also the air-chambers below the stomata are conspicuously larger in the tetraploid species than in the diploid one.

Onobrychis viciaefolia in its wider sense is a considerably variable species, distributed in West Asia, Central Europe, and the Mediterranean region. The species is clearly a collective one, and Širjaev in his monograph of the genus *Onobrychis* split it up into several species. The genuine *O. viciaefolia* is wild-growing in Eastern Europe, but was introduced in the greatest part of Europe as a forage plant. It is not wild-growing in Italy, where *O. tommasinii* and another diploid species, *O. arenaria* Ser. (Favarger 1953), are found.

Securigera securidaca Deg. et Doerfl. — A Mediterranean therophyte in which Tschechow and Kartaschowa (1932) counted 2n=12. The same number was found by me in material from Italy: dry grassland vegetation, promontory between Amalfi and Atrani, alt. 175 m (No.: 54—8).

Trifolium procumbens L. — A West Asiatic, European, annual herb in which n=7 was counted in a fixation from Italy: *Quercus pubescens* wood at Minute, alt. 400 m (No.: S.C. 17). This is in accordance with the number found by Bleier (1925), Karpechenko (1925) and Wipf (1939).

Vicia bithynica L. — A Central and South European herb, in which Heitz (1931 b) and Sveschnikowa (1927) counted 2n=14. This has been confirmed by the present author in material from Italy: *Castanea* wood at Campidoglio, alt. 500 m (No.: S.C. 8).

**Vicia ochroleuca* Ten. — This species is found in woods in Italy and Algeria. The chromosome number was found to be n=6 (Fig. 1 i) in a fixation from Italy: *Castanea* wood near Campidoglio, alt. 500 m (No.: S.C. 1).

Vicia pseudo-cracca Berth. — A West Mediterranean species in which Sveschnikowa (1927) counted 2n=14. This is in accordance with the results of the present author, who counted n=7 in a pollen metaphase in a fixation from Italy: *Castanea* wood at Campidoglio, alt. 500 m (No.: S.C. 5).

Scrophulariaceae

**Digitalis micrantha* Schrad. — In this Mediterranean species the chromosome number was counted at n=24 by Haase-Bessell (1921). 2n=56 (Fig. 1 j) was found by me in material fixed in Italy: dry grassland vegetation in gravelly scree in Valle d. Ferriera opposite to Pogerola, alt. 550 m (No.: S.C. 19).

Labiatae

**Cleonia lusitanica* L. — This West Mediterranean annual species is found on the Iberian Peninsula and in Algeria. It has been regarded as a close relative of the genus *Prunella,* in which 2n=28 must be considered the only valid chromosome number (see Böcher 1949). The material of *Cleonia* studied by me was sent from the Botanical Gardens in Paris (No.: 3570, Fig. 1 k), and from the Botanical Gardens in Dijon (No.: 3571). Both seed lots were sent as material of wild origin; the origin of the seeds, however, is obscure, as the species is not wild-growing in these parts of Europe. In both cultures 2n=20 was counted. This number is very rare in the *Labiatae*; in the related genus *Drachocephalum* L., however, two basic numbers have been reported, viz. 5 and 7:

D. imberbe Bge	2n=10 (Sokolovskaja and Strelkova 1938)
D. moldavicum L.	2n=20 (Panutina-Muchina 1933)
D. altaicense Laxm.	2n=14 (Sokolovskaja and Strelkova 1938)
D. ruyschiana L.	2n=14 (Löve, Á. and D., 1944 b)

Briquet's arrangement (1895) of the genus *Drachocephalum* does not seem to agree with the cytological data. It would, however, be premature to draw any conclusions about the intergeneric relationships before further studies have been made, but perhaps a closer relationship between *Cleonia* and *Drachocephalum* can be supposed.

Compositae

**Galactites tomentosa* Moench. — Distributed over Mediterranean Europe and Boreal Africa, the Canary Islands and Madeira. Mitosis has

been studied in RT from seeds collected in Italy: in gravelly scree in Valle d. Ferriera opposite to Pogerola, alt. 500 m (No.: H. 107). 2n=22 (Fig. 1 l).

**Reichardia picrioides* Roth. — A Mediterranean perrennial herb. Two other species of *Reichardia* have been studied cytologically. *R. gaditana* (Wk.) Samp. (Mesquita Rodrigues 1953) and *R. tingitana* Roth. (Teleżyński in Tischler 1931), in these n=8 was counted. I have studied material of *R. picrioides* from Italy, fixed from a wall in the garden of San Cataldo (No.: S.C. 10), in this a normal meiosis with n=7 bivalents was found (Fig. 1 m).

	n	2n
Ranunculus cortusaefolius Webb et Berth.	8	16
Aethionema saxatile R. Br.	24	
Lobularia maritima Desv.		24
**Poterium spinosum* L.		28
Sedum dasyphyllum L.	28	
Anthyllis vulneraria L. coll.		12
**Anthyllis vulneraria* L. var. *polyphylla* (Kit.) Ser.		12
Astragalus glycyphyllus L.	8	
**Coronilla emerus* L.		14
**Coronilla scorpioides* (L.) Koch		12
Hedysarum coronarium L.		16
**Hedysarum sibiricum* Poir.		14
Medicago orbicularis Bart.		16
Melilotus neapolitanus Ten.		16
**Onobrychis caput-gallae* (L.) Lam.		14, 21
**Onobrychis tommasinii* Jord.	7	
Securigera securidaca Deg. et Doerfl.		12
Trifolium procumbens L.	7	
Vicia bithynica L.		14
**Vicia ochroleuca* Ten.	6	
Vicia pseudo-cracca Berth.	7	
**Digitalis micrantha* Schrad.		56
**Cleonia lusitanica* L.		20
**Galactites tomentosa* Moench		22
**Reichardia picrioides* Roth.	7	

III. Summary

The chromosome numbers of 24 species mostly of Mediterranean origin have been given. 12 of these have not previously been studied

cytologically, or new chromosome numbers were found; these are marked with an asterisk in the text and in the table p. 273.

These stray contributions to the caryological knowledge of the Mediterranean flora do not allow far-reaching conclusions. In some cases, however, the taxonomic arrangement of a genus has been supplemented in a considerable way. Thus the genus *Coronilla* gives a clear example of a minor taxonomic group in which the cytological data have rendered it possible to elucidate the evolution in a probable way. In the genus *Hedysarum* further studies will in all probability appear to be quite as valuable for the understanding of the interrelationship. The *Onobrychis viciaefolia* complex has been split up into three species on account of cytological and morphological data, and *Cleonia lusitanica,* which previously had often been regarded as a near relative of the genus *Prunella,* has proved to be more closely related to the genus *Drachocephalum,* in which unfortunately few cytological data are known.

Literature

For literature not cited in the list below see TISCHLER 1950.

ATCHISON, E., 1949: Studies in the Leguminosae IV. — J. Elisha Mitchell Sci. Soc. 65: 118—130.

BRIQUET, J., 1895: Labiatae. — A. Engler and K. Prantl. Die natürl. Pflanzenfam. IV. 3 a: 183—375.

DELAY, C., 1939: Recherches sur le noyau des Legumineuses. — Rev. Cyt. et Cytophys. Vég. 4: 183—223.

FAVARGER, C., 1953: Note de caryologie alpine. II. — Bull. Soc. Neuchâtel. Sci. Nat. 76: 133—169.

FEDTSCHENKO, B. A., 1902: A survey of the species of the genus Hedysarum (in russian). — Leningrad.

HAASE-BESSELL, G., 1921: Digitalisstudien. II. — Zeitschr. indukt. Abst.- u. Vererb.-Lehre. 27: 1—26.

LARSEN, K., 1954: Chromosome numbers of some European flowering plants. — Bot. Tidsskr. 50: 163—174.

— 1955: Cytotaxonomical studies in Lotus. II. — Bot. Tidsskr. 52: 8—17.

MESQUITA RODRIGUES, J. E., 1953: Contribução para o cohencimento cariológico das halófitas e psamófitas litorais. — Diss. Coimbra.

REESE, G., 1953: Ergänzende Mitteilungen über die Chromosomenzahlen mitteleuropäischer Gefässpflanzen. II. — Ber. Deutsch. Bot. Gess. 66: 65—73.

ŠIRJAEV, G., 1925: Onobrychis generis revisio critica. I. — Publ. Fac. Sci. Univ. Masaryk. 56: 1—198.

TISCHLER, G., 1927: Pflanzliche Chromosomen Zahlen. — Tabul. Biol. 4: 1—83.

— 1931: Idem. — Tabul. Biol. 7: 109—226.

— 1936: Idem. — Tabul. Biol. 11: 281—304, 12: 57—115.

— 1938: Idem. — Tabul. Biol. 16: 162—218.
— 1950: Die Chromosomenzahlen der Gefässpflanzen Mitteleuropas. — 's-Gravenhage.
UHROVÁ, A., 1935: Revision der Gattung Coronilla L. — Beih. Bot. Centralbl. 53 B: 1—174.

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Anteckningar om flora och vegetation i Kebnekaise-området

Av Torsten Håkansson

Universitetets Botaniska Museum, Lund

(Meddelanden från Lunds Botaniska Museum. Nr 110)

Sommaren 1945 fick jag i samband med en växtbiologisk exkursion till Abisko tillfälle till ett kortare besök i Kebnekaise under tiden den 31 juli—4 augusti i sällskap med Gunnar Degelius, Samuel Hansen och Eva Melander. Därvid gjorde jag en del anteckningar om flora och vegetation i Ladtjovagge och i Kebnekaisemassivet, vilka områden ännu äro botaniskt bristfälligt kända när det gäller kärlväxterna och bryologiskt så gott som okända. Anteckningarna gälla främst de närmaste omgivningarna kring Kebnekaise turiststation. I övrigt gjordes de under en uppstigning till Sydtoppen längs östra leden över Kebnetjåkkoglaciären och Björlings glaciär den 2 augusti och under en tur upp genom Tarfaladalen till Tarfalajaure den 3 augusti. Uppgifterna hänföra sig till största delen till det lågalpina bältet (Du Rietz 1942 a) och dess övergångszon till björkskogsregionen. Fig. 1 visar begränsningen av Kebnekaiseområdet och läget av de inom detta anförda lokalerna.

De mossor jag insamlade bestämdes efter hemkomsten till Lund till övervägande delen av fru Elsa Nyholm, som alltså stått för det grundläggande arbetet rörande mossorna i denna uppsats. Min tacksamhet till henne vill jag här framföra. Min färdkamrat docent Gunnar Degelius har varit vänlig överlämna en lista över mossor, som han tagit vid undersökning av lavvegetationen i området (Degelius 1945). De ha bestämts av fil. dr Herman Persson och förvaras nu på Riksmuseum. Det övriga mossmaterialet liksom insamlade kärlväxter har överlämnats till Botaniska Muséet i Lund.

I fråga om kärlväxternas nomenklatur har Hylanders förteckning av 1941 följts och för bladmossorna Jensens Skandinaviens bladmoss-

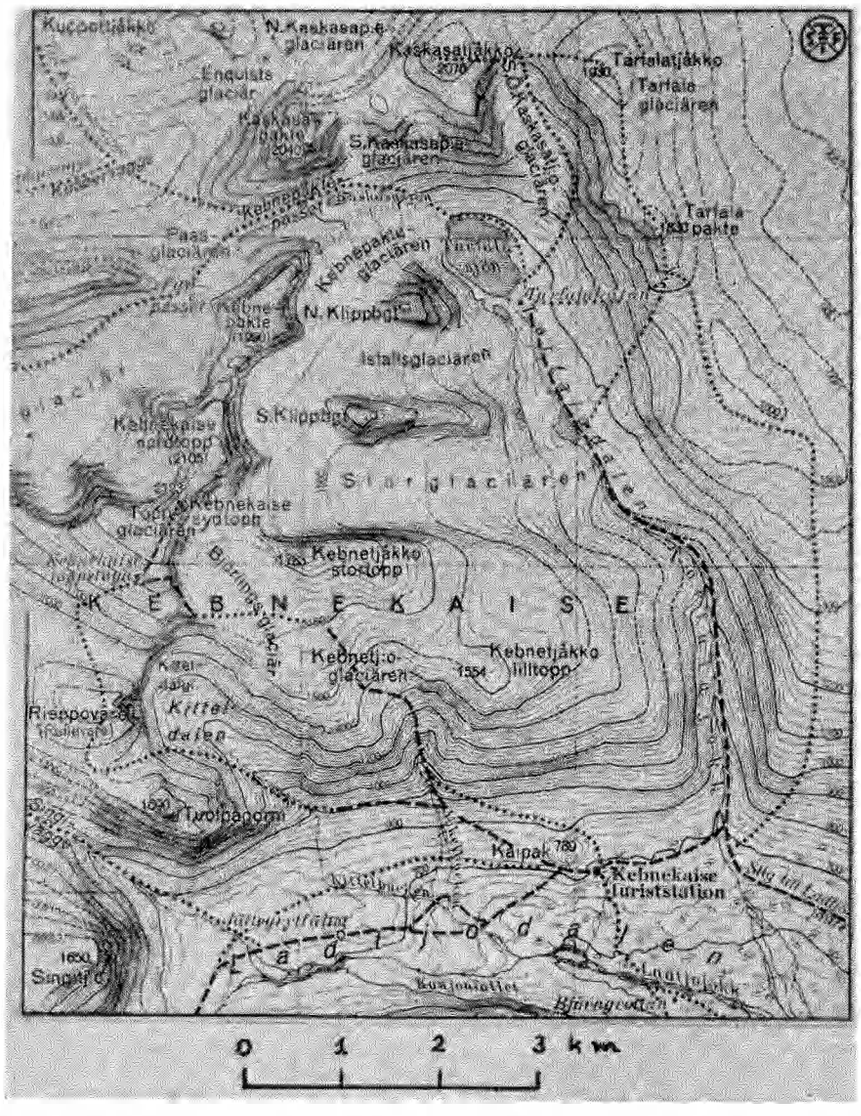

Fig. 1. Kebnekaises topografi och vandringsleder. Efter H. W:son Ahlmann 1951, Pl. 1. — Kartan publicerad med tillstånd av Svenska Turistföreningen. För publicering godkänd i rikets allmänna kartverk den 8 december 1951.

flora och E. Nyholms Illustrated moss flora of Fennoscandia. II Musci. Fasc. I. 1954 samt för levermossorna Buchs Suomen maksasammalet. 1936.

Någon rikare vegetation var ej att vänta i Kebnekaiseområdet.

I Ladtjovagges botten från i höjd med Kaipak och vidare österut dominera surare bergarter, syenitporfyr och kvartsiter. Detta är även fallet inom Tarfaladalens nedre, södra hälft. Därovan följa i de båda dalarnas sidor svarta skiffrar och myloniter. Efter en växellagring av glimmerskiffer och amfibolit komma amfiboliter att dominera om-

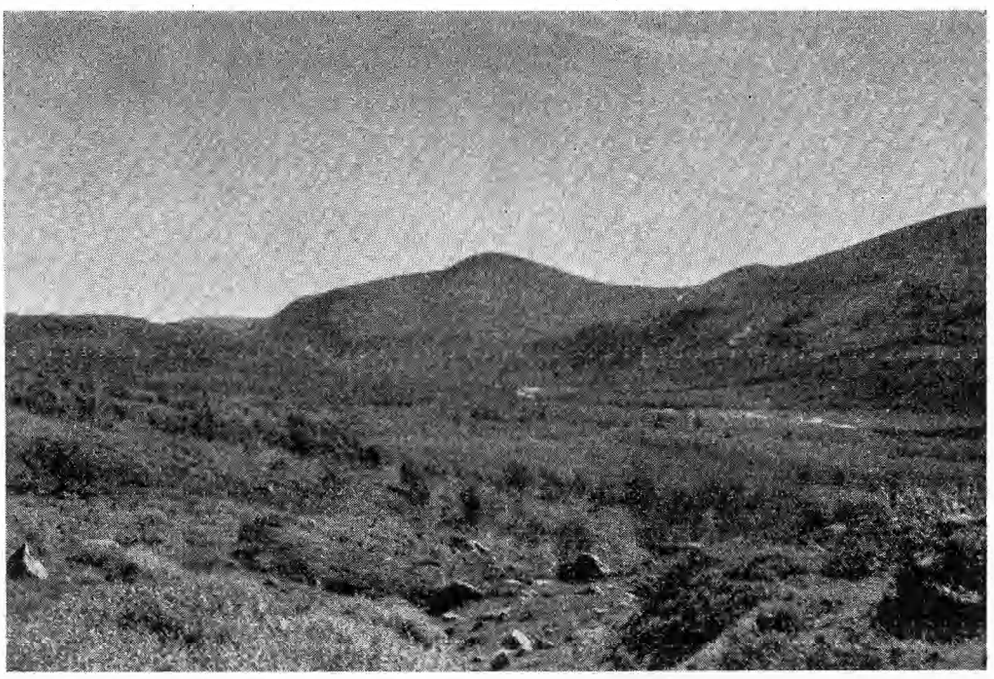

Fig. 2. Ladtjovagge österut från sluttningen söder om Kebnekaise turiststation. Berget i bakgrundens mitt är Juovavare. Foto T. Håkansson, aug. 1945.

rådets högre delar (Quensel 1919, Johansson 1951). I större delen av området härska alltså mot den kemiska vittringen mera motståndskraftiga bergarter och härav präglas växtsamhällena, som i stort sett äro artfattiga och tämligen triviala. Småfläckar med artrikare samhällen uppträda dock i välbevattnade sluttningar och framförallt i anslutning till de mera lättvittrade skiffrarna. På vittringsjorden från dessa finner man de kalkgynnade arterna.

