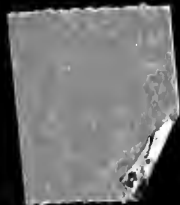


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PLATE I.



A DARWIN CENTENARY

THE REPORT OF THE
CONFERENCE

HELD BY

THE BOTANICAL SOCIETY
OF THE BRITISH ISLES

IN 1959

to mark the Centenary of the
publication of

THE ORIGIN OF SPECIES

EDITED BY

P. J. WANSTALL

1961

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THE FRONTISPIECE

This portrait was taken from a Daguerrotype in the possession of Sir Charles Darwin, who very kindly loaned it through Lady Barlow for this frontispiece. The original crayon drawing which was photographed is probably the one now at Down House. According to an unpublished catalogue of Samuel Lawrence portraits by Frank Miles, in the National Portrait Gallery, this was a possible study for an oil painting intended for the British Association, but the project was interrupted by the artist's departure for the United States in 1853 and no more came of it.—
EDITOR.

EDITORIAL NOTE

On November 24th, 1859, the *Origin of Species* was first published; almost exactly one hundred years later a number of well-known botanists, invited by the Botanical Society of the British Isles, presented papers covering the development and modern aspects of work in the fields of evolution, phylogeny, plant breeding, genetics, and cytotaxonomy, all of which have received an impetus from this monumental work.

Lady Nora Barlow provided the Conference with an admirable background in which she included an intimate account of her grandfather's home environment and the influences which must have been shaping his thoughts and unconsciously directing him towards the way of life which proved so productive. The President and Lady Barlow both emphasised Darwin's contacts with the outstanding botanists of his day—people such as Hooker and Henslow—and his regard for one of these men is well shown by a note written on the back of a letter to his wife in August 1854 indicating that Hooker was by far the best man to edit his 'species volume' if he should die before it was ready for publication.

The papers read at the Conference are all printed here, with the discussions which followed them, in the order in which they were given. That part of the exhibition which was particularly designed to illustrate recent research work on the subjects of Darwin's botanical monographs has been included in this volume in the form of short reports submitted by the exhibitors. The rest of the Exhibition reports for 1959 will be found in Volume 4, Part 1, of the *Proceedings*.

Dr. H. J. M. Bowen and members of the Meetings Committee were responsible for the excellent arrangements for this centenary meeting which was held in the rooms of the British Academy on November 27th and 28th. During the evening of the 28th a conversazione was held at Crosby Hall, Chelsea, and on Sunday, 29th, members went by car and coach to Downe, Kent, where they visited Down House and were shown the Darwin Museum by Lady Barlow. During the afternoon a memorial service was held in Downe Church, when an address was given by the Rev. L. G. Vedy.

I would particularly like to thank my friends and colleagues, Mr. B. M. G. Jones, Mr. D. T. Streeter and Dr. S. R. J. Woodell, for help in recording the discussions during the conference; Mr. D. H. Kent and Mr. J. E. Lousley for valuable advice in the course of preparation of this report and who, with other members of the Publications Committee, generously assisted with the task of proof reading.

P. J. WANSTALL.

Queen Mary College, London, E.1.

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The Editor is grateful to John Murray (Publishers) Limited for permission to include quotations from *The Life and Letters of Sir J. D. Hooker* by Leonard Huxley and the *Life and Letters of Charles Darwin* by Francis Darwin.

INTRODUCTORY REMARKS

The Conference was opened by the President, Professor T. G. Tutin, who said:—

We are meeting to-day to celebrate the centenary of the publication of what may truly be called a book that radically changed man's view of the world.

In the last year much has been written and said about Darwin's life and work. I would like now to remind you first of his extraordinary variety of interests and knowledge. His monograph of barnacles is still, I believe, the standard work on the subject; his theory of atoll formation has not been disproved, though there are now alternative suggestions; his book, *The Expression of the Emotions in Man and Animals* is one of the earliest investigations of a branch of psychology; and his numerous botanical works must be well-known to you.

There you have the complete biologist: botanist, zoologist, geologist and psychologist all in one. From this broad and solid foundation of fact and observation rises the splendid edifice known throughout the world as the *Origin of Species*.

The idea of evolution so permeates our thinking now that it is probably impossible to imagine what it was like to be without it. It has enabled us to connect up and make sense of a great number of previously disconnected facts and, what is just as important, it has directed our attention to phenomena that had been ignored or overlooked, and given new life and meaning to the whole of biology.

The idea has spread far beyond biology and has proved equally enlightening in other fields. Astronomers make theories about the evolution of the Universe, while Professors of English study the evolution of the modern novel. In fact it is easy to get the impression that the only things immune from the effects of the evolutionary process are *Ginkgo biloba* and the domestic ball-cock.

Darwin, though his knowledge of these different fields was great, relied to some extent on experts for detailed information, and discussed with them the evidence for and against his views. He was fortunate in counting among his friends the geologist Lyell, the botanist Hooker, and the zoologist Huxley, each of them still regarded as an outstanding man in his own field.

As the botanical aspects of Darwin's work are of special interest to this Society, I should like to say a little about Hooker

in connection with Darwin, and, indeed, Hooker also deserves to be remembered by us on this occasion as a very great botanist. He was eight years Darwin's junior and lived to attend the celebration of the centenary of his friend's birth in 1909. In the course of his long life he was not only an energetic member of the staff of the Geological Survey and, for many years one of the most able Directors of Kew, but travelled extensively, carrying out both botanical and geographical exploration in very difficult conditions.

He collected plants, painted quite remarkably good water-colours of Himalayan scenery, and made a map of part of Sikkim which was in use until recently. In addition to all this he wrote, or contributed largely to, numerous floras, the most noteworthy perhaps being the famous *Flora of British India*. His essays on the geographical distribution of plants and his travel books are classics which should be read more frequently than they perhaps are.

In industry and knowledge, though within a more limited field, he was a man of the same calibre as Darwin himself. He describes his first meeting with Darwin as follows: "My first meeting with Mr. Darwin was in 1839 in Trafalgar Square. I was walking with an officer who had been his shipmate for a short time in the *Beagle* seven years before, but who had not, I believe, since met him. I was introduced: the interview was of course brief, and the memory I carried away and still retain was that of a rather tall and rather broad-shouldered man, with a slight stoop, an agreeable and animated expression when talking, beetle brows, and a hollow but mellow voice; and that his greeting of his old acquaintance was sailor-like—that is, delightfully frank and cordial".

Later on in their friendship he says: "I at any rate always left with the feeling that I had imparted nothing and carried away more than I could stagger under"; a feeling reciprocated by Darwin, who wrote after a visit to Hooker, "I learn more in these discussions than in ten times over the number of hours reading".

Hooker was at first sceptical about the efficiency of Natural Selection, but became somewhat, though not entirely, converted after reading the manuscript of the joint paper which Darwin and Wallace presented to the Linnean Society in 1858. This partial change of view was obviously a relief to Darwin, as can be seen from the following quotation from a letter he wrote to Hooker shortly afterwards: "You cannot imagine how pleased I am that the notion of Natural Selection has acted as a purgative on your bowels of immutability. Whenever naturalists can look on species-changing as certain, what a magnificent field will be open—on all the lines of variation—on the genealogy of all living beings—on their lines of migration,"

When the "Origin" was published on 24th November 1859, as is well known, it enjoyed a remarkable success, the whole edition being sold immediately.

It is interesting to see its impact, even on someone already so well acquainted with its main theme as Hooker, so perhaps I may be allowed another quotation:

"Dear Darwin,

You have, I know, been drenched with letters since the publication of your book and I have hence forbore to add my mite. I hope that now you are well through Edition II, and I have heard that you were flourishing in London. I have not yet got half through the book, not from want of will, but of time—for it is the very hardest book to read to full profit that I ever tried; it is so cram-full of matter and of reasoning". (I am sure all of us would agree with Hooker on this point). "I am all the more glad that you have published in this form, for the 3 vols., unprefaced by this, would have choked any Naturalist of the XIX century and certainly have softened my brain in the operation of assimilating their contents. I am perfectly tired of marvelling at the wonderful amount of facts you have brought to bear, and your skill in marshalling them and throwing them on the enemy. It is also extremely clear as far as I have gone, but very hard to fully appreciate. Somehow it reads very different from the MS., and I often fancy that I must have been very stupid not to have more fully followed it in MS."

Bentham, like many others, held out against the new doctrine for a time and Hooker writes about this, and other matters, in another letter to Darwin early in 1860:

"Dear Darwin,

I have had another talk with Bentham, who is greatly agitated by your book—evidently the stern keen intellect is aroused and he finds it too late to halt between two opinions; how it will go we shall see. I am intensely interested in what he shall come to and never broach the subject to him.

I finished Geolog. Evidence Chapters yesterday; they are very fine and very striking, but I cannot see that they are such forcible objections as you still hold them to be. I would say that you still in your secret soul *underrate* the imperfections of Geol. Record, though no language can be stronger or arguments fairer and sounder against it. Of course I am influenced by Botany, and the conviction that we have in a fossilized condition 1/100,000 of the plants that have existed, and that not 1/100,000 of those we have are recognisable specifically. I never saw so clearly just the fact that it is not intermediates between existing species we want but between these and the unknown *tertium quid*.

You certainly make a hobby of Nat. Selection and probably ride it too hard—that is a necessity in your case. If improvement of the creation-by-variation doctrine is conceivable, it will be by unburdening your theory of Natural Selection, which at first sight seems overstrained: i.e. to account for *too much*. I think too that some of your difficulties which you override by Nat. Selection may give way before other explanations—but oh Lord! how little we do know and have known, to be so advanced in knowledge by one theory. If we thought ourselves to be knowing dogs before you revealed Nat. Selection, what d.....d ignorant ones we must surely be now we do know that law”.

It is interesting to speculate what effect it might have had on the progress of biology if Darwin had known of Mendel’s experiments and Strasburger’s discovery of the constancy of chromosome number and of meiosis—events which occurred during Hooker’s lifetime.

In spite of prolonged ill-health, Darwin’s household must have been a very happy one. I had the privilege of knowing one of Hooker’s daughters, Lady Thistleton-Dyer, in her vigorous old age. She remarked one evening as we were sitting by the fire, “I think quite the nicest people we used to stay with when we were children were the Darwins”. The memory of those pleasant visits was evidently still vivid after 70 years or so.

It is now my pleasant duty to welcome all our visitors and especially those who are going to address us.

DARWIN AS A BOTANIST

NORA BARLOW

When I received your invitation to address your opening meeting I felt greatly honoured by this vicarious and genetic distinction. My grandfather would have been mildly astonished, I think, but wholly delighted that botanists, those students of his latest love in the biological sciences, should still choose to show him homage in 1959.

To-day the second year in succession of Centenary Celebrations is drawing to a close. On both sides of the Atlantic, and on both sides of the Iron Curtain, there has been a bumper crop of books and articles on Charles Darwin from historical, biographical, philosophical and modern scientific angles. The fine comb of historical criticism has been passed through his words and motives, and more and yet more sources of his ideas have been brought to light. Scholars in every discipline of new knowledge are still exploring the far-reaching effects of a scientifically grounded belief in evolution.

His reputation has had to stand up to a hundred years of a violently changing epoch, with new discoveries relevant to his theories, which might easily have relegated them to oblivion. In your Conference the modern aspects of some of the branches of botanical knowledge will be discussed, where Darwin laid tentative foundations. With cytology unborn, and the chromosome and gene not yet conceived; with Mendel's contemporary papers ignored, Darwin could only discuss the vital problems of variability, heredity, reversion, cross-fertilisation and embryology within the terms of the day, lit by his flair for the significant. It is remarkable how often he was on the right ladder, though necessarily near the bottom rung.

We shall hear from you in the next two days how real is the debt that present pioneer work owes to Darwin. I would remind you that he would still be the first to exclaim now, as he did in 1869:—"How much the views on all points will have to be modified". He knew that change even affected scientific theory and that problems are always being solved afresh under the impact of new discovery.

My contribution will be to try to give you a picture of the man in relation to his botanical work; and also in relation to the botanical traditions which were his background. As I myself experienced other kinds of traditions that were handed on by Charles Darwin to his sons and daughters—to my father, my uncles, and my aunts, I can perhaps throw a faint reflected beam

back on to their father. For I never saw him; he died before I was born.

All Charles Darwin's children were of an enquiring cast of mind; my own father, whose gifts were mainly mechanical, would show sudden and deep interest in the way country gates latched in different parts of England or wherever we might be; or in such matters as the shafts of farm waggons, harness or other examples of man's primitive mechanical ingenuity. He taught us the rigging of sailing ships; and made us stand on the edge of a cliff with a strong off-sea wind blowing, to note the dead calm experienced—especially round one's feet and legs. This, I afterwards found, must have been a traditional game learnt from their father's experiences on the *Beagle*. In his small pocket notebook dated July, 1836, there is a small diagram of a man on a cliff in St. Helena. Put your hand out over the edge of the cliff as we were made to do, and the upward current of air is felt in full force from the impact of the wind on the cliff face; and if the wind is strong enough, also an off-shore current to fill the vacuum. Of Darwin's five sons; only Francis showed detailed biological interest, though all had a deep love for the country and respect and kindness to all living things.

There was undoubtedly a strong botanical as well as medical tradition in the earlier generations of Darwin. Robert Waring Darwin, Charles's great-grandfather, had been termed a "man of curiositie" by Stukeley, the archaeologist. His son, another Robert Waring, wrote *Principia Botanica*, first published in 1787, which ran into three editions, and is now rarely obtainable. In Charles Darwin's *Life of Erasmus*, Charles mentions his botanical great-uncle appreciatively. Charles writes of *Principia Botanica*:—"This book in MS. was beautifully written, and my father declared that he believed it was published because his old uncle could not endure that such fine caligraphy should be wasted. But this was hardly just, as the work contains many curious notes on biology—a subject wholly neglected in the last century".

Many of the observations in *Principia Botanica* also show the ingenuousness of the age. Under Grasses, Robert Waring Darwin explains them thus economically:—

"The leaves are food for cattle, the small seed for birds, and the largest grain for man. And it is observed, that nature hath so provided, that cattle (in grazing) seldom eat the flowers, intended to produce seed, unless compelled by hunger".

In his Preface, and reasons for the book, he says:—

"Nothing is more pleasing and instructive to the human mind than to contemplate the harmony of Creation, as nothing more strongly evinces the existence of a Supreme Cause It is impossible for the most laboured harangues, or the most subtle reasoning, to make so deep or lasting impressions on the mind as the works themselves".

The most squeamish of eighteenth century matrons would be reassured by the following:—

“That this science may be divested of indelicacy in an English dress, for the word bastard, which frequently occurs in Botany, the word base is substituted; and the word hermaphrodite is entirely discarded”.

More prognostic of modern thought is the footnote:—“That Dr. Darwin [this was Dr. Erasmus, his younger brother by seven years] suggests improvements on the Linnean System to make it ‘more natural’.” The two brothers, born in 1724 and 1731, respectively, were deeply influenced by the work of Linnaeus, whose concept of classification was built on a basis of immutable components. It is of interest to note that Dr. Erasmus was advocating a ‘more natural’ system of classification so early, and that the one true meaning of ‘natural’ in this context, based on phylogeny, only became generally accepted two generations later after the publication of the *Origin of Species*.

In the third edition of *Principia Botanica*, Robert added many notes referring to his brother, Dr. Erasmus Darwin’s works, suggesting that the two Darwin brothers learnt from one another. A botanical dichotomy existed between them; Robert, the systematist, must have helped Erasmus, the medical philosopher, with taxonomic food for his evolutionary speculations.

Many of the themes which claimed the attention of Erasmus were to be re-examined by his grandson Charles in the last years of his life with a very different scientific vision. The insistent themes of adaptation remained latent but compelling, until the key of Natural Selection could unlock their mysteries.

Under the plate of *Cypripedium* from *The Botanic Garden*, Erasmus remarks in a foot-note that an allied American species much resembles an American spider that “catches small birds as well as insects and has the venomous bite of a serpent” “The similitude of this flower to this great spider seems to be a vegetable contrivance to prevent the humming-bird from plundering its honey”. Erasmus knew, too, of the movement of the tentacles of the *Drosera* leaf—the mucilaginous drops at the ends of the threads he said resembled “an earl’s coronet”. He had observed that the tentacles caught and entangled flies. But his explanation of this elaborate insect trap was that it prevented them from “infesting the leaves”.

This was the type of botanical reasoning that Charles must have been familiar with as a boy. Though his grandfather and great uncle were symptomatic of the enlarging interest in the subject, their facile teleological explanations may well have served to alienate Charles.

How much effect—negative or positive—the family tradition had upon Charles, who can say? It is impossible to know where the seed of tradition will germinate upon fertile ground. However, in a room full of botanists, it is worth a moment’s searching

of heart to trace any definable influence that set you on your paths:—a parent or a teacher, or for the perverse, a determination to blaze a new trail?

Robert Waring Darwin, Charles's father, followed his father Erasmus in his love for his garden; for Erasmus not only wrote *The Botanic Garden*, he made two botanic gardens as well. Robert, Charles's father, built an early hot-house in the first decade of the 19th century, and planted trees and unusual shrubs in his Shrewsbury garden high above the Severn. The white poplars in Pope's Villa at Twickenham came from Dr. Robert Darwin. He had his two younger children portrayed with botanical specimens in their hands; this was in 1815, when Charles was six, and I leave you to speculate whether the pot plant is a *Lachenalia* or *Veldtheimia*. Both plants were introduced from the Cape at the turn of the century, and are figured in *The Botanical Magazine*.

All this might be—and indeed has been—brought forward to prove what a perfect home the young Charles Darwin had for his training as a naturalist. But I should like to suggest that some of those family influences disinclined him for close botanical study in his early years. His father was a much loved but stern parent, somewhat disapproving of his younger son's inability to toe the prevailing classical educational line, so that Charles developed an early need to assert his independence. It is my belief that the absence of juvenile records of any keen interest in botanical study, was due to this need to follow his own path, with perhaps the added memory of his grandfather's and great uncle's unsatisfying reasoning. His youthful notebooks are curiously bare of botanical remarks, though the embryo ornithologist, geologist and entomologist are there. At the age of ten he may be said to have gained his first notion of geographical distribution when he noticed the specific differentiation between the insects on the Welsh coast and those around his Shrewsbury home. In old age he still remembered the stories he concocted as a boy of the rare birds he had seen, his matured conscience shocked at having trespassed on the sacred ground of exact observation. His aspiration to know every pebble on his father's front drive is often quoted. But I know of no botanical precocity—his school-boy boast that he could alter the colour of primroses at will by watering them hardly fills the bill. His early powers of noticing were there; he had the normal collector's urges, with the keen eye and delight in detecting new species, the search for rarities and the tabulating instinct. But there are no records of these urges in his botanic infancy. For Darwin's association with botany has a different approach from that of most botanists, and therein lies its interest, as I shall hope to show.

During his maturing period on the *Beagle*, there are still remarkably few botanical records in the small pocket-books he carried with him on expeditions. One entry from a catalogue of

specimens sent home from Port Desire, in South America, is of interest as the first evidence as far as I know, of any observation of his on the movement of plant organs, and of pollination. The entry runs:—"Cactus—the stamens when touched collapsed rapidly and with force on the pistil as did the petals in a less sudden manner". He must have been observing such matters as early as the last days of 1833.

This entry is the clue to his late botanical development. His searching eye, and his growing need to reason on the causation behind the outward form was taking possession more and more. The organism with its adaptive devices had begun to absorb him—those accretions which had become the hall-marks of specific form. He always pronounced himself an ignoramus in professional botany, and was not equipped as a systematist for the *Beagle* voyage. He had not at that time met Joseph Dalton Hooker, his later botanical mentor, and his friendship with John Stevens Henslow at Cambridge, had not made a botanist of him, though it had obtained the post of naturalist for him on board H.M.S. *Beagle*.

These two men were amongst the great influences of Darwin's life. The elder, Henslow, 13 years Darwin's senior, was Professor of Botany at Cambridge during Darwin's time at the University. This dim but saintly figure aroused in everyone a profound personal affection. Darwin describes the expeditions with Henslow and his band of enthusiastic pupils around Cambridge. Darwin writes:—"Two or three times in each session he took excursions with his botanical class; either a long walk to the habitat of some rare plant, or in a barge down the river to the fens, or in coaches to some more distant place, as to Gamlingay, to see the wild lily of the valley, or to catch on the heath the rare natter-jack".

There is the story, which turned out so creditable to both Darwin and Henslow, which also proves incidentally that Darwin did sometimes look through a microscope at botanical specimens whilst at Cambridge. In his Autobiography he wrote:—

"I cannot resist mentioning a trifling incident which showed his kind consideration. Whilst examining some pollen-grains on a damp surface I saw the tubes exerted, and instantly rushed off to communicate my surprising discovery to him. Now I do not suppose any other professor of botany could have helped laughing at my coming in such a hurry to make such a communication. But he agreed how interesting the phenomenon was, and explained its meaning, but made me clearly understand how well it was known; so I left him not the least mortified, but well pleased at having discovered for myself so remarkable a fact, but determined not to be in such a hurry again to communicate my discoveries". Henslow and Darwin were so often to be seen walking together that Darwin was termed "the man who walks with Henslow".

