

THE CYTOGENETICS OF *CAREX FLAVA* AND ITS ALLIES*

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1. INTRODUCTION

This group of closely allied species included in the section *Extensae* of the subgenus *Carex* is represented in Great Britain by : *Carex flava* L., *C. lepidocarpa* Tausch, *C. demissa* Hornem., *C. serotina* Mérat, and *C. scandinavica* E. W. Davies. The taxonomy of these species has caused difficulty for many years, and, although the chromosome numbers have been investigated by workers in Sweden, Japan and America, there has been considerable discrepancy in their results (see below), and no counts have previously been made on British material.

Species	Haploid Chromosome Number	Determined by :	Date
<i>C. extensa</i> Good.	30	Wulff	1937
<i>C. flava</i> L.	29	Tanaka	1942, 1948
	30	Heilborn	1939
	30	Wahl	1940
<i>C. lepidocarpa</i> Tausch	29	Tanaka	1942, 1948
	34	Heilborn	1924
"C. oederi Retz" = <i>C. serotina</i> Mérat	36	Heilborn	1922, 1924, 1928
	35	Tanaka	1948

2. CYTOLOGICAL TECHNIQUE

The cytological technique employed throughout this investigation is a modification of the aceto-carmine squash method by the addition of a drop of iron alum. The *Carices* have exceedingly small chromosomes and hard wiry roots, which make them difficult cytological material.

The original attempts to count the chromosomes of this genus were made at mitosis using root tips. First embedding and sectioning methods were tried and later the root tip squash technique was used, staining with Feulgen, aceto-carmine, or a combination of the two stains together. However, the results throughout were unsatisfactory, as the cytoplasm was overstained and contained oil globules, while the chromosomes remained faint and aggregated together. Thus the counts were never accurate enough to detect a difference of two chromosomes at mitosis, which is essential when examining a genus

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like *Carex* which has an aneuploid series with many allied species with consecutive chromosome numbers.

Finally young male spikes were fixed and meiosis was investigated using the modified aceto-carmin method. This produced well stained and spread chromosomes and, in contrast, a light background, as the cytoplasm absorbed little stain.

3. CHROMOSOME NUMBERS

The chromosome numbers have perhaps not proved as valuable a criterion in the taxonomy of these species as had formerly been hoped. However, the chromosomes of the British members of the *Extensae* and of *C. mairii* Coss. & Germ., a closely allied species from southern Europe, have been examined from several localities, and are remarkably similar and uniform in number and morphology (Plates 12 and 13, figs. 1-14). This is further evidence that they are a naturally closely united group distinct from the other sections, such as *Distantes*, *Acutae*, *Montanae*, etc., which differ from them in size and morphology of their chromosomes.

The chromosome numbers of these species together with their subspecies and varieties are given in Table 1. The number of plants of each species and their localities is stated in each case.

Thus this aggregate of species forms a short aneuploid series with chromosome numbers ranging from 30 to 35. If this series is ascending, the low numbered members are assumed to be primitive, while the species with more numerous chromosomes are secondary and advanced. If this is the case, *C. flava* is the oldest and original member of this aggregate, and the other species are derived and more recent in origin. This aspect of the problem will be referred to, and elaborated, later, when the curious abnormalities, found at meiosis in hybrid sedges, have been discussed in the next section.

4. HYBRIDS AND HYBRIDISATION

The study of the interspecific hybrids of a critical group such as the *C. flava* aggregate is of great importance, as it frequently yields information about the relationships of the species, their age and evolution. The natural and artificial hybrids will now be discussed separately.

(a) *Natural Hybrids*

Natural hybrids are found between members of this aggregate, whenever two or more of the species grow together and their flowering periods overlap. However this is rather infrequent in this country, except in the case of the widespread *C. demissa*, and it appears that ecological barriers prevent much introgression between the species. The hybrids found in the field are listed in Table 2, and these will be discussed later, after some of the abnormalities seen at meiosis have been briefly outlined.