Från turiststationen gjordes anteckningar längs en linje söderut ned till Ladtjojokk genom gränszonen mellan björkskogsregionen och det lågalpina bältet på 600—700 m ö.h. Denna gränszon (fig. 2) domineras av alpina växtsamhällen. Vegetationen består här till övervägande delen av kråkrishedens förband, *Empetrion* (Du Rietz 1942 b) motsvarande krypljunghedens förband hos Kalliola 1939 och Nordhagen 1943. Det har över stora ytor följande sammansättning i fältskiktet: *Arctostaphylos alpina, Betula nana, Empetrum hermaphroditum* (dominerande), *Loiseleuria procumbens, Vaccinium uliginosum, Diapensia lapponica, Carex Bigelowii, Festuca ovina* ssp. *vulgaris* och *Juncus trifidus*.

De mest exponerade kullarna, som under vintern tydligen äro snöfria ha en ännu torftigare kärlväxtflora, som endast täcker 10—20 % av markytan. Från en sådan kulle antecknades: *Arctostaphylos alpina, Betula nana, Loiseleuria procumbens, Vaccinium uliginosum, Diapen-*

sia lapponica och *Juncus trifidus*. Detta är Vestergrens (1902) *Cesiolichen*-samhälle och Nordhagens (1943) association *Loiseleurieto-Diapensietum* inom *Loiseleurieto-Arctostaphylion*.

Den snöskyddskrävande blåbärsheden, Du Rietz' *Myrtillion* (1942 b), motsvarande Nordhagens (l.c.) *Phyllodoco-Myrtillion* förekommer längs den ovannämnda linjen vackert utbildad i den branta, sydexponerade, skålformiga sluttningen omedelbart SV om Turiststationen. Den representeras här av associationen *Phyllodoco-Vaccinietum myrtilli*. I dess nedersta del stå enstaka exemplar *Betula tortuosa*. Den dominerande arten är *Empetrum hermaphroditum*, därnäst spela *Vaccinium Myrtillus* (d) och *V. uliginosum* den viktigaste rollen. I övrigt förekommer *Arctostaphylos uva-ursi, Betula nana, Phyllodoce coerulea, Sorbus aucuparia* (ungplantor), *Vaccinium vitis-idaea, Chamaenerium angustifolium, Cornus suecica, Lycopodium annotinum, Pedicularis lapponica, Solidago virgaurea* (d), *Thelypteris Dryopteris, Deschampsia flexuosa* (d) och *Luzula pilosa*. De arter, till vilka fogats (d), anges av Du Rietz (1942 a) som skiljearter mot *Empetrion*.

Söder om denna sluttning ligger en mycket artfattig myr dominerad av *Carex aquatilis* och med rikligt inslag av *Salix glauca* ssp. *eu-glauca*. Av kärlväxter förekomma i övrigt blott *Potentilla palustris, Betula nana* och *Salix phylicifolia* ssp. *Weigeliana*. Bottenskiktet utgöres av *Calliergon sarmentosum, C. stramineum, Drepanocladus procerus* och *Sphagnum teres*. Denna myr är ett medelfattigkärr (Du Rietz 1949, 1954), där *Drepanocladus procerus* och *Sphagnum teres* bilda ett inslag av rikkärrsarter. Förekomsten av de nämnda mera krävande arterna i bottenskiktet kan kanske förklaras av att myrens yta lutar mot väster och dess vatten alltså är rörligt.

Fuktiga svackor och bäckdalar i sluttningen intas av videsnår. I ett sådant antecknades *Betula nana, Salix glauca* ssp. *eu-glauca* (dominerande), *S. phylicifolia* ssp. *Weigeliana, Alchemilla glomerulans, Cirsium heterophyllum* (steril), *Cornus suecica, Equisetum pratense, Potentilla palustris* (steril), *Ranunculus acris* ssp. *Boraeanus* (steril), *Rubus arcticus, Stellaria calycantha* och *Viola biflora*. Samhället på denna säkerligen sent framsmältande mark är närmast en artfattig variant av Nordhagens (l.c.) association *Salicetum geraniosum alpicolum* tillhörande förbandet *Mulgedion alpini*. Regional ledart i fjällen för detta förband är bl.a. *Cirsium heterophyllum*.

Artrika och representativa högört-videsnår, som höra till *Salicetum geraniosum alpicolum* finnas i dalbottnen i nedre delen av Tarfaladalen 750—800 m ö.h., Fig. 3. I ett sådant 500 m N bron över Tarfala-

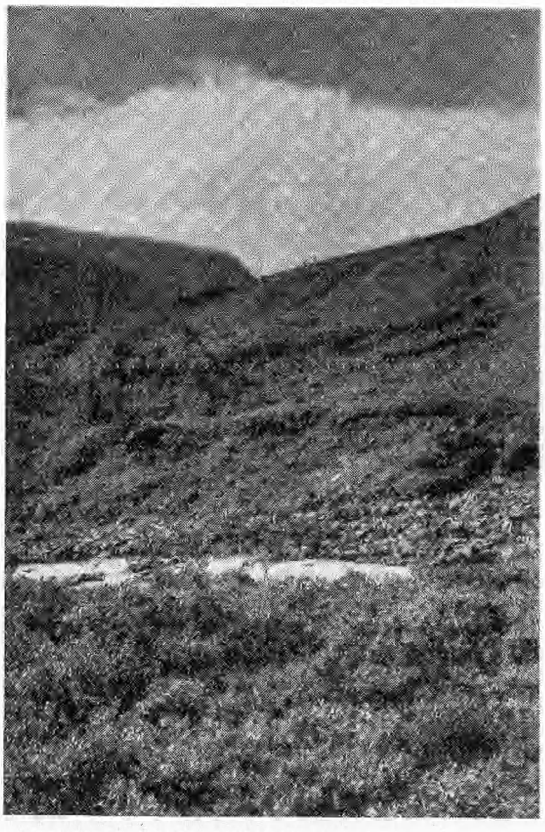

Fig. 3. Videsnår i nedre delen av Tarfaladalen, c:a 800 m ö.h. Foto T. Håkansson, aug. 1945.

jokk bestod buskskiktet av *Salix lanata* ssp. *eu-lanata* (dominerande) jämte *S. phylicifolia* ssp. *Weigeliana*. I fältskiktet ingingo *Vaccinium Myrtillus, Alchemilla glomerulans, A. Murbeckiana, Astragalus alpinus, A. frigidus, Bartsia alpina, Cerastium alpinum, Chamaenerium angustifolium, Geranium silvaticum* (regional ledart enl. Nordhagen l.c.), *Hieracium silvaticum* coll., *Melandrium rubrum, Oxyria digyna, Polygonum viviparum, Pyrola minor, Ranunculus acris* ssp. *Boraeanus, Rumex acetosa* ssp. *lapponicus, Saussurea alpina, Solidago virgaurea* (fläckvis dominerande), *Taraxacum crocodes* coll., *Thalictrum alpinum, Trollius europaeus, Veronica alpina, Viola biflora, Anthoxanthum odoratum, Carex Bigelowii, Deschampsia flexuosa, Festuca ovina* ssp. *vulgaris, Phleum commutatum, Poa alpina* och *Trisetum spicatum*.

I det frodiga bottenskiktet påträffades följande mossor: *Aulacomnium palustre, Dicranum scoparium, Drepanocladus uncinatus, Hylocomium Schreberi, H. splendens, Lescuraea mutabilis* var. *saxicola, Mnium spinosum, Polytrichum juniperinum, Sphagnum Girgensohnii* och *Barbilophozia lycopodioides*.

Strax nordväst om turiststationen avbryts Kebnetjåkkos jämna sydsluttning av det brant stupande Kaipak, som höjer sig 150 meter över

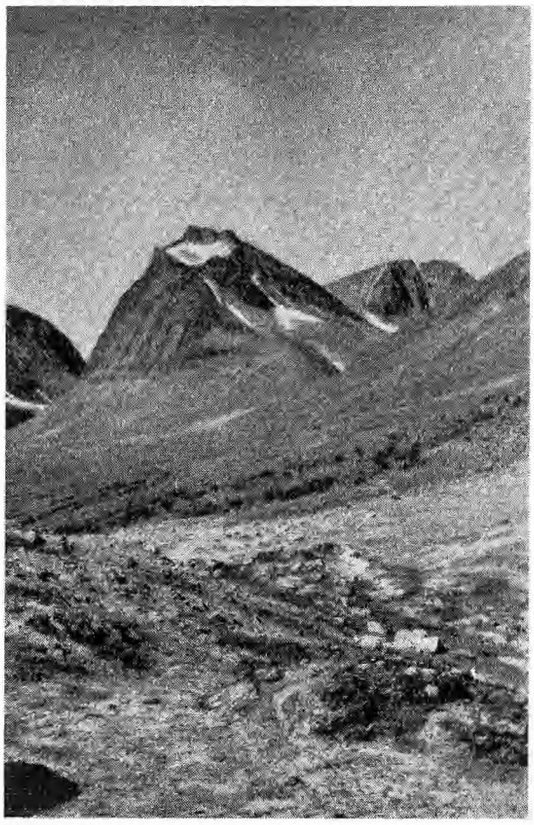

Fig. 4. Kebnetjåkkos sydsluttning nedanför Kaipak. I bakgrunden Tuolpagorni. Foto T. Håkansson, aug. 1945.

Ladtjotjokks dal. I blåbärsheden i sluttningen nedanför bergets brant, Fig. 4, ingå utom det dominerande blåbärsriset följande arter: *Empettrum hermaphroditum, Juniperus communis* var. *montana, Phyllodoce coerulea, Vaccinium Vitis-idaea, Angelica Archangelica* ssp. *norvegica, Chamaenerium angustifolium, Cornus suecica, Euphrasia frigida, Hieracium alpinum* coll., *Linnea borealis, Pedicularis lapponica, Polygonum viviparum, Potentilla Crantzii, Carex Bigelowii, C. vaginata, Deschampsia flexuosa, Festuca ovina* ssp. *vulgaris, Juncus trifidus* och *Poa nemoralis*. På blocken i denna hed förekom av mossor *Cynodontium strumiferum, C. tenellum, Dicranum fuscescens, Rhacomitrium microcarpon, Barbilophozia Hatcheri, Sphenolobus minutus* och *Temnoma setiformis*.

Floran i Kaipaks brant ovanför den beskrivna blåbärsheden har skildrats av S. Birger (1912). Utöver de av honom angivna arterna fann jag här *Luzula arcuata*. I klippbranten växte vidare följande mossor: *Ceratodon purpureus, Hygrohypnum Smithii, Mnium orthorrhynchum, Schistidium apocarpum* och *Tortula ruralis*.

De talrika av bäckar och rännilar bevattnade sänkor, som löpa över Kebnetjåkkos sydsluttning på 7—800 m:s höjd ö.h. intas av snölegesamhällen av ängstyp. I ett sådant 400 m N Turiststationen förekommo

Epilobium anagallidifolium, Gnaphalium norvegicum, Polygonum viviparum, Ranunculus acris ssp. *Boraeanus* (dominerande), *Rumex acetosa* ssp. *lapponicus, Veronica alpina, Viola biflora, Viola palustris, Carex aquatilis* och *Phleum commutatum.* Samhället hör till Gjaerevolls (1950) förband av ängssnölegor, *Ranunculo-Anthoxanthion.*

En artrik äng av samma förband påträffade jag 950 m ö.h. i Tarfaladalens östra sida. Den genomdrogs och översilades delvis av en bäck. Fältskiktsarterna voro *Salix herbacea, Alchemilla glomerulans, Bartsia alpina* (steril), *Cerastium cerastioides, Oxyria digyna, Pedicularis lapponica, Polygonum viviparum, Ranunculus acris* ssp. *Boraeanus, Sedum Rosea, Rumex acetosa* ssp. *lapponicus, Saxifraga rivularis, Sibbaldia procumbens, Taraxacum* sp., *Veronica alpina, Anthoxanthum odoratum, Carex Bigelowii, Phleum commutatum, Poa alpina* och dess f. *vivipara.* Närmast intill bäcken i det fuktigaste stråket växte *Epilobium anagallidifolium, Equisetum scirpoides, Ranunculus nivalis, Saxifraga cernua, S. stellaris, Carex norvegica* och *Juncus biglumis.* I bottenskiktet fanns *Brachythecium latifolium, Drepanocladus uncinatus, Hylocomium pyrenaicum, Polytrichum alpinum, Webera albicans* och *W. commutata* (för kontroll av dessa mossbestämningar tackar jag fil. dr Herman Persson).

Under bestigningen av Kebnekaises sydtopp den 2 augusti längs den östra leden klättrade vi i tät dimma uppför den brant som begränsar Björlings glaciär i väster. Här påträffade vi på c:a 1800 meters höjd i en skreva i branten *Cerastium Edmondstonii, Saxifraga cernua* och *Saxifraga groenlandica.* Dessa arter ha tidigare meddelats härifrån jämte *Papaver radicatum* ssp. *hyperboreum* och *Saxifraga tenuis* av docent Börje Åberg, som besteg toppen den 6 augusti. Utom de nämnda arterna funno vi här också *Cardamine bellidifolia.* Lokalen utgör med all sannolikhet höjdrekord i Nordskandinavien för *Cardamine bellidifolia* liksom enl. Åberg för övriga arter. De tidigare angivna högsta höjderna för *Cardamine bellidifolia,* som jag i litteraturen lyckats uppspåra är: Nissontjårro 1667 m, Du Rietz 1925; Tarfalatjåkko 1590 m, Du Rietz 1925; Kebnetjåkko 1530 m, S. Birger 1912.

Lokalen ligger som antytts i en klippbrant, som stupar från blockhavet kring Sydtoppen 300 m rakt ned till Björlings glaciär och är exponerad mot öster. Den erbjuder de arter, som där fresta tillvaron, miljöbetingelser, som äro så pass identiska med förhållandena på istidens nunatakker som det i Nordskandinavien är möjligt under nutida förhållanden. De sex fanerogamer, som här påträffats: *Cardamine bellidifolia, Cerastium Edmonstonii, Papaver radicatum* ssp. *hyper-*

boreum, Saxifraga cernua, S. groenlandica och *S. tenuis,* bör alltså ha kunnat överleva den sista istiden under utpräglat arktiska betingelser som teorin antar för de istidsöverlevande arterna. *Papaver radicatum* ssp. *hyperboreum,* som är endem i Nordskandinavien, och *Cerastium Edmondstonii,* som hör till de s.k. västarktiska arterna och enl. Hultén 1950 till de arktiskt cirkumpolära arterna med stor utbredningslucka i Sibirien, äro båda med stor sannolikhet istidsöverlevande. *C. Edmondstonii* förekommer utanför Skandinavien närmast på Island, Spetsbergen, Grönland och på Shetland och Hebriderna samt i Skottland och Wales. Att den från dessa arealer i postglacial tid skulle ha spritts till Skandinavien kan med vår bristande kännedom om artens biologi ej helt uteslutas, men måste anses föga sannolikt.

I blockmarkerna kring toppstugan på 1920 m ö.h. och under vägen upp till Sydtoppens jökel insamlades en del prov av den sparsamma mossvegetationen. Den visade sig omfatta följande arter: *Andraea Blyttii, A. rupestris, Arctoa fuvella, Kiaeria falcata, Polytrichum hyperboreum, P. piliferum* och *Rhacomitrium lanuginosum.* I allt är detta arter, som man kunde vänta sig finna på dessa höga höjder. Några kärlväxter påträffades ej i dessa extrema blockmarker. Ej ens *Ranunculus glacialis* trivs i sådana.