Though Darwin owed so much to Henslow on the study of specific differentiation in every branch of natural history,

Darwin's growing absorption in the origin of these specific forms led them apart in the end. Henslow died in 1862, whilst the upheaval of existing beliefs was still raging over the *Origin of Species*. He was never converted to evolution; and his creationist view of the species question may have helped to open Darwin's eyes after their many discussions, as I believe Captain FitzRoy's Fundamentalist opinions must have done on board the *Beagle*. I do not mean to suggest more than that some obstruction of a truly fundamental nature must have begun to loom up between both Henslow's and FitzRoy's explanations of a general pattern, and the facts as Darwin began to see them. The time soon came when Darwin could no longer look for Henslow's helping hand, and it was then that Joseph Dalton Hooker's immense knowledge stood him in such good stead.

It was during the vital years of self-development on the *Beagle* voyage that the collector's power of noticing differences and pigeon-holing began to take on a different form. Then, when panoramic vistas of geological change were presented to him, besides the procession of living forms, both in their existing representatives and in the fossil relics he disembedded from past ages, a change began to take place. The reasoner on the causes of transformation slowly took possession. The aesthetic pleasure in the form of the organism became itself transformed into the aesthetic pleasure of the conformity of the whole plan by which they had arrived at their present state. Transformation and change became more absorbing than the transformed, though the detail he loved was never abandoned as the mainstay of all his reasoning. If sometimes Charles Darwin laid himself open to the accusation of worshipping Natural Selection as an active force shaping the organism, I think the explanation lies in the homage he felt for the final form that had been achieved. He would always acknowledge the passivity of Natural Selection, and knew it could only act as a sieve to discard the worthless—the losers in the race—and never did he think it had a directive power of value-making, beyond the value of existence itself. The cause of Life and its resistless urge he treated as beyond human reason to determine.

When once his passion to rationalize the processes that were at work on all matter, living or mineral, became dominant, then his old pleasure in the detail of beetle or fossil took on a new sense of relationship—it was the sense of the symphony instead of the chord. Thus the adaptation of the final form as we know it, became one of his main quests; variation took on a new interest as the essential attribute of living matter on which adaptation could work.

It was at this stage, within a few years of his return from the *Beagle*, that his friendship with Joseph Dalton Hooker began, which was to develop into a close intimacy until Darwin's death. Hooker was at the time working at Kew Gardens under Sir William Hooker, his father; he did not become Director until

1865, on his father's death. He was eight years Darwin's junior, and became Henslow's son-in-law. This, the most intimate of all Darwin's friendships, came at precisely the right time for the botanical work that so largely filled the remaining years of his life. His half traditional yet rejected familiarity with botany gave him a huge new field on which to work out old theories and new. Detailed exploration into different aspects of plant life absorbed him in turn as grist to the evolutionary mill. His delight in detailed observation of the performance of the organism as a whole and in its parts, and in its relation to its surroundings, gave him engrossing matter for experiment. The marvels of the forms of flowers, with the intricate devices for pollination; the devices of insectivorous plants for acquiring their nitrogen needs, the means of seed dispersal and the means by which climbers and twiners obtained their necessary light—all assumed new importance as evidence before the Bar to prove Evolution by means of Natural Selection. His detailed work on the fertilization of orchids; his largely pioneer work on trimorphic and dimorphic plants; on the movement of the tentacles of *Drosera*, and of other experimental observations, produced in himself an almost devotional surprise and admiration that became a tribute to the powers of Natural Selection. His love of detailed observation, which never made him a botanical taxonomist, here found an ample field, and also took him to the very foundation of the ultimate needs of the classifier, the basis of a common descent. Charles Darwin's grandfather and great-uncle had called for an improvement in the Linnean system to make it more "natural"; our historical memories are short, and it needs an effort to keep in mind that when Darwin began to write his botanical books, the genealogical tree was not yet firmly established as the assumed fundamental basis of all classification. The Creationist view still reigned supreme in many quarters, shifting to Multiple Creations when the position became strained.

Thus Darwin may be said to have achieved botanical eminence through the back door; his theory called for detailed botanical study late in his life. He always regretted that he had never been through the mill of plant physiology and morphology; he had no equivalent to his self-imposed study of Cirripedes (Barnacles) which gave him his insight into animal specific form. When Hooker was working with great labour and prolonged microscopical examination on the anomalous *Welwitschia*, Darwin wrote to him:—"I expect it is going to be your Barnacles"; and Darwin expressed envy as well as admiration for the hours of work to determine the analogies and meaning of every part of that remarkable plant.

The first actual contact between Hooker and Darwin was in 1843, after Hooker's return from the *Erebus* and *Terror* expedition under Ross. But already in 1839 the proofs of *The Journal of Researches*, or *The Naturalist's Voyage* sent him by Lyell, had made a deep impression on Hooker, who slept with them under

his pillow to read on waking, at the time when he was taking his M.D. degree. The printed volume went with him on his four years' absence, and it was soon after his return that he got into personal touch with Darwin over the Galapagos flora. Darwin's collection had been sent back to Henslow, the good go-between for all Darwin's material. This Galapagos collection was by no means negligible, in spite of Darwin's secondary interest in plants; in reading the "Journal" we certainly get a distinct impression that the silicified *Araucaria* of the Andes were more significantly exciting to him than living specimens of the tree or plant; whereas the excitement of specific differences of living mammal, bird and reptile is still captured by the reader. Darwin had kept the vegetable products from the different Galapagos islands separate—an important piece of evidence that he had in his mind even at that time the distribution of species in isolated islands. He regretted later that he had omitted to do so with some of his other collections. This first work undertaken for Darwin, Hooker describes to Bentham as "a very slow work indeed . . . there are more new species than I expected . . . am now amongst the grasses, which are terrible. Fancy two new Panicums; I cannot make them agree with any others, yet everyone will say I only made them new species to save the trouble of finding out their proper names . . ."

Darwin's first letter to Hooker in 1843 was the foundation of their lasting friendship. There was immediately a sense of understanding, both in their serious problems and in their jokes. Darwin admired the systematist's vast knowledge, whilst Hooker already held the young philosophic naturalist in high esteem.

Darwin began his letter by congratulating Hooker on his safe return, continuing with the pleasure he had received on hearing that Henslow had relinquished his "small collection of plants" to Hooker for examination. "You cannot think how pleased I am", Darwin wrote, "as I feared they would have been all lost, and few as they are, they cost me a good deal of trouble . . . I have long thought that some general sketch of the Flora of the point of land (Patagonia and Tierra del Fuego) stretching so far into the southern seas, would be very curious. Do make comparative remarks on the species allied to the European species for the advantage of botanical ignoramuses like myself".

Hooker's findings were finally published in the *Journal of the Linnean Society* for 1849, and filled Darwin with fresh admiration. But by then their friendship was firmly established, and Darwin had already communicated to Hooker his ideas on the origin of species by sending him the sketch of 1844, before he had told any of his other friends. This famous letter is so important in the history of Darwin's developing ideas, as well as in their developing friendship, that I must quote parts of it once more. It shows Darwin's anxious approach to upsetting the creationist creed: although his own views were so far advanced in January 1844, when he wrote it, yet he did not venture to remove the many

creationist passages in Murray's edition of *The Naturalist's Voyage* published more than a year later in 1845—and fifteen more years of maturation were needed before the fruit was ready to drop, as you well know, and then it was forced from the tree by the strange coincidence of A. R. Wallace's simultaneous arrival at the solution of the evolution puzzle by means of Natural Selection.

Hooker had only recently returned from the Antarctic when Darwin wrote:—

“Besides the general interest about the southern lands, I have been now ever since my return engaged on a very presumptuous work, and I know no one individual who would not say a very foolish one. I was so struck with the distribution of the Galapagos organisms, etc., etc., and with the character of the American fossil mammals, etc., etc., that I determined to collect blindly every sort of fact, which could bear in any way on what are species At last gleams of light have come, and I am almost convinced (quite contrary to the opinion I started with) that species are not (it is like confessing a murder) immutable. Heaven forbid me from Lamarck nonsense of a ‘tendency to progression’, ‘adaptation from the slow willing of animals’, etc.! But the ideas I am led to are not widely different from his; though the means are wholly so. I think I have found out (here's presumption!) the simple way by which species become exquisitely adapted to various ends. You will now groan, and think to yourself, on what a man I have been wasting my time and writing to! I should, five years ago, have thought so”.

Hooker was slow in accepting the whole force of the 1844 sketch for the “Origin”—he, too, was a slow convert and no iconoclast. Nevertheless, he had already expressed his views on the mutability of species forcibly in his *Introductory Essay to the Flora of Tasmania* which appeared a few months before the “Origin” and such a well-founded opinion paved the way in botanical circles for the acceptance of the revolutionary view of 1859. Hooker wrote in his *Flora of Tasmania*: “In the *Introductory Essay to the New Zealand Flora*, I advanced certain general propositions as to the origin of species, which I refrained from endorsing as articles of my own creed: amongst others was the still prevalent doctrine that these are, in the ordinary acceptance of the term, created as such and are immutable. In the present Essay I shall advance the opposite hypothesis, that species are derivative and mutable; and this chiefly because, whatever opinions a naturalist may have adopted with regard to the origin of species every candid mind must admit that the facts and arguments upon which he has grounded his convictions require revision since the recent publication by the Linnean Society of the ingenious and original reasonings and theories of Mr. Darwin and Mr. Wallace”. He continues that “everyone is free to adopt such a theory as may best harmonize with the facts adduced by their own experience”.

That such a man as Hooker, with his vast botanical knowledge, should thus have attacked the foundations of the creationists through his trial of the hypothesis of Natural Selection, used as an aid in describing the taxonomy of his floras, with the new evidence of variation and mutability, is specially noteworthy as being pre-“Origin”.

In Darwin and Hooker’s two aspects of botanical work, each needed the other. “How few generalizers there are among systematists”, Darwin wrote to Hooker in 1853, “I really suspect there is something absolutely opposed to each other and hostile in the two frames of mind required for systematizing and reasoning on large collections of facts”. Hooker writes: “If you knew how grateful the turning from my ‘professional botany’ to your philosophic botany was, you would not fear bothering me with questions”. This deep mutual regard lasted to the end, and Hooker wrote in his recollections after Darwin’s death, of those discussions they had had together in the study of Darwin’s house at Down: “I at any rate always left with the feeling that I had imparted nothing and carried away more than I could stagger under”.

In enumerating and describing Darwin’s seven major botanical works, I can only briefly list them as they appeared, to remind you of their scope.

The list is impressive enough for an “ignoramus” in botany as he called himself. The first work on plant fertilization came out only three years after *The Origin of Species*, entitled *On the various Contrivances by which Orchids are fertilized by Insects*. I will only mention here some personal points about this famous book. The wild British orchids were amongst the plants of the chalk flora which charmed him most and which attached him to his home at Down in Kent. There, only 16 miles from St. Paul’s Cathedral, in good years, the Fly and Bee Orchid can still be found, whilst *Cephalanthera* and *Epipactis* grow in the woods, in spite of encroaching building and population. His memorable prediction that the insect fertilizer of *Ophrys insectifera* would be found, you will remember, was realised by Godfrey, who observed the male of the small burrowing wasp, *Gorytes mystaceus*, visiting the flowers, but only in the early part of the season, before the true female wasps emerge. This pseudo-copulation ensuring fertilization in a manner in accord with Darwin’s expectation forms a curious hark-back to his grandfather’s note on *Cypripedium*.

In 1861 Darwin was trying to analyse the morphology of the flower of orchids, and had put forward the view that the labellum was compounded of one petal and two petaloid stamens. Whilst trying to trace the ducts he wrote in despair to Hooker: “I was a fool ever to touch orchids”. Hooker answered in a comforting vein. In his reply Darwin wrote: “You rather astound me with respect to value of grounds of generalisation in the morphology of plants. It reminds me that years ago I sent you a grass to

name, and your answer was: 'It is certainly *Festuca* (so-and-so), but it agrees as badly with the description as most plants do'. I have often laughed over this answer of a great botanist", and ends his letter: "But I must stop; otherwise, by Jove, I shall be transformed into a botanist. I wish I had been one, this morphology is surprisingly interesting".

"Climbing Plants" was first published as a paper in the *Journal of the Linnean Society* in 1865; and was enlarged into a book in 1875.

Insectivorous Plants, published 1875, of which more later.

Effects of Cross- and Self-Fertilisation in the Vegetable Kingdom, 1876.

Different Forms of Flowers on Plants of the same Species, 1877.

The Power of Movement in Plants. Assisted by Francis Darwin, 1880.

Animals and Plants under Domestication is a work in rather a different class, as it was largely the material for the longer unfinished work from which the "Origin" was hastily compiled after Wallace's communication to him in 1857.

Besides these seven major works, he was constantly contributing botanical papers to periodicals, mainly to the *Journal of the Linnean Society*; *Nature*; *Gardener's Chronicle*; *Annals and Magazine of Natural History*.

Each of the books just enumerated had a history behind it, often lasting over many years. The first observations that set his mind working concerned the problem of some particular parts of a plant, and their use and behaviour, besides their origin. I thought it of interest in throwing light on the workings of Charles Darwin's mind to trace one book in greater detail from its inception to its publication. I have chosen *Insectivorous Plants*; the book opens with Darwin's description of exactly what happened: "During the summer of 1860, I was surprised by finding how a large number of insects were caught by the common sun-dew (*Drosera rotundifolia*) on a heath in Sussex". This was whilst he was staying at Hartfield, the home of Wedgwood relations. He probably remembered his grandfather's comments, for he continues:—"I knew that insects were caught; but knew nothing further on the subject". He then gathered plants, counted their prey, and the experimental work involving microscope and weighing began, which only culminated in 1875. He wrote:—"It was soon evident that *Drosera* was excellently adapted for the special purpose of catching insects, so that the subject seemed well worthy of investigation". He discusses the results of his experiments in 367 pages of close reasoning, and the movement of the tentacles and why, has pride of place. He correlates the movement with the other known movements of plant organs—which takes us right back to that first botanical observation on the cactus in 1833. Thus each minutest fact

became part of a wider interpretation. He says:—"Such movements imply irritability or sensitiveness . . . it is probable that all leaves are to a slight degree irritable". He concludes his chapter with a comparison of these impulses with animal nerve mechanisms:—" . . . the greatest inferiority of all is the absence of a central organ, capable of receiving impressions from all points, to transmit their effects in any direction, to store them up and reproduce them". Experiment and observation continued intermittently for over fifteen years, and during much of this time the traffic between Down and Kew—of plants, letters and ideas—was constant. Whilst Darwin worked on *Drosera* at Down, Hooker at Kew experimented on the carnivorous *Nepenthes*, in spite of pressure of over-work; "I have three plants set out in inviolable places—a very sanctum—", Hooker wrote, "and shall make a point of now going on—all other duties, social, scientific and parental, notwithstanding". Darwin wrote quite early in his experiments to Hooker, "I sometimes think *Drosera* is a disguised animal!" Later when experiment and observation were over, Darwin wrote:—"I don't think any discovery gave me more pleasure than proving a true act of digestion in *Drosera*". But no certainty was ever achieved without moments of agonised doubt.

William Marshall, a friend of Darwin's sons, was staying at Down during the *Drosera* period and records the following story. Some of them were playing tennis on the lawn, when Charles Darwin put his head out of an upper window and exclaimed with obvious distress:—"This confounded *Drosera* has gone all wrong this morning, upsetting my theories and spoiling a year's work". By lunch time the reason for the aberrant behaviour had been discovered, so that previous results remained valid. This was after a period when Darwin had been at work on other matters, and he felt that the astonishing results of the extreme sensitiveness of the tentacles of *Drosera* to 1/78,000th of a grain of phosphate, needed confirmation. He had to make sure, and this story shows his readiness to share his disappointments as well as his triumphs.

His experimental enthusiasm carried him through the early stages of all his books. But the writing up the results in book form remained always a veritable drudgery. He wrote to Hooker on the progress of *Insectivorous Plants*:—"You ask about my book, and all I can say is that I am ready to commit suicide; I thought it was decently written, but I find so much wants re-writing, that it will not be ready to go to printers for two months, and will then make a confoundedly big book . . . I begin to think that everyone who publishes a book is a fool".

Not even the shortest account of Darwin as botanist can be concluded without some account of the last publication he was to set in motion, but was never to see completed. I mean, of course, the *Index Kewensis*. Towards the end of 1881, only a few months before his death, Darwin wrote to Hooker stating that he wished to aid in some way the scientific work carried on at

the Royal Gardens by setting aside a considerable sum to complete and publish a new Kew 'Nomenclator' under a scheme drawn up by Hooker. Hooker informed his official masters, with whom he had already had strained relations, and wrote to Darwin:—"I, as a matter of course, informed the Board of your munificent offer, showing what a grand aid it would be to our own work, as well as to science in general, and how honourable to Kew. The First Commissioner (one of your d—d Liberals) wrote a characteristically illiberal and ill-bred minute on it, addressed to me, in effect warning me against your putting the Board to any expense!—and this though I expressly stated that 'your offer involved the Board in no expense or other responsibility whatever'."

The work was put finally into the hands of Benjamin Daydon Jackson and a vast undertaking it was. He worked on the basis of the Kew Herbarium copy of Steudel's *Nomenclator*, which was laid down in folio. Jackson wrote:—"It was ever a matter of regret on my part that his (Darwin's) life ended before any progress had been made on the last work originated by him, with the object of helping others in a field in which he had himself sometimes vainly sought for information".

Francis Darwin, who collaborated with his father during his last years, can give us the most vivid picture of Charles Darwin's affectionate attitude to flowers and to all plants, with which I must end. Francis writes: "He had great delight in the beauty of flowers—for instance in the mass of Azaleas which generally stood in the drawing-room. I think he sometimes fused together his admiration of the structure of a flower and of its intrinsic beauty; for instance, in the case of the big pendulous pink and white flowers of *Dielytra*. In the same way he had an affection, half artistic, half botanical, for the little blue *Lobelia*. In admiring flowers, he would often laugh at the dingy high-art colours, and contrast them with the bright tints of nature. I used to like to hear him admire the beauty of a flower; it was a kind of gratitude to the flower itself, and a personal love for its delicate form and colour. I seem to remember him gently touching a flower he delighted in; it was the same simple admiration that a child might have".

THE DEVELOPMENT OF CYTOTAXONOMY SINCE DARWIN'S TIME

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Charles Darwin was 22 years old when Robert Brown discovered the cell nucleus, he was 39 when Hofmeister discovered the chromosomes, and 65 when the intensive study of the nucleus began. He died at the time when Strasburger and Boveri established the constancy within the species of the chromosome number. Six years after the death of Charles Darwin, Waldeyer introduced the word chromosome, but the importance of chromosome structures for heredity and evolution did not become evident until the first part of this century. The famous Wilhelm Johannsen was for a long time, perhaps to the end, very sceptic. As late as 1916 he wrote "that chromatin often has been pointed out as the seat of the genes, but this hypothesis is still completely uncertain". In fact, a real proof that chromosomes are the seat of inheritance was probably first given in 1931 by Creighton & McClintock for *Zea mays* and by Stern for *Drosophila*.

It is difficult to establish the year of birth of that field of science which now is called cytotaxonomy. Undoubtedly, one of the first steps was taken when Rosenberg in 1909 established the three numbers 2_0 , 3_0 , and 4_0 for *Drosera rotundifolia*, its hybrid with *D. anglica*, and *D. anglica* itself. But the idea that chromosome numbers of related species are related constituting regular series of multiples goes back to the years 1915-1917 when Tischler, Tahara and Winge published their papers on chromosome numbers and their significance. From Tischler's paper of 1915 we may cite the following conclusive remark: "Also mit dem Ausschneiden der grossen phylogenetischen Probleme auf der Basis der Chromosomenuntersuchungen is es wohl noch zu früh. Wohl aber meine ich, dass wir auch jetzt schon die Chromosomenzahlen verwerten können, wenn wir die Gattungen oder gar die Species mit verschiedenen Zahle ins Auge fassen". Some few years later in his *Allgemeine Pflanzen-karyologie*, 1921-22 Tischler says a little more, namely: "Planmässige Verbindung der Cytologie mit der Systematik liegt aber im allgemeinen nicht vor. Solche schöne Arbeiten, wie sie Täckholm (1920) sowie Blackburn & Harrison (1921) für die Gattung Rosa anstellten werden da sicherlich sehr anfeuernd wirken". I think that the 1920 paper by Täckholm in the best way fixes the year of birth of cytotaxonomy. It was a preliminary paper. The large monographic cytological treatment

of *Rosa* appeared in 1922, the same year as Heilborn's first paper on *Carex*. Täckholm and Heilborn were both pupils of Professor Rosenberg in Stockholm. No doubt this very outstanding cytologist had worked as an obstetrician for cytotaxonomy by teaching Täckholm, Heilborn and others. Also Winge had studied in Stockholm. There was at that time an intimate co-operation between Professor Ostenfeld in Copenhagen, who in the years 1910-1919 studied apomixis and species formation in *Hieracium*, and Rosenberg, who worked with the cytological background for apomixis.