The meiosis of hybrid *Carices* is always highly irregular, and cytology produces conclusive evidence of hybridity in a suspected plant. However, the arrangement of the chromosomes and their behaviour at metaphase and anaphase is very different from what is usually seen in hybrids of most genera. First, and perhaps of most fundamental importance, there are no lagging chromosomes at anaphase I, but these can usually be seen to a small extent at anaphase II. Thus the normal sequence of events generally accepted for hybrids in most genera, with the possible exception of *Luzula*, is reversed. Secondly, at metaphase I, instead of the occurrence of tri- and bi-, or univalents, depending on the nature of the hybrids, there are frequently chains or even rings formed of from 3 to 6 or even 8 chromosomes (Plate 13, fig. 16) and round the periphery of the metaphase plate univalents are often seen.

TABLE 1
Chromosome numbers of the *C. flava* aggregate

Species	Haploid number	Number of plants sampled	Locality
1. <i>C. extensa</i> Good.	30	4	Rhos Neigr, Anglesey.
2. <i>C. flava</i> L.	30	4	Roudsea Wood, Haverthwaite, Lancs.
	30	1	Malham Bog, Yorks.
	30	2	Preda, Graubünden, Switzerland.
	30	1	Lake Carezza, W. Dolomites, N. Italy.
3. (a) <i>C. lepidocarpa</i> Tausch	34	1	Wicken Fen, Cambs.
subsp. <i>lepidocarpa</i>	34	1	Fulbourn Pond, Cambs.
	34	3	Wittering Marsh, Northants.
	34	1	Gordale Scar, Malham, Yorks.
	34	1	Malham Tarn, Yorks.
	34	1	Moughton Scar, Yorks.
	34	3	Widdybank Fell, Teesdale, Durham.
	34	1	Gotland, Sweden.
	34	1	Tiefencastel, Switzerland.
3. (b) <i>C. lepidocarpa</i> subsp. <i>scotica</i>	34	1	Cwm Glas, Snowdon, Caernarvon.
E. W. Davies	34	1	Carn Eige, Cannich, Inverness.
	34	1	Inchnadamph, W. Sutherland.
	34	1	Preda, Graubünden, Switzerland.
	34	1	Albula, Graubünden, Switzerland.
4. <i>C. mairii</i> Coss. & Germ.	34	4	Lumbreras, Spain.
5. <i>C. demissa</i> Hornem.	35	2	Shapwick peat moor, Somerset.
	35	1	Bredon Cloud Wood, Leics.
	35	3	Strines Moor, Derbyshire.
	35	1	Little Dun Fen, Westmorland.
	35	3	Loch Tummel, Perth.
	35	2	Cannich, Inverness.
	35	1	Cwm Glas, Snowdon, Caern.
	35	1	Furnols, Echandelyse, Auvergne, France.
	35	1	Lac de la Faye, Auvergne, France.
	35	1	Issoire, Central France.
	35	1	Font Romeu, E. Pyrenees, France.
6. <i>C. serotina</i> Mérat	35	1	L'Ancrese, Guernsey.
	35	1	Frensham Pond, Surrey.
	35	2	Fulbourn Pond, Cambs.
	35	2	Rhos Neigr, Anglesey.
	35	2	Hale Moss, Bentham, Lancs.
	35	1	Monea, Ireland.
	35	2	Hökatorp, Skåne, Sweden.
	35	2	Alvar, Öland, Sweden.
	35	2	Gotland, Sweden.
<i>C. serotina</i> var. <i>cyperoides</i>	35	1	Shapwick peat moor, Somerset.
7. <i>C. scandinavica</i> E. W. Davies	35	1	Sweden.
	35	1	Loch Torridon, W. Ross.

The meiosis appears to be more abnormal and irregular when the parents of the hybrid are very dissimilar, and have widely different chromosome numbers. The metaphase I, described above, represents a hybrid between *C. demissa* ($n = 35$) and *C. hostiana* ($n = 28$). In an interspecific hybrid between two more closely related species such as *C. demissa* ($n = 35$) and *C. lepidocarpa* ($n = 34$), or *C. demissa* ($n = 35$) and *C. serotina* ($n = 35$), meiosis is more normal, and apart from a few univalents and perhaps one conglomerate group of chromosomes forming a chain, the rest are arranged on the metaphase plate as bivalents (Plate 13, figs. 17-20). Thus a fairly high degree of homology

is indicated between these species with similar and consecutive chromosome numbers; for the pollen of hybrid plants is never completely sterile, and fertility usually ranges from 20 to 35 per cent (Table 2).