Som tidigare nämnts utgöres floran i Kebnekaiseområdet helt övervägande av arter, som trivas med en kalkfattig grund. Ett inslag av kalkgynnade arter förekommer dock på några lokaler. I dalgången, som från Kebnetjåkkoglaciären leder söderut till Ladtjovagge (i fortsättningen kallad Jökelbäcksdalen) påträffade jag på 1000 m ö.h. (2 km NV Turiststationen) *Melandrium apetalum* och *Gentianella tenella.* Den förra arten är tidigare känd från Singitjåkko (Birger 1912), medan den senare är ny för Kebnekaiseområdet. Även i Tarfaladalen fann jag en del kalkgynnade arter, *Dryas octopetala, Elyna Bellardii, Pedicularis hirsuta, Rhododendron lapponicum, Salix reticulata* och *Carex atrata.* Den sistnämnda är ny för Kebnekaiseområdet. De övriga ha meddelats härifrån av Du Rietz (1926) i hans artlista. De kalkgynnade arterna förekomma i dalens mellersta del på 900—1000 m:s höjd (höjdvärden enl. Woxnerud 1951, Pl. 1). Där växte också den kalkgynnade mossan *Tortula norvegica.* Just här bildar dalen en brant vettande mot söder, i vilken Hyolithus-zonens bergarter, svarta skiffrar och kvartsiter blottlagts (muntl. uppgift av lic. H. Johansson).

Vid genomgång av litteraturen och kontroll av herbariematerialet i Riksmuséets botaniska avdelning och i de botaniska muséerna i Göte-

borg, Lund och Uppsala visade sig följande nio av de av mig antecknade arterna vara nya för Kebnekaiseområdet:

Botrychium boreale, 1,5 km NV Kebnekaise turiststation, hed i lågfjällbältet vid mynningen av Jökelbäcksdalen, c:a 800 m ö.h.

Carex atrata, Tarfaladalens östra sida, *Trollius*-äng, c:a 950 m ö.h.

Gentianella tenella, 2 km NV Kebnekaise turiststation, äng i Jökelbäcksdalens östra sida, c:a 1000 m ö.h.

Melampyrum silvaticum, 150 m N Kebnekaise turiststation, bäckdal med viden, c:a 700 m ö.h.

Pinguicula alpina, 1 km S Kebnekaise turiststation, bäckdal med viden, c:a 600 m ö.h.

Pyrola norvegica, Tarfaladalens östra sida, c:a 800 m ö.h. och c:a 1000 m ö.h., hed.

Sagina saginoides, Tarfaladalens östra sida, äng, c:a 950 m ö.h.

Veronica fruticans, Tarfaladalens östra sida, hed, c:a 950 m ö.h.

Viola palustris, 400 m N Kebnekaise turiststation, snölegeäng, c:a 750 m ö.h.

Under vägen till och från Kebnekaise gjordes uppehåll vid det artrika sydberget Tarfalaålke i Ladtjodalen invid leden Nikkaluokta—Kebnekaise, c:a 4 km Ö turiststationen. Frödin (1918) har lämnat utförliga uppgifter om kärlväxtfloran här och Degelius (1945) har skildrat bergets lavflora. Utöver de av Frödin meddelade arterna anträffades i ängsbjörkskogen nedanför branten följande: *Arabis alpina, Cerastium fontanum* ssp. *scandicum, Epilobium Hornemanni, Equisetum pratense, Linnea borealis, Luzula pilosa, Lycopodium annotinum, Melampyrum silvaticum, Ribes spicatum, Rubus arcticus, Selaginella Selaginoides, Stellaria calycantha* och *Trientalis europaea.* På ett större block växte *Woodsia alpina.*

I branten ovanför björkskogen förekom utöver Frödins arter enligt uppgifter, som välvilligt lämnats av docent Degelius, även *Carex adelostoma, Potentilla nivea* s. str., *Rhododendron lapponicum, Salix caprea* ssp. *sericea, Saxifraga tenuis, Sedum Rosea* och *Thelypteris Dryopteris.*

Mossfloran i den väl bevattnade sydexponerade ängsbjörkskogen visade sig vara rik. Som bottenskikt på marken påträffades *Brachythecium Starkei, Mnium pseudopunctatum* och *Orthocaulis Floerkei.* På de talrika stora stenarna och blocken växte *Dicranoweissia crispula, Dicranum fuscescens, Grimmia funalis, G. ovalis, Hylocomium splendens, Leucodon sciuroides, Oncophorus virens, Paraleucobryum longifolium, Plagiothecium silvaticum* var. *Roeseanum, Polytrichum alpinum, Pterygynandrum filiforme, Rhytidium rugosum, Ulota curvifolia, Webera cruda, Barbilophozia barbata* och *Scapania subalpina.* I och vid kanterna av en bäck genom björkskogen förekommo *Calliergon*

Richardsonii, C. stramineum, Campylium stellatum, Drepanocladus uncinatus och *Philonotis tomentella.*

I den följande förteckningen över de i Kebnekaiseområdet och Ladtjovagge insamlade mossorna och deras lokaler ha de av docent Degelius insamlade och av fil. dr Herman Persson kontrollbestämda arterna speciellt markerats. De övriga ha insamlats av förf. och bestämts eller kontrollerats av fru Elsa Nyholm. Följande förkortningar ha använts för muséer, där materialet förvaras: L=Botaniska Muséet, Lund, S= Riksmuseum, Stockholm, U=Botaniska Muséet, Uppsala.

Andraea Blyttii Br. & Sch. — Kebnekaiseområdet, mellan toppstugan och sydtoppen, blockmark, 1900 m ö.h., 2.8.1945, L.

A. rupestris Hedw. — Kebnekaiseområdet, mellan toppstugan och Sydtoppen, blockmark, 1900 m ö.h., 2.8.1945, L; SV Kebnetjåkkoglaciären, block, 1400 m ö.h., 2.8.1945, L.

Arctoa fulvella Br. Eur. — Kebnekaiseområdet, blockfältet V toppstugan, 1940 m ö.h., 2.8.1945, Degelius, S.

Aulacomnium palustre Schwaegr. — Kebnekaiseområdet, Tarfaladalen, 500 m N bron över Tarfalajokk, videsnår, 800 m ö.h., reg. alp., 3.8.1945.

A. turgidum Schwaegr. — Kebnekaiseområdet, Tarfalajokks kanjon, östsidan nedom bron, 680 m ö.h., reg. subalp., 3.8.1945, Degelius, S.

Bartramia ithyphylla Brid. — Kebnekaiseområdet, Tarfaladalen, ängsmark i östsidan 4,5 km SO Tarfalajaure, 950 m ö.h., 3.8.1945, L.

Brachythecium latifolium Philib. — Kebnekaiseområdet, Tarfaladalens östsida 4 km SO Tarfalajaure, översilad *Ranunculus*-äng, 950 m ö.h., 3.8.1945, L.

Br. salebrosum Br. & Sch. ssp. *turgidum* Hn. — Kebnekaiseområdet, Tarfaladalens östsida, torr backe 4 km SO Tarfalajaure, 1000 m ö.h., 3.8.1945, L.

Br. Starkei Br. & Sch. — Ladtjovagge, bottenskikt i ängsbjörkskogen nedanför Tarfalaålkes sydbrant, 1.8.1945, L. Kebnekaiseområdet, Tarfaladalens östsida 4,5 km SO Tarfalajaure, ängsmark, 950 m ö.h., 3.8.1945, L.

Bryum obtusifolium Lindb. — Kebnekaiseområdet, Tarfalajaures östra strand, vid smältvattensbäck, 1200 m ö.h., 3.8.1945, L.

Campylium stellatum J. Lange & C. Jens. — Ladtjovagge, bäck i ängsbjörkskogen nedanför Tarfalaålkes sydbrant, 1.8.1945, L.

Calliergon Richardsonii Kindb. — Ladtjovagge, bäck i björkskogen nedanför Tarfalaålkes sydbrant, 1.8.1945, L.

C. sarmentosum Kindb. — Kebnekaiseområdet, 500 m S Kebnekaise turiststation, *Carex aquatilis*-kärr, 650 m ö.h., reg. alp., 4.8.1945, L.

C. stramineum Kindb. — Ladtjovagge, kärr mellan Bogdanovkåtan och Ladtjojokk, 7 km Ö Kebnekaise turiststation, 1.8.1945, L. Kebnekaiseområdet, NNO turiststationen, *Ranunculus*-äng, c:a 700 m ö.h., reg. alp., 1.8.1945; 800 m S turiststationen, bäckdal, 4.8.1945, L.

Ceratodon purpureus Brid. — Kebnekaiseområdet, Kaipak, klippor i sydbranten, c:a 720 m ö.h., 1.8.1945, L.

Cynodontium strumiferum DNot. — Kebnekaiseområdet, Kaipaks sydbrant block, c:a 700 m ö.h., 1.8.1945, L.

C. tenellum Limpr. — Kebnekaiseområdet, Kaipaks sydbrant, 720—740 m ö.h., reg. alp., 1.8.1945, Degelius, S.

Desmatodon latifolius Br. & Sch. — Kebnekaiseområdet, Tarfaladalens östsida 4,5 km SO Tarfalajaure, äng, 950 m ö.h., 3.8.1945, L.

Dicranoweissia crispula Lindb. — Kebnekaiseområdet, SV Kebnetjåkkoglaciären, block, c:a 1400 m ö.h., 2.8.1945, L; Tarfalajaures östra strand, block, 1200 m ö.h., 3.8.1945, L; Tarfaladalen 500 m N bron över Tarfalajokk, videsnår, 3.8.1945, L. Ladtjovagge, sten i ängsbjörkskogen nedanför Tarfalaålkes sydbrant, 1.8.1945, L.

Dicranum fuscescens Turn. — Kebnekaiseområdet, Kaipaks sydsluttning, block, reg. alp., 1.8.1945, L. Ladtjovagge, ängsbjörkskogen nedanför Tarfalaålkes sydbrant, fuktigt block, 1.8.1945, L.

D. scoparium Hedw. — Kebnekaiseområdet, Tarfaladalen 500 m N bron över Tarfalajokk, videsnår, 800 m ö.h., reg. alp., 3.8.1945, L.

Drepanocladus exannulatus Warnst. s. str. — Ladtjovagge, Bogdanovkåtan 7 km Ö Kebnekaise turiststation, *Carex rostrata*-kärr, 1.8.1945, L.

Dr. procerus Warnst. — Kebnekaiseområdet, 500 m S turiststationen, *Carex aquatilis*-kärr 650 m ö.h., reg. alp., 4.8.1945, L.

Dr. purpurascens Loeske — Kebnekaiseområdet, 200 m N turiststationen, bäck, 700 m ö.h., reg. alp., 2.8.1945, L.

Dr. revolvens Warnst. — Ladtjovagge, Holmajärvi båtlänning, kärr, 31.7. 1945, L; mellan Bogdanovkåtan och Ladtjojokk, 7 km Ö Kebnekaise turiststation, kärr, 1.8.1945, L.

Dr. uncinatus Warnst. — Ladtjovagge, i bäck och på block i ängsbjörkskogen nedanför Tarfalaålkes sydbrant, 1.8.1945, L; Bogdanovkåtan 7 km Ö Kebnekaise turiststation, stranden av Ladtjojokk, 1.8.1945. Kebnekaiseområdet, 400 m NNO turiststationen, *Ranunculus*-äng, reg. alp., 1.8.1945; Tarfaladalen 500 m N bron över Tarfalajokk, videsnår, 800 m ö.h., reg. alp., 2.8.1945, L; Tarfaladalens östra sida, äng, 950 m ö.h., 3.8.1945.

Grimmia funalis Schpr. — Ladjtovagge, ängsbjörkskog nedanför Tarfalaålkes sydbrant, block, 1.8.1945, L. Kebnekaiseområdet, Kaipaks sydbrant, c:a 730 m ö.h., reg. alp., 1.8.1945, Degelius, S.

Gr. ovalis Lindb. — Ladtjovagge, ängsbjörkskog nedanför Tarfalaålkes sydbrant, block, 1.8.1845, L, S. Kebnekaiseområdet, Tarfaladalens östra sida, stort block, 1120 m ö.h., 3.8.1945, Degelius, S.

Hygrohypnum ochraceum Loske — Kebnekaiseområdet, Tarfalajaures östra strand, smältvattensbäck, 1200 m ö.h., 3.8.1945, L.

H. Smithii Broth. — Kebnekaiseområdet, Kaipaks sydbrant, klippor, reg. alp., 3.8.1945, L.

Hylocomium pyrenaicum Lindb. — Kebnekaiseområdet, Tarfaladalens östra sida 4 km SO Tarfalajaure, översilad *Ranunculus*-äng, 950 m ö.h., 3.8.1945, L.

H. Schreberi Brid. — Kebnekaiseområdet, Tarfaladalens östra sida 4,5 km SO Tarfalajaure, äng, 950 m ö.h., 3.8.1945, L; Tarfaladalen 500 m N bron över Tarfalajokk, videsnår, reg. alp., 3.8.1945, L.

H. splendens Br. & Sch. — Ladtjovagge, ängsbjörkskog nedanför Tarfala-

ålkes sydbrant, block, 1.8.1945, L. Kebnekaiseområdet, Tarfaladalen 500 m N bron över Tarfalajokk, videsnår, 800 m ö.h., reg. alp., 3.8.1945, L.

Kiaeria falcata Hag. — Kebnekaiseområdet, mellan toppstugan och Sydtoppen, blockmark, 1900 m ö.h., 2.8.1945, L.

K. Starkei Web. & Mohr. — Kebnekaiseområdet, 300 m SV Kebnetjåkkoglaciärens sydkant, block, 1400 m ö.h., 2.8.1945, L.

Lescurea mutabilis Lindb. var. *saxicola* Hag. — Kebnekaiseområdet, Tarfaladalen 500 m N bron över Tarfalajokk, videsnår, reg. alp., 800 m ö.h., 3.8. 1945, L.

Leucodon sciuroides Schwaegr. — Ladtjovagge, ängsbjörkskog nedanför Tarfalaålkes sydbrant, block, 1.8.1945, L. I Torne lappmark är den vidare känd från Paddos S om Abisko, där den tagits 1916 av G. Samuelsson, S, U och av E. Jäderholm, U samt 1944 av H. Persson, S, U och O. Hedberg, U och 1948 av P. O. Nyman, U, från Keron, H. Persson 1944, S, U, från Nissontjårro, G. Samuelsson 1916, S, U och E. Jäderholm, S, från Nissonjokks kanjon, G. Arnell, O. Mårtensson 1954, U, från området mellan Abisko och Paddos, E. Evans, E. Nyholm och O. Mårtensson 1953, U och P. O. Nyman, 1948, U, från Maivattjåkko N om Torne träsk, E. Nyholm, 1949, U och från Masugnsbyn, Rautasjoki kanjon, E. Nyholm 1946, S.

Mnium orthorrhynchum Br. eur. — Kebnekaiseområdet, Kaipaks sydbrant, klippor, c:a 730 m ö.h., reg. alp., 1.8.1945, L.

Mn. pseudopunctatum Br. & Sch. — Ladtjovagge, Bogdanovkåtan, 7 km Ö Kebnekaise turiststation, stranden av Ladtjojokk, 1.8.1945; ängsbjörkskog nedanför Tarfalaålkes sydbrant, i bäck och i bottenskiktet i skogen, 1.8.1945, L.

Mn. spinosum Schwaegr. — Kebnekaiseområdet, Tarfaladalen 500 m N bron över Tarfalajokk, videsnår, reg. alp., 3.8.1945, L. Tidigare är arten endast en gång iakttagen så högt som i lågfjällbältet av regio alpina nämligen på fjället Kätavare N om Riksgränsens station av E. Jäderholm och G. Samuelsson 1916, S.

Oncophorus virens Brid. — Ladtjovagge, ängsbjörkskog nedanför Tarfalaålkes sydbrant, block vid bäck, 1.8.1945, L.

Paraleucobryum longifolium Loeske. — Ladtjovagge, lokal=föreg., 1.8. 1945, L.

Philonotis seriata Lindb. — Kebnekaiseområdet, 200 m N turiststationen, vid bäck, 700 m ö.h., reg. alp. 1.8.1945, L.

Ph. tomentella Mol. — Kebnekaiseområdet, 800 m S turiststationen, bäckdal, reg. subalp., 1.8.1945; 300 m NV turiststationen, vid bäck, reg. alp., 1.8.1945, L. Ladtjovagge, ängsbjörkskog nedanför Tarfalaålkes sydbrant, bäck, 1.8. 1945, L.