Thus cytotaxonomy as a separate field started its life about 1920, but it first became conscious much later. Of fundamental importance for its further development was, of course, the discovery of occurrences of different chromosome numbers within some of the Linnean species. Who were the pioneers using for the first time the chromosome number as a fundamental criterion for the subdivision or the bipartition of a species? Already in Tischler's first lists we find instances of polyploidy in a species, but the use of such chromosomal differences in taxonomy may go back to the years 1923-1927. Some of the first pioneers were from my own country and worked at that time at the plant-anatomy laboratory, that institute which now after the modernization last year is the Institute of Plant-anatomy and Cytology, of which I have the pleasure to be the director.

One of the pioneers was undoubtedly C. A. Jørgensen who, in his paper on the *Callitrichaceae* in 1923, stated that different strains of *Callitriche stagnalis* had 5 or 10 bivalents during meiosis. His comments are of great interest; he says that both forms undoubtedly belong to *C. stagnalis* and that he, notwithstanding the fact that they are almost morphologically identical, is inclined to consider them as belonging to different species. A difference in chromosome number, he says, is a characteristic of greater import than many purely intrinsic differences, and must definitely be indicated as something substantial. Bearing in mind that the difference in numbers would certainly, on crossing the two types, produce sterile seed, one inclines, he says, towards considering them as different.

In fact, with these words he opened a discussion which is still going on. The next papers of importance came in 1926-1927. One concerned Jordan's microspecies of *Erophila verna*, which according to Winge's investigations had three different chromosome numbers, thus $n=7$, 15, and 32, and almost simultaneously at least 9 cytotaxonomical papers appeared, namely Hagerup's on *Empetrum*, Jørgensen's on *Vallisneria*, Helms & Jørgensen's on *Betula*, Jens Clausen's on *Viola*, Heilborn's on *Draba*, Langlet's on *Ranunculaceae*, Percival's on *Ægilops*, Senjaninova's on *Valeriana*, and Lewitsky & Kuzmina's on *Festuca elatior*. This appears to have been a cytotaxonomical explosion, and it became rather an explosion wave which continues to our days. I was as a young student much influenced by the cytological atmosphere

in Copenhagen, which was stamped by Ø. Winge, Jens Clausen, C. A. Jørgensen, and Hagerup. As Hagerup was in the same house his influence perhaps became strongest. His *Empetrum* paper is, from a historical point of view, of particular interest, giving rise to two trends. By establishing a tetraploid as a separate species, *Empetrum hermaphroditum*, it became a challenge to orthodox taxonomy and an inspiration for cytotaxonomy and by involving plant geographical and ecological questions, it brought about a swarm of papers about cyto-ecology, and geographical distribution of chromosome numbers. Thus, while the birth of cytotaxonomy based upon chromosome numbers perhaps took place in Copenhagen and Stockholm, another branch was born simultaneously in Russia in the famous school of Navashin. Here the chromosome ideograms and the karyotypes of the species became early the main point of investigation. Among the early papers, two by Delaunay in 1922 and 1926 on *Muscari*, *Bellevalia*, and *Ornithogalum* raised a fruitful discussion leading to the important papers by Lewitsky and Tron in 1930 and Lewitsky 1931a & b. In the same period, however, Navashin himself published his two fundamental papers about the cytology of the genus *Crepis* in relation to species formation. It was in 1925 and 1926.

The early stage of cytotaxonomy in the twenties is well illustrated by a prophecy of Ruggles Gates in 1924. He said that the time would come when the description of a species was not considered complete until the morphology of its chromosome group was known, for visible chromosome differences, where they occur, throw important light on relationship.

The study of meiotic chromosomes, which was initiated in 1909 with Janssen's theories about chiasma formation, was rapidly developing, particularly, perhaps, in the United States under the influence of Morgan. Again some of the most important results for cytotaxonomy were gained in the twenties and early thirties. In 1922 Cleland described the ring-formation in *Oenothera*, and in the same year Blakeslee published his paper about variations in *Datura* due to changes in chromosome number. A few years later in 1925-26 the study of segmental interchange, inversions and other structural changes was intensified through the works of Belling, Sturtevant and others. This branch of cytology was from the thirties onwards very much developed by McClintock, Darlington and others and was for the first time synthesized by Darlington in the first edition of his book *Recent Advances in Cytology*, which appeared in 1932.

Another not strictly cytological branch had also been developing. It was the study of apomixis and the mechanisms which are responsible for the many micro-species in *Alchemilla*, *Hieracium* and others. But while the two first branches—the study of chromosome numbers and the karyotypes—supplied the taxonomists with cytological evidence of great value in their work with delimitation or subdivision of species, the two other branches

dealing with structural hybridity and apomixis sometimes brought great complications. In the many groups which we now call agamic or amphi-apomictic complexes or in complex heterozygotic groups as *Eu-Oenothera* as well as in certain groups with much introgression between the units, the conditions may be so intricate and the units so unstable or difficult to define that any attempt of systematization is rather hopeless. Cytology has thus given modern taxonomy many tools or toys: Chromosome numbers, chromosome morphology and size, but also—and it is not the most unimportant contribution—it has supplied taxonomists with a knowledge of permanent structural hybridity and of accidental crossing-over or fertilization in apomicts. These ought to make him strongly against attempting species-making in groups where any cutting up into described taxa will, at the most, have only local or temporary importance.

The study of the so-called constant species hybrids led to one of the greatest triumphs not only for cytotaxonomy, but for the theory of evolution. In 1917 Winge published his theory about doubling of chromosomes in species hybrids resulting in series of multiple chromosome numbers. His theory was amply corroborated through, for instance, the study of *Primula kewensis* and the artificial synthesis of *Nicotiana digluta* (Clausen & Goodspeed, 1925), *Raphanobrassica* (Karpetchenko, 1927-28) and Jørgensen's synthesis (in 1927) of a constant species hybrid between *Solanum nigrum* and *S. luteum*. In 1933 Winge himself was able to produce an allotetraploid constant species-hybrid within the species aggregate *Erophila verna*. For the understanding of the species formation in nature it was of particular interest to demonstrate that already known species had originated as allotetraploids. Most famous perhaps is Müntzing's synthesis in 1930-32 of *Galeopsis tetrahit* from a cross between the diploid species *Galeopsis pubescens* and *G. speciosa*. He got a single triploid hybrid plant and backcrossed it to *G. pubescens*. Only one seed developed, but it grew up to a plant, which was almost identical with *Galeopsis tetrahit* and crossed with natural *G. tetrahit* it gave fully fertile hybrids. But evidence of allopolyploid evolution and species formation were also gained through purely cytological and morphological comparisons. We are able to gather a group consisting of *Æsculus carnea* (Skovsted, 1929; Upcott, 1936), *Spartina townsendii* (Huskins, 1931), *Pentstemon neotericus* (J. Clausen, 1933), the new world cotton (Skovsted, 1934, 1937), *Iris versicolor* (Anderson, 1936), *Rorippa microphylla* (*Nasturtium uniseriatum*) (Howard & Manton, 1940), *Madia citrigracilis* and *M. gracilis* (Clausen, Keck & Hiesey, 1945), *Anemone janczewskii* (Gajewski, 1946), the last being produced experimentally and found spontaneous in many gardens, and finally *Poa annua* which, according to many important pieces of evidence including cytological, is an allotetraploid (Tutin, 1957). One less known, but very interesting allotetraploid species from my own field of activity is *Saxifraga nathorstii*, a peculiar species endemic to

north-east Greenland (Böcher, 1941). It is completely fertile, but morphologically it is intermediate between the purplish flowered *Saxifraga oppositifolia* and the yellow flowered *Saxifraga aizoides*. Now these two supposed parents have both 13 chromosome pairs while *Saxifraga nathorstii* has 26. *S. aizoides* has two pairs of particular large size and *S. oppositifolia* has one small pair, which as a rule is precosiously separated. In the PMCs of *S. nathorstii* the two large as well as the small pair occur, thus making the allotetraploid origin quite evident. The curious fact is that the parent species grow side by side in many areas other than north-east Greenland and that sterile hybrids between them are not reported anywhere. The Greenland flora may further contain other allopolyploids, e.g. *Melandrium triflorum* as shown to be probable by Nygren 1951.

What is the situation to-day? Cytotaxonomy is a fertile scientific field, which gets its support from many sides, from pure cytology and genetics, from plant geography, ecology and last, but not least, comparative morphology and taxonomy. It is, therefore, not surprising that its students come from different quarters. Some are clearly more cytogenetically minded, some are more taxonomically minded and others tend towards ecology or plantgeography. This, in my opinion, is as much an advantage as a disadvantage. It is very good that experiences from other fields are brought into contact with cytological findings, but too frequently the synthesis of widely different fields makes so heavy demands on the scientists, that he or she stops too early. It is not uncommon that cytotaxonomists have been too much cytologists and only poor taxonomists. A species like *Plantago lanceolata* was long considered to consist of races on three ploidy-levels. But later work disclosed that the tetraploids as well as the high polyploids belonged to two other species. Thus the species is exclusively diploid. In too many cases differences in chromosome number have been based on very few samples from only a limited area of the total range of the species and in too many cases the published cytological data are only counts of root-tip-mitoses. Of course in such mitoses the number can be established, but a knowledge of the meiotic behaviour may be of fundamental importance to the understanding of the species problem in question. Saying this I expose also myself to criticism. When I first published the chromosome number of *Arabis holboellii*, a most peculiar species of Greenland and N. America, I thought that it was safe to use clear pollen mitoses. Thus I published $n=21$, but fortunately my further studies disclosed that the species was apomictic and that the 21 number was the somatic one in several populations, while others had $2n=14$ and were diploid. More illuminating is the case of *Campanula rotundifolia*. In my first paper in 1936, diploids were reported from Greenland only and tetraploids both from Greenland and temperate Europe. Later Guinochet (1942) found diploids in the Alpes Maritimes and thought that these were ter-

tiary relics. Now *Campanula rotundifolia* or rather the *C. rotundifolia* complex has been investigated from 60 localities, which has disclosed quite another picture. Diploids are found also in the lowland of formerly glaciated areas as on two islands in the Baltic Sea as well as at Moscow. These diploids are morphologically almost inseparable from the tetraploids in the same area. It is also very difficult to separate arctic diploids from arctic tetraploids (see Böcher, 1960). The whole complex consists of rather well separated diploids and badly separated tetraploids, which may be allo- or autoallopolyploids. So far only a single triploid has been found by Guinochet. The striking variation, however, in *Campanula rotundifolia* is not only a result of polyploidy. It is also, and perhaps to a much higher degree, the result of structural changes. In diploids, as well as in tetraploids, inversions, as indicated by the occurrence of bridges and acentrics, are frequent, and associations of many chromosomes occur frequently indicating segmental interchanges. The structural hybridity for inversions and interchanges has probably contributed to the subdivision of the complex into a great number of not very well defined nor well separated geographical races or subspecies. Finally in two of the tetraploid strains we have found accessory chromosomes. The whole story is getting more and more interesting and complicated, but the hope through chromosome studies to be able to subdivide the species into two separate species is lost. *Campanula rotundifolia* is a polyploid complex, which moreover already at the diploid level contains many structural deviations. It is therefore not surprising, that even thorough taxonomical investigations as those by Witasek in 1902 did not lead to any satisfactory classification. In many other cases, e.g. in *Galium boreale*, which was studied eagerly from many areas by Løve & Løve (1954), the accumulation of more evidence has altered the picture. We have now tetraploids and hexaploids of this species growing side by side on the experimental field and find it very difficult or perhaps impossible to distinguish them. Our material is from Europe where, according to the previous investigations, only one of the chromosome numbers ought to occur. Thus the area of the two chromosome races overlap. No doubt an adequate cytotaxonomical investigation should always be very time-consuming in order to avoid premature conclusions, but who has time enough? Many species must be studied for years by many in order to reach a final conclusion.

Fortunately there are many cases where cytology suddenly discloses the true foundations of a problem. This was evidently the case when Løve & Løve two years ago began a cytotaxonomical study of the *Triglochin maritimum* aggregate. They disclosed a series of polyploids ranging from diploids up to 24-ploids and were able to elevate a western America variety with 96 chromosomes to specific rank and re-establish *Triglochin elatum* of Nuttall, which was shown to have 144 chromosomes. I saw this

plant in a marl bog in the Gaspé Peninsula and must admit that its ecological behaviour, its growth habit and size is striking and deviates very much from our European plant, which has only 48 chromosomes. From my own field of observations I may here mention two cases. We have in Greenland a *Luzula* of the *multiflora* group with a much contracted head-like inflorescence. It is the subsp. *frigida* var. *contracta*, which is a hexaploid and occurs in rather poor soils. Now in the interior along the margin of the inland ice another morphologically very similar plant occurs. But its ecology is widely different from that of subsp. *frigida*, being found mostly near alkaline or salty lakes on open neutral or basic soils. This ecologically deviating plant appeared to be tetraploid and a thorough investigation disclosed that it had smaller seeds and shorter perianth leaves; evidently a good new species which was called *L. grønlandica* and which further occurs in the Canadian Arctic (Böcher, 1950). In the *Trisetum spicatum*-complex we had a similar experience (Böcher, 1959). The true widespread arctic *Trisetum spicatum* is a tetraploid, but in low- or subarctic areas another type occurs, which is hexaploid. This is what at one time was called *Trisetum molle* Kunth and it is an American temperate to low arctic species radiating over Greenland to Iceland. The rediscovery of this species, which happened almost simultaneously and independently in Copenhagen (by me) and in Montreal (by Dr. Morrison), has now made the world range of the complex much more clear. On the recent map published by Hultén, 1959, we see that this complex keeps to the north in Eurasia, while in America it goes far to the south. This local American southern range extension is clearly due to the existence here of *Trisetum molle*, which has quite another ecological behaviour from the true *Trisetum spicatum*. *Trisetum molle* grows on dry rocks in the lowlands as far south as in the Gaspé Peninsula, it is very easy to cultivate in Copenhagen. This cannot be said of *Trisetum spicatum*, which is much more likely to die. As a whole the Arctic North-Atlantic flora is from a cytological point of view perhaps now the best known. In 1952 appeared the paper by K. Holmen about the chromosome numbers in the flora of Peary Land and in 1956 Løve & Løve's cytotaxonomical conspectus of the Icelandic flora, and in 1958 Jørgensen, Sørensen & Westergaard worked out their cytotaxonomical treatment of the whole flora of flowering plants in Greenland.

The *Triglochin*, *Luzula* and *Trisetum* studies may exemplify cytotaxonomical approaches on the specific level. Others may be on a subspecific level, for example the very fine study of *Gilia capitata* by Grant, 1950. But before I finish my lecture with some words about the taxonomical treatment of chromosome races I should like to deal with some cytotaxonomical works on the generic level and on the level of families or orders.

There are many impressive cytotaxonomic investigations of genera. Some of them are exclusively based on chromosome

numbers and karyotypes, others on crossability and chromosome homology. This, for example, is the case with the famous investigations by Clausen, Keck & Hiesey on genera like *Zauschneria* and *Layia*. In *Layia* the species are arranged according to their chromosome number, their morphology, crossability and the degree of pairing between specifically different chromosomes.

Another genus, which has been subject to a thorough cytotaxonomical investigation is *Narcissus*, which was studied in the years 1939-1951 by A. Fernandes. In this genus cytological studies have revealed the occurrence of almost all kinds of evolutionarily important chromosome changes. Auto- and allopolyploidy as well as polysomy have been active which result in some species groups with euploid, others with aneuploid numbers. Many other important investigations of various genera might have been mentioned in more detail, among more recent ones, e.g. the genus *Calamagrostis* studied by Nygren and Westergaard, *Luzula* by Nordenskjöld, *Geum* by Gajewski.

One of the best known families is probably the *Ranunculaceae*. Thanks to previous investigations by Langlet, Lewitsky and many others, as well as his own observations, Gregory in 1941 was able to make a summary, which lead to a new and probably better arrangement of the genera according to basic numbers, and chromosome size. He removed two genera, *Anemonella* and *Thalictrum*, from the *Anemoneae*, and placed them together with *Aquilegia* and *Isopyrum* in a special tribe with small chromosomes, the *Thalictriceae*. Also in the *Gramineae*, which was studied carefully by Avdulov in 1931, there are similar size differences, which, however, in most cases correspond to the groups already described by taxonomists. Other from a cytological point of view particularly well known families are, e.g. the *Cruciferae* (Manton, 1932), the *Malvaceae* (Skovsted, 1935, 1941), and the *Saxifragaceae* (Hamel, 1953).

The impressive and very suggestive work about the Pteridophytes by Manton, first the book about the cytology and evolution in 1950 and later the paper on the cytotaxonomy of the Pteridophyte flora of Ceylon in 1954, may serve as the best example of a cytological treatment of one of the large plant groups. It was possible on the basis of comprehensive cytological data—using Professor Manton's own words—"to recommend a splitting of two of Copeland's fern families". The word *recommend* reflects a charming cautiousness on the part of the authoress. About the limitations of the cytological method she says that cytological difference is probably a slightly more trustworthy guide to absence of affinity, but even this may perhaps on occasion be misleading. The most that cytology can attempt to do is to add significant comment to proposals based on other types of evidence. This modest attitude towards cytological methods in plant taxonomy ought, in my opinion, to be a little more common among cytotaxonomists. In this connection I

would like to say that although I have used the word cytotaxonomy many times I do not like it. Cytotaxonomy is going to be a scientific box; the word may invite people to limit their research to chromosomal and morphological differences. But our progress depends on many-sidedness and vision. In fact, as compared with cytotaxonomy, names such as experimental taxonomy, a term which was introduced by Clausen, Keck & Hiesey, or biosystematy, as proposed by Camp & Gilly, in 1943, are much better, being more embracing, but they contain a weak, but in our day unnecessary, challenge to the so-called orthodox taxonomy. Why not, as proposed by Turrill, 1955, say *synthetic taxonomy* or merely *taxonomy* presupposing that all taxonomists now and in the future to the best of their ability are "cyto-geno-eco-choro-taxonomists".

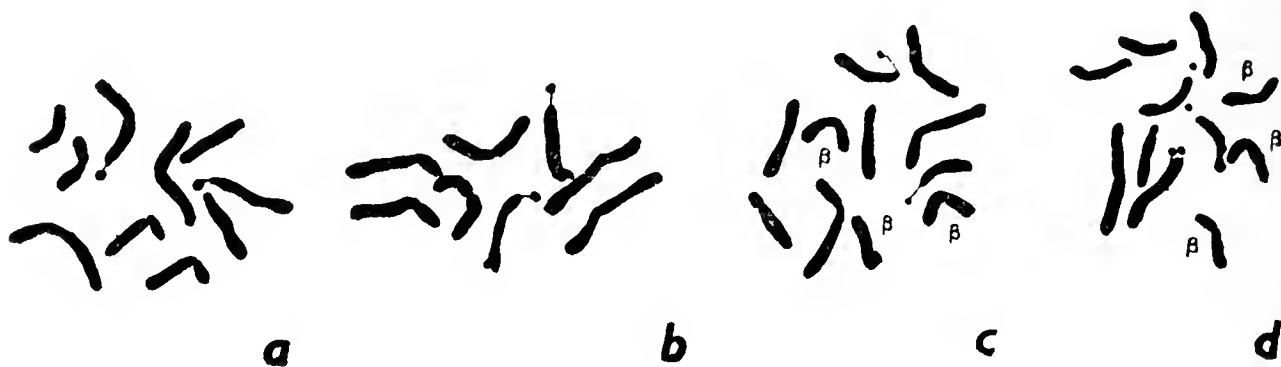


Fig. 1.

Metaphase plates from root tips of three strains of *Plantago coronopus*. a, from Venezia (normal, $2n=10$). b, from a *Chenopodium*-steppe community in Morocco (nullisomic, $2n=8$). c and d, from Beira Alta, Portugal (trisomic, $2n=11$; the chromosome represented in triplicate condition marked β).

We were just discussing the limitation of the cytological method. Those who believe in differences in chromosome numbers as a fundamental criterion for separation of species ought to take into consideration how little in certain cases the number itself means. In a species like *Plantago coronopus* we found $2n=10$, 11, 20, 30, and 31, but the trisomic strains were not morphologically distinguishable and the hexaploid with 30 chromosomes was only a little coarser than the largest among the diploids. The supernumerary chromosome is in this case probably almost inert; this is deduced from the fact that a strain has now been found with the chromosome number $2n=8$ indicating that this whole chromosome pair, one of which sometimes may be supernumerary, can be lost without clear morphological consequences. A chromosome of this kind behaves like many accessory ones, but has the normal size. Also in *Clarkia* additional chromosomes occur in some populations without being associated with any morphological or physiological traits, that have been detected (Håkansson, 1942; Lewis, 1951). Aneuploidy itself is not enough to justify taxonomical separation and in genera with diffuse centromeres the same genecomplement may be found in plants with different chromosome numbers.