The hybrids detected in the field between British members of this aggregate will now be briefly discussed.

TABLE 2
Natural hybrids in the *C. flava* aggregate

		% Pollen fertility	Localities
1. <i>C. flava</i>	× <i>C. lepidocarpa</i>	29%	Lake Carezza, Dolomites, N. Italy.
2. <i>C. flava</i>	× <i>C. demissa</i>	22%	Roudsea Wood, Haverthwaite, Lancs.
3a. <i>C. lepidocarpa</i> subsp. <i>lepidocarpa</i>	× <i>C. demissa</i>	22%	Teesdale, Durham.
"	× "	24%	Derby Fen, Norfolk.
"	× "	30%	S. Cerney, Glos.
"	× "	35%	Hökatorp, Skåne, Sweden.
"	× "	25%	Krogenbund Mose, Zealand, Denmark.
b. <i>C. lepidocarpa</i> subsp. <i>scotica</i>	× <i>C. demissa</i>	32%	Loch Tummel, Perth.
"	× "	35%	Creag-na-Caillich, Perth.
"	× "	33%	Creag-an-Lochan, Perth.
"	× "	35%	Ben-y-Vrackie, Pitlochry, Perth.
"	× "	28%	Ben Dorain, Argyll.
"	× "	30%	Glen Doll, Clova, Angus.
"	× "	31%	Cwm Glas, Snowdon, Caernarvon.
4. <i>C. lepidocarpa</i>	× <i>C. serotina</i>	25%	Wicken fen, Cambs.
"	× "	20%	S. Cerney, Glos.
5a. <i>C. demissa</i>	× <i>C. serotina</i>	29%	S. Cerney, Glos.
b. <i>C. demissa</i>	× <i>C. serotina</i> var. <i>cyperoides</i>	26%	Shapwick, Somerset.
6a. <i>C. hostiana</i>	× <i>C. lepidocarpa</i> subsp. <i>lepidocarpa</i>	0%	Chippenham Fen, Cambs.
b. "	× <i>C. lepidocarpa</i> subsp. <i>scotica</i>	0%	Loch Tummel, Perth.
"	× "	0%	Waulk Mill Bay, Mainland, Orkney. Lech, Voralberg, Austria.
7. <i>C. hostiana</i>	× <i>C. demissa</i>	0%	Loch Tummel, Perth.
8. <i>C. distans</i>	× <i>C. lepidocarpa</i>	0%	Totternhoe, Beds.

(1) *C. flava*

This rare British plant, with its specialised ecological requirements, seldom meets the other members of the group in this country. However, at Roudsea Wood (Lancashire), *C. demissa* occurs with *C. flava*, and there is a range of intermediate forms, which are clearly of hybrid origin. These plants revealed a highly irregular meiosis, and the pollen showed between 70 and 80 per cent sterility. It certainly seemed as if back crosses with the parent species were present as well as F_1 plants, for there was a great range of forms and it appeared that, in time, *C. demissa* would completely oust *C. flava* by hybridisation, for the latter species was scarce compared with the abundance of hybrid plants and *C. demissa*. This is the only record of a *C. flava* hybrid from this country; as this species has never been found growing with or near *C. lepidocarpa*, *C. serotina* or *C. scandinavica*, and as their ecological requirements are rather different, hybrids between *C. flava* and these species seem unlikely to occur naturally. However, hybrids and back crosses between this species and *C. lepidocarpa* were abundant by Lake Carezza in the Western

Dolomites. Here, in North Italy, the habitat and the topography seemed suitable for both species and they were hybridising freely.

(2) *C. lepidocarpa*

Subsp. *lepidocarpa* frequently hybridises with *C. demissa*, and a hybrid swarm often predominates, while the parent species are comparatively rare, and sometimes difficult to detect. This certainly is the case on the lower slopes of Widdybank Fell in Upper Teesdale (Plate 13, fig. 17) and at Hökatorp (Plate 13, fig. 18), a calcareous fen by the sea in S.E. Skåne, Sweden. Likewise, on base-rich Scottish and Welsh mountains hybrid swarms between *C. demissa* and subsp. *scotica* are common at about 1,000 m. where the distribution areas of these two species overlap, whereas below and above this altitude the two species remain quite distinct.