Plagiothecium silvaticum B. & S. var. *Roeseanum* Lindb. — Ladtjovagge, ängsbjörkskog nedanför Tarfalaålkes sydbrant, fuktigt block, 1.8.1945, L.

Polytrichum alpinum Hedw. — Ladtjovagge, som föreg., block, 1.8.1945, L. Kebnekaiseområdet, 400 m NNO turiststationen, *Ranunculus*-äng, reg. alp., 1.8.1945, L; 300 m SV Kebnetjåkkoglaciären, 1400 m ö.h., 2.8.1945; sydöstra stranden av Tarfalajaure, 1200 m ö.h., 3.8.1945; 3 km NV turiststationen, hed i Jökeldalen, 1000 m ö.h., 2.8.1945; Tarfaladalens östra sida, *Ranunculus*-äng, 950 m ö.h., 3.8.1945.

P. hyperboreum R. Br. — Kebnekaiseområdet, mellan toppstugan och Sydtoppen, blockmark, 1900 m ö.h., 2.8.1945, L.

P. juniperinum Hedw. — Kebnekaiseområdet, 700 m S Kebnetjåkkoglaciären, hed i Jökeldalen, 1000 m ö.h., 2.8.1945, L; Tarfaladalen 500 m N bron över Tarfalajokk, videsnår, 800 m ö.h., reg. alp., 3.8.1945, L.

P. norvegicum Hedw. — Kebnekaiseområdet, 300 m NV turiststationen, 700 m ö.h., reg. alp., 1.8.1945, L.

P. piliferum Hedw. — Kebnekaiseområdet, Kaipaks sydbrant, 700 m ö.h., reg. alp., 1.8.1945, L; mellan toppstugan och Sydtoppen, blockmark, 1900 m ö.h., 2.8.1945, L.

Pseudoleskea incurvata Dix. — Kebnekaiseområdet, Tarfaladalens östra sida 4 km SO Tarfalajaure, 1100 m ö.h., 3.8.1945, L.

Pterygynandrum filiforme Hedw. — Ladtjovagge, ängsbjörkskog nedanför Tarfalaålkes sydbrant, block, 1.8.1945, Degelius, S.

Rhacomitrium canescens Brid. — Kebnekaiseområdet, 1 km S Ladtjojokk, klappersten på holme i Ladtjojokk, 4.8.1945, L.

Rh. fasciculare Brid. — Kebnekaiseområdet, 300 m NV turiststationen, vid bäck, 700 m ö.h., reg. alp., 1.8.1945, L.

Rh. lanuginosum Brid. — Kebnekaiseområdet, 500 m S Kebnetjåkkoglaciären, 1200 m ö.h., 2.8.1945, L; Kaipaks sydsluttning, block, reg. alp., 1.8. 1945, L; mellan toppstugan och Sydtoppen, blockmark, 1900 m ö.h., L.

Rh. microcarpon Brid. — Kebnekaiseområdet, Kaipaks sydsluttning, block, reg. alp., 1.8.1945, L.

Rhytidium rugosum Kindb. — Ladtjovagge, ängsbjörkskog nedanför Tarfalaålkes sydbrant, block, 4.8.1945, Degelius, S.

Schistidium apocarpum Br. eur. — Kebnekaiseområdet, Kaipaks sydbrant, klippor, reg. alp., 1.8.1945, L.

Sch. apocarpum Br. eur. var. *gracile* Br. eur. — Ladtjovagge, ängsbjörkskog nedanför Tarfalaålkes sydbrant, block, 4.8.1945, Degelius, S.

Scorpidium scorpioides Limpr. — Ladtjovagge, Holmajärvi båtlänning, kärr, 31.7.1945, L.

Tortula norvegica Wg., Lindb. — Kebnekaiseområdet, Tarfaladalens östra sida 4 km SO Tarfalajaure, torr backe, 1000 m ö.h., 3.8.1945, L.

T. ruralis Schwaegr. — Kebnekaiseområdet, Kaipaks sydbrant, klippor, reg. alp., 1.8.1945, L.

Ulota curvifolia Brid. — Ladtjodalen, ängsbjörkskog nedanför Tarfalaålkes sydbrant, block, 1.8.1945, L.

Webera albicans Schpr. — Kebnekaiseområdet, Tarfaladalens östra sida 4 km SO Tarfalajaure, översilad *Ranunculus*-äng, 950 m ö.h., 3.8.1945, L.

W. commutata Schpr. — Lokal=föreg. 3.8.1945, L.

W. cruda Bruch — Ladtjovagge, ängsbjörkskog nedanför Tarfalaålkes sydbrant, block, 4.8.1945, Degelius, S.

W. cucullata DNot. — Kebnekaiseområdet, Tarfalajaures östra strand, smältvattensbäck, 1200 m ö.h., 2.8.1945, L.

Sphagnum Girgensohnii Russ. — Ladtjovagge, Bogdanovkåtan 7 km Ö Kebnekaise turiststation, kärr, 1.8.1945, L. Kebnekaiseområdet, 800 m S turiststa-

tionen, bäckdal, reg. alp., 4.8.1945, L; Tarfaladalen 500 m N bron över Tarfalajokk, videsnår, 800 m ö.h., reg. alp., L.

Sph. teres Ångstr. — Kebnekaiseområdet, 500 m S turiststationen, *Carex aquatilis*-kärr, 650 m ö.h., reg. alp., 4.8.1945, L.

Barbilophozia barbata Loeske — Ladtjovagge, ängsbjörkskog nedanför Tarfalaålkes sydbrant, block, 1.8.1945, L, S.

B. Hatcheri Loeske — Kebnekaiseområdet, Kaipaks sydsluttning, block, 1.8.1945, L; Tarfaladalens östra sida, äng, 950 m ö.h., 3.8.1945, L. Ladtjovagge, ängsbjörkskog nedanför Tarfalaålkes sydbrant, block, 1.8.1945, Degelius, S.

B. lycopodioides Loeske — Kebnekaiseområdet, S Kebnetjåkkoglaciären, hed, 1000 m ö.h., 2.8.1945; 400 m NNO turiststationen, *Ranunculus*-äng, 1.8. 1945, L; Tarfaladalen 500 m N bron över Tarfalajokk, videsnår, 800 m. ö.h., 3.8.1945, L.

Gymnomitrium concinnatum Corda. — Kebnekaiseområdet, SV Kebnetjåkkoglaciären, block, 1400 m ö.h., 2.8.1945, L.

G. coralloides Nees. — Kebnekaiseområdet, Tarfalajaures södra strand, 1200 m ö.h., 3.8.1945, L.

G. varians Schiffn. — Kebnekaiseområdet, Tarfalajaures södra strand, blockmark, 1200 m ö.h., 3.8.1945, L.

Diplophyllum albicans Dum. — Kebnekaiseområdet, SV Kebnetjåkkoglaciären, block, 1400 m ö.h., 2.8.1945, L.

Harpanthus Flotowianus Nees. — Kebnekaiseområdet, 400 m NNO turiststationen, *Ranunculus*-äng, 700 m ö.h., 1.8.1945, L.

Lophozia Wenzelii Schiffn. — Kebnekaiseområdet, Tarfaladalen 4,5 km SO Tarfalajaure, 950 m ö.h., 3.8.1945, L.

Orthocaulis Floerkei Buch. — Ladtjovagge i bottenskiktet i ängsbjörkskog nedanför Tarfalaålkes sydbrant, 1.8.1945, L.

O. Kunzeanus Buch. — Kebnekaiseområdet, 400 m NNO turiststationen, *Ranunculus*-äng, 700 m ö.h., 1.8.1945, L.

Pleuroclada albescens Spruce — Kebnekaiseområdet, Tarfalajaures södra och sydöstra strand, 1200 m ö.h., 3.8.1945, L; NV turiststationen, vid bäck, 700 m ö.h., 1.8.1945; L.

Ptilidium ciliare Hampe. — Ladtjovagge, ängsbjörkskog nedanför Tarfalaålkes sydbrant, fuktigt block, 1.8.1945, L.

Radula complanata Dum. — Ladtjovagge, ängsbjörkskog nedanför Tarfalaålkes sydbrant, block, 4.8.1945, Degelius, S.

Saccobasis polita Buch. — Kebnekaiseområdet, Tarfaladalen 500 m N bron över Tarfalajokk, videsnår, 800 m ö.h., 3.8.1945, L.

Scapania paludosa K. Müll. — Kebnekaiseområdet, N turiststationen vid bäck, 700 m ö.h., 2.8.1945, L.

Sc. subalpina Dum. — Ladtjovagge, ängsbjörkskog nedanför Tarfalaålkes sydbrant, block vid bäck, 1.8.1945.

Sphenolobus minutus St. — Kebnekaiseområdet, Kaipaks sydsluttning, block, 1.8.1945, L.

Temnoma setiformis M. A. Howe — Kebnekaiseområdet, nedanför Kaipaks sydsluttning, block, 700 m ö.h., 1.8.1945, L.

Summary

A description is given of some of the main plant communities in the low alpine belt east of the highest mountain of Sweden in the Kebnekaise region, northernmost Lappland. These communities are dwarf-shrub heaths of the poor type of the *Empetrion-* and *Myrtillion*-alliances (Du Rietz 1942 a), willow scrubs of the association *Salicetum geraniosum alpicolum* in the alliance *Mulgedion alpini* (Nordhagen 1943) and meadows of the alliance *Ranunculo-Anthoxanthion* (Gjaerevoll 1950), all characteristic of poor, non-calcareous soils.

Cardamine bellidifolia is reported from 1800 m s.m., the highest locality in northern Scandinavia. In the boulder ground at Kebnekaise sydtopp at 1900 m s.m. the following mosses are growing: *Andraea Blyttii, A. rupestris, Arctoa fulvella, Kiaeria falcata, Polytrichum hyperboreum, P. piliferum* and *Rhacomitrium lanuginosum,* but no vascular plants.

The bryological flora of the Kebnekaise-region and the adjoining Ladtjo-valley, which was hitherto unknown, is listed with 68 species of mosses, 19 species of hepatics and 2 *Sphagnum* species.

Litteratur

AHLMANN, H. W:SON, 1951, Scientific investigations in the Kebnekajse massif, Swedish Lappland. I. General outline of the investigations in 1946—1951. — Geogr. Annaler. Bd 33. Stockholm.

ALM, C. G., 1921, Bidrag till Kebnekaisetraktens flora. — Sv. Bot. Tidskr. 15. Stockholm.

ALMQUIST, E., 1918, Växtlokaler från Torne och Lule lappmarker. — Ibid. 11. Stockholm.

BIRGER, S., 1912, Kebnekaisetraktens flora. — Ibid. 6. Stockholm.

DEGELIUS, G., 1945, Ett sydberg i Kebnekaiseområdet och dess lavflora. — Bot. Not. Lund.

DU RIETZ, G. E., 1925, Studien über die Höhengrenzen der hochalpinen Gefässpflanzen im nördlichen Lappland. — Veröff. Geobot. Inst. Rübel. 3 Heft. Zürich.

— 1926, Bidrag till Kebnekaiseområdets flora. — Sv. Bot. Tidskr. 20. Stockholm.

— 1942 a, Rishedsförband i Torneträskområdets lågfjällbälte. — Sv. Bot. Tidskr. 36. Stockholm.

— 1942 b, De svenska fjällens växtvärld. — Ymer, h. 3—4. Stockholm.

— 1949, Huvudenheter och huvudgränser i svensk myrvegetation. — Sv. Bot. Tidskr. 43. Stockholm.

— 1954, Sydväxtberg. — Sv. Bot. Tidskr. 48. Stockholm.

FRÖDIN, J., 1918, Iakttagelser i Kebnekaiseområdets sydberg. — Sv. Bot. Tidskr. 11. Stockholm.

GJAEREVOLL, O., 1950, The snow-bed vegetation in the surroundings of Lake Torneträsk, Swedish Lappland. — Sv. Bot. Tidskr. 44. Stockholm.

HEDBERG, O., 1947, Bidrag till Torne lappmarks flora. — Bot. Not. Lund.

HULTÉN, E., 1950, Atlas över växternas utbredning i Norden. Fanerogamer och ormbunksväxter. — Stockholm.

JOHANSSON, H. F., 1951, The petrology and tectonics of the Kebnekajse region and their morphological importance. — Geogr. Annaler. Bd 33. Stockholm.

KALLIOLA, R., 1939, Pflanzensoziologische Untersuchungen in der alpinen Stufe Finnisch-Lapplands. — Annales Bot. Soc. Zool.-Bot. Fenn. Vanamo. Tom 13. N:o 2. Helsinki.

MÅRTENSSON, O., 1952, A contribution to our knowledge of the moss flora of the Pältsa area. — Bot. Not. Suppl. Vol. 3: 2. Lund.

NORDHAGEN, R., 1943, Sikilsdalen og Norges fjellbeiter. — Bergens museums skrifter 22. Bergen.

QUENSEL, P., 1919, De kristallina sevebergarternas geologiska och petrografiska ställning inom Kebnekaiseområdet. — Geol. Fören:s Förhandl. Bd 41. Stockholm.

VESTERGREN, T., 1902, Om den olikformiga snöbetäckningens inflytande på vegetationen i Sarekfjällen. — Bot. Not. Lund.

WOXNERUD, E., 1951, Kartografiska arbeten i Kebnekajse. — Geogr. Annaler. Bd. 33. Stockholm.

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New or Otherwise Interesting Swedish Lichens. XV

By A. H. MAGNUSSON

Gothenburg, Sweden

147. New Taxa

Lecidea (Eulecidea) atriuscula H. Magn. n. sp.

Thallus effusus, fuscoater, areolatus, areolis minutis, planis, angulosis, opacis, I−, CaCl−, KOH+ flavis, demum rubris, Pd± flavis, hypothallo atro. Apothecia numerosa, leviter prominentia, minuta, disco fuscoatro, plano, opaco, immarginato. Excipulum intus incoloratum, extus tenuiter caeruleo-viride. Hypothecium cum thecio incoloratum, KOH+ flavum, epithecio sordide caeruleo-viridi. Paraphyses contiguae, clavatae. Sporae octonae, globoideae.

Bohuslän: par. Öckerö, Hönö, in its southern part, on oxidated rock 1916, H. Magn., associated with *Rhizocarpon oederi*.

The specimen observed is uniform, several cm in diam.; areolae 0.3—0.5 mm wide, separated by narrow cracks, most of them opaque from a thin cover of sordid grey-green algae. Apothecia 0.3—0.4 mm wide, 0.2—0.35 mm thick, constricted at base; when young they have a very thin, inconspicuous, concolorous margin which is soon depressed.

Thallus 0.2—0.35 mm thick, without cortex. Algae dense, 8—11 μ in diam., forming a 70—100 μ thick stratum. Medulla consisting of densely interwoven, thick-walled hyphae, 3.5—4 μ in diam. Lower side pale or dark. Large parts of the thallus surface are covered by a thin stratum of algae, solitary or in groups, 20—25 μ wide with grey-green surface. The algae resemble soredia and are covered by very short-celled hyphae, but the thallus surface below is not broken up. — The exciple is laterally 50 μ thick with outermost 10 μ blue-green, hyphae in KOH distinct, radiate, thick-walled. Hypothecium with interwoven hyphae. Thecium, 50 μ high, like exciple becomes red in Pd, yellow in KOH like hypothecium, epithecium sordid blue-green. Apices of para-

physes distinct in KOH, 3.5—4 μ thick. Spores ovoid to globoid, 6.5—9×7 μ.

The new species seems to be a near relative to *L. turjaënsis* Räs. which has similar reactions, broad spores, 6—10.5×5—7 μ, and a similar colour, brown-grey to castaneous. But *turjaënsis* is described with a 75 μ high thecium, a brown epithecium, unchanged in KOH, and small concave to plane apothecia, only 0.1—0.3 mm wide.

Lecidea (Eulecidea) inaequalis H. Magn. n. sp.

Thallus effusus, caerulescenti-albo-cinereus, crassiusculus, granulosus, granulis contiguis, difformibus, basi constrictis, I−, KOH−, CaCl−, Pd+ leviter flavescentibus. Apothecia crebra, mediocria, sessilia, atrofusca, mox convexa, immarginata, saepe composita. Excipulum pallidum, granulosum, KOH−. Hypothecium altum, incoloratum. Thecium mediocre, superne tenuiter viridi-fuscum. Paraphyses in KOH discretae, apicibus haud incrassatis. Sporae subglobosae vel ovoideae.