Nor is polyploidy itself enough. If the analysis of the chromosome number of a species is extended so that very many strains from the whole range are studied the result will probably in most cases be that some strains are found having a number of another ploidy-level. Thus, I believe, it will be possible in most diploid species to find accidental tetraploids. Such as have been found by us in *Dryas octopetala*, *Cynanchum vincetoxicum*, *Trifolium arvense* and *Pulsatilla pratensis*. In the latter species the accidental tetraploids, which occur very rarely in the populations of diploids, have been given varital rank because they can be distinguished by gigas characters, but in *Dryas octopetala* and *Trifolium arvense* a similar practise cannot be followed. In *Veronica officinalis*, which most frequently is tetraploid, two diploid strains with leaves of medium size have been found, one in Gotland in the Baltic and another in southernmost Jutland. In this case the diploids probably represent a basic ancient type, which of course is extremely interesting, but it is not sufficient to give it specific status considering the great range of variability among the tetraploids, which include size classes on both sides of the size of the diploids. Some cytotaxonomists have summarized a number of cases, where the occurrence of polyploidy justifies the division into two or more species. But it is also possible to make another summary of cases, where such a division is impossible, and it will be a long one including, for example, *Silene ciliata* (Blackburn, 1933), three species of *Tradescantia* (Anderson & Sax, 1936), *Valeriana officinalis* (Skalinska, 1947), three species of *Eupatorium* (Grant, 1953), three species of *Delphinium* (Lewis, Epling, Mehlquist & Wyckoff, 1951), *Sanicula crassicaulis* (Bell, 1954), *Luzula multiflora* (Nordenskjöld), very many grass species as summarised by Jones, 1957, and many others. As Winge says: "What is to be done, for instance, with *Narcissus bulbocodium*, which appears in nature with 14, 21, 28, 35 and 42 somatic chromosomes (Fernandes)". Such types with different chromosome numbers exhibit frequently a higher or lower degree of sterility in reciprocal hybridization, but scarcely anybody would think of designating them as different species. They are types of different atomicity, if I may be allowed an analogy with chemistry where, e.g., sulphur appears with the valence of 2, 4, or 6.

As pointed out by Camp, homoploids are usually interfertile and heteroploids intersterile, but autotetraploids may be almost indistinguishable from their ancestral diploids and are at the same time highly interfertile with morphologically quite different tetraploids.

It is not the doubling up of a chromosome complement, which is crucial, but rather the success of the tetraploids. If they are able to find a separate ecological niche isolation mechanisms will soon remove them from their diploid ancestors—and as evolution proceeds—they will one day reach a stage, which makes it natural to regard them as species. To find the right day—

the right stage—however, is difficult and will always be a matter of opinion. As already pointed out a useful piece of cytotaxonomic work was carried out by Winge in *Erophila*. In his final paper from 1940 he mentions 10 aneuploid chromosome numbers found in 117 strains from different European countries. In the F_7 - F_9 after a cross between plants with $n=15$ and 32 he got a number of fertile, cytologically constant plants with 6 different chromosome numbers. In this situation it is not easy to be a taxonomist, but according to Winge it is possible to delimit 4 true species with 7, 12, 15 to 20 and 26 to 32 chromosomes respectively. These species are characterized by different ecological demands and different geographical ranges. We see here a striking example of a difficult adaptation of cytogenetic evidences to practical taxonomy. It is impossible or unscientific to name all the chromosome races as species. Therefore a compromise is the only solution.

In fact no species are comparable, looked upon from an evolutionary point of view. Some of them are, and well-defined and well-established, others just in *status nascenti*. Some are complex and may in time produce a swarm of species, others are monotypic, little varying and may sooner or later become extinct.

Even in our day some taxonomists are inclined to consider species to be more or less fixed units of almost the same dimensions and nature. But we may only try to compare species like *Erophila quadruplex*, which is a member of a species aggregate, *Geum urbanum*, which only is separated from *Geum rivale* by ecological barriers, *Calluna vulgaris*, which is monotypic, the only member of a genus, and *Campanula rotundifolia*, which includes a series of ill-defined smaller taxa being at the point of species formation. I think this is enough to be convinced that species are not on the same level or of the same nature. If so, why then try to enclose them in fences of the same size? The species should never be procrustian beds. Cytotaxonomists as well as experimental taxonomists must admit that no biological law has universal validity. The law formulated by Løve, 1951, that "*every polyploid level is a distinct taxonomical species*" is of this kind; it is a formulation which stimulates discussion and opposition and thus is perhaps of importance. Another law of the same kind is "*that hybrid fertility is an expression of relationships between the species, which are crossed*". But in *Lamium* it has been proved by Bernström (1953-55) that crossability or non-crossability give no clues at all to the relationships between the species.

The synthetic taxonomy, which utilizes every kind of knowledge about the plants has by Tutin been called a botanical revolution. Its many workers will continue to split up old species in order to describe the real bricks of living nature. But as many of the species, which now are cut up, form interdependent evolutionary groups, it is quite natural to hold them together in

species aggregates just as recently proposed by those working with "Flora Europaea" Aggregates are plastic. They can include species of the *Erophila*-type as well as apomictic species. They are able to adapt taxonomical regularity to biological multiplicity, but it involves an increasing use of a ternary nomenclature, which I personally accept.

Cytology is by some going to be reduced to an auxiliary science for taxonomy. This, however, will imply stagnation. Comparative cytology is a separate field as are comparative anatomy, embryology, and morphology. Like these three fields, cytology can be used in the study of evolution, but by dealing with cell structures which are the seat of genetic active materials, comparative cytology can supply us with evolutionary informations, which are much more fundamental. Thus my hope is that cytotaxonomy will never forget its duty to contribute to the understanding of the evolution of species, genera and families. It should always include the phylogenetic aspect, thus—I am sure—quite in the spirit of our great late colleague Charles Darwin, who, in spite of his ignorance about chromosomes, should be regarded as the great genius also of cytotaxonomy.

Darwin's country has been and is a genial soil for the study of evolution, and species formation. Some of the most important cytotaxonomical papers were produced in his country. The Botanical Society of the British Isles was probably the first to publish a journal—*Watsonia*—which is stamped by cytotaxonomy or better, synthetic taxonomy. British papers are rarely quantity of material only, but contain usually a good deal of philosophy, which is stimulating to read. We from the other side of the North Sea are listening intently to the fruitful discussion between you all. As seen from outside, British botany is in a period of rapid growth.

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Professor D. H. VALENTINE enquired whether any further studies of *Empetrum hermaphroditum* had been made since the original investigation by Hagerup? Has meiosis in the tetraploid been investigated and is there anything known of its phylogeny?

Professor BÖCHER replied that Hagerup's was the only published work and in it he had been mistaken in his interpretation of meiosis. It might be an allopolyploid but the parents are unknown. The diploid *Empetrum nigrum* may be one parent. The chromosome number had been confirmed by Arvidsson from root-tips of Swedish material.

THE PATTERN OF VARIABILITY AND EVOLUTION IN PLANTS

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We are met here to-day in conclave to celebrate the centennial of the publication of probably the most important and far-reaching single work of a secular nature ever to come from the pen of an author. It is not my purpose to detail its impact on the mind of man; others have done, and for a very long time will continue to do this in a manner far more scholarly than I possibly could. The best I can do is to pay tribute to its influence on my own thinking, for it began very early.

It was, I recall, a cold winter's night during my fifteenth year. My usual nightly struggle with mathematics and Latin lessons for the morrow had been finished and so I wandered into father's study looking for something to read. I rarely did this, for his shelves always seemed forbiddingly replete with ecclesiastical writings and commentaries, sets of the Old Testament in Hebrew, the Gospels in Greek, and the usual so-called inspirational writings of the day. But that night I found a series of volumes on a high shelf I somehow had missed before. Among them were translations of Ovid and Aristotle; there also was Bacon's *Novum Organum* and other works certainly not especially written to interest a lad of my age. However, among those volumes I spotted one whose title somehow caught my attention for, already, I had heard—and perhaps not too favourably—of its author. As you doubtless already have suspected, it was Darwin's *Origin of Species*.

How this particular volume came to be in the library of a staunch fundamentalist parson will never be known. I suspect, however, that father—doughty old warrior that he was—wished to have personal contact with the “enemy”. The underlined passages and marginal notes in his own handwriting indicated that father had read the book, which is to his credit. More to his credit is the fact that, several evenings later when he discovered me with my nose still buried between its covers, all he asked was whether I first had finished my usual struggle with those too often insoluble mathematical puzzles and indeclinable Latin verbs. Little did I then realise that the reading of that book ultimately would lead me into a profession where, always with discomforture, I should be required to write the Latin descriptions of new species of plants and also wrestle with the all but incomprehensible mathematics of population statistics. Perhaps, then, there has been some sort of destiny that has shaped

my end, at least that end which makes it possible for me to stand here on this platform and on this particular occasion.

What was it on those pages of the "Origin" that could capture the rapt attention of a lad of fifteen years? I have tried to analyse it in retrospect, but the secret rather eludes me. Had it been the account of high adventure into strange lands as narrated in the "*Voyage of the Beagle*" it would be much more understandable. Perhaps what caught and held my attention was the impact of great truths based on the observation of simple and, when explained, comprehensible natural phenomena, and these expounded in simple, even humble, phrases easily understood by one who was entirely unsophisticated in scientific matters. What ever it was the fact remains that I was not only totally absorbed in that book the first time I read it, but returned to it again and again that winter until many of its details were far more familiar to me than my necessary schoolboy lessons. I soon forsook the classics and became ever more deeply interested in certain phases of biology.

What were those great truths that Darwin presented in his *Origin of Species*? The traditional approach, perhaps, would be to delve through the great body of critical evaluations of his concepts by the many learned scholars of Darwiniana, then summarise them at length, adding the necessary citations and a welter of footnotes. Instead, I purpose to do no more than let my mind wander back across the years to rediscover just what it was a lad of fifteen got out of those memorable pages. To-day, save as I were to refresh my memory from the original text, the details and background data are somewhat less than crystal clear, but what then appeared to be the really important ideas were so deeply etched on my consciousness that they have become an essential part of my present thinking. These are:

- That organisms usually produce far more offspring than the environment can support;
- That the offspring of individual matings often are variable among themselves;
- That these variations have an hereditary basis;
- That there are natural forces which somehow select from among these variable and too numerous offspring those which are most successful in a given habitat; and
- That these naturally selected forms, in some manner, give rise to different kinds of organisms which—in time—may become new species.

How simple, how almost self-evident, these five great truths now seem, so that it is almost incomprehensible that they had not been thought of in proper sequence centuries earlier by the many great natural philosophers who preceded Darwin.

Perhaps the philosophical temperament tends more toward analysis than synthesis, so that only a very few of the world's great minds have been capable of analysis followed by logical

resynthesis and the simplification needed to make the truth self-evident. We must not forget that Darwin, in accumulating his great mass of data, never got lost in its details, so that one might say that he had one of those rare minds capable of recognizing the truth when he saw it. It is an obvious fact that men had been seeing and making note of the same phenomena for untold centuries before him, but had not understood their significance. That he did recognize them for basic truths, and also was able to arrange them in logical sequence, constitutes the very essence of his true greatness.

It is not my intention critically to analyze these five great dicta, or truths. In fact, I am not certain that they have been stated correctly for, as you already have been warned, they are what a man with grey in his beard recalls that a lad of fifteen remembered. Rather, I will but briefly remark on the first three, leaving the fourth and fifth for the text of my remarks to-day.

Darwin, himself, gave credit to Malthus for having furnished the key concept. In turn, one can but wonder what sort of wrestling old Parson Malthus had with his own conscience as he pondered on whether the Deity, in commanding Noah and his sons to go forth and repopulate the world, actually intended that they *over*-populate it.

The variability of offspring resulting from individual matings was an observation that man had been making for many centuries, for there now is good evidence that man has been consciously selecting for better breeding stock from among his domesticated plants and animals for at least ten thousand years. It needed only a good field naturalist to re-observe this phenomenon and give it universal application in nature; this Darwin did in masterly fashion.

The problem of the actual basis of these hereditary variations was one that troubled Darwin. One only can wonder how he would have handled the situation had he known of Mendel's experiments, then in progress but not yet completed, in the little monastery garden at Brünn. Chromosomes had not yet been discovered, and a concept of genes had not yet been invented when Darwin made his remarkable inductions concerning the nature of inheritance. The rediscovery of Mendel's work in 1900, and this soon to be followed by the DeVriesian concept of mutations, and these when coupled with the facts of both mitotic and meiotic phenomena, soon pushed Darwin's concept of inheritance into the background. Genic mutations followed by recombinations were all we thought were necessary to keep our biological structure in balance. But our rapidly expanding pyramid of concept had not been built on a sufficiently broad base of observation and knowledge; instead, it was precariously balanced on its apex.

To-day we are beginning to realize that the "large" mutations inferred by DeVries are not so effective in successful evolution as we once had supposed. It is the minute and scarcely detectable

mutations that really count, and these usually evident only after a considerable series of accumulations and accretions of change in associated genetic material. To-day we even dare doubt the reality of the gene, at least the concept we have held concerning its particulate nature for a half century. Certainly, we no longer dare think in terms of "one gene—one effect". Now that we can go far beyond a study of the gross structure of the chromosome and are beginning to understand the physico-chemical nature of the highly complex deoxyribonucleic-acid molecules, as well as the source and action of the microsomes, we dare at last return to Darwin's concept of the ultimate effectiveness, in evolution, of minute changes and permutations in the genetic mechanism.

For a century biologists have been paying little more than lip-service to Darwin so that, in truth, it may be said that what we actually have had is a century *without* Darwinism for, until recently, we had but little concept of the real mechanism of evolution. It was something in which, as biologists, we thought we ought to believe, but we had no sound basis for our belief. For a century our writings have been replete with what we all too glibly have called "the proofs of evolution". Usually when we have attempted to prove it, we have done little more than dig up the dry bones of the past, presenting them to our colleagues and students in an apologetic manner, hedging our remarks about with half-truths based on incomplete knowledge, hiding behind the comforting petticoats of the obvious incompleteness of the fossil record, so that in the end we never did convince them that *evolution is a primary and continuing force in nature*. The trouble was that we never had convinced ourselves. We were not real Darwinists.

There are times when one can point to the exact turning place in one's concepts. Mine probably was a slow evolution. In spite of my early contact with Darwinism, I had been trained to hunt plants, to press them as neatly as possible, and then on returning to my home herbarium to affix the correct names to them in traditional manner and file them in the proper pigeon-holes. The only other chore, if a few seemed not to be something that already had been described, was to write the necessary Latin descriptions and publish them as "new species". Perhaps the turning point came one day on the bleak tundra in Alaska when I garnered a large series of dwarf Arctic willows, no two of which were precisely alike. Perhaps it was while riding through that amazingly complex oak forest in the State of Oaxaca, high in the mountains of southern Mexico. Perhaps it was another time when I was caught in a sudden storm on the ledges above the grinding, booming glaciers of Mount Rainier in the Cascade Mountains and took shelter behind a great rock, only to discover there a glandular, yellow, tubular flowered sort of *Phyllodoce* hybridizing with an eglandular, rosy-magenta, campanulate flowered kind, together with a wide assortment of obvious segregate forms, some

of them exactly comparable to those which already had been described from adjoining areas as the nomenclatural types of "species".

Perhaps it was these and the thousands of other specimens that a plant explorer jams into his presses, as well as the millions more he walks past with something of a critical eye but doesn't collect, that set me to wondering more and more about the basic concepts of evolution in relation to the practice of plant classification. If evolution is a fact applicable to the past, is it not equally applicable to the present? And, if so, do these species which we so carefully describe and delimit on the basis of only a relatively few specimens have any stable reality in nature? Or are they little more than ephemeral points, within the present, of a great plexus of genic material existant within the space-time continuum? Does the species have fundamental reality in both space and time? Or is it only the product of a much too limited definition? What is a species? The elements of these problems were forming in my mind but never had become concrete questions.

It was approaching midnight, and I was seated at my desk in the Herbarium of the New York Botanical Garden reading a manuscript for the printer. For a taxonomist, it had been a pleasurable experience "cleaning up" a series of collections of *Vaccinium* from North and Central America, for the paper contained the descriptions of about twenty-five new species. Finished with the task, I paused and looked out across the lights of that great restless city and, somehow, the previous series of questions welled up inside of me. Half-thought thoughts which I had suppressed for years finally became articulate. I did not begin asking myself questions, the questions began asking themselves of me. And for the first time I realized that I was not able to answer them, and that I had never been able to answer them. Suddenly, I became aware that for years I had been doing something about which I really knew nothing. I had been describing "new species" without knowing what a species was. The shock was such that I tore that manuscript into shreds and threw it in the waste basket. And from that day to this I have never written the description of a "new species" without a great deal of soul-searching. No, I did not cease being a plant explorer, for I was still to garner many specimens from frigid mountain tops and steamy jungles where no plant collector ever had been before. But I was no longer hunting "new species" or extensions of range; instead, I was primarily interested in ascertaining "the pattern of variability and evolution in plants", hoping from that sort of activity to discover something of the true nature of the species. Inevitably, this led me into the field of population dynamics.

There are some who equate the study of population genetics with experimental systematics. The techniques of the two may be somewhat comparable, but the approaches are very different. The experimental systematist usually begins with the classical

interpretation of species and works backwards so as to understand the genetic mechanics of his material. The population geneticist begins with the raw population, discarding in his own mind any classical concept of species, and works from there into a series of group concepts which may, or may not, be comparable to the taxonomist's concepts of species. Furthermore, there are several rather different types of population genetics. One deals with limited populations in culture plots; the other attempts to assess the broad pattern of a group as it occurs in nature. Now I do not at all imply that one type of activity is more important or yields more significant results than the other. All I would wish to note is that the methodologies of these two types of population genetics usually have to be different because of the nature and availability of the "populations" being studied. Because of the differences in method of attack, that phase of population genetics which seeks to assess the broad pattern of variability and evolution in nature as it applies to systematics has been called "Biosystematics" (Camp and Gilly, 1943).

The biosystematist welcomes assistance from standard research by means of the plot method, but too often he discovers that it is a practical impossibility to use orthodox genetic methods on the material he is studying. For example:—Suppose that a person were to begin studying the oaks of the *Quercus robur* × *Q. petraea* complex. What chance would he have of seeing the F_2 generation in its mature state? He would indeed be fortunate to see the F_1 generation in a sufficiently mature stage to be reproductive, save as he began as a very young person. And he would have little or no chance of making the necessary back-crosses and inter-crosses among the various segregative types to find those comparable to the confusing forms he is so likely to discover in nature. And so the biosystematist, in many instances, is forced to use paragenetic methods. He must assume that the same genetic phenomena are present in natural populations as are to be found under controlled conditions in culture plots and green houses. But he also must make certain careful observations and critical preliminary tests, usually of a cytological nature, so that he is on relatively sure ground, for such things as the presence in a population of polyploidy, disploidy, cleistogamy, heterogamy and apomixy create pitfalls of interpretation into which the biosystematist dare not fall. (For example:—It was lack of knowledge of the heterogamic nature of his *Oenotheras* that led DeVries to suppose he was discovering mutations; instead, he was dealing with a scattering of genetic segregates capable of maintaining their morphological stability only because of the presence of balanced lethals. There is no evidence that DeVries ever saw a single real mutation among the Evening-primroses in his plots.)

It is not my intention to describe in detail the methods of the biosystematist; these are a matter of record in the writings of an increasingly large number of workers. Furthermore, they are too complex to be outlined in any brief manner, for the

methods are as varied as the material. The concept of approach to a problem, and not the method, is the important thing. The biosystematist must work, even live, with his material until he knows it in all its seasonal moods; he must know its reproductive pattern as well as what pollinates it, and how; he must be steeped in the lore of genetics, but also fully understand the manifold limitations of this discipline; he must be more than passing familiar with the working end of a high-power microscope; and he must have an ability to see minute differences in form and texture, as well as the training to handle large amounts of material in some sort of statistical manner. Far and beyond this, he must be able to obliterate from his mind the narrow conceptual limits of biotic units forced on him by a century of intensive traditional taxonomy almost wholly devoid of any working concept of evolution as a continuing force in nature. In brief, he must be a skilled biologist, and also really believe in evolution.

Without further ado, let us see what happens when a biosystematist is turned loose among natural populations of different sizes and types. It is hoped I will be pardoned if I have not searched the literature for examples, but have limited myself to certain of those with which I am personally familiar.

WHY ARE THE BARKS OF THE HIGH ALTITUDE FORMS OF *CINCHONA* IN ECUADOR SO VARIABLE IN ALKALOID CONTENT?