In the same way hybrids might be expected between *C. lepidocarpa* and *C. serotina* in the few calcareous localities where these species are known to occur together. However, this hybrid is rare, apparently because *C. serotina* flowers and fruits at least one month later than the other four species. At Fulbourn Pond (Cambridgeshire), where *C. lepidocarpa* and *C. serotina* grow completely intermixed, there is no sign of hybridisation, and, in late June, the former species is in ripe fruit while the latter is still in flower.

Consequently, it was rather unexpected to find a plant at Wicken Fen, Cambridgeshire, which appeared to be a hybrid of this parentage, growing with *C. serotina* and *C. lepidocarpa*. This plant had an irregular meiosis and the pollen showed 80 per cent sterility. The only other locality examined where these two species were found growing together is a disused gravel pit on the Cotswolds near S. Cerney, and, as *C. demissa* also grows at the edge of the pit, the situation is complicated further. A complex hybrid swarm involving all three species occurs, and the range of forms is very great. Although the majority of plants seem to be intermediate between *C. lepidocarpa* and *C. serotina*, and some forms contain *C. demissa* also, there is a large stand of pure *C. serotina* at one side of the gravel pit. This can almost certainly be correlated with the late flowering period of this species, for specimens of pure *C. lepidocarpa* and *C. demissa* were not seen and these species had clearly been ousted by hybridisation.

(3) *C. demissa*

This species, which is tolerant of a wide range of habitats, is frequently found growing with, or near, the other species, and hybrids are fairly common.

The hybrids with *C. flava* and *C. lepidocarpa* have already been mentioned, but on Shapwick peat moor in Somerset, this species forms a hybrid swarm with *C. serotina* var. *cyperoides*. The latter is rather uncommon, and it seems likely that it may, in time, be lost completely, if hybridisation with *C. demissa* continues, for an enormous range of intermediate forms is now abundant on the moor, and *C. serotina* var. *cyperoides* is becoming increasingly rare. The cytology of this hybrid has been examined, and reveals a highly irregular meiosis (Plate 13, fig. 19), with a conglomerate ring of chromosomes surrounded by univalents.

(4) *C. serotina*

The few hybrids that are known between *C. serotina* and the other members of the aggregate have already been discussed, and it undoubtedly seems to be the late flowering of this species that acts as the main barrier, and keeps it distinct from the other members of the group.

(5) *C. scandinavica*

C. scandinavica, in the British Isles confined to northern and western Scotland, has

as yet never been found growing with any of the other species in this country. Hence no hybrids have been recorded.

(6) *C. hostiana* and *C. distans*

This study would not be complete without mentioning *C. hostiana* DC. and *C. distans* L., two members of the closely related section *Distantes*, for the former species very frequently hybridises with *C. lepidocarpa* and *C. demissa*. *C. hostiana* ($n = 28$), like *C. demissa*, grows in a wide range of habitats and tolerates many different soil conditions, which probably accounts for the frequency of its hybrids.

The hybrid between *C. hostiana* and *C. lepidocarpa* is sufficiently well known to have a name (*C. × xanthocarpa*), and is of fairly frequent occurrence. It grows (Table 2) at Chippenham Fen, Cambridgeshire, where the hybrid forms a large clone, which appears to multiply entirely vegetatively and now covers a considerable area, surrounded by the parent species.

Likewise *C. hostiana* hybridises with *C. demissa*. This hybrid was collected by Loch Tummel, Perthshire, and the plant showed a highly irregular meiosis with several chains of chromosomes and numerous univalents.

Lastly a hybrid between *C. distans* ($n = 37$) (Plate 13, fig. 15) and *C. lepidocarpa* was recorded from Cow Common, Totternhoe, Bedfordshire. This hybrid formed a clonal stand like *C. × xanthocarpa*, and had highly sterile pollen and a very irregular meiosis.

Thus it seems that all the members of this aggregate are capable of hybridisation, and considerable gene-flow between species is possible. It seems also that it is not genetical incompatibility but ecological and topographic barriers that keep *C. flava*, *C. lepidocarpa*, *C. demissa* and *C. scandinavica* apart, as distinct entities, while, in contrast, late seasonal periodicity seems to play the major role in the case of *C. serotina*.