Värmland. Munkfors, Bryngelstorp, on the hill to the north east 1951, S. W. Sundell (315) associated with *Stereocaulon vesuvianum.*

The thallus probably covers a rather large area but no edge has been observed. It is coarsely granular, uniform; the granules 0.3—0.5 mm thick and equally wide, very uneven; groups of them separated by cracks. No hypothallus discernible. — Apothecia 0.5—1.0 mm wide, some simple, plane or slightly convex; most of them soon convex and composed of several confluent parts, the irregular groups more or less constricted at the base.

Apothecia 0.35—0.45 mm thick, inside pale, Pd+ yellow. Exciple excluded at edge, below and laterally 50—85 μ thick, grey to brownish grey from granules unchanged in KOH, yellowish in Pd, hyphae radiate to parallel. Hypothecium 100 μ thick or more, colourless, hyphae mainly perpendicular. Thecium 75—80 μ high, colourless, upper 6—8 μ brownish green, colourless in KOH. Paraphyses distinct, 1.5 μ thick, lax in KOH, uniform to the apices. Asci 45—50×12 μ, clavate; apical wall 6—8 μ thick. Spores 8, 9—11×7—8 μ, broadly ellipsoid or subglobose, uniseriate or ±biseriate. — Pycnidia indiscernible.

The new species belongs to the *goniophila*-group on account of the lax paraphyses and the broad spores but differs from most of these species in the brownish colour of the apothecia, the pale, granular exciple and the composed areolae.

Lecidea (Eulecidea) vermlandica H. Magn. n. sp.

Thallus ater, tenuissimus, continuus, inaequalis, indistincte areolatus, KOH−. Apothecia numerosa, adpressa, minuta, tenuia, disco atro, plano, margine tenui, atro, leviter prominente cincto. Excipulum fusco-atrum, integrum. Hypothecium fuscescens, KOH+ subviolascens. Thecium tenue, leviter smaragdulum, superne caeruleo-viride. Sporae octonae, minutae, late ellipsoideae.

Värmland: par. Sunnemo, Heftersbol, on shady rock wall north of the farm 1952, S. W. Sundell (371).

Thallus in the single specimen observed 2×2 cm in diam., minutely areolate or rugulose and opaque upon a blackish hypothallus. — Apothecia 0.2—0.4 mm wide, concolorous with the thallus, inconspicuous, slightly constricted at base and 0.15 mm thick. Exciple at edge 35 μ thick, black-green, at base 50 μ, brown-black, entire with distinct limitation. Hypothecium 35 μ thick, at conical centre up to 70 μ, pale brown with considerable oily content. Thecium 50 μ high, pale emerald, I+ blue like hypothecium; upper 8 μ blackish blue-green. Paraphyses firmly contiguous; in KOH 1.5 μ thick, distinct, apices thicker. Asci 45×12 μ. Spores rare, 7—8×5.5—6 μ.

The new species seems to be closely related to *Lecidea lugubris* Nyl., described from Fretum Behringii (St. Lawrence Bay) in Flora 1885. According to the description the distinguishing character of importance here seems to be the subglobose spores, 8—9×7—8 μ. *Lecidea collatula* Nyl. from France is a rather similar species but from the description it has black exciple and an epithecium which in HNO_3 becomes "obscure caerulescens" (in *vermlandica* violet-red). Its spores are 7—9×3.5—4.5 μ in size.

Lecidea (Eulecidea) scotoplaca H. Magn. n. sp.

Thallus tenuissimus, ater, saepius saxo nudo interruptus, medulla I+ caerulescens. Apothecia dispersa, mediocria, atra, sessilia, crassa, plana, margine leviter prominente. Excipulum solum laterale, obscure fuscum, usque ad basin continuatum. Medulla apothecii granulis nubilata, I+ caerulea, sensim in hypothecio ±fusco transiens. Thecium incoloratum, superne obscure caerulescens. Paraphyses arcte conglutinatae. Sporae octonae, minutae, ellipsoideae.

Härjedalen: Anderså cataract 1925, E. P. Vrang (in herb. H. Magn.) on siliceous rock.

The exceedingly thin thallus developed around and partly between the apothecia, smooth, minutely cracky, inside white. — Apothecia

0.5—0.7(1) mm wide, about 0.6 mm thick, greatly constricted at base. Most part of the interior is greyish from rather large and dense granules, soluble in HCl. There is no reaction with KOH, CaCl or Pd but the rather lax, long-celled hyphae with 1—1.5 μ thick lumina assume in iodine a blue colour. Outermost 20—35 μ dark brown down to base, KOH−. Hypothecium diffuse, 30—40 μ thick. Thecium 50—70 μ high, I+ blue; upper 20 μ black-olive or -green. Paraphyses difficult to separate even when treated with KOH and thereafter with HCl, 1.5—2 μ thick, apices widened to 3 μ, conglutinated and also blue-green in KOH, simple. Spores rare, about 10—12×5 μ. — Algae, 6—8 μ in diam., have been seen only in the thallus.

L. scotoplaca may be more or less closely related to *L. lapicida* on account of the positive I-reaction and the habitus, but is distinctly separated by the black thallus, the high apothecia, the firmly contiguous paraphyses and the absence of a yellow KOH-reaction (common in *lapicida*). A real exciple can hardly be said to exist, the dark outer surface resembles more a cortex.

Lecidea (Biatora) frustulenta H. Magn. n. sp.

Thallus effusus, fuscus, diffractus, areolis crassis, verruculosis, rimis latis separatis, crustam frustulosam formantibus, KOH−, I−, CaCl−, Pd−, hypothallo indistincto. Apothecia pauca, minuta, arcte adpressa, fuscoatra, disco convexo, immarginato. Excipulum extus fuscescens, intus pallidum, hyphis radiantibus. Hypothecium fulvescenti-pallidum. Thecium tenue, superne lutescenti- vel viridescenti-fuscum. Paraphyses ramosae. Sporae octonae, late ellipsoideae vel subglobosae, minutae.

Västergötland: par. Råda, Mölnlycke, on steep gneissose rock near the highroad on its southern side 1927, H. Magn. (10380), associated with *Lecidea fuliginosa.*

The thallus probably covers a large area but no edge was observed. Areolae 0.5—2.0 mm wide, 0.3—0.5 mm thick, very irregular, in shape with densely verruculose, opaque surface of a reddish-brown tint, mostly constricted at base and loosening easily. Algae 5—7 μ in diam., yellow-green. — Apothecia 0.3—0.5 mm wide, inconspicuous, without algae. Exciple about 35 μ thick, also lower surface dark brown, inwardly gradually paler and grading into the pale brownish-yellow hypothecium. Lumina of the hyphae, turgid in KOH, interwoven, very narrow and branched. Thecium 50—60 μ high, sordid, only asci I+ blue. Paraphyses 1 μ thick, ±branched. Ripe asci few, 35—40×13 μ. Spores not numerous, 9—7×6 μ.

The new species must be placed in the *rivulosa* (*cyathoides*) group on account of the apothecial structure with brownish exciple, low thecium and broad spores, resembling those in *L. tenebrica*. But the habitus with diffractive, verruculose areolae is very different from all species in this group.

Thelidium corticola H. Magn. n. sp.

Thallus continuous only in patches, 0.5—1.0 cm wide, upon the rough verrucae fertiles contiguae vel dispersae, minutae, apice atro excipuli prominenti visibili. Excipulum integrum, globosum, atrum, uniforme. Paraphyses dissolutae sed periphyses superne longae, distinctae. Sporae incolores, ellipsoideae, transversim 5—7-septatae.

Bohuslän: par. Kville, on *Fraxinus* in the cemetery 1934, H. Magn. (14436) with *Collema flaccidum, Physcia orbicularis* and *Bacidia populorum.*

Thallus continuous only in patches, 0.5—1.0 cm wide, upon the rough bark between the above-mentioned lichens, rather thin and uneven between the ±dense, fertile verrucae, without visible hypothallus. Thallus 70—100 µ thick outside the exciple without distinct cortex, Pd−, KOH− or yellowish, CaCl−. Algae 4—6.5 µ in diam., yellow-green, in dense crowds between the medullary cells, 3.5—5 µ large, or between hyphae. Cells often filled with oil.

Fertile verrucae 0.5—0.7 mm wide, about 0.5 mm high, black top 0.2—0.5 mm wide, naked, half globose. Exciple 0.4—0.7 mm in diam., globose; wall uniform, about 50 µ thick, black, HNO_3−; mouth 25 µ wide, not depressed. Inner part 17 µ thick, colourless to near the mouth. Hypothecium at base 20 µ thick, faintly greyish, laterally attenuated half way to the top. Paraphyses dissolved, but periphyses up to 50 µ long, 1 µ thick, indistinctly branched, occupying upper 70 µ of nucleus. Asci about 70×16 µ, wall at apex about 5 µ thick. Spores 8 or lying in asci-resembling groups of 4—8, 24—32×7—8.5 µ, fusiform with 5—7 horizontal septa.

Th. corticola has a certain resemblance to *Th. acroglyptum* Norm. apud Th. Fr. in Bot. Not. 1867 p. 154, pictured in Rabh., Krypt.flora *9*/1: 365, 1934 and in Servit, Lich. Fam. Verrucariacearum Pl. 1, fig. 26, 1954, but this species grows on moss and has (according to the holotype in Oslo) white, flattened thallus consisting of rather thin, irregular parts of different size, more naked apothecia with distinctly impressed mouth. Its exciple with 25 µ dark stratum and 50 µ thick, colourless stratum has parallel, thin-walled hyphae.

I find it appropriate to cite Norman's excellent description on this occasion. "Thallo latius expanso, cinereo, tenui, deliquescente, e plagulis v. squamulis adnatis parvulis, irregularibus, erosis, remotioribus constante; apotheciis mediocribus, atris, basi innatis v. fere totis emersis, e globoso truncato-conicis, vertice, circa ostiolum profunde impressum, pertusum, peripherice saepe radiatim striolatum, tumidulo; sporis 8:nis, pure hyalinis, elongate oblongis, 6-locularibus, 0.030—34 mm longis, 0.005—6 mm latis; gelatina hymenii jodo post caerulescentiam levissimam intense coccineo-rubescente. — Hab. supra muscos in rupibus Nordlandiae meridionalis". "Ad Indyr par. Gildeskaal Nordlandiae" (Label in Oslo). — "Plagulae thalli vegetationi algarum, hypothecium fusco-nigrum simulanti, sparse insident, cui apothecia post deliquescentiam thalli passim nuda imposita sunt. Perithecium integrum, post evacuationem nuclei vulgo persistens, sed saepe diffractum conflexum. Paraphyses in mucum diffluxae."

Dermatocarpon daedaleum (Krmph.) Th. Fr. v. *corticola* H. Magn. n. var.

Thallus squamuloso-verrucosus, cinereus, squamulae ad marginem dilatatae, convexae sublobataeque, ceterum irregulariter verruciformes, rimis profundis separatae subtus obscurae. Apothecia in quavis squamula evoluta, saepius numerosa, apice leviter prominentia.

Västergötland: par. Skallsjö, Drängsered 1933, H. Magn. (14123). At base of *Fraxinus*.

Radiating squamules about 1×1 mm in diam., ±incised and partly discrete, appressed, inner squamules 1—3 mm wide, very irregular, almost bullate with a great number of black, solitary apothecia visible at apices. Only few radiating squamules sterile. — Thallus about 0.35 mm thick, lower part, 100—150 μ thick, ±dark brown from interwoven, lax, brown hyphae, 3—4 μ thick, moderately thin-walled with very long cell-lumina. No lower cortex. Medulla 50—100 μ thick, colourless, of similar hyphae; limitation toward dark stratum very distinct. Algal stratum 50—60 μ thick with dense, yellow-green algae, 6—7 μ in diam. Upper cortex 30—35 μ, colourless; its cells very thin-walled, 4—7 μ in diam.; only upper 7—8 μ pale brown, mostly with 5—6 μ thick gelatinous cover. No reactions with KOH or Pd.

Apothecia 150—200 μ deep, 120—150 μ wide, entirely immersed, subglobose, colourless except in upper 50 μ where they are brown; surface in thallus level 70 μ wide, dark brown; mouth very narrow, about 10 μ. Exciple wall at base 30 μ, laterally 20 μ thick, of closely parallel, thin

hyphae. No paraphyses visible. Periphyses at mouth 1.5 μ thick, about 20 μ long, indistinct. Asci about 40 μ, with narrow foot to 50 μ high. Spores 8, (10)12—14×6(7) μ, simple, ellipsoid.

This plant resembles most *D. daedaleum* in colour, thallus structure and arrangement of the apothecia and it is perhaps only a variety growing on bark. To my knowledge it is the southernmost find in Sweden together with a poor specimen from irrigated rock in Västergötland: par. Sätila, Svansjön, collected 1926 by me (9557). *D. arboreum* (Schweinitz) Fink, not rare in N. America, has much larger squamules. *D. cinerascens* Nyl. on soil in France is unknown to me.

Pilophorus distans (Hult.) H. Magn. n. comb. — *P. robustus* f. *distans* Hult. in Bihang K. V. A. Handl. *26*, 3/3: 17 1900. — *P. cereolus* f. *distans* (Hult.) H. Magn. in Förteckn. Skand. växter. 4. Lavar p. 43, 1937.

I have found this plant, mostly in heaths, in many places along the Swedish West Coast. It always grows on slight seepages, often abundantly. Its thallus is coarsely granular with contiguous, very uneven surface, or it is areolate-cracky with the areolae composed of granules. In the greyish-white thallus there occur more or less frequently dark red-brown cephalodia, applanated or verruciform, up to 2 mm in diam. The podetia are 1—3(5) mm high, very irregular in shape, narrow with a small apothecium at top, or they are partly 1—2 mm thick as excrescences from a thallus verruca and divided. There is usually one apothecium at the top but sometimes several, confluent, up to 1.5 mm wide. All are very convex, immarginate, mostly constricted at base, black and resembling *Lecidea*-apothecia. When the stalk is narrow like the apothecium they may resemble a minute *robustum*. — Inner structure agrees with that in the other two Swedish species, but many apothecia must be considered monstrous or abortive. I have found no spores larger than 12×6 μ, but spores seems to be rare.

It was found by Hulting in Dalsland: Vågsäter, Hattefjäll 1870 and 1895 according to specimens in Bot. Garden, Göteborg. From my herbarium I can record the following localities: Bohuslän, Forshälla, St. Hasselön 1929 (12033) on seepage near northern shore, together with G. Degelius; Orust, Röra, Näverkärr 1938 (16345) and Långelanda, Svanesund 1926 (10121); Tjörn, Stenkyrka, Kållekärr 1920 (4594); Jörlanda, Toröd 1946 (19963) under overhang; Solberga, Rörtången 1928 (11331). — Västergötland: Partille, Bokedalen 1939 (16547), on moist rock in the wood. — Halland: Idala 1932 (13676).

The following localities were kindly communicated by G. Degelius: Småland: Slätthög, Moheboda 1945, on moist rock wall, coll. I. Söderberg. — **Norway.** Forsand hd, Frafjorddalen, by Brålandsfossen 1947, Degelius, a meager specimen; Nordland, Lofoten, Moskenesöy, Sörvågen by a cataract 1937, Degelius, a fine specimen. It is issued in Havås: Lich. Norv. Occid. 150 from Hordaland: Granvin, Daemmedalene, collected on steep, shady, slaty rock facing the north, 525—575 m s.m. 1936, sometimes irrigated.

I think this plant is a good species separated from *P. robustus* by the well-developed, horizontal thallus (in *robustus* soon disappearing), the low, mostly simple podetia (in *robustus* high, branched) and by its distribution (apparently western, coast-bound). It can also not be placed under *P. cereolus* which has usually low, sterile, ±sorediate podetia. All three Scandinavian species have a negative Pd-reaction. It is not recorded from the British Isles but may occur there.

148. Species new to Scandinavia

Arthopyrenia salwei (Leight.) Zahlbr. — Collected by me 1918 on Gotland: par. Öja, Burgsvik, on calcareous rock. It resembles *A. conoidea* (Fr.) Zahlbr. but has an entire, black exciple (in *conoidea* "dimidiate" e.g., the base is pale). It is recently found also in Poland by Z. Tobolewski.

Bacidia hemipolioides (Nyl.) Zahlbr., Catal. Lich. *4*: 114, 1927. — *Lecidea* Nyl. in Flora *56*: 274, 1873. — Collected by S. W. Sundell in Värmland: Övre Ullerud, Bergsby, on rock wall south of the farm, 1952 (164).