Because of the acute need for antimalarial drugs early in World War II, resulting from lack of access to the primary commercial plantations in south-eastern Asia, a small band of plant explorers was sent into the areas of the wild stands in the South American Andean region to locate *Cinchona* barks yielding the highest possible amounts of these alkaloids. It soon was discovered that the more easily accessible and classically known high-yielding barks such as the low elevation "Roja" (*Cinchona succirubra*) and the middle elevation "Costrona fina" and "Urituzinga" (of the *Cinchona officinalis*-complex) had been riddled by over-exploitation. Therefore, it was necessary to push the explorations into areas where little disturbance of the natural stands had taken place. This took the explorers on to the essentially trackless and excessively rugged upper slopes in the region of the "mossy forest" just below the treeless, windswept and inhospitable páramo. Here, between the 9,000 and 10,000 foot elevations, in southern Colombia and northern Ecuador, was found a type known to the local Cascarilleros (or bark hunters) as "Pitaya" bark. Its total crystallizable alkaloids (usually abbreviated as TCA) averaged about 5 per cent of dried bark weight, up to 2 per cent of this being quinine. This, of course, was considerably lower than the better plantation strains but, as noted, these no longer were accessible. And so it was decided to open up trails in order to exploit this type of bark. It also was known that rather similar stands of *Cinchona* were present at the

same elevation in central and southern Ecuador. Therefore, in April 1944, I was assigned the task of ascertaining the extent of this stand in southern Ecuador, and also whether its alkaloid content would make its exploitation worthwhile. An additional task was to organise work crews to exploit such remaining stands of the classically known high-yielding barks as might still be found. This latter chore has no bearing on our immediate problem, and so we will concern ourselves only with the *Cinchona*-population at the higher elevations.

There are four primary alkaloids in the bark of *Cinchona*: quinidine, cinchonidine, quinine and cinchonine. Three of these, quinine, cinchonine and cinchonidine, may be classed as anti-malarials. Quinidine has importance in the treatment of auricular fibrillation. As may be seen from the chart (Figure 1), there are remarkable differences both in the amounts and kinds of alkaloids produced by this high-altitude population. Taxonomically it has never been resolved. Some workers of the past, relying largely on alkaloid content, have attempted to equate the northern "Pitaya" type with the alkaloidally similar *C. officinalis*. Morphologically, the two are quite different in their botanical characters. In Ecuador, this "Pitaya" type (*C. pitayensis*) is found in the two northern Andean provinces of Carchi and Imbabura (Nos. 1 and 2 on the sketch map).

Figure 1, based on the bark analyses of individual test trees, also will indicate that the high altitude population in the Province of Pichincha is transitional between the two northern provinces and the central provinces of Cotopaxi, Bolivar and Chimborazo, where the trees yielded almost pure cinchonine, with only a few traces of quinidine. This type is called "Serrana" by the local cascarilleros. In the province of Cañar (No. 7) the population swings across a "nudo" or cross-range to the Cordillera Oriental, or eastern range. Here, in Cañar, there is another sharp change in alkaloid content, especially on the eastern escarpment, where the TCA drops sharply. In the two southern provinces, Azuay and Loja, little or no alkaloid is to be found; in fact, I have omitted a fairly large number of individual-tree analyses which yielded no alkaloids, merely to save space on the chart. This essentially alkaloid-free type is locally called "Pata de gallinazo". Its presence was known to the local cascarilleros only because, in the old days, the thin branch bark of it from the Loja area was regularly used to adulterate that of the characteristically thin trunk bark of "Costrona fina", the classical bark of the Loja region, at a time when "Loja bark" carried a premium price in European markets, and when buying bark by appearance and locality of collection rather than by analysis was the practice. (For several centuries before the establishment of the high-yielding types in the plantations of south-eastern Asia, Loja was the traditional source of commercial quinine-yielding barks.)

The individual-tree analyses of this high-altitude population now establishes the inherent chemical difference of its segments. However, the taxonomist, using only traditional morphological

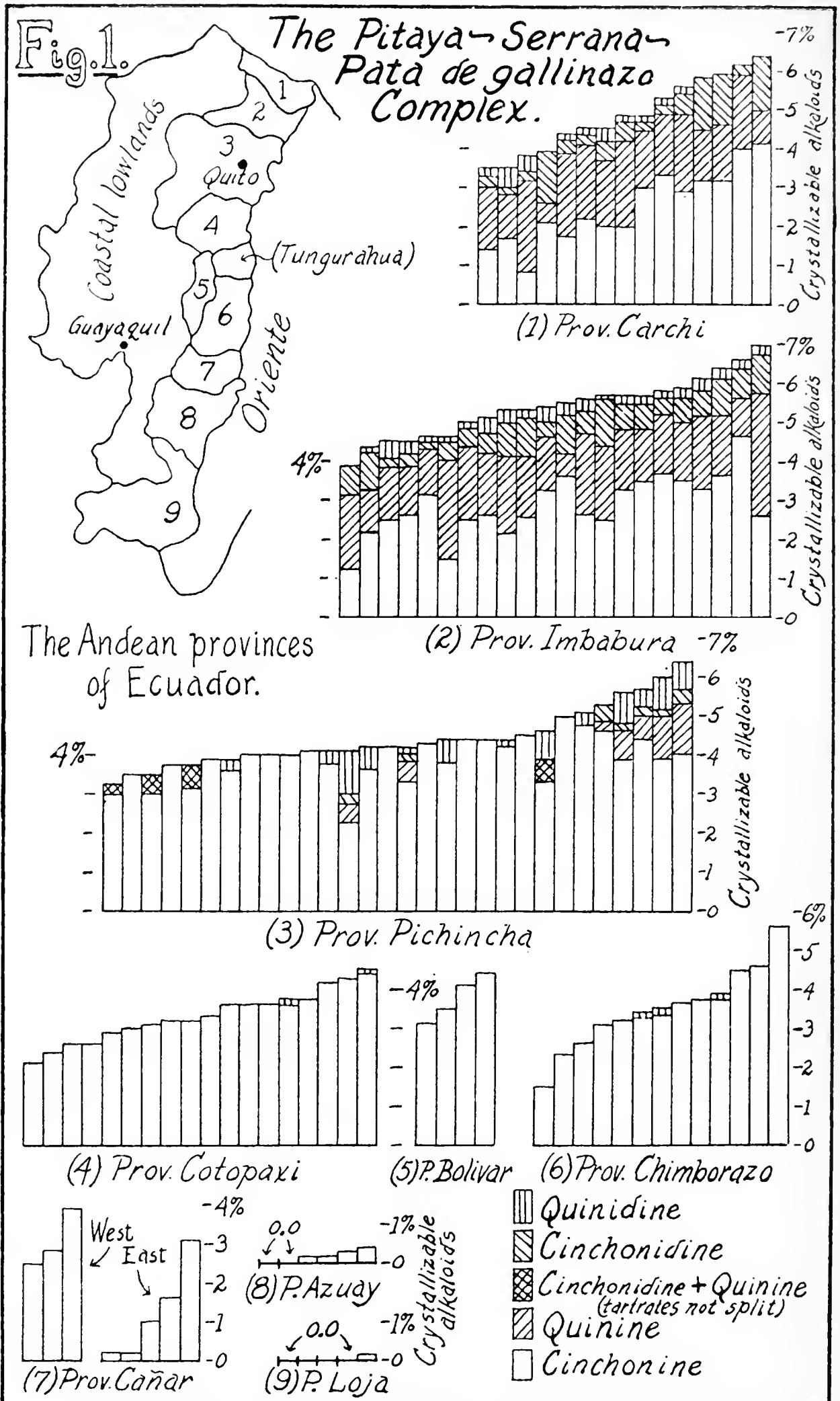


Fig. 1. Analyses of the total crystallizable alkaloids of representative individual trees of wild stands of *Cinchona* occurring between the elevations of 9,000 and 10,000 feet in the Andean provinces of Ecuador.

criteria, finds it difficult to separate the "Pitaya", "Serrana" and "Pata de gallinazo" types when studying herbarium materials, so similar are they and so seemingly continuous is the relatively small amount of morphological variation from the northern to the southern provinces of Ecuador. A confirmed taxonomic "splitter" might be tempted to erect several varieties, but even he would have to search his conscience.

What, then, is the source of this rather remarkable variation of yield in both amount and kind of alkaloid in this population? Following current trends of thinking, it would seem that a series of mutations involving genes primarily affecting the alkaloid yield would be the most likely explanation. It certainly would be a simple one, but it probably is not the correct one. Elsewhere (Camp, 1949) I have presented in some detail what I consider to be the more nearly true situation. This will be here presented only in greatly condensed form.

To-day, in the region of the equator in Ecuador, the permanent snow line is at about 17,000 feet elevation. Also, in various areas, evidence is to be found of rather recent glaciations, perhaps even more recent than those of our own late Pleistocene in the northern hemisphere, extending down to as low as 11,000 feet, or sometimes to 10,000 feet elevation. This means that, in rather recent times, these upper level *Cinchona*-populations must have been forced considerably farther down the slope (for they will not stand frost, high as they are to be found to-day). Down slope they would have had opportunity to come into contact with other species of the genus.

Such work as has been done on the genus indicates that various of the species are homoploid, that is, they have the same chromosome number. Breeding work also indicates a high degree of interfertility between an even wider series of species. During the work of the "Misión de *Cinchona* del Ecuador" there was little time for any activity except that primarily associated with the discovery of stands of potentially high-yielding trees. However, after the cessation of hostilities, I remained in Ecuador for an additional six months doing general plant exploration (Camp, 1952), and so was able to return to certain of these areas for more intensive work of a basically botanical type and thus give the problem somewhat more study.

In the Province of Pichincha, and especially in the Río Saloya-Corazon Pass area, there is ample evidence that the northern "Pitaya" type at one time had made solid contact with the middle elevation "Bofuda" type (*C. pubescens*), which characteristically contains only cinchonine. Likewise, in the Province of Azuay this high-altitude material comes into contact and hybridizes with a form locally called "Crespilla de Cuenca" (*C. rugosa*) and, similarly, in the province of Loja with another type, "Crespilla de Loja" (*C. microphylla*); in neither of these sorts had we earlier been able to detect alkaloids.

Briefly, then, it would appear that at some time in the past, the "Pitaya" type, genetically attuned to the upper levels of the forest zone in this region, had made contact in several areas with morphologically and alkaloidally considerably different kinds. During those contacts there were exchanges of genetic material with these species. It is to be remembered that this phenomenon is to be seen in active progress to-day in selected areas in Pichincha, Azuay and Loja where, because of situations of penetrating deep valleys and favourable slopes, the several types still make contact. In these zones of contact one easily may discover, not just a few putative hybrids, but whole local populations exhibiting every conceivable set of morphological combination between the forms involved. In the Río Saloya-Corazon Pass area, the alkaloids also indicate a highly introgressed genic condition (see Camp, 1949). In Azuay and Loja the relative absence of alkaloids makes this sort of analysis impossible; however, the considerable differences in morphology of the forms there involved makes an analysis of hybridity on this basis a relatively easy matter.

Of course, one does not know, but one who has something of a genetic background and who has lived and worked with this high-altitude population for a year and a half, would be more than tempted to come to the conclusion that there had been an even more active exchange of genetic materials—by means of introgressive hybridization—between these several species in the past than there is to-day, at a time when the high altitude population must have been forced to a somewhat lower elevation. On the climatic swing back to present conditions there appear to have been selective pressures favouring the retention of the morphological characters of the "Pitaya" type by those forms migrating up the slopes. In a more extensive discussion of this situation I also pointed out the possibility of soil types as being influencing factors. In the region there is a vast complex of ancient sedimentary and volcanic rocks, together with more recent ones, all these superficially further disturbed at the higher elevations by recent glaciations, and these glacial soils in turn modified by a covering of even more recently, even currently, deposited volcanic ash in certain localities, these all yielding to the region a series of soil types with considerably different chemical characteristics. Perhaps, then, the climate has selected out of this series of genetic combinations a relatively homogeneous morphological type suited to the high elevations; in like manner, it seems to have gained a series of different physiological races attuned to different soil types. Certainly, in this high altitude population, there appears to be little if any genetic linkage between the morphological characters of the plants and their alkaloid content, so that it seems likely that several sets of selective pressures have been operating on the same genetically complex population.

The alkaloidal differences between these physiological races cannot be charged to responses to differences in soil chemistry,

or any other detectible factor, save that of differences of a genetic nature. Where the currently active hybrid complexes are to be found (as in the Río Saloya-Corazon Pass area, in which tree-to-tree analyses were made from the 3,000 to the 10,000 foot elevation), it was not unusual to find two trees of similar age and appearance, so close that their branches touched and their roots entwined, but with very different amounts and kinds of alkaloids. The point cannot be overemphasised that, in this and similar situations, we are not dealing with variant physiological responses induced by changes in the environment, but with compatible hereditary characters sorted out of genetic complexes by the variant selective pressures present in the environment. The situation poses a fundamental problem for the taxonomist.

I do not intend to settle this particular taxonomic matter in this place. I have included these *Cinchonas* only as an example of one of the many sorts of problems the biosystematist encounters when, for a time, he forsakes the comfort of his beloved herbarium and begins working with living populations.

[**Note:**

A section on the variability of the American Beech (*Fagus*) has been deleted at this point. Chromosomal samplings originally indicated that the group was homoploid. After delivering the paper a complex polyploid situation was discovered on a single mountain in the Southern Appalachians. It is unknown whether this situation is limited to this single mountain or whether there is a scattering of ancestral diploids among the more than 10,000 individual trees sampled for morphological variability throughout the range of the group in eastern North America. Until this has been systematically ascertained it would seem unwise merely to publish the data on morphological variability without a more complete assay of possible correlated chromosome numbers, as was done in the other groups here reported on.]

WHY IS VACCINIUM CORYMBOSUM SO VARIABLE?

The northern high-bush blueberry (*Vaccinium corymbosum*) is one of the most variable species of its genus. It achieves reality in our current manuals only by a type of taxonomic legerdemain or, one might better say, a sort of necromancy performed by our taxonomic high priests over the well-fumigated corpses of a few very dead specimens. As generally defined, less than half of the total population of which it is comprised is at all accounted for; the remainder usually is conveniently ignored. Its extreme variability, coupled with the fact that it occurs only north of the glacial boundary, should be warning enough that there is something unusual in its genetic background.

Figure 2 may be used as a basis for our discussion. This figure in no manner attempts to delineate the entire geographic ranges of the materials involved; instead its sole purpose is to

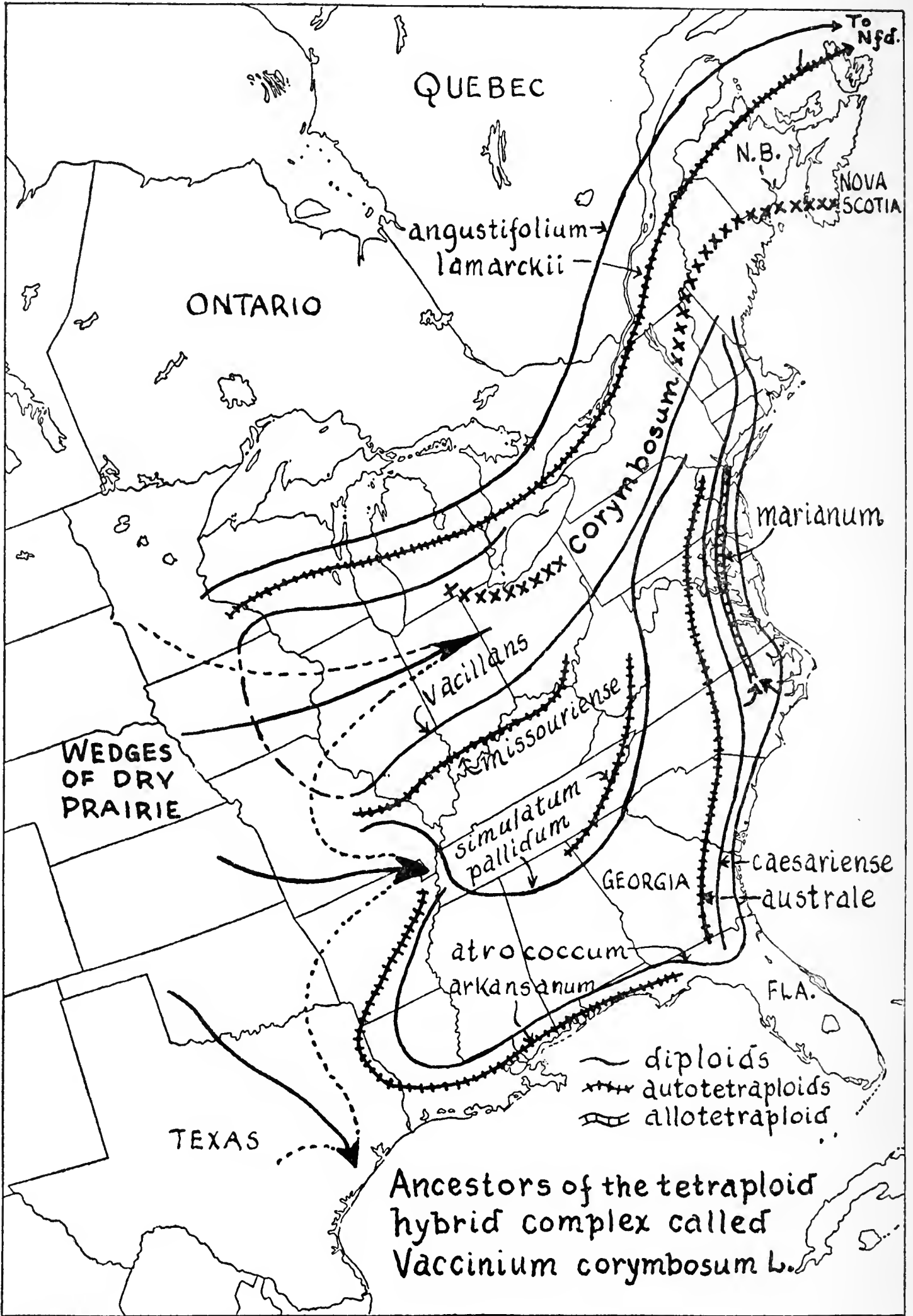


Fig. 2. The origin of the tetraploid hybrid complex called *Vaccinium corymbosum* L. The lines indicate only the generalized distributions of the ancestral diploids and their derived tetraploids which, during the Pleistocene, gave rise to this highly variable hybrid complex. In post-Pleistocene time invading wedges of dry prairie eliminated former close association between various of the western populations.

give a general concept of the pattern of distributions of the ancestral elements of the population we are to consider. First, however, it should be noted that the genus *Vaccinium* is prone to two things—the production of polyploids, as well as effective interfertility of those forms with the same chromosome number. The polyploids are of two types, autopolyploids and allopolyploids; of the allopolyploids there are two subtypes, those which arise by the union of chromosomally unreduced gametes (a fairly common phenomenon in *Vaccinium* and elsewhere in the Ericalean complex), and by the autopolyploidic doubling of the chromosomes of hybrids; in both allopolyploidic subtypes the end results are genetically comparable.

As can be noted from the chart the diploids (with $2n=24$ chromosomes) usually have associated autotetraploids ($2n=48$); although ecologically comparable, the autotetraploids usually are somewhat more able to compete with other shrubby materials because of their greater stature so that the diploids tend to be on the more open sites and the tetraploids in thickets or among second-growth coppice. Of the tetraploids directly concerned with our immediate problem, only *Vaccinium marianum* appears to be an allopolyploid, combining as it does the very different characters of the diploids *V. caesariense* and *V. atrococcum*. The 24 populations of blueberry within the subgenus *Cyanococcus* which I deemed worthy of recognition under a binomial have been described elsewhere (Camp, 1945); to repeat these descriptions in any detail here would needlessly encumber the discussion. Since that time I have recognized a 25th population, *V. missouriense*, which appears to be a polyploid (probably an autopolyploid) derivative from the western portion of the *V. vacillans* population. (*Vaccinium vacillans* itself is a diploid hybrid complex; a south-eastward projecting spur extending along the Piedmont as far south as Georgia has given rise to another autopolyploid population which seems never to have made contact with the more western *V. missouriense*, nor does it seem to have had more than casual relation to our immediate problem, and so was omitted from the chart. Others of the 25 species, not related to our problem, also have been omitted from our map.)

In stature these derived tetraploids vary considerably, being genetically paced by their diploid ancestors. Thus, the northern *V. lamarckii* rarely is over 3 decimetres high; *V. missouriense* only occasionally reaches a meter, even in the most favourable situations; *V. simulatum* varies between 1 and 2 metres; and *V. arkansanum*, *V. australe* and *V. marianum* usually are 2 to 3 metres high at maturity. In general the individuals of these basic populations are rather cohesive so that reasonably adequate keys may be constructed for their identification. Individually, their leaves may be small or relatively large with entire or sharply serrate margins, and their surfaces glabrous or densely pubescent. The flowers may be clear white, straw coloured or with a deep pink tinge, and be narrowly urceolate or almost campanulate.

And the fruit may be black or a bright frosty blue. A relative cohesiveness of character is lacking in *V. marianum*. At first it was thought it might be of hybrid origin between *V. australe* and *V. arkansanum*, but this latter tetraploid does not enter the necessary area; instead, *V. marianum* has been found to be a highly segregative allotetraploid, in which it differs from our standard concept of the sometimes more stable amphidiploid. The age of these derived tetraploids is a moot question. The East Coast *V. marianum* may be of rather recent origin; the others appear to be considerably older. Certainly they antedate the origin of *Vaccinium corymbosum*, which came into being not later than the latter stages of the Pleistocene. And now to the subject of our enquiry.