(b) *Artificial Hybrids*

These flavoid species of *Carex*, like all those in the subgenus *Carex*, lend themselves to artificial hybridisation, as the male spike is easily removed without damaging the female organs. The crosses were carried out during May and early June, and the ripe seeds collected at the end of July and sown immediately.

The artificial hybridisations included all possible combinations between the five British members of the aggregate, and some crosses between these and *C. mairii*, *C. extensa* and *C. hostiana* (Table 3). However, although in most combinations some apparently ripe seed was produced, germination is slow and spasmodic in this genus, so as yet only a few of the hybrid seedlings have produced fertile spikes. These are listed in Table 3, and Plate 13, fig. 20 shows the very irregular meiosis of these artificial hybrids.

Thus it would seem that these five British species included in the *C. flava* aggregate, are capable of considerable gene-flow from one to another, and produce F_1 plants with between 20 and 30 per cent good pollen. They should therefore be regarded as ecospecies, and the group as a whole as one coenospecies (Gregor, 1939; Clausen, Keck & Hiesey, 1939).

6. DISCUSSION

The cytology, evolution and origin of the aneuploid series in the genus *Carex* will be discussed more fully in another paper.

However, it seems reasonable to postulate from the present cytological, ecological (Davies, 1954) and taxonomic (Davies, 1953a, b, c) evidence that, within this coenospecies,

TABLE 3
Artificial hybrids in *C. flava* aggregate

Female Parent		Male Parent	No. of seedlings	% Pollen Fertility of hybrid
1.	<i>C. flava</i> Roudsea, Lancs.	× <i>demissa</i> Loch Tummel, Perth.	4	20
2.	<i>C. flava</i> Roudsea, Lancs.	× <i>lepidocarpa</i> subsp. <i>scotica</i> Cannich, Inverness.	1	—
3.	<i>C. lepidocarpa</i> Tiefencastel, Switzerland.	× <i>flava</i> Preda, Switzerland.	4	—
4.	<i>C. demissa</i> a. France b. Bredon, Leics.	× <i>flava</i> Roudsea, Lancs. Roudsea, Lancs.	1 2	— —
5.	<i>C. demissa</i> a. Shapwick, Somerset. b. France c. Wild Boar Fell, Westmorland	× <i>lepidocarpa</i> Teesdale, Durham. Wicken, Cambs. Wittering, Northants.	5 3 5	25 — —
6.	<i>C. demissa</i> a. Strines Moor, Derbyshire. b. France. c. Shapwick, Somerset. d. France.	× <i>C. serotina</i> Anglesey. Hökatorp, Sweden. Anglesey. Monea, Ireland.	2 1 5 1	29 30 — —
7.	<i>C. demissa</i> Strines Moor, Derbyshire.	× <i>scandinavica</i> Sweden.	3	—
8.	<i>C. demissa</i> Bredon, Leics.	× <i>mairii</i> Lumbreras, Spain.	2	—
9.	<i>C. serotina</i> Hökatorp, Sweden.	× <i>lepidocarpa</i> Pyrenees.	6	24
10.	<i>C. mairii</i> a. Pyrenees. <i>C. mairii</i> b. Pyrenees.	× <i>lepidocarpa</i> subsp. <i>lepidocarpa</i> Gordale, Yorks. × <i>lepidocarpa</i> subsp. <i>scotica</i> Cannich, Inverness.	1 2	— —
11.	<i>C. mairii</i> Pyrenees.	× <i>serotina</i> Fulbourn, Cambs.	2	—
12.	<i>C. extensa</i> Anglesey.	× <i>serotina</i> Sweden.	1	—
13.	<i>C. hostiana</i> Teesdale.	× <i>lepidocarpa</i> Pyrenees.	2	—

C. flava is the relict and primitive member, with the lowest chromosome number, specialised ecological requirements and relict distribution (Davies, 1953 d). The development of the other ecospecies from *C. flava* has been accompanied by an increase in chromosome numbers, a greater variation within the species and an ability to grow in a wider range of plant communities. Thus *C. lepidocarpa*, with four more chromosomes, is more abundant, adaptable and probably of more recent origin, although not so recent as the very widespread and variable *C. demissa* with a capacity to flourish under various ecological conditions. Lastly, *C. serotina*, with the same chromosome number as *C. demissa*, yet requiring more specialised conditions, seems to be a more primitive and possibly a reduced form, which needs the low sparse vegetation of an open habitat with little competition.