As the species is known only from the authentic locality in England. Jersey Is., Rozel, where it was collected by Larbalestier 1873 "near Archirondel Tower" (acc. to Leight., Lich. Flora Great Brit., ed. 3) the find in central Värmland seemed almost incredible. I therefore asked for the authentic specimen in Nylander's herbarium (no. 18713) which was kindly sent to me from Helsingfors. The plants were almost identical! Here is the description: Thallus effuse, thin or very thin, greyish green or sordid ochraceous (from the oxidated rock), hardly continuous. Apothecia numerous, 0.3—0.5 mm in diam., variegated, young ones like those in shady situation pale testaceous, older or more exposed ones dark brown, often with paler circumference, at first slightly convex with ±distinct, pale margin, then convex to half globose with excluded margin.

One good section of an apothecium 0.55 mm wide, 0.2 high, very

convex, with thallus below it 100—200 μ thick. Exciple very diffuse, at depressed edge 35—50 (80) μ thick, pale, partly blue-greenish in inner part, with radiating, 4—5 μ thick hyphae, exciple narrower downwards and colourless, confluent with ± colourless hypothecium to a tissue, 100 μ high, I—. Thecium 60—70 μ high with indistinct lower limitation, in most parts faintly blue-greenish, surface not darker or outermost 10 μ partly ± bright blue-green. A sordid thin cover of detritus sometimes visible on the surface. Paraphyses firmly conglutinated, simple, in KOH 1.5 μ thick to the apices. Asci about 50×17 μ, clavate. Spores 8, 14—16×4 μ, 3-septate, usually ± bent (12—18×4.5 μ acc. to Nyl.).

Algae in thallus yellow-green, in clusters. Apothecia KOH—. Thecium and hypothecium I+ dark blue about 100 μ deep, mainly the asci coloured.

Bacidia inornata (Nyl.) Blomb. & Forss., Enum. Plantae Scand. 1880 p. 81; Vain., Lichenogr. Fenn. *2*: 166, 1922 (with descr.). — *Lecidea* Nyl. in Flora *57*: 11, 1874. — Västergötland: par. Lerum, Skafsås 1926, H. Magn. (10227 a), on rock wall with *Lecidea tuberculata* Smrft.

Bacidia propinqua (Hepp) Arn. in Flora *49*: 531, 1866; Th. Fr., Lich. Scand. *2*: 353, 1874; Vain., Lichenogr. Fenn. *2*: 152, 1922. — Bohuslän: par. Hjärtum, at lake St. Vector 1940, H. Magn. (17486), on *Quercus*. Agrees well with the descriptions given by Th. Fr. and Vain. Formerly known only from Tavastia: par. Tammela, on *Populus tremula*.

Catillaria confusior (Nyl.) Zahlbr., Catal. Lich. *4*: 35, 1927. — *Lecidea* Nyl. in Flora *57*: 315, 1874. — *Biatorina* conf. A. L. Smith, Brit. Lich. *2*: 142, 1926. — Bohuslän: par. Långelanda, Åsen 1926, H. Magn. (9836), on stones under overhang. Formerly recorded only from Scotland: Pertshire, Blair Athole, Craig Tulloch, on mica-schist.

Apothecia 0.45 mm wide, 0.2 mm thick, with thallus below. Exciple laterally 20 μ thick, brown-yellow with a violet shade as also in the 12 μ thick epithecium, both red-violet in KOH. Hypothecium colourless, hyphae densely intricate, in exciple radiating, 5 μ thick. Thecium 70 μ high, colourless; epithecium in water dark sordid blue-green with a thin gelatinous cover, KOH+ red-violet on the whole but tips of paraphyses dark greenish and thicker, about 3 μ, ± distinct in KOH. Spores 9—13×4—4.5 μ, ellipsoid or oblong. — Algae below exciple dense, 5—8 μ in diam., not in glomerulae.

Catillaria subnigrata (Nyl.) Zahlbr., Catal. Lich. *4*: 74, 1927. — *Lecidea* Nyl. in Flora *59*: 370, 1866. — *Biatorina synothea* **subnigrata* A. L. Smith, Brit. Lich. *2*: 133, 1926. — Halland: Fjärås bräcka, on stone fence 1926, H. Magn. (9790). Described by Nylander from England:

Merioneth, Cader Idris and also recorded from Somerset and Pertshire on schistose rock.

Apothecia 0.5 mm wide, 0.2 mm thick, KOH−. Exciple at edge 50 μ thick, pale, surface brown-yellow, at base colourless. Hypothecium 50—70 μ high, colourless to sordid. Thecium 50 μ high, upper 7—10 μ pale olive-brown, I+ blue. Paraphyses greatly branched (Nyl.: non discretae). Sporae 8—10(12) ×5 μ.

Zahlbruckner quotes in Catal. *4*: 74 Blomb. & Forss., Enum. Plant. Scand. 1880, p. 92, which is wrong, because these write *subnigra* (Nyl.) which is another species described by Nylander in Flora 1873 p. 21 and by Vainio in Lichenogr. Fenn. *5*: 423, 1934. It grows on limestone in Finland. This lichen is quoted as *Lecidea subnigra* (no. 6779) in Zahlbr., Catal. *3*: 702, 1925.

Lecidea (*Biatora*) *cinereopallens* Vain., Lichenogr. Fenn. *4*: 397, 1934. — Värmland: Övre Ullerud, Förby 1952, S. W. Sundell (152), on *Sorbus aucuparia* in northern slope west of the road. Vainio records the only specimen collected from Tavastia, Hollola, on decaying wood.

Lecidea fuscoferruginea Vain., Lichenogr. Fenn. *4*: 91, 1934. — Bohuslän: Romelanda, Lysegården 1925, H. Magn. (9428 a) in a brook. Agrees well with Vainio's description of the authentic and only specimen, collected in Karelia borealis, Leksa by a cataract.

Lecidea (*Biatora*) *lygaeoplaca* Vain., Lichenogr. Fenn. *4*: 327, 1934. — Västergötland: Borås, Ryaåsen, Ålegård 1923, H. Magn. (7463), on boulder in talus slope. It was first named *L. tenebrica* Nyl. but at a recent revision of *tenebrica* it struck me that this locality lay far outside the area of distribution of *tenebrica* given on my map in Sv. Bot. Tidskr. *29*: 13, 1925. The suspicion arose that the determination was wrong and a further study of the specimen and comparison with a small sample from herb. Vainio showed their identity. The most obvious distinctive character is the persistent apothecial margin in *lygaeoplaca* against the disappearing one in *tenebrica*.

Lecidea (*Eulecidea*) *paraclitica* Nyl. in Flora *55*: 355, 1872; Vain., Lichenogr. fenn. *4*: 243, 1934. — *L. erratica* Kbr in Zahlbr. Catal. *3*: 575, 1925. — *L. expansa* f. *paraclitica* in Norrl. Exs. 762. — Värmland: N. Råda, Nyberget 1954, S. W. Sundell (270) on wooden fence by a road.

Rhizocarpon subgeminatum Eitn. in 88 Jahresber. Schles. Ges. vaterl. Kultur (1910) 1911 p. 42; Schade in Sitz.ber. u. Abhandl. Naturwiss. Ges. Isis, Dresden (1933/34) 1935. — *Rh. phaeolepis* Vain., Lichenogr. Fenn. *2*: 290, 1922.

Närke: par. Svennevad, Österkvarn 1951. G. Kjellmert, on siliceous stone. — Bohuslän: Stenungssund, Stenungsön 1953, 1954, H. Magn., on faint seepage over open rock in wood, associated with *Rhiz. hochstetteri* f. *incrassatum, Pyrenopsis* sp. (ster.), *Sarcogyne clavus, Lecidea macrocarpa* and *Ephebe lanata.*

Biatorella pinicola (Mass.) Anzi; H. Magn. in Rabh. Krypt.flora *9,* 5/1: 33, 1936. — Göteborg: V. Frölunda, Saltsjönäs 1948, H. Magn. (21316 a) on *Sorbus aucuparia,* a small specimen associated with *Lecanora* cf. *chlarotera.* — Värmland: Karlstad, on *Ulmus* by the old cemetery 1953, S. W. Sundell (417) a very good specimen. According to Skytte Christiansen in Bot. Tidskr. *48*: 173, 1947 it has recently been collected also in Själland. It is distinguished from the commoner *B. moriformis* in the brown- or reddish-yellow surface of the thecium. Apothecia therefore more or less brown.

149. Species new to Sweden or Norway

Lecidea distensa Vain. in Adjum. Lich. Lapp *2*: 81, (1883); Lichenogr. Fenn. *4*: 190, 1934. — Värmland: par. Sunnemo, Gräsberget at Skärjen 1952, S. W. Sundell (468); Bohuslän: par. Spekeröd, E of Groland 1954, H. Magn. (24161 a), on old stone fence in heath. — Norway: Stadtlandet, Svarthorn Havås 1911, perhaps uncertain. The only Finnish specimen was collected in Karel. Bor.: Nurmes. The Swedish specimens have been compared with a sample from Vainio's herbarium.

Lecidea latypizodes Nyl. in Flora *57*: 12, 1874; H. Magn. in Nyt Magasin f. Naturvid. *87*: 209, 1949. — Värmland: Munkfors, Granhöjden, eastern slope 1951, S. W. Sundell (223). In 1939 I collected it in Norway: Vestagder, Lyngdalsfjord, inner part.

Lecidea lithophiloides Müll. Arg. in Flora *57*: 188, 1874; H. Magn. in Ark. Bot. 33 A, 16: 17, 1948 (with description). — Värmland: Munkfors, Bryngelstorp, rock wall on northeast hill 1950, S. W. Sundell (77). In Norway found in Möre by me 1947, see Ark. Bot. l.c.

Catillaria hemipoliella (Nyl.) Blomb. & Forss. in Enum. Plantae Scand. 1880 p. 92; Vain., Lichenogr. Fenn. *4*: 462, 1934. — Hedmark Fylke: Grua, in a valley near St. Rögden, on southern shore, about 300 m from the frontier 1954, S. W. Sundell (199), on trunk of *Picea* in shade.

150. New localities for Swedish lichens

Verrucaria obnigrescens Nyl. in Flora *58*: 362, 1875; Vain., Lichenogr. Fenn. *1*: 43, 1921. — Södermanland: Huddinge, Tullinge 1938, H. Magn., on rock wall. — E. Småland: par. Gladhammar, Hörlingerum 1949, H. Magn., on shady rock. — Värmland: par. Sillerud, Elgtån 1912, on rock wall by crossroad, H. Magn.; Sunnemo, Skärjen, E of the western end of the lake 1951, S. W. Sundell (255) on rock wall with *Lecidea stigmatea.*

This species which has a thin, usually minutely areolate thallus with ±blue-grey shade and very small, prominent apothecia seems to be distributed in Sweden. The exciple is entire, and the involucrellum reaches the base. *V. obnigrescens,* recorded by Hulting from Dalsland (1900 p. 85), is according to Vainio another species.

Dermatocarpon michelii (Mass.) Zw. was found by me in Bohuslän: par. Hjärtum, Yttre Torp 1946 (20143) on earthy slope with grass during the excursion of the Botanical Association in Göteborg. While the participators during a halt looked for phanerogams I could see no substrate for lichens and sat down on a slope where I detected this rare lichen growing there in small quantity. By the courtesy of Dr R. Santesson I could examine the species from the following localities in Sweden in the Botanical Museum, Uppsala. Västergötland: Kinnekulle, Martorp heath, 1860, Graewe, 1873, Hellbom; Närke, St. Mellösa 1866, Hellbom; Värmland: Ölme, Leksåsen 1872, H. Falk; Östergötland, near Navestad in the environs of Norrköping 1881, Hulting; Småland, Jönköping, Rosenlund 1868, Blomberg.

Lecidea atomaria Th. Fr., Lich. Scand. *2*: 561, 1874. — Dalsland: Dalskog, Idala 1938, H. Magn. (16432), on stone fence of black (Liane) slate. Thallus verruculose, very dark. Apothecia about 0.2 mm in diam., dense, plane, marginate. Exciple 15—20 μ thick, dark brown to black-green, entire. Thecium 30—35 μ high. Asci about 20×8 μ. Spores 4—6× 2—3 μ. Recorded by Th. Fr. from Västergötland: Billingen, coll. P. T. Cleve.

Lecidea (*Biat.*) *commixta* H. Magn. in K. Vet. o. Vitterh. Samh. Handl. Göteborg *29/4*: 16, 1925. The holotype was collected in Bohuslän: par. Foss 1851 by M. M. Floderus and lay in Uppsala under the name of *L. caesiopruinosa* Schaer. (Th. Fr., Lich. Scand. *2*: 453, 1874, in part). Now I have found it in Bohuslän: par. Spekeröd, east of Groland 1954 (24162) on stone fence in the heath, and at Bräcketorp mill, under overhang in forest (24113). Formerly in Västergöt-

land: par. Partille, NW of the railway station 1943 (18473) on perpendicular rock in the heath.

Lecidea homosema Nyl. in Flora *55*: 551, 1872; H. Magn. Ark. Bot. 2/2: 119, 1952. Except from the three localities in Torne Lappmark now known from Jämtland: Undersåker, Vällista, at 900 m, on boulder, G. Kjellmert 1953 and from Bohuslän: par. Valla, Hammar, under overhang 1920, H. Magn. (4500).

Lecidea peralbida (Th. Fr.) H. Magn., Ark. Bot. 2/2: 124, 1952, collected 1951 by S. W. Sundell (137) in Värmland: Munkfors, Bryngelstorp, rock wall on hill to northeast. Formerly recorded by me from Torne Lappmark and Jämtland.

Lecidea plebeia Nyl.; Vain., Lichenogr. Fenn. *4*: 240, 1934; Blyttia *6*: 47, 1948. — Värmland: Munkfors, N. Stensdalen, on wood in marshy ground 1954, S. W. Sundell (5). In Norway I collected it 1947 in Akershus (see Blyttia l.c.).

Lecidea (*Eulecidea*) *subcinerascens* Nyl. in Flora *60*: 228, 1877; Vain., Lichenogr. fenn. *4*: 98, 1934. — Jämtland: par. Frostviken, Gäddede, Brännklumpen 1934, H. Magn. (14486), on rock at 730 m.

Rhizocarpon intersitum Arn. in Lich. Ausfl. in Tyrol *17*: 537 and 544, 1877 (description p. 554); Malme in Sv. Bot. Tidskr. *8*: 289, 1914. — Värmland: Munkfors, Gersheden 1951, S. W. Sundell (38) upon a stone mark by the old highroad. This specimen agrees very well with Malme's description. Spores rarely fully developed, either 8 young ones seen or a few ripe, dark ones. Epithecium blue-green, KOH−; but hypothecium, especially upper part, in KOH ±violet-brown. Thallus KOH−, Pd−. Formerly recorded by Malme from Jämtland: Enafors.

Lecanora subradiosa Nyl. in Flora *55*: 549, 1872; H. Magn. in Ark. Bot. *33* A, 1: 113, 1946 and *16*: 30, 1948; Harm., Lich. France *5*: 999, 1913. — Bohuslän: par. Ödsmål, Kolhättan 1928, H. Magn. (11682), under overhang. — Västergötland: par. Angered, Gunnilse 1945, H. Magn. (18983), under overhang. — E. Småland: northwest of Gamleby 1949, H. Magn. (21560 a) on vertical rock of a hill. Formerly recorded from Lycksele Lappmark and Jämtland, from Norway, Finland, France and Poland.

Rinodina cinereovirens Vain.; H. Magn. in Medd. Göteborgs Bot. Trädg. *17*: 266, 1934. — Värmland: Karlstad, Knappstad, on *Sorbus suecica,* by the highroad (400), Växnäs, on *Sorbus aucuparia* (388) and Hammarö, Dingelsundet, on *Alnus glutinosa* (401) all collected 1953 by S. W. Sundell. A northern species formerly collected in Jämtland, Medelpad, Västerbotten and Norrbotten.

151. *Ramalina landroënsis* Zopf = *R. sinensis* Jatta.