Vaccinium corymbosum occurs only within the glaciated area; therefore it could not have been in its present location during the height of the ice advances. Being tetraploid and highly variable, none of the known diploids possibly could have been its particular ancestor; it is to the tetraploid populations themselves that we must look. The events of the Pleistocene were a bit more complex in America than in Europe, but the principles were the same with a series of advances and wanings of the ice fronts resulting in drastic northward and southward shiftings of all biota, not just a small, limited, or special part of it. Therefore the distributions of the blueberries were equally affected. It also is important to remember that the blueberries have an unusually high light requirement; therefore they are not part of the forest association, being limited to openings in the forest cover. Under primeval conditions, they were to be found on rocky outcroppings or the edges of cliffs, and in the lowlands along water courses, around the soggy, but sunny, margins of ponds and bogs, or in sandy flat-woods where, because they are mycorrhizal and can garner nutrients in soil too sterile to support a dense forest, there is sufficient light for their growth and reproduction. The blueberries continue to be in those habitats, but they follow quickly after man when he cuts down the forest; they also have ventured as weedy growth into his pastures and meadows and along his fence rows.

If the situation following the earlier ice maxima were at all like the last (and there is every reason to believe they were), it will be obvious that the waning of the ice left much of the terrain without an established drainage pattern, so that a multitude of lakes, ponds, bogs and swamps existed, often with ridges of sterile glacial soil between; all of these afforded ideal habitats for the development of a large population of blueberries. And so, each time the ice fronts pushed southward, elements of the northern blueberry populations were forced ahead of them; and each time the ice fronts waned, these populations almost exploded into the newly available habitats northward. In the end this population in the zone of active migration became a large hybrid complex, the tetraploids forming the dominant element because of their larger size and greater competitive

ability as the forests and forest-margin shrubs encroached on the territory. It is the somewhat isolated segments of this once genetically churned population of tetraploids which we now call *Vaccinium corymbosum*.

The western end of this population is dominated by "arkansanoid" and "missourienoid" forms, these grading into "simulatoid" forms. (The western connections have been partly obliterated by the wedges of dry climate, too dry for blueberries, which drove eastward at the maximum of the post-Pleistocene Xerothermic period which reached its greatest severity about six thousand years ago.) Eastward the population leans heavily towards "australoid" and "marianoid" forms. Sporadically throughout the population the genetic elements of *V. lamarckii* are evident; intermediate and low-growing "lamarckioid" forms segregate and persist as part of this complex interbreeding population wherever rocky bluffs, cut-over forest land or abandoned sterile pastures are contiguous to the "high-bush" forms of the swamps. In parts of eastern Canada these low-growing tetraploid "lamarckioid" forms are so quickly adventive after clearing of the forest, and form so dense a ground cover, that they greatly retard natural reforestation. Burning them off only kills the few tree seedlings that have taken hold; the blueberries sprout from the rootstocks the next spring, more vigorous than ever because of the fertilizing ash.

Is *Vaccinium corymbosum* a species? Certainly it is not the tidy sort of species with which the taxonomist likes to deal. The biosystematist, however, sees it as an interbreeding population having a common background, its extreme variability being only what he would expect from its ancestry and the history of its development. Until someone invents a better term within the confines of the binomial system, the biosystematist will continue calling it a species. It is only one of the many different kinds of populations with which he has to deal under this systematic category.

HOW DO VIOLETS REACT TO CHANGES IN THE ENVIRONMENT?

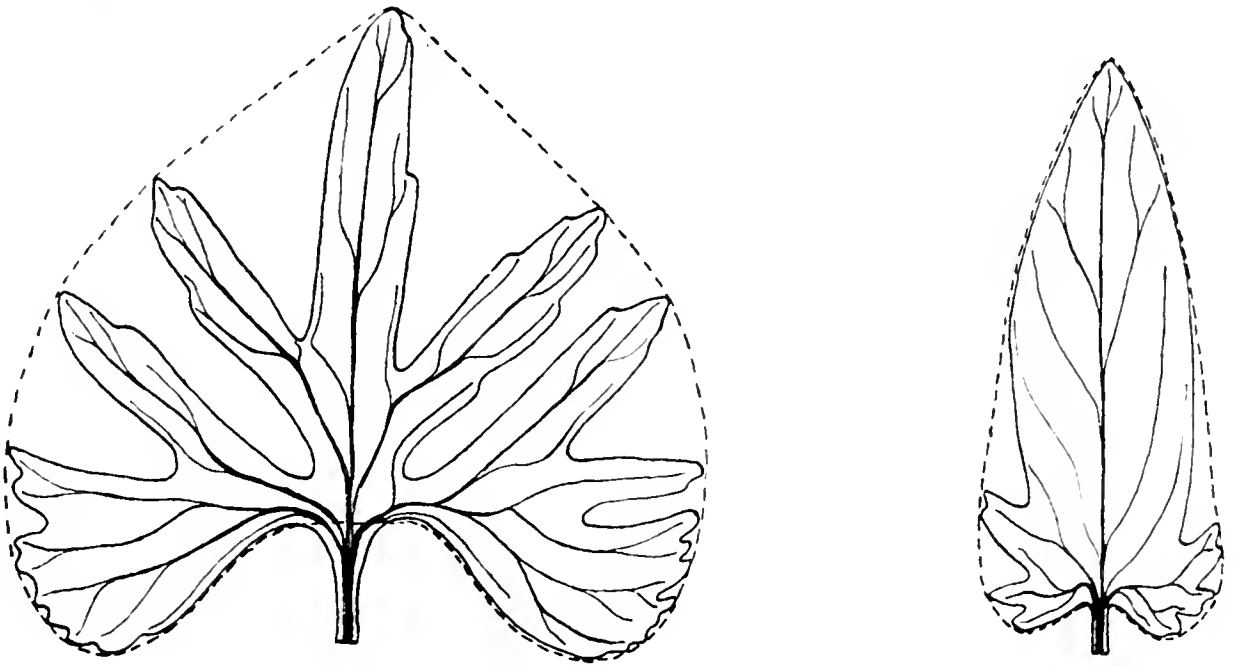
In the previous sections of this discussion we have seen how various of the underlying forces of evolution have reacted in the production of variant and often new kinds of populations over large areas and through relatively long periods of time. The question immediately arises whether the biosystematist is able to detect evolution actually taking place in wild populations, or is he limited by his methodologies and observations to the postulation that evolution has taken place in the past and, therefore, that it *should* be a continuous process. In brief, can he *see* evolution taking place to-day, or must he only *assume* that it is. Obviously, long-term perennials such as forest trees are not the most ideal material for study, for the turn-over in individuals in the population is far too slow. Therefore, we have chosen a group of violets for this phase of our work.

Of the fifty-odd species of *Viola* recognized as occurring in the north-eastern United States, about half belong to that group known as the "stemless (or acaulescent) blue" violets (which only sporadically have recessively mutant white flowered forms). A fair number of these occur in Connecticut. The term "stemless" is applied to the group because, characteristically, the rhizome is very short and often erect, neither producing runners or stolons, nor the elongated branches of some of our violets, which may sprawl or clamber to almost a half metre during a single season. As may be seen in the figures which follow, the leaves of the various sorts of "stemless blues" are exceedingly different in general outline and also in the amount of marginal lobing; they also differ in their pubescence. "Good" differential characters also are to be found among the flowers and fruits. (See Gleason, 1952.) However, so as not to encumber the text, I am limiting our discussion to leaf shape.

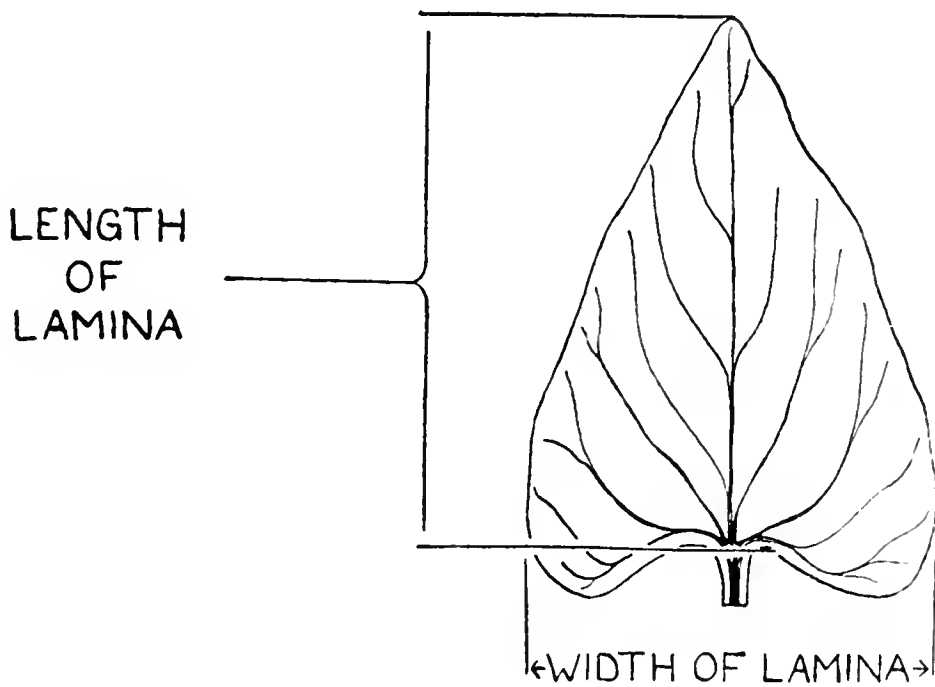
The acaulescent blue violets comprise a group of polyploids, having been compounded out of forms with 12, 20 and 22 chromosomes. Tests indicate that these 54-chromosome materials are amply interfertile; only rarely does an individual lack almost complete compatibility with others of the group, so that many so-called "hybrids" have been described. Biomechanically, this group of complex polyploids has an interesting breeding pattern. For a brief time during the early spring they produce open flowers, easily pollinated by insects; soon only cleistogamic flowers are formed and these are produced during the rest of the growing period. Photoperiodicity is the controlling mechanism. Under glass in midwinter one can induce either open flowers for use in controlled crossings or a large amount of obligately selfed seed from the cleistogamic flowers merely by shifting the points on the time clock controlling a few electric lights hung over the plants.

Although classed as perennials, the individual plants often are not so long-lived as one might suspect. Individual plants moved into outside garden plots have the disconcerting habit, in a few seasons, of leaving one only with a label stuck into the ground, and this surrounded by a lusty colony of obvious seedlings. Or, in too many instances, the seeds germinate but the seedlings refuse to grow, for the plants appear to be exceedingly sensitive to minor differences in habitat. This genetically controlled sensitivity of the various plant types is the basis of the situation which one discovers in nature.

Thus, within a fairly narrow compass one can often find a considerable variety of plant types, as where shrubs and trees cast a variant pattern and depth of shade, or where this difference in pattern, or a minor change in slope and exposure to the sun's rays, results in small differences in moisture near the soil surface, or where grasses and weeds have come in and induced small changes in available moisture or sunlight. Thus, beginning with the brief period of open pollination in the early spring, there is ample opportunity for insects to make crossings between very diverse plants. The catapult-like mechanism of the bursting fruits then



METHOD OF ASCERTAINING OUTLINE AREA/REAL AREA
RATIO OF LOBED LEAVES



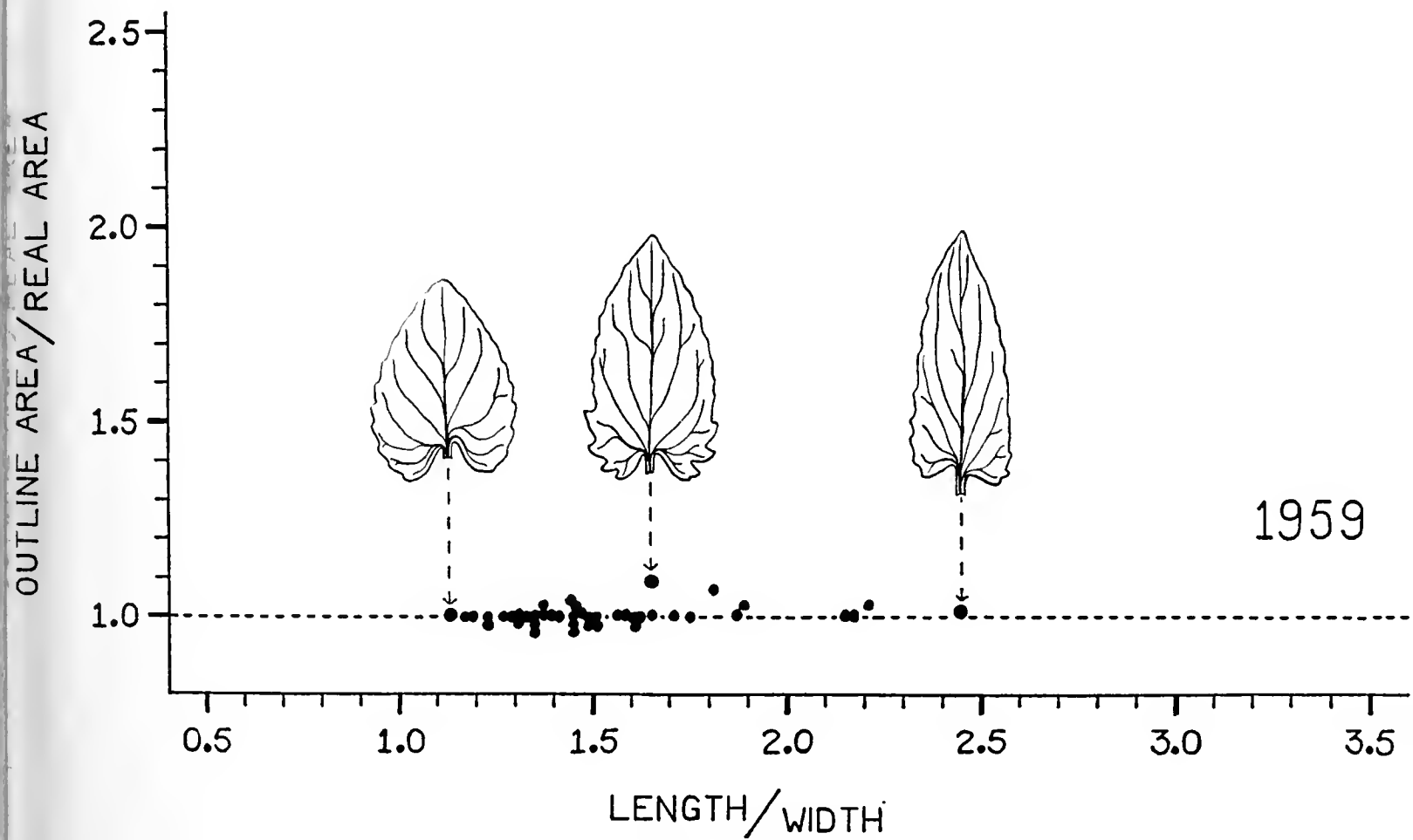
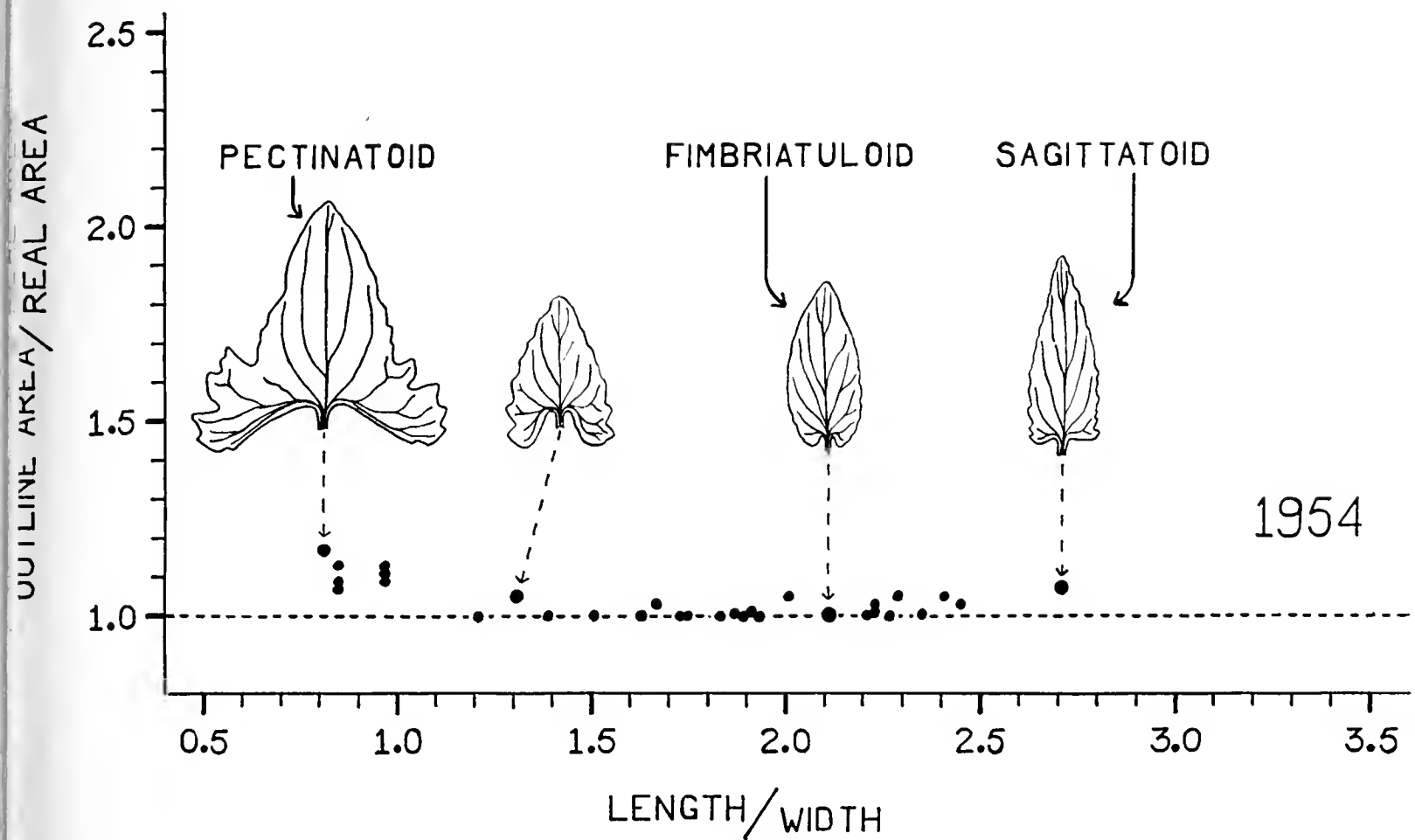
METHOD OF ASCERTAINING LENGTH/WIDTH
RATIO OF LAMINA

Fig. 3. Methods determining leaf shape in *Viola*.

scatters the seed from these crossings over a considerable area; some of the consequent seedlings persist and some do not, depending on the precise nature of the microhabitat in which the seed germinated. If genetically attuned to a particular spot the plants soon mature and, themselves, are capable of cross pollination. But it must be remembered that the open flowers are few in comparison with the many cleistogamic self-pollinated flowers produced by the plants. Therefore, following a primary hybridization, the successful of the hybrid offspring are capable of producing a great abundance of selfed seed, leading to a wide series of potentially highly variant forms possessing, according to normal Mendelian mechanics, new combinations of characters not found in either of the parental types. And these seeds are scattered widely in the area, and so further complicate the pattern of variation. Let us now turn to several examples.

First, however, it might be of interest to know how we are going about our problem. In these studies, instead of the usual randomized samplings, definite colonies are selected and representative leaf, flower or fruit samples made from each plant so that we have a record of every plant in each colony at the time of sampling. These are pressed and filed on appropriate cards with complete data. The leaves then are measured and the pubescence counted from predetermined standard areas in the usual manner under the microscope. The flowers and fruits present other problems; since we will not be dealing with them, these items will here be omitted. In fact, the pubescence counts, important as they are, also will be omitted for to include this item with the leaf measurements would greatly encumber the following charts and lead to no conclusion that cannot be obtained from leaf shape alone.

Figure 3 indicates how the leaves are measured. If lobed, a line is drawn around the leaf connecting the apices of the various lobes, resulting in something very much like the traditional shape of various of the unlobed sorts. This *outline area* is then measured by means of a planimeter. Then, by following around the convolutions of the lobings, the *real area* of the leaf also is arrived at by the planimeter. From these two figures then can be calculated the ratio of the outline area to the real area, resulting in a figure larger than unity. Obviously, the unlobed leaves have a ratio of 1. Because many of the leaves are basally auricled, or have backwardly flaring lobes, the length of the lamina is taken to be the measurement from the base of the petiolar sinus to the apex of the leaf; the width measurement is taken at the widest part, whether basally or farther up the blade. From these latter two measurements then are calculated the length/width ratio. With the two ratios at hand, a representative leaf from each plant can then be plotted by means of a single point on a two-way graph. Where the non-lobed forms are abundant in a colony, so that representative dots began to pile up on the unity line, the dots are extended below the line in their proper places in relation to their length/width ratios.