It seems likely that this species, with the widest geographical distribution (Davies, 1953 d) of the group, spread rapidly during and after the last glaciation, recolonising the open habitats produced by the retreating ice. Within recent times, owing to its specialised requirements, this species has become confined to scattered and local areas; probably the presence of different forms which are not true ecotypes (as these differences do not seem

related to ecology) can be correlated with this fact. The isolated populations throughout the British Isles show minor differences, which are retained in cultivation; the most striking examples of such isolated populations are some of the forms which are found in Ireland and the Baltic Islands of Gotland and Öland, for these plants are almost worthy of recognition as distinct taxa. This continued isolation is probably the reason for the existence of a form on Shapwick peat moor, Somerset, sufficiently different to be considered a variety (*C. serotina* var. *cyperoides*). Further results of this isolation are possibly to be seen in the origin of *C. scandinavica* and *C. viridula* Michx. (Davies 1953 d). These two plants, which are rather similar to *C. serotina* but have different and more limited geographical distributions, have only recently been considered distinct species. They may have been evolved within comparatively recent times owing to geographic separation.

6. CONCLUSION AND SUMMARY

A cytogenetical survey of the *C. flava* aggregate (*C. flava* L., *C. lepidocarpa* Tausch, *C. demissa* Hornem., *C. serotina* Mérat, *C. scandinavica* E. W. Davies) is made, and the origin and evolution of the species discussed.

These five members of section *Extensae* and *C. mairii* are found to form a short aneuploid series, with their haploid numbers ranging from $n = 30$ to $n = 35$.

The interspecific hybrids between the members of this group, with the exception of *C. demissa*, were found to be rather uncommon. This seems to be due to the different and specialised ecological requirements of the species, topographic separation and the late flowering season of *C. serotina*. Hybrids were examined and synthesised whenever possible, and in every case the pollen showed at least 20 per cent fertility; this increased when the parent species had the same or nearly similar chromosome numbers.

Thus these five closely related species, which are capable of considerable gene-flow from one to another, and produce natural and artificial hybrids with between 20 and 30 per cent good pollen, are regarded as ecospecies and the group as a whole as one coenospecies.

C. flava seems to be a relict and stable plant with an isolated and scattered distribution. *C. lepidocarpa*, with its three subspecies, namely subsp. *lepidocarpa* and subsp. *scotica*, which form a discontinuous topocline in the British Isles, and subsp. *jemtlandica*, so far only known from Scandinavia, is more widespread.

The abundant *C. demissa* appears to be a variable plant, but the range of variation is continuous, and within the limits of one adaptable species. In contrast, *C. serotina*, with its local and fragmentary distribution, has a number of forms which, owing to long isolation, seem to give rise to varieties, such as var. *cyperoides*, and eventually species; such is probably the origin of *C. scandinavica* and *C. viridula*.

7. ACKNOWLEDGMENTS

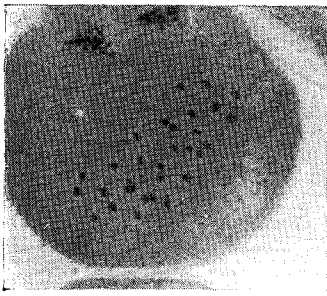
I have pleasure in recording my gratitude to Professor T. G. Tutin for his advice and encouragement throughout this work. I should also like to express my thanks to the Research Board, University College, Leicester, for the award of a scholarship during the period 1950-53, and for giving considerable financial help towards my field studies during this period.

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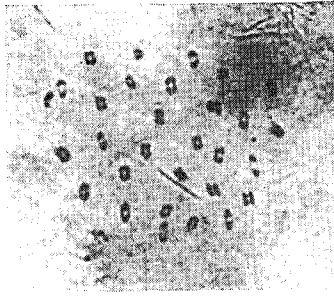
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 CLAUSEN, J., KECK, D. D. & HIESEY, W. M., 1939, The concept of species based on experiment, *Amer. J. Bot.*, **26**, 103-106.