During my studies on the genus *Ramalina* I have had the opportunity of seeing authentic specimens of many species, among others *R. asahinana* Zahlbr., described in Bot. Mag., Tokyo *41*: 355, 1927 with Pl. 11, fig. 4, pictured also by Asahina in Journ Jap. Bot. *15*: 209, 1939, fig. 14, and by Sato in Saito Ho-on Kai Mus. Res. Bull., no. 4, 1934, Pl. 1, fig. 3. Asahina there suggests that *R. sinensis* Jatta (Nuov. Giorn. Bot. Ital. *9*: 462, 1902) could be a synonym to *asahinana*. I therefore borrowed Jatta's holotype from Naples (collected in China) and found it identical to *asahinana*. Another species, *R. laciniata,* described by Jatta in Malpighia *17*: 4, 1903 and collected in Himalaya could not be found in Jatta's herbarium, but I soon detected it in material from Kew Gardens and found that is also must belong to *sinensis,* though the laciniae were partly narrower. It struck me that we had a similar species in Sweden, viz. *R. landroënsis* Zopf described and pictured by Branth in Hedwigia *45*: 147, 1906, Pl. 7, fig. 1—5, and Pl. *8,* fig. 7—10. There is material of this species from several provinces: Västerbotten, Gästrikland, Uppland, Jämtland and Värmland, and it is issued in my exsiccatas under no. 261. Different forms have been collected, some identical with the material from East Asia.

In Räsänen's herbarium I had the opportunity of seeing his *R. foliosa* described in Die Flechten Estlands *1*: 30, 1931, note, and collected in Siberia, at Tomsk, being a slight variety of *R. sinensis* with leaf-like laciniae found also in Japanese specimens. Finally I detected that *R. tucumanensis* Räs., described in Arch. Soc. Zool. Bot. Fenn. *2*: 46 (1947) 1949 was only very young specimens of *sinensis,* interesting because it was the only hitherto known locality from the southern hemisphere. Other names of this species are: *R. fastigiata* v. *nervosa* Nyl. also called *R. nervosa* Räs., or *R. calicaris* v. *nervosa* Räs.

Thus, the oldest name of this species is *sinensis* Jatta (1902) and *laciniata, landroënsis, asahinana, foliosa, tucumanensis* and *nervosa* are synonyms. The species has a wider distribution than any other *Ramalina* species I have seen: Japan, China, Siberia, Himalaya, Finland, Sweden, Tyrol, Italy and Argentina. It is natural that a species with this wide distribution varies considerably: the laciniae may be broad, leaf-like or rather narrow (as in specimens from Jämtland and Värmland), but good characteristics are the usually very distinct nerves with depressions between them where the cortex disappears so the white

medulla becomes more or less visible (a kind of pseudocyphellae) or, there are perforations instead. The specimens are mostly fertile with apical, large, plane, thin apothecia, and the disc is not rarely ±brown-rose coloured and thinly marginated. Spores 12—14×5—6(7) μ, straight or somewhat bent. Frequently the thallus is dorsiventral with paler back. Once known it seems to be easily recognized in its different forms.

(Received March 23rd, 1955)

Additional note with a Correction and an Information

The name *Acarospora geophila* H. Magn. in Bot. Not. 1954 p. 194, described by me from U.S.A.: Washington, has to be changed because it has previously been used by me for a species from Southern Mongolia: Lichens from Central Asia II: 38, 1944. I will therefore rename it and call it ***A. geogena*** H. Magn.

The name *Buellia schisticola* H. Magn. in Bot. Not. 1954 p. 199, however, will be valid against *B. schisticola* B. de Lesd. in Bull. Soc. Bot. France *101*: 225, 1954 because my description was published June 30th and B. de Lesdain's description towards the end of the same year. The descriptions are both made on material from the same locality, collected by C. Sbarbaro.

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Smärre uppsatser och meddelanden

En storvuxen Nuphar luteum från Dalarna

Den 18 augusti 1954 fann jag i Lars Olstjärn, nära Skramsen, Järna socken, Dalarna ett individ av *Nuphar luteum* (L.) Sm., som var betydligt större och kraftigare än de andra i denna och angränsande sjöar. Lars Olstjärn är en liten c:a 250 m lång sjö med klart vatten (transparens 6,7 m) på alla sidor omgiven av fuktiga marker. Djupet omedelbart utanför stränderna, som bestå av gungfly, är 1—2 m. *Nuphar luteum* förekommer flerstädes från stranden till 2,5—3,9 meters djup. Det stora individet växte några meter från stranden, och i det klara vattnet kunde man tydligt se de på två meters djup på sedimentbottnen liggande undervattensbladen. Flytbladen och i synnerhet frukterna voro hos detta individ mycket större än vanligt. Ett flytblad, som pressats, är 26 cm långt och 19 cm brett. En frukt (konserverad i sprit) är 5,5 cm

Frukt av storvuxen *Nuphar*. — Naturlig storlek.

Tab. 1. **Några storleksuppgifter om Nuphar luteum.** — Mått i cm.

	Flytblad		Frukt		Foderblad	
	längd	bredd	längd	diameter	längd	bredd
Individet från Lars Olstjärn	26	19	5,5	5,0	3,4	2,8
Hegi	10—30	—	3—4	—	(1,5) 2—3	—
Lagerberg enl. fig. 327	—	—	c:a 3,5	3	c:a 2,5	c:a 2
Neuman	12—25	10—15	—	—	—	—

lång och 5 cm i diameter, och ett av de på frukten kvarsittande foderbladen är 3,4 cm långt och 2,8 cm brett. I ovanstående tabell ha måttuppgifter för *Nuphar luteum* sammanställts från Hegi (sid. 445), Lagerberg (sid. 627) och Neuman (sid. 516).

Litteratur

HEGI, G.: Illustrierte Flora von Mittel-Europa. III. München.
LAGERBERG, T.: Vilda växter i Norden. II. — Stockholm 1947.
NEUMAN, L. M.: Sveriges Flora. — Lund 1901.

Limnologiska institutionen, Lund, februari 1955

FOLKE LUNDBERG

Ett nytt fynd av Rubus radula i norra Halland

Vid en exkursion i Onsala socken den 31 oktober förra året påträffade jag i en liten skogsdunge i närheten av gården Häcklehagen ett ganska stort bestånd av *Rubus radula* Whe.

Denna sällsynta art blev för ett par år sedan känd från två andra lokaler i socknen, nämligen Ledet och Kråkelid enligt Stellan Holmdahl i Hallands Naturskyddsförenings årsbok 1953, men ännu i Hulténs Atlas (1950) finnes ingen annan lokal i Halland än den i Ahlfvengrens Hallands växter (1924) uppgivna, nämligen »nära Båstad, Östra Karups socken». Däremot finns i Hulténs Atlas en lokal i västra Småland ungefär i höjd med Falkenberg, och vidare finns ju den kända lokalen på Koön i Bohuslän. Det kan nämnas, att *Rubus radula* på denna lokal, där den enligt Harald Fries: Göteborgs och Bohus läns fanerogamer och ormbunkar (1945) skulle föra ett tynande liv, är vacker och livskraftig, och att det påträffats ytterligare ett bestånd 100—200 meter från den ursprungliga lokalen, men denna sistnämnda lokal lär redan vara förstörd genom bebyggelse.

Göteborg i april 1955

A. WENNERBERG

Notes on South African Hepatics II

1. Taxonomical Notes

Pallavicinia pilifera Steph. — This species, described from San Thomé, was growing on stream banks in the Knysna Forest, where it was also found fruiting. As a perianth is lacking it belongs to the genus *Symphyogyna* and not to *Pallavicinia.*

Frullania sylvestris Sim and *F. natalensis* Sim. — I have had the opportunity of comparing type specimens and they seem to belong to the same species. As *F. sylvestris* is placed first in the handbook of Sim this name must be the correct one.

Frullania Rehmanii St. and *F. capensis* G. — These two species are frequently very difficult to distinguish when sterile. I have collected fertile specimens of both and have found that they differ in the following points:

Frullania capensis G.	*Frullania Rehmannii* St.
Reddish brown.	Brown.
Leaves: Apex rounded, size 340×360 μ.	Apex rounded-pointed, size 150×250 μ.
Cells rounded.	Cells roundly polygonal.
Oil bodies compound, 4×4—4×8 μ.	Homogenous, 2—4 μ.
Lobuli often parallel to the stem or inclined to it, cells up to 18 μ long.	Lobuli generally diverging from the stem, cells up to 25 μ long.
Lateral margin of the amphigastria slightly arched.	Lateral margin with a shoulder.
Female bracts sharply pointed, margins entire.	Female bracts with long and acute teeth.

Lepidozia succulenta Sim. — The amphigastria are usually only one cell long and four cells wide and the perianth has a ventral fold as in *Arachniopsis.* The name must be *Arachniopsis succulenta* (Sim).

Lepidozia truncatella Nees. — I have compared a rich material of this species from Table Mountain in Cape Province with *L. cupressina* (Sw.) Ldbg from South America. I cannot find any real difference between them, and I think they are identical. The name should be the older one: *L. cupressina* (Sw.) Ldgb.

Plagiochila corymbulosa Pears. and *P. natalensis* Pears. — The size of the trigones as well as of the teeth of the basal portion of the upper margin of the leaves vary greatly and, therefore, I do not think it possible to separate the two species by these characters. In my opinion they are only modifications of the same species, *Plagiochila corymbulosa* Pears.

Cephalozia atro-virens Sim and *C. Pillansi* Sim. — The construction of the stem in both these species is that of the genus *Cephaloziella,* the insertion of the leaves is, however, somewhat oblique. I think they are best classified in *Cephaloziella* and the names must be *Cephaloziella atro-virens* (Sim) and *Cephaloziella Pillansi* (Sim).

Jamesoniella oenops (L. et L.). — I found this species on the south side of

Table Mountain as new to Africa. It occurs in Chile, Tierra del Fuego, and I have also found it in material from Tristan da Cunha.

Odontochisma variabile Sim. — I have examined the type specimen and found that this species belongs to the genus *Jungermania*. The name thus must be *Jungermania variabilis* (Sim).

Odontoschisma africanum Sim. — In specimens from Knysne I have found female organs characteristic of the genus *Notoscyphus*. The name must be *Notoscyphus africanus* (Sim).

Chiloscyphus expansus Nees. — The perianth has the shape characteristic of the genus *Mylia* (=*Leptoscyphus*). I have examined specimens collected by Ecklon in "Promontorium Bonae Spei" named *Plagiochila gottscheana* and *Jungermania expansa* (from Herbarium Lehmann) and found that they belong to the same species. As *Jungermania expansa* Lehm. is the oldest one the name of the plant must be *Mylia expansa* (Lehm.). The synonymes are: *Jungermania expansa* Lehm., Hep. Cap. in Linnaea IV p. 361 (1829), Pug. pl. III p. 46 (1831); *Chiloscyphus expansus* Nees. Syn. Hep. p. 179 (1844); *Leptoscyphus gottscheanus* (Ldbg) St. Bull. Herb. Boiss. 2me sér. p. 227 (1906); *Plagiochila gottschana* Ldbg in Pug. VIII p. 2; Syn. Hep. p. 646 (1844).

Leioscyphus Iversenii Pears. and *Leptoscyphus Iversenii* Sim also belong to the genus *Mylia*; the name should be *Mylia Iversenii* (Pears.).

Leptoscyphus Leightonii Sim. — I have examined the type specimen and found that it belongs to *Lophocolea Newtoni* Steph.

Leptoscyphus Stephensii Sim is identical with *Lophocolea cuspidata* (Nees) Limpr.

Lophocolea diversifolia Gottsche belongs, as E. W. Jones suspected [Trans. Brit. Bryol. Soc. II/2 p. 196 (1953)], to the genus *Mylia*. I have examined the type specimen and found a perianth with the characteristic shape. The name must be *Mylia diversifolia* (G.) E. W. Jones.

Lophocolea subrotunda Mitten seems to be identical with the older *L. semiteres* (Lehm.) Mitt.

Chiloscyphus lucidus (L. et L.) Nees. — A portion of Ecklon's original collection of *Jungermania lucida* from "Cap. Bon. Spei" is preserved at the Naturhistoriska Riksmuseum, Stockholm. It is sterile and has the appearance of *Lophocolea opposita* Mitt. I think it must belong to this species, and the name should be *Lophocolea lucida* (L. et L.) with the synonymes: *Jungermania lucida* L. et L. in Lehmann, Pug. V p. 2 (1833); *Chiloscyphus lucidus* (L. et L.) Nees, Syn. Hep. p. 182 (1844); *Lophocolea opposita* Mitten, Phil. Trans. 1879 p. 397. *L. rubescens* St., Bot. Gaz. 15 p. 288 (1890); *L. obscura* St., Sp. Hep. 3 p. 1777 (1907); *L. Duseni* St. p.p. Sp. Hep. 3 p. 178 (1907).

Chiloscyphus fasciculatus Nees. — This species has, as already described by Stephani in Spec. Hep. III p. 227, the perianths on long branches and it belongs to the genus *Lophocolea*. It seems to be closely related to the South American species *L. gayana* (Mont.) Mitt.

Lejeunea convexa S. Arn. is a *Cheilolejeunea* with the slime papilla distally at the base of the tooth. The perianth is compressed. The correct name is *Cheilolejeunea convexa*.

Symphyomitra tabularis S. Arn. — The South African plant is identical with *S. africana* St. from Central Africa and with *Jungermania congesta* Lehm. from

"Promontorium Bonae Spei". As the name *Lethocolea* Mitt. (App. to N. Z. Fl. 1867) is older than *Symphyogyna* Spruce (1885), the name must be *Lethocolea congesta* (Lehm.) S. Arn. It is probably identical or at least very closely related to *L. prostrata* Mitt from Tristan da Cunha.

Porella capensis (G.) nov. comb. (*Madotheca capensis* Gottsche). — The material from Philipstown (collected 1832 by Ecklon) contains two species, one with the ventral margin straight and marginal cells about 20 μ wide, the other with the ventral margin undulate and marginal cells about 10 μ wide. The former is *P. capensis* proper, the latter is identical with *P. vallis-gratiae* (St.).

Jungermania elongata L. et L. in Linn. IX p. 426 (*Frullania trinervis* ε *elongata* in Syn. Hep.) appears to be identical with *Frullania Hildebrandtii* St. It seems to me to be a modificatio leptoderma of *Frullania trinervis,* growing on moist and shady localities.

Lejeunea krakakammae Ldbg is identical with *Strepsilejeunea knysnana* S. Arn. and the right name is *Strepsilejeunea krakakammae* (Ldbg) S. Arn.

Jungermania sphagni Dicks. — A specimen of this name, collected by Ecklon on Table Mountain, contains only *Jamesionella colorata. Odontoschisma sphagni* (Dicks.) Dum. probably does not occur in South Africa.

Riccardia submarginata S. Arn. is, as E. W. Jones has pointed out, identical with *R. pinguis* (L.) Gray.

Lepidozia spinosa S. Arn. is, as Th. Herzog has pointed out, identical with *Psiloclada clandestina* Mitt.

2. Geographical Distribution of the South African Hepatics

In Revue Bryologique T. XXII, Fasc. 1—2, p. 3 (1953) I have made some remarks about *Hepaticae* occurring also outside of South Africa. Since that was written I have found some new interesting species from Table Mountain, namely *Lepidozia bicuspidata* Mass. and *Jamesoniella oenops* (L. et L.) St., both earlier known only from southern South America, and *Metzgeria violacea* (Ach.) Evs., earlier known from South America, Belgian Congo and the district of Lake Edward and Kivu in Africa. Furthermore, I have found some South African species growing on Tristan da Cunha, namely *Calypogeia fusca* Lehm., *C. bidentula* (Web.) Nees, *Frullania serrata* G., *F. Lindenbergii* (Lehm.) Spreng., *Lepidozia tabularis* St., *Mylia expansa* (Lehm.) S. Arn.

There are more connections between the South African and the South American Flora than previously recognized. The group of *Hepaticae* known to be common to both continents now number:

Adelanthus sphalerus (H. et T.) St.
— *unciformis* Lehm. (also in Madagascar and Ireland)
Bazzania convexa (Thunb.) Mitt.
Frullania arecae (Spreng.) Sw. (also in Mexico, Galapagos and Madagascar)
— *Ecklonii* (Spreng.)
Jamesionella colorata (Lehm.) Spr. (also in the Antarctic Islands, Tristan da Cunha and Tasmania)
— *grandiflora* (L. et G.) Spr. (also known from Tristan da Cunha and Tasmania)
— *oenops* (L. et L.) Spr. (also in the Antarctic Islands)

Jamesionella paludosa St. (also known from Tristan da Cunha)
Lepicolea ochroleuca (Spreng.) Lindb. (also from Tristan da Cunha)
Lepidozia bicuspidata Mass.
— *cupressina* (Sw.) Ldbg
Marchantia berteroana L. et L. (also in the Antarctic Islands and Australia)
Metzgeria violacea (Ach.) Evs.

and of species widely spread in tropical and subtropical regions:

Dumortiera hirsuta (Sw.) R. Bl. et Nees
Lunularia cruciata (L.) Dum.
Lophocolea muricata Nees
Reboulia hemisphaerica (L.) Raddi
Telaranea nematodes (Aust.) Howe.