PACHAUG FOREST ~ WOODLAND TRAIL

Fig. 4. Selective modification of leaf shape in a small colony of violets within five years, following increase in shade.

The violets of a woodland trail in the Pachaug State Forest

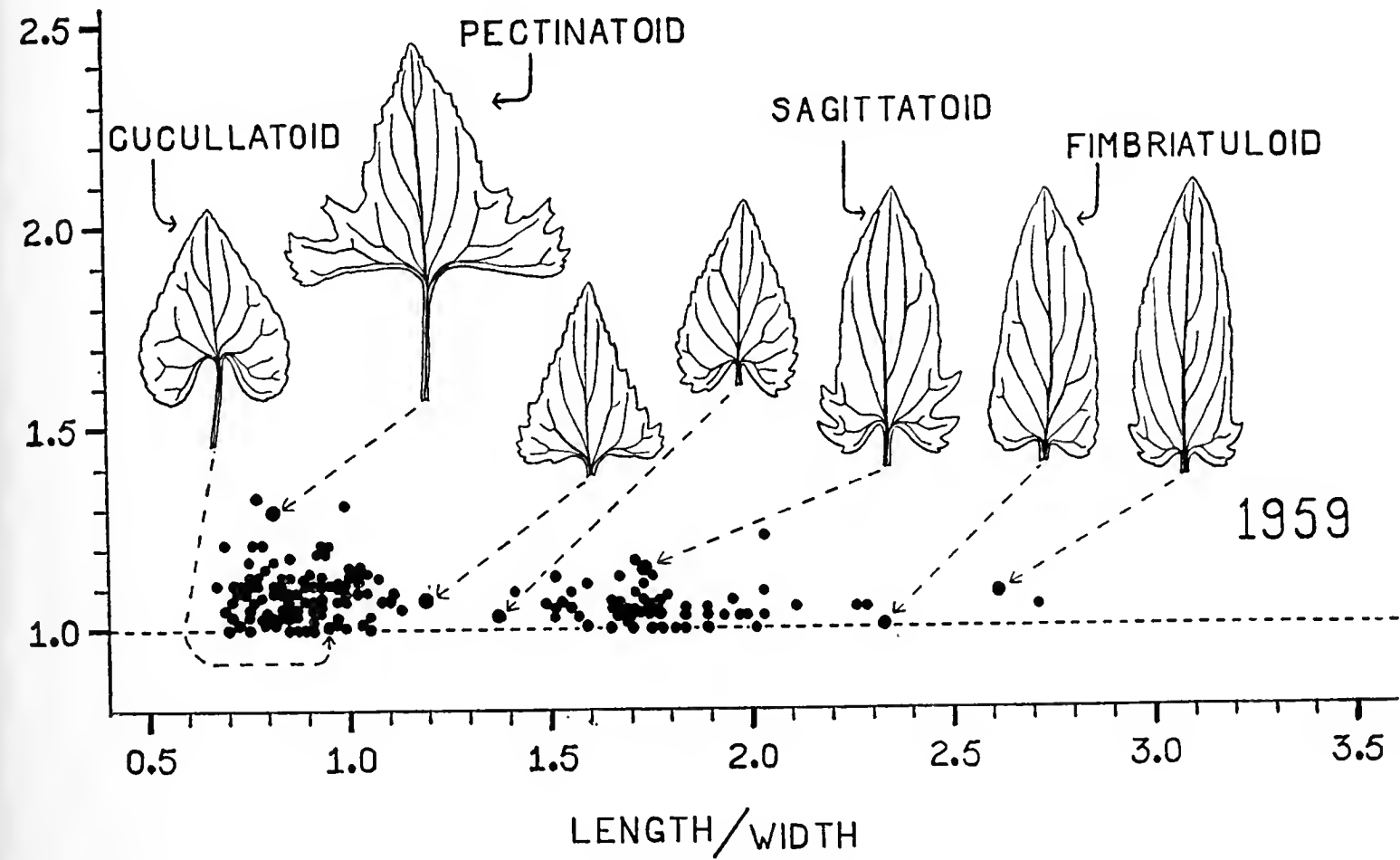
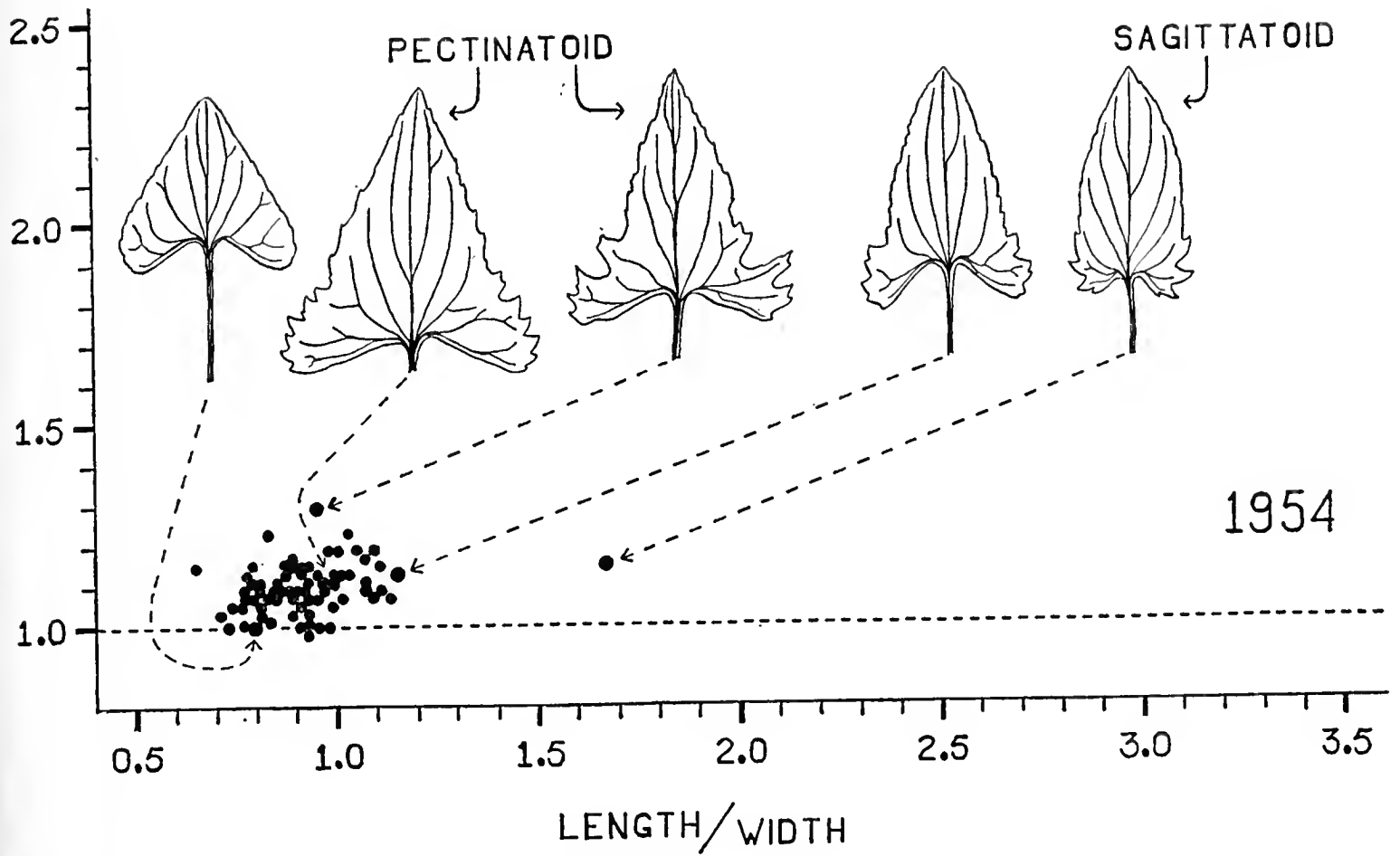
Figure 4 indicates what happened in a small colony in a five year period along a woodland trail in the Pachaug State Forest Preserve. For further aid in this and subsequent charts, selected leaf forms also are included on the graphs to assist with visualizing the type of individuals of which the colonies are composed. In 1954 the colony varied from broad leafed forms to those which were rather narrow. The almost continuous nature of the variation from plant to plant may easily be seen from the chart. It also should be noted that here, and on the subsequent charts, legitimate specific names have not been used. For example, the leaves of *Viola fimbriatula* typically are heavily pilose, while those of *V. sagittata* are essentially glabrous. Other colonies examined involving only these two kinds indicate that genetic recombinations often have placed the pilosity of *V. fimbriatula* on leaves with the basal lobings of *V. sagittata*, and vice versa, together with all the intermediate combinations one might expect in a multifactorial, polyploid hybrid complex. The names placed on the charts, therefore, indicate only the shapes; thus, the word "fimbriatuloid" means only that a particular leaf has a shape comparable to that of typical *V. fimbriatula*, and so on through this and the other charts.

By the current season, or 1959, this particular colony has become greatly modified. In five years the trees had so overgrown the trail that the shade and sun pattern had sufficiently changed so as to eliminate the broadest forms yet, as a whole, the colony had segregated a new series of forms very different from the original plants and tending towards the broad type of leaf, but without the wide basal and more sharply defined marginal lobings. The bulk of the colony now resembles nothing as yet taxonomically recognized in the genus, yet it is highly reproductive and successful under the new set of environmental conditions.

Plants of a picnic area in the Pachaug State Forest

The area represented in Figure 5 seems almost to have been made to order for this type of study, for these violets are weedy things and stand a considerable amount of abuse. Some years ago the authorities of the Pachaug State Forest opened up what they thought would be a good picnic area, putting in permanent tables and fireplaces. But the spot never has been popular for it lies between several extensive White Cedar (*Chamaecyparis thuyoides*) bogs, the breeding places of myriads of hungry mosquitoes, so that picnic parties soon leave for other areas, often not even bothering to unload their lunches.

In 1954, when newly cleared and while still sunny, the area was dominated by a group of wide leafed "pectinatoid" forms; even the marginally unlobed forms had something of the deltoid shape of this type. Only a single "sagittatoid" plant was present.



PACHAUG FOREST~PICNIC AREA

fig. 5. Modification of leaf shapes in a colony of violets in five years following the migration of several additional forms into the area.

By 1959 the overhanging trees had spread their branches considerably. Also, being unpopular as a picnic site, the Forest authorities have not done much to keep the invading shrubs under control so that these also produce considerably more shade than previously. During the interval of five years some "cucullatoid" forms entered the area, or perhaps had segregated out of the original "pectinatoid" materials. The more shade tolerant "fimbriatuloid" and "saggitatoid" forms soon began invading the area and, as will be noted by the chart, already have begun to join genetic forces with the still-dominant "pectinatoid" material, forming a genetic bridge between the narrow and wide leafed forms. Remembering our experience of what happened to the previous colony along a woodland trail, you will understand our interest in seeing what modifications another five years will bring to this particular colony. No matter what happens, it will not remain the same, so dynamic is the evolution among these violets, so closely do they adjust themselves to minor changes in the environment.

The violets of the Bluffhead fire tower trail

The State of Connecticut, although heavily industrialized, has about half of its area now covered by forest in various stages of reproduction; much of this forest has reverted from abandoned farmland, now too stony and sterile to be productive. Some years ago the State Department of Forests built a fire watch tower on a rocky promontory called Bluffhead, maintaining a trail for the use of the forest wardens going to the tower. This trail later was widened, regraded, and made usable for vehicles. This entailed clearing away the brush and some of the trees, so that the trail, converted to a woods-road, was opened to considerable sunlight. Because of its steepness and consequent washing in heavy rains, periodical regrading was necessary, resulting in disturbance of the habitat.

Figure 6, left graph, indicates the type of violet population which occupied this periodically disturbed and sunny woods-road in 1954. A shady area near a brook supported a small colony of "cucullatoid" forms, the remainder of the colony along the woods-road consisted of all possible genic combinations between the somewhat lobed and pubescent *Viola palmata* and the more deeply lobed and glabrous *V. brittoniana*, which is not supposed to occur in the area, being a plant of the coastal sandy areas. (In early post-Pleistocene time, the waters of the Atlantic stood not far from the base of what now is Bluffhead; to-day they are miles away. But lest we get into an argument with our taxonomic friends, we will speak of these narrow-segmented, glabrous materials on Bluffhead only as "brittonianoid" forms.) In 1954, only a few plants bridged the genetic gap between the "palmatoid" and "cucullatoid forms.

At about that time the State of Connecticut changed from tower watching to aeroplane patrol, a more efficient and rapid

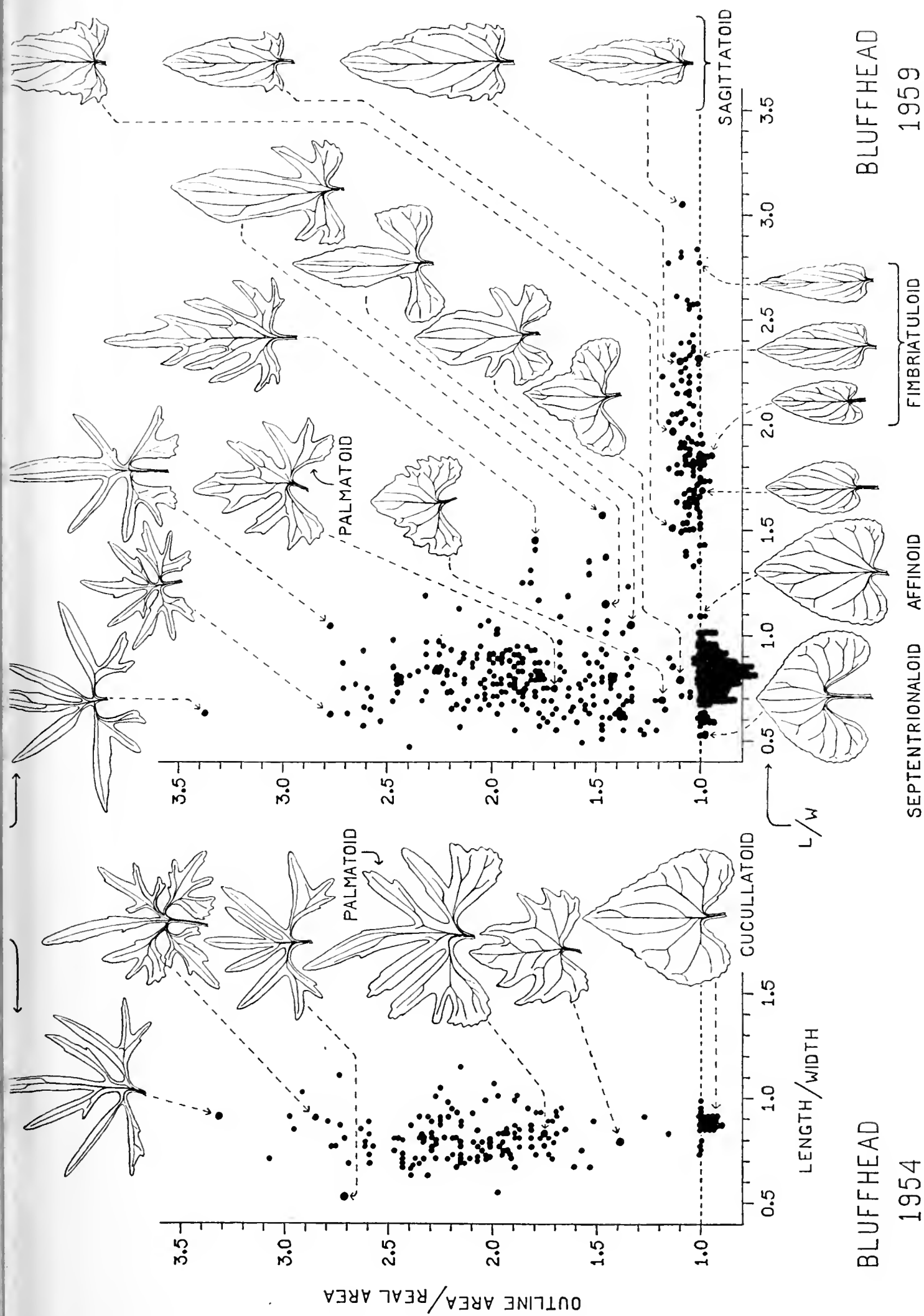


Fig. 6. The various leaf forms of violets along a disturbed woods-road, and the modification of the colony after the road was abandoned for five years, leading to the migration of more shade tolerant species into the area and the production of numerous intermediate fertile forms.

means of forest fire detection. Consequently, the fire tower on Bluffhead was dismantled and removed. With no further reason for maintenance of the woods-road it was abandoned. Already the trees are overgrowing the trail and the shrubs again moving on to its margin, so that the conditions of sunlight and moisture are beginning to be somewhat different.

Converging on to the original road is a series of abandoned and shady trails, marking the access roads of a former cycle of lumbering operations, these so shady that, search as we would in 1954, no forms save a scattering of the narrow leafed "fimbriatuloid" and "saggitatoid" forms could be found. Since 1954, these forms have been migrating out of these side trails and on to the main trail where conditions are becoming suitable to them. The basally broadly auriculate "septentrionaloid" forms are appearing where only the "cucullatoid" forms were present before. And, as the chart indicates, a wide variety of unnamed and unnameable forms are beginning to appear in the total population.

What the future of the population along this trail will be time only will reveal. This much is certain. The violets of Bluffhead never have heard about the neatly compartmented species of the taxonomist. Instead, they are working out their destiny in the only way they can, by a continuous and vigorous genetic adjustment to the demands of a constantly changing environment. This is the story of evolution as it is proceeding to-day among the violets, and as it will continue to proceed so long as they exist on the face of the Earth.

I have no profound conclusions to make at the end of these remarks, for there is no conclusion to evolution. It is a continuous process spanning the whole of the space-time continuum, a process so vast and genetically so complex as almost to defy the mind of man, and yet one so simple that it easily may be grasped if we but pause in our mad rush to nowhere in particular and carefully examine a single colony of violets growing along a woodland trail. It now is a century since Charles Darwin did much the same sort of thing, arriving at much the same sort of conclusion:—That groups of organisms have evolved and are evolving, each in its own genetically peculiar manner, being guided by the selective forces of a continually changing environment.

Perhaps, in these latter days, a century after Darwin, we may say that evolution is not necessarily the production of new species. Perhaps it is the genetic ability of organisms to fill up the multitudinous sorts of new habitats ever being presented by a constantly changing environment. Perhaps evolution is the perpetuation of a continually changing and modified genetic reticulum within the time-space continuum and that the species, so cherished by us taxonomists, are only ephemeral nodes in this genetic reticulum. Often, in the quiet of my study, I feel that

this is what Darwin meant when, so astutely, he anticipated what only recently we have discovered regarding the manner in which natural populations react to the manifold changes in the environment.

ACKNOWLEDGMENTS

The writer wishes to thank various agencies of the U.S. Government for permission to make use of the various records pertinent to his studies on *Cinchona*. As a matter of record it is to be noted that representative bark samples and complete files of the laboratory analyses of both field samples and commercial lots of bark collected from wild stands in South America and handled by representatives of the Board of Economic Warfare, the Office of Economic Warfare, the Foreign Economic Administration and the U.S. Commercial Company during World War II, together with the complete files of the field reports of the various exploring parties, recently have been placed on permanent loan in the Department of Pharmacognosy of the College of Pharmacy, the University of Connecticut.

Thanks also are due Dr. Geo. M. Darrow and his former associates in the Bureau of Plant Industry, the U.S. Department of Agriculture, Beltsville, Md., for making a large series of special test crossings between individuals of different species of *Vaccinium* at my personal request, and also for permitting me to examine large amounts of basic genetic data (most of it never published) from breeding and progeny test plots accumulated during a period of intense activity in the production of new horticultural forms of blueberries, using plants from the wild as sources of breeding material.

Special recognition should be given my colleague, Miss Mary M. Hubbard, for her willingness to keep the accumulating data on *Viola* populations organized; during the summer of 1959 we were assisted by Mr. Lee Warner, whose work was supported by a special grant from the National Science Foundation. Miss Hubbard also made the *Viola* charts.

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Dr. S. M. WALTERS disagreed with Professor Camp and said that the experimental taxonomist cannot divest himself of all concepts of

orthodox taxonomy for Professor Camp himself goes into the field armed with orthodox taxonomy in saying that he is interested in violets.

Professor CAMP agreed, and pointed out that he had rejected the traditional views of taxonomists in order to arrive, without prejudice, at an understanding of the situation in *Vaccinium*. He had worked from a concept of a major group to those of minor groups; he had not commenced with species in mind although he had arrived at entities which could be described as such. He found that his present research students rejected species but he expected that in ten years time they would return to binomials.