PLATE 12

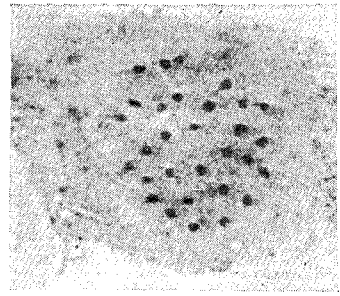
Figure 1 shows a pollen grain mitosis and two of the three aborting nuclei, and Figs. 2-9 show meiosis in the pollen mother cells. All photographs $\times 2,400$.



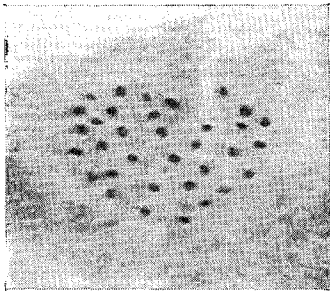
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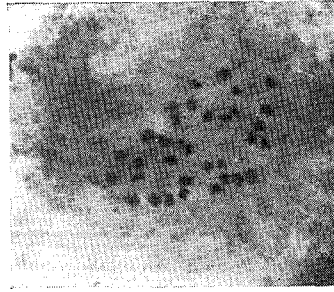
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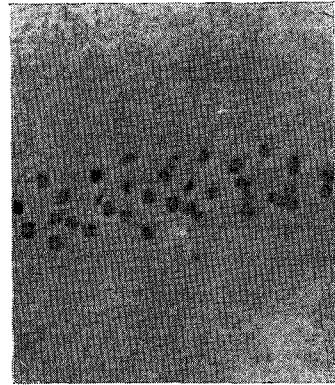
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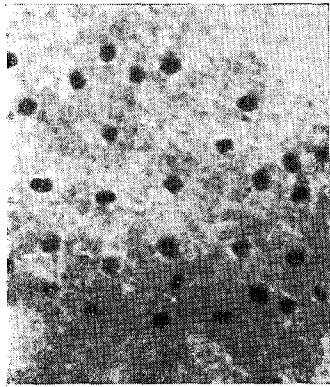
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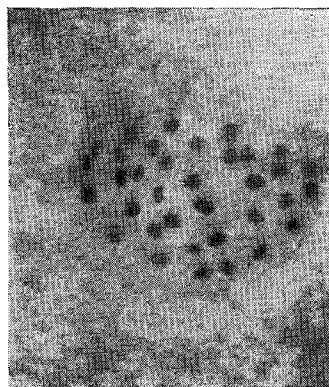
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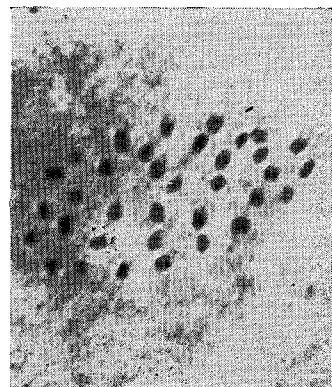
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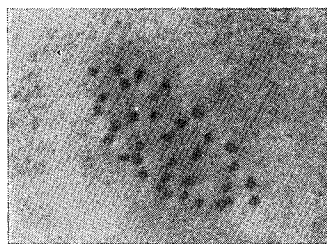


9

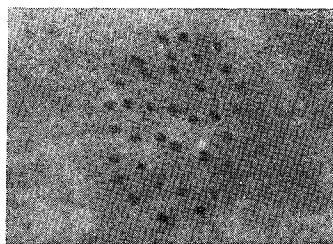
- Fig. 1. *Carex flava*, Roudsea Wood, Lancs., $n = 30$.
 Fig. 2. *C. flava*, Malham Tarn Moss, Yorks., $n = 30$.
 Fig. 3. *C. flava*, Preda, Graubünden, Switzerland, $n = 30$.
 Fig. 4. *C. lepidocarpa* subsp. *lepidocarpa*, Wicken Fen, Cambs., $n = 34$.
 Fig. 5. *C. lepidocarpa* subsp. *scotica*, Inchnadamph, Sutherland, $n = 34$.
 Fig. 6. *C. demissa*, Loch Tummel, Perthshire, $n = 35$.
 Fig. 7. *C. demissa*, Furnols, Central France, $n = 35$.
 Fig. 8. *C. serotina*, calcareous marsh, Fulbourn, Cambs., $n = 35$.
 Fig. 9. *C. serotina*, salt marsh, Hökatorp, Sweden, $n = 35$.