There are also closely related forms of *Isotachis, Lethocolea* (=*Symphyomitra*), *Lophocolea, Symphyogyna* and *Tylunanthus* in South America and South Africa.

It is possible that these species represent a relict of a flora living in an old continent consisting of the united South America and Africa. They cannot, however, be used as a relevant proof of the theory of Wegener. The spreading of the *Hepaticae* is not quite comparable with the spreading of higher plants. The *Hepaticae* frequently have very small spores and are also dispersed by small fragments of leaves and gemmae. These small particles are easily carried long distances by the air. The *Hepaticae* thus have a facility for "jumping" from one place to another. In this respect they differ widely from phanerogams with heavy seeds, as for instance *Leucadendron argenteum* R. Br., which is able to spread only a few meters.

The group of *Hepaticae* known to be common to South Africa and Europe (mostly with bicentric distribution) consists of

Adelanthus decipiens (Hook.) Mitt.
— *unciformis* Lehm. (also in South America and Madagascar)
Calypogeia arguta N. et M.
Clevea Spathysii (Ldbg) K. Müll.
Exormotheca pustulosa Mitt.
Gongylanthus ericetorum (Raddi) Nees
Lophocolea cuspidata (Nees) Limpr.
Marsupella sparsifolia (Lindb.) Dum.
Plagiochila tridenticulata Tayl.
Riccia Crozalsi Lev.
— *plana* Tal. (also in Australia)
— *sorocarpa* L.
Targionia hypophylla L.

and the wide-spread species:

Dumortiera hirsuta (Sw.) R. Bl. et Nees
Lunularia cruciata L.
Reboulia hemisphaerica (L.) Raddi
Riccardia pinguis (L.) Gray
Telaranea nematodes (Aust.) Howe.

There are also many closely related species in South Africa and Europe, such as:

Anthoceros natalensis St. — *A. multifidus* L.
Phaeoceros carolinianus (Mich.) Prosk. — *P. laevis* (L.) Prosk.
Calypogeia bidentula (Web.) Nees — *C. fissa* Raddi
Cephalozia crassicaulis St. — *C. connivens* (Dicks.) Lindb.
Cephalozia vallis-gratiae St. and *C. robusta* St. — *C. bicuspidata* (L.) Dum.

Cololejeunea capensis S. Arn. — *C. calcarea* Spr.
Fossombronia montaguensis S. Arn. — *F. pusilla* (L.) Dum.
Inflatolejeunea capensis S. Arn. — *Lejeunea Macvicari* Pears.
Lejeunea Ecklonii Ldbg — *L. cavifolia* Lindb.
Lophocolea Moelleri St. — *L. bicuspidata* (Nees) Limpr.
Marchantia berteroana L. et L. — *M. polymorpha* L.
Marchesinia chrysophylla (L. et L.) — *M. Mackai* (Hook.) Gray
Metzgeria violacea (Ach.) Dum. — *M. fruticulosa* (Dicks.) Evs.
M. tabularis St. — *M. furcata* (L.) St.
Microlejeunea ocellifera S. Arn. — *M. gracillima* (Mitt.) Carr. et Pears.
Pallavicinia capensis S. Arn. — *P. Lyellii* (Hook.) Gray
Radula capensis St. — *R. lindbergiana* G.

South African plants common to Australia are of special interest, but they are few in number. *Riccia plana* Tayl. occurs, however, also in Europe. *Psiloclada clandestina* Mitt. is found in Tasmania, New Zealand, New Guinea and Amboina.

Frullania serrata G. is the only that has a range from Indonesia over East and South Africa to Tristan da Cunha in the west.

SIGFRID ARNELL

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In Memoriam

Åke Åkerman

26/8 1887—13/4 1955

Ernst Åke Åkerman föddes den 26 augusti 1887 i Norra Vram, där fadern var inspektor på Vrams Gunnarstorp för att några år senare på arrende övertaga Ahleborgs gård. Från hemmet ärvde Åkerman intresset för jorden; hos fadern — som var känd som framstående jordbrukare — mötte han förståelse för sin önskan om teoretisk utbildning. Fadern kände personligen till Svalöf och redan som ung gymnasist kom Åke Åkerman 1904 som sommarassistent till den institution, han sedan kom att ägna huvuddelen av sitt livsverk; han återkom sedan varje sommar fram till 1908.

Under tiden hade han, 1906, blivit student i Hälsingborg och börjat sina studier vid Lunds Universitet. Enligt vad han själv omtalat, var hans avsikt att avlägga fil. kand. i Lund för att sedan på Alnarp vidareutbilda sig till agronom. Han fångades emellertid efterhand av den teoretiska forskningen och fortsatte i Lund sina studier, som avslutades med disputation i december 1915 på en avhandling, betitlad »Studier över trådlika protoplasmabildningar i växtcellerna».

Under lundatiden var Åke Åkerman intresserad medlem av Lunds Botaniska förening, och han blev där 1908 revisor för samlingarna, sedan för kassa och växtbyte. Hösten 1909 blev han föreståndare för samlingarna, vilket uppdrag 1911 utbyttes mot sekreterarens, som han behöll till och med vårterminen 1915. 1910 var han föreningens stipendiat och 1914 blev han medlem av en kommitté för omarbetande av föreningens stadgar.

Då Herman Nilsson-Ehle 1915 utnämndes till professor i Lund, utsåg styrelsen för Sveriges Utsädesförening Åkerman till hans efterträdare som föreståndare för vete- och havreavdelningen på Svalöf. Så småningom efterträdde han 1939 Ehle även som föreståndare vid Utsädesföreningen, en befattning som han med okuvlig vilja uppehöll även de månader, då ohälsa bröt hans fysiska krafter — ännu dagen före sin död arbetade han ivrigt med förberedelserna för ett styrelsemöte i föreningen.

Den första generationen på Svalöf var skolad i floristik, och med Nilsson-Ehle gjorde den moderna ärftlighetsläran sitt intåg i den svenska växtförädlingen. Åkerman var också ärftlighetsforskare och har lämnat några värdefulla bidrag till denna forskningsgren. Hans akademiska studier hade dock framförallt ägnats fysiologin och denna hade kanske hans innersta kärlek. Så snart han börjat arbetena med veteförädling, tog han upp frågan om vinterhärdighetens natur. Resultaten av hans undersökningar — utförda i samarbete med Utsädesföreningens kemist, dr. J. E. Lindberg — redovisades i en avhandling av 1927: »Studien über den Kältetod und die Kälteresistenz der Pflanzen», vilken nu räknas bland de klassiska på området. Det sista tryckta bidraget från hans hand var en populär översiktsuppsats i Lantmannen av den 4 april detta år om växternas vinterhärdighet, författad på sjukbädden. I denna visar han sin förmåga att överblicka problemen, likaså att han helt följt med utvecklingen på området, och slutligen är artikeln ifråga en god exponent för hans eminenta förmåga att på ett klart, redigt och lättfattligt sätt framlägga vetenskapliga fakta för en publik, som icke är vetenskapligt skolad.

Ett annat av Åkermans huvudintressen kom snart att bli brödsädens, särskilt vetets, bakningskvalitet. På detta område gjorde han, ånyo i samarbete med Lindberg, insatser, som kom hans namn att nämnas med respekt ej blott här i Europa utan även på andra sidan Atlanten. Hans kunskaper och hans initiativkraft ha här haft större betydelse för vår svenska brödsädesförsörjning under kritiska tider än vad man nu kan med full rättvisa uppskatta.

För Sveriges Utsädesförenings utveckling kom Åkermans insats att betyda oerhört mycket. Den som haft förmånen att personligen känna föreningens samtliga tre föreståndare sedan 1890 vill ju gärna göra jämförelser. Man måste då konstatera, att alla tre — N. Hjalmar Nilsson, Herman Nilsson-Ehle och Åke Åkerman — varit personligheter av rang, envar med sin särpräglade läggning. Ett försök till inbördes värdesättning vore oförlåtligt naivt, det må vara

tillräckligt konstatera, att Åkerman på ett värdigt sätt sällar sig till raden av föreståndare av sådan kvalitet, att få svenska instituioner torde ha förmånen kunna uppvisa motsvarande. Hans organisationsförmåga, hans vida kunskaper och hans säkra förankring hos vetenskap, jordbruk och industri gav honom en position, som han målmedvetet utnyttjade för att främja den sak, för vilken han arbetade.

Det är självklart, att en man med de ovan uppräknade egenskaperna kom att tagas i anspråk för åtskilliga värv utanför det, som var hans huvuduppgift. Det må här främst erinras om hans insatser som föreståndare för livsmedelskommissionens produktionsavdelning under andra världskriget, insatser, vilkas betydelse kanske kan bli föremål för olika slag av historieskrivning men utan vilka vårt försörjningsläge under svåra år varit sämre än det blev. Medlemskap i flera styrelser för viktiga institutioner på jordbrukets område och i olika utredningar gjorde det också möjligt för Åkerman att nyttiggöra sina kunskaper och sin erfarenhet — en detaljuppräkning skulle inför detta forum föra alltför långt.

Detsamma gäller en uppräkning av de skilda utmärkelser, som kom honom till del. Medlemskap i svenska och utländska lärda samfund med biologi och agrikultur bland agenda, två hedersdoktorat och innehavet av ordensutmärkelser från fem länder utom Sverige gav honom rätt att sätta större delen av alfabetet efter sitt namn. Den sista stora utmärkelse, han erhöll, var Kungliga Lantbruksakademiens Nilsson-Ehlemedalj, och det är väl knappast för mycket sagt, att han gladdes mer åt den än åt någon annan.

Liksom alla mänskor med en stark vilja att uträtta någonting i livet hade Åke Åkerman sina skarpa kanter, som stundom kunde framkalla friktion och irritation hos omgivningen — det är ett faktum, som ej bör förtigas. Det må emellertid tillåtas den, som känt honom personligen i fyrtio år — varav i det närmaste tjugofem som nära medarbetare — att betyga, att kantigheterna voro ganska betydelselösa i jämförelse med Åkes positiva egenskaper. Bland dessa vill man väl först nämna ett brinnande intresse för de arbetsuppgifter han påtagit sig — ett intresse som ingen kunde misstaga sig på. Därnäst kommer hans oerhört omfattande kunskaper. Han trängde väl som forskare sällan särskilt djupt i enstaka problem, men han visste och kunde oerhört mycket, både om forskningens resultat och på de områden — tillämpad forskning, jordbruk och med jordbruket lierad industri — inom vilka han var verksam. Han hade slutligen ett rikt tillmätt mått av den klokt balanserade inställning, som med ett stundom underskattande tonfall brukar nämnas »sunt bondförstånd».

Dessa egenskaper i förening gjorde honom till en sällsynt god rådgivare i fackliga ting för den, som i likhet med honom själv arbetade på gränsområdet mellan teoretisk biologi och dennas tillämpning inom jordbruket. Härtill skall läggas, att han städse var lyhörd för nya idéer och uppslag, gärna understödde dem med sin auktoritet och ofta lyckades framskaffa de nödvändiga resurserna för idéernas verkställande. Som exempel kan nämnas, att om det var Nilsson-Ehle, som gav uppslaget till att inducerade mutationer infördes i växtförädlingsprogrammet, så var det Åkerman som skaffade de första ekonomiska bidrag, vilka gjorde det möjligt att i för den tiden ganska stor skala pröva dessa mutationers praktiska värde.

Bilden av Åke Åkerman är inte fullständig, om man inte tager med hans förmåga att koppla av från arbetsuppgifterna. Hans levande musikintresse kom då med i bilden. Han sjöng, han smekte sin flöjt och han spelade piano — gärna som ackompanjatör till någon annan förmåga, som ville hjälpa till att underhålla vänkretsen. Har man sett Åke Åkerman på Barnens Dag i Svalöf sitta i kabaréns lilla musikkapell, blåsa flöjt och applådera föreningens yngste assistent, när han från estraden sjöng smädevisan om chefen — då har man lätt att med glädje minnas inte bara den utomordentlige organisatören, den framstående samhällsmedlemmen, utan också mänskan Åke Åkerman.

OLOF TEDIN

Litteratur

Tore Linnell, Nyttoväxter i färg. — Almqvist & Wiksell. Stockholm 1955. 220 s. — Pris 11: 75, inb. 13: 75.

I den av Almqvist & Wiksells Bokförlag utgivna serien om naturböcker i färg har nyligen utkommit en liten bok om nyttoväxter. Som textförfattare stå Tore Linnell och Nils Hylander medan de 128 färgplanscherna äro utförda av Edgar Hahnewald.

Boken behandlar både svenska och utländska nyttoväxter och icke bara odlade utan även vildväxande. Alltefter nytta och användning delas växterna upp i 17 grupper, t.ex. stärkelse-, olje-, krydd-, stimulans- och medicinalväxter. En avdelning om virkesväxter är särskilt värdefull i och med att illustrationerna kompletteras med vedprover. Bildmaterialet, i sexfärgstryck, är f.ö. av mycket hög klass. Texten är genomgående innehållsrik och saklig. Man får uppgift icke bara på växtens användning utan även förekomst och egenskaper.

Denna lilla handbok, som väl i första hand vänder sig till allmänheten, borde även kunna bli till god nytta vid undervisningen på såväl låg- som högstadiet. Ordförklaringar samt latinskt och svenskt namnregister underlätta begagnandet. För dem, som önska ytterligare upplysningar om nyttoväxter finns en förteckning över modern litteratur på området.

Bo Peterson

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Notiser

Ny hedersledamot av Lunds Botaniska förening. Den 4 maj 1955 uppvaktades professorskan, fru Anna Murbeck av styrelsen för Lunds Botaniska förening, som framförde föreningens beslut att utse henne till hedersledamot och överlämnade ett diplom med tack för hennes välvilja mot och intresse för föreningen och gynnande av botanisk forskning.

Doktorsdisputationer. Fil. lic. Alf Liljefors försvarade den 2 april 1955 å Stockholms Högskola en gradualavhandling med titeln »Studies on Species Formation in the Genus Sorbus in Scandinavia». Fil. lic. Sven Kilander försvarade i Uppsala den 28 april en akademisk avhandling över »Kärlväxternas övre gränser i sydvästra Jämtland samt angränsande delar av Härjedalen och Norge». Fil. lic. Lars Ehrenberg disputerade den 17 maj i Stockholm på en avhandling med titeln »Studies on the Mechanism of Action of Ionizing Radiations in Plant Seeds». Fil. lic. Peter Bernström försvarade den 18 maj i Lund en gradualavhandling med titeln »Cytogenetic Studies in Lamium». Samma dag försvarade fil. lic. Börje Norén i Uppsala en avhandling med titeln »Studies on Myxobacteria with special Reference to growth Conditions and bacteriolytic Activity». Fil. lic. Nils Quennerstedt försvarade i Uppsala den 26 maj en akademisk avhandling över »Diatoméerna i Långans sjövegetation».

Lunds Botaniska Förenings stipendier. Ur Murbeckska fonden har föreningen utdelat 400 kr. till fil. kand. Lennart Eliasson för undersökningar över sambandet mellan ämnesomsättning och tillväxt hos veterötter.

Forskningsanslag. Lunds universitet har ur Anna och Svante Murbecks minnesfond utdelat 1.175 kr. till fil. mag. Gunvor Rasmusson för fältstudier över vegetationen och de ekologiska förhållandena på Skanörs ljung och 725 kr. till fil. lic. Hans Runemark för studier av material av lavsläktet *Rhizocarpon* i British Museum; ur P. O. Lundells fond 1.200 kr. till fil. licc. Pär Fransson och Henry Rufelt för undersökningar över auxiners och antiauxiners fysiologiska verkningar samt ur C. F. O. Nordstedts fond 395 kr. till fil. lic. Henry Rufelt för studieresa till Norge.

Av K. Vetenskapsakademien har ett av de Lindahlska stipendierna å 8.000 kr. utdelats till fil. lic. Lars Ehrenberg för utarbetande av gradualavhandling över den joniserande strålningens verkningsmekanism.

K. Fysiografiska sällskapet i Lund har utdelat bl.a. följande anslag: till fil. licc. Pär Fransson och Henry Rufelt 1.000 kr. för undersökningar över tillväxtsubstansers fysiologiska verkningar och till docent Bertil Hylmö 600 kr. för undersökning över disackaridbildningens betydelse för köldhärdigheten hos olika *Brassica*-arter.