PLATE 13

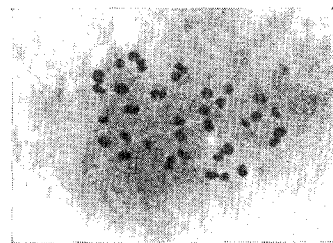
Figures 10-15 show normal meiosis in the pollen mother cells, and Figs. 16-20 show highly irregular meiosis in the pollen mother cells of some hybrid sedges, with univalents marked by arrows, and a few multivalents forming chains and rings of chromosomes. All photographs $\times 2,400$.



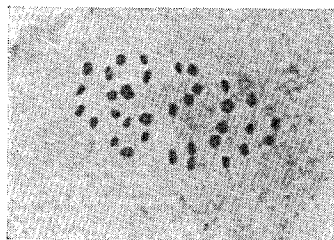
10



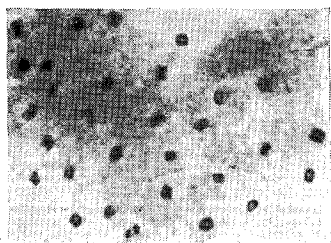
11



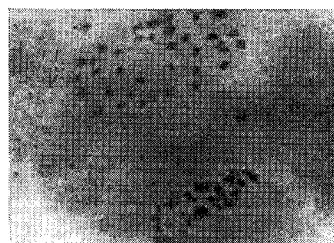
12



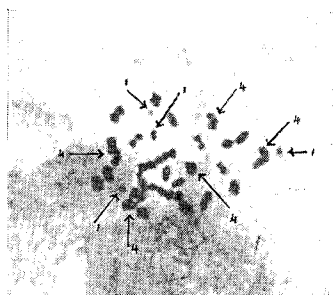
13



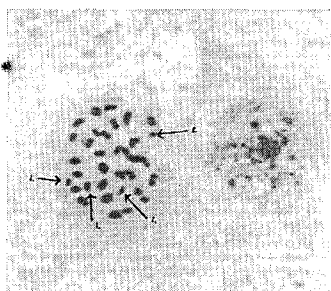
14



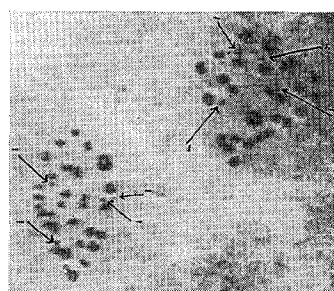
15



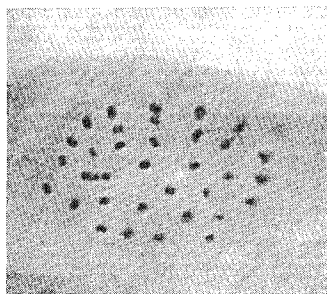
16



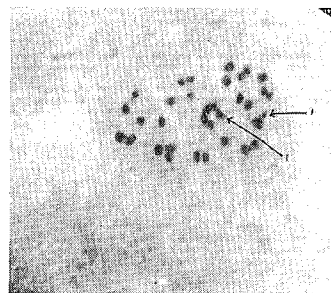
17



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Fig. 10. *Carex serotina* var. *cyperoides*, Shapwick peat moor, Somerset, $n = 35$.

Fig. 11. *C. scandinavica*, Loch Torridon, W. Ross, $n = 35$.

Fig. 12. *C. scandinavica*, Sweden, $n = 35$.

Fig. 13. *C. mairii*, Lumbreras, Spain, $n = 34$.

Fig. 14. *C. extensa*, Rhos Neigr, Anglesey, $n = 30$.

Fig. 15. *C. distans*, St. Nectaire, Central France, $n = 37$.

Fig. 16. *C. demissa* \times *C. hostiana*, Loch Tummel, Perthshire.

Fig. 17. *C. lepidocarpa* \times *C. demissa*, Teesdale, Durham.

Fig. 18. *C. lepidocarpa* \times *C. demissa*, Hökatorp, Sweden.

Fig. 19. *C. demissa* \times *C. serotina* var. *cyperoides*, Shapwick, Somerset.

Fig. 20. *C. demissa*, Shapwick, Somerset, \times *C. lepidocarpa*, Teesdale, Durham; hybridised 10 May, 1951.

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