Professor I. MANTON wondered whether violets will always evolve as Professor Camp had concluded? Surely, as the size of populations decreases biotypes become limited and the species may not subsequently be able to readapt or readjust itself and recolonise the surrounding habitats. The end of the natural life of a population is when it cannot readjust itself to changing conditions.

Professor CAMP said that the violets are now in an explosive phase in their evolution and that in any case relics are not deficient in biotypes. He pointed out that many epibiotic species showed remarkable genetic variability, for example *Sequoia gigantea* in which seedlings of seventy-three biotypes have been recognised in England. The environment limits the survival of these by selection in the plants' native stations in California, but in cultivation the careful gardener preserves all of them. Similarly the taxonomist unwittingly thwarts himself if he rejects the dillings and runts in a box of seedlings! These may be among the more important plants he should study.

Mr. J. E. DANDY remarked that the tearing up of the descriptions of twenty-five new species was good advice which others would do well to follow!

EVOLUTION IN THE GENUS PRIMULA

D. H. VALENTINE (The Durham Colleges, University of Durham)

In the first edition of the *Origin of Species*, Darwin discussed the differences between the primrose and the cowslip, and decided that although they were generally very distinct in morphology and habitat, they appeared to be linked by numerous intermediates, and hence should be classified as varieties of the same species. Later (1868) he investigated the point more carefully; he made many experiments in which the primrose and the cowslip were crossed reciprocally and were also crossed with the 'common Oxlip', a group which appeared to consist of natural primrose-cowslip hybrids. He concluded that this latter group was, in fact, composed of first or second generation hybrids which were more or less sterile; and these facts, taken together with the other data, were sufficient to convince him that his former decision must be reversed and that the primrose (*P. vulgaris*) and the cowslip (*P. veris*) must be given specific rank. This paper of Darwin's is of special interest as one of the earliest contributions, if not the first, to what is known to-day as experimental taxonomy.

Since Darwin's time, there have been several studies of the group of Primulas to which these species belong, known now as the section Vernales; and it is perhaps appropriate that at this centenary meeting, one of the papers should be devoted largely to this group. It will not be possible, in the time available, to treat it at all exhaustively. Thus, no attempt will be made to describe any of the work (e.g., Clifford, 1958) on hybridization and introgression in natural populations; and the interesting problems of heterostyly and homostyly, also studied by Darwin, will be omitted. What will be done is to give some idea of variation in the group, and to discuss some of the phylogenetic questions which arise. The paper will conclude with a few general comments on the genus as a whole.

Because of insufficient knowledge, it is not possible at present to say with certainty how many species there are in the Vernales, though the number is probably between 10 and 15. In this paper, we shall be concerned with nine taxa; their names and geographical distributions are given in Table 1; and all of them have been grown in cultivation at Durham. *P. veris*, *P. vulgaris* and *P. elatior*, as defined for example by Wright Smith and Fletcher (1947), are large polytypic complexes with numerous subspecies. Only one of the four main subspecies of *P. veris* is included here, and only one of the three main subspecies of *P. vulgaris*, as sufficient living material of the others has still to be examined

TABLE 1

(1) <i>P. veris</i> L. subsp. <i>veris</i>	N. Europe, from Britain to the Urals.
(2) <i>P. vulgaris</i> Huds. subsp. <i>vulgaris</i>	W. and S. Europe.
(3) <i>P. elatior</i> (L.) Hill subsp. <i>elatior</i>	N.W. and C. Europe.
(4) <i>P. intricata</i> Godr. et Gren.	Pyrenees, S. Alps, N. Balkans.
(5) <i>P. pallasii</i> Lehm.	Turkey, Caucasus, Urals, Altai.
(6) <i>P. amoena</i> M. Bieb.	Caucasus, Turkey.
(7) <i>P. megaseaefolia</i> Boiss.	W. Transcaucasia, N.E. Turkey.
(8) <i>P. juliae</i> Kusn.	E. Transcaucasia, Dagestan.
(9) <i>P. lofthousei</i> Harr.	S. Spain.

Of the eight or nine subspecies of *P. elatior*, three are included here as species (*intricata*, *pallasii* and *lofthousei*), though their status is controversial; the remainder are not as yet available.

The differences between these nine taxa will be described below; but it may be said at once that they represent very adequately the range of form in the Section, and also the range of distributional types. The variation in geographical range, from what may be called "wides", such as *P. veris*, to endemics, such as *P. juliae* and *P. lofthousei*, is characteristic of groups of allied species such as are found in sections or genera; in larger groups, as was clearly demonstrated by Willis (1922), the proportion of endemics is commonly much greater than it is here. If we regard number of individuals and extent of geographical area covered as criteria of success, then it may be said that in a group such as a section or a genus, there are generally many unsuccessful species and a few which are very successful. The most obvious interpretation of these facts is that the most successful species are those which, both in the past and up to the present, have best been able to adapt themselves to their environments. We should then expect that, at any one time, comparatively few species would be both fit enough in themselves, and fortunate enough in the environments they happened to be in, to achieve great success; and that most species, either because of lack of innate fitness, or because of an unfavourable environment, would be comparatively unsuccessful. This interpretation is more comprehensive, and, we think, more convincing, than the alternative and anti-selectionist theory of *Age and Area* of Willis (1922). However, to demonstrate the differences in fitness in present, let alone past environments, between successful and unsuccessful species is a difficult task. Doubtless some of the difficulties will become apparent in the account which follows.

The criteria on which taxonomic groups such as genera and sections are based are generally those of morphological resemblance. We shall consider the morphological characters in some detail: but it may be stated that not all systematists have

been in agreement as to the exact limits of the Vernales. Thus, while Wright Smith and Fletcher (1947), following Bruun (1932), place all the taxa of Table 1 in a single section, the Vernales Pax, Fedorov (1952) puts them into three different sections, viz., Julia Fed. et A. Los., Carolinella (Hemsl.) Pax and Euprimula Schott. The criterion which we regard as decisive comes from hybridization experiments. Such experiments, carried out over a period of many years, have shown that all the nine taxa listed in Table 1 can be connected, directly or indirectly, by viable hybrids. The results to date are summarised in Fig. 1, which is a crossing

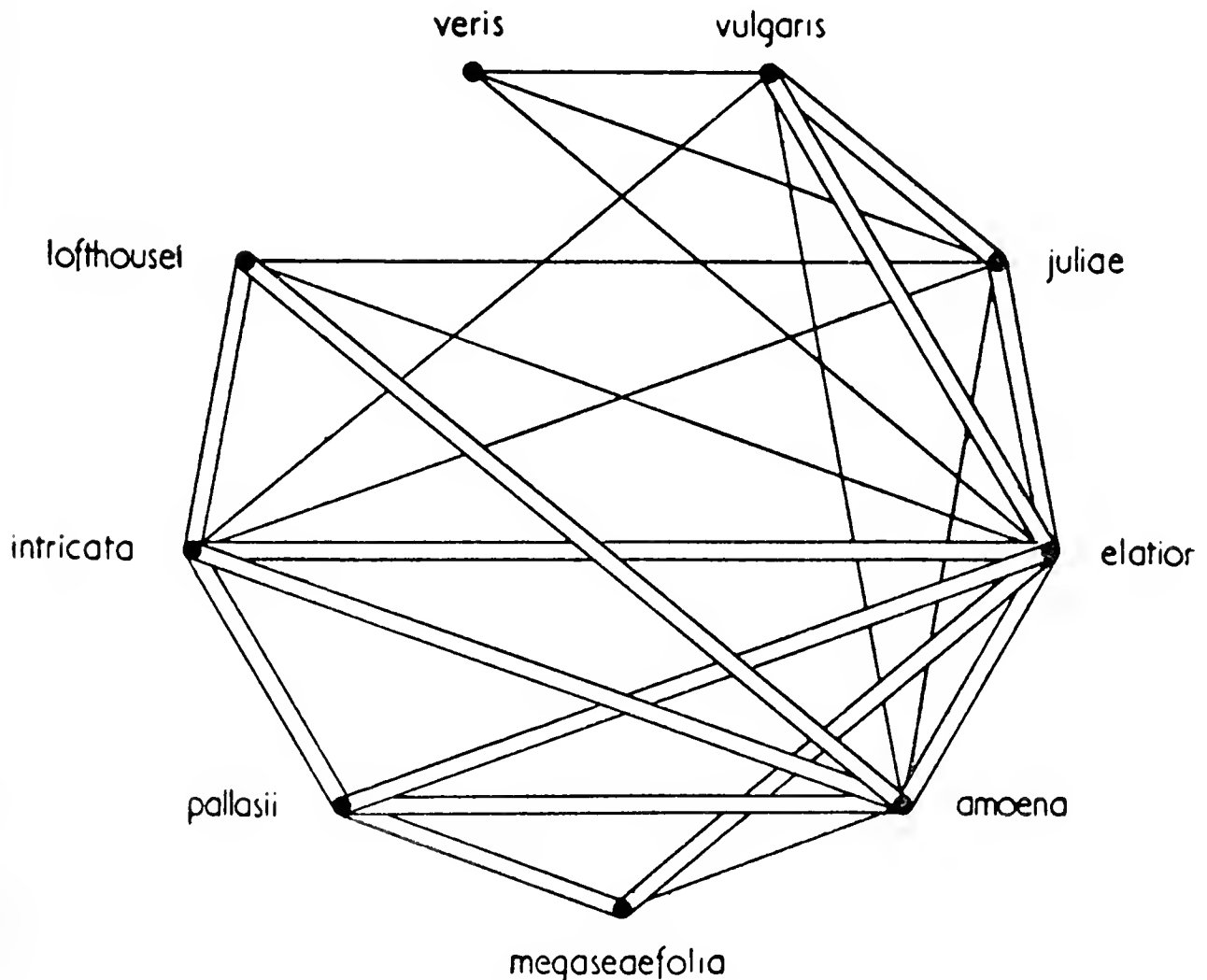


Fig. 1. Crossing polygon for 9 taxa of the Vernales.

polygon. Some of the gaps in the polygon, e.g., that between *P. veris* and *P. lofthousei* mean that repeated experiments have failed to produce hybrids; others, such as that between *P. intricata* and *P. megaseaeifolia*, mean that it has not yet been possible, because of practical difficulties, to attempt the cross.

The fact that viable hybrids can be produced in this way may be taken as evidence that the plants concerned are phylogenetically rather closely related. Further, none of these species is known at present to form hybrids with any species of *Primula* from any of the other sections of the genus. The facts that all the species also have the same chromosome number ($2n=22$) and a similar chromosome morphology [Bruun, 1932], and that the hybrids all show fairly good pairing at meiosis and are at least

partially fertile, are evidence in favour of the closeness of the relationship. Figures for pollen fertility for the hybrids of *P. elatior* with the other 8 species range from 43% for the *P. elatior-veris* hybrids to 84% for the *P. elatior-juliae* hybrids. Some data for meiotic pairing are given below in Table 4.

To indicate clearly and concisely how the species differ from one another is by no means easy; and this difficulty is one which has often caused confusion in discussions of evolution. It is perhaps worth saying here that a good knowledge of the range of form of a group of organisms, such as is obtained, for example, in a monograph or a revision, is essential to an appreciation of the problems of evolution. Darwin realised this; and he spent no less than eight years (1846-1854) on a monographic study of the Cirripedia (the barnacles), the results of which were eventually published. Later, in writing his autobiography, he doubted whether the work was worth so much consumption of time, but according to Hooker (F. Darwin, 1887) he alluded to it at the time as a valued discipline; and there can be little doubt that it had an important influence on his scientific thinking.

It should also be realised that the converse is true; and that a knowledge of modern evolutionary theory is essential to a proper appreciation of systematics. Systematics, of course, provides an indispensable basis for research in many fields; but if it is to be more than a mere tool and is to make its full contribution to the biological sciences, it needs to be integrated with its evolutionary background.

It is possible, in the limited time available, to describe here only certain characters of the Vernales. Some of these are illustrated in Figs. 2, 3, 4, 5.

- (i) *Leaf-shape* (Fig. 2). The leaves of all the species are rugose (except *megaseaefolia*) and more or less hairy (except *juliae*). At one extreme are the petiolate and cordate leaves of *megaseaefolia* and *juliae*, at the other the spatulate leaves of *vulgaris* and *intricata*, in which there is no distinct petiole; species such as *elatior* and *amoena* are intermediate.
- (ii) *Flower-size* (Fig. 3). Here there is a clear gradation from *vulgaris* and *juliae*, which have the largest flowers, to *lofthousei* and *veris*, which have the smallest.
- (iii) *Flower-colour*. Two main groups can be distinguished. The corolla of *juliae*, *amoena* and *megaseaefolia* always has anthocyanin, the flowers being pink, purple or blue. The corollas of the remaining species, except *vulgaris*, normally lack anthocyanin, and are yellow. In *P. vulgaris* agg., the subspecies differ in flower colour; the corolla may be yellow, white, pink or purple.
- (iv) *Calyx teeth* (Fig. 4). There is a fairly well-marked gradation from *veris*, in which the calyx teeth are as broad or rather broader than long, to *vulgaris*, in which the teeth are much longer than broad.

PLATE II.

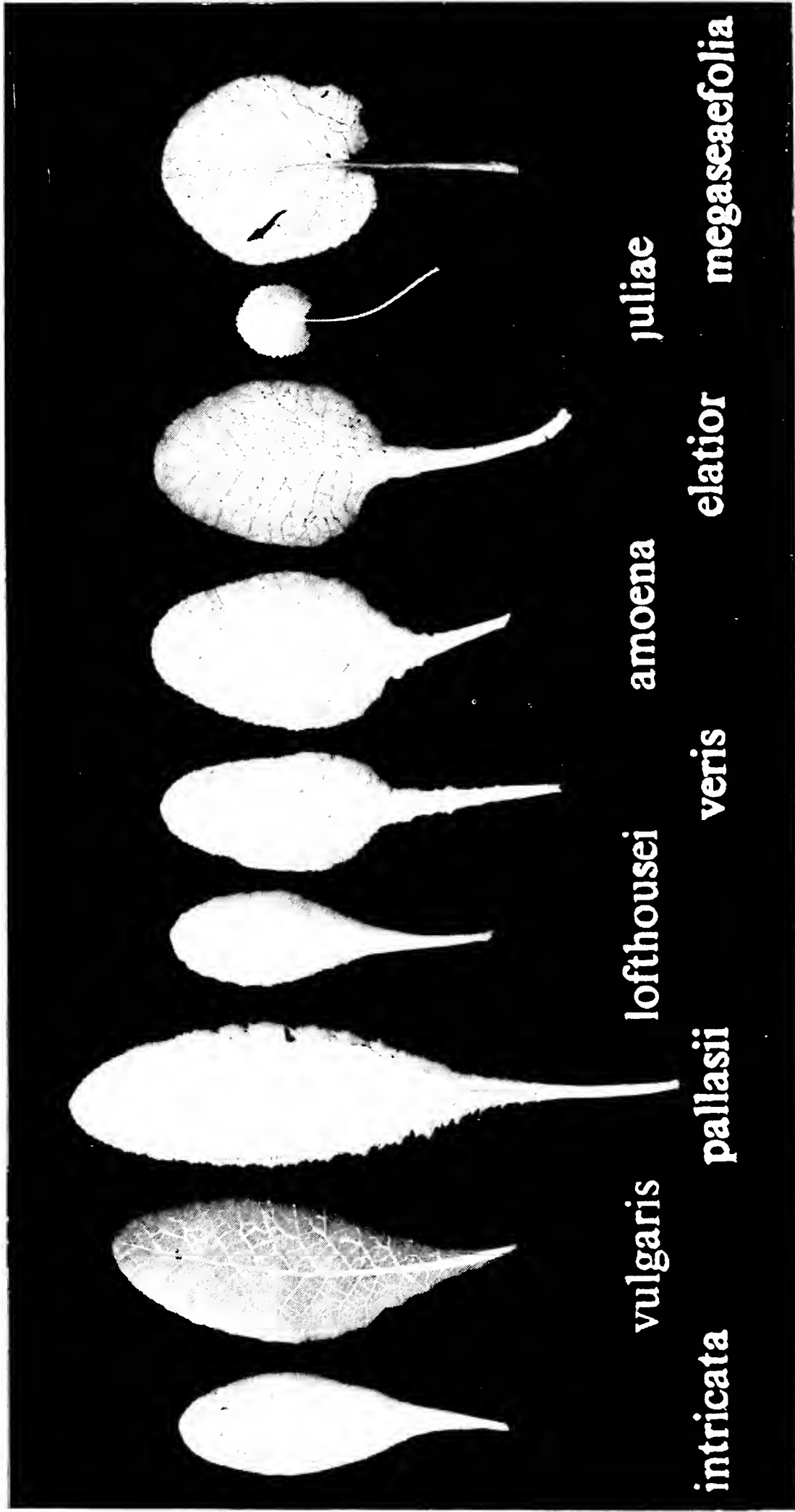


Fig. 2. Leaf-shape in the *Veris*. (Length of *P. veris* leaf = 14 cms.)

PLATE III.

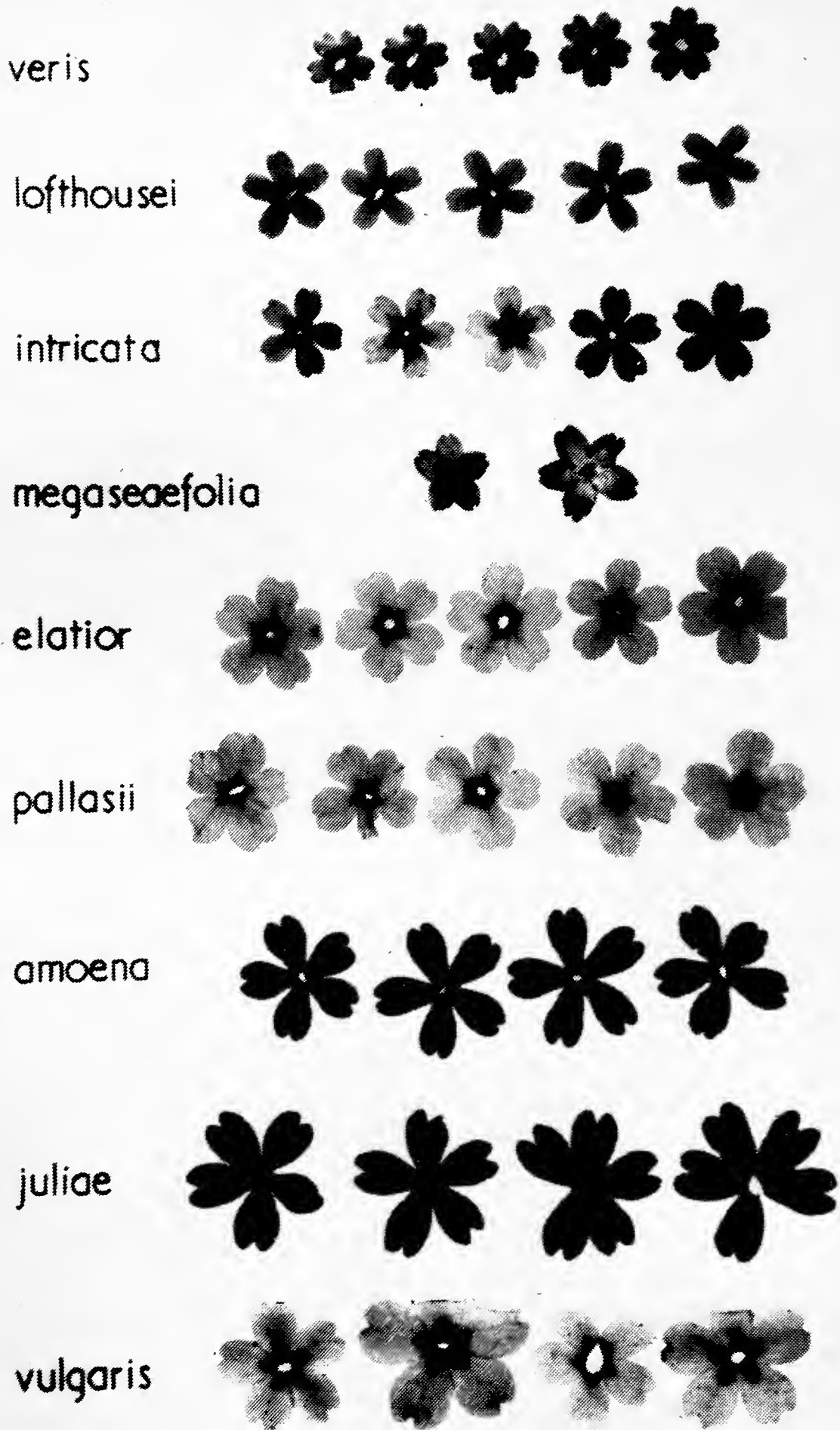


Fig. 3. Corolla diameter in the Vernales.
(Mean diameter of *P. veris* corolla = 14 mm.)

PLATE IV.



Fig. 4. Calyces of the Vernaes. (Mean length of *P. veris* calyx = 12 mm.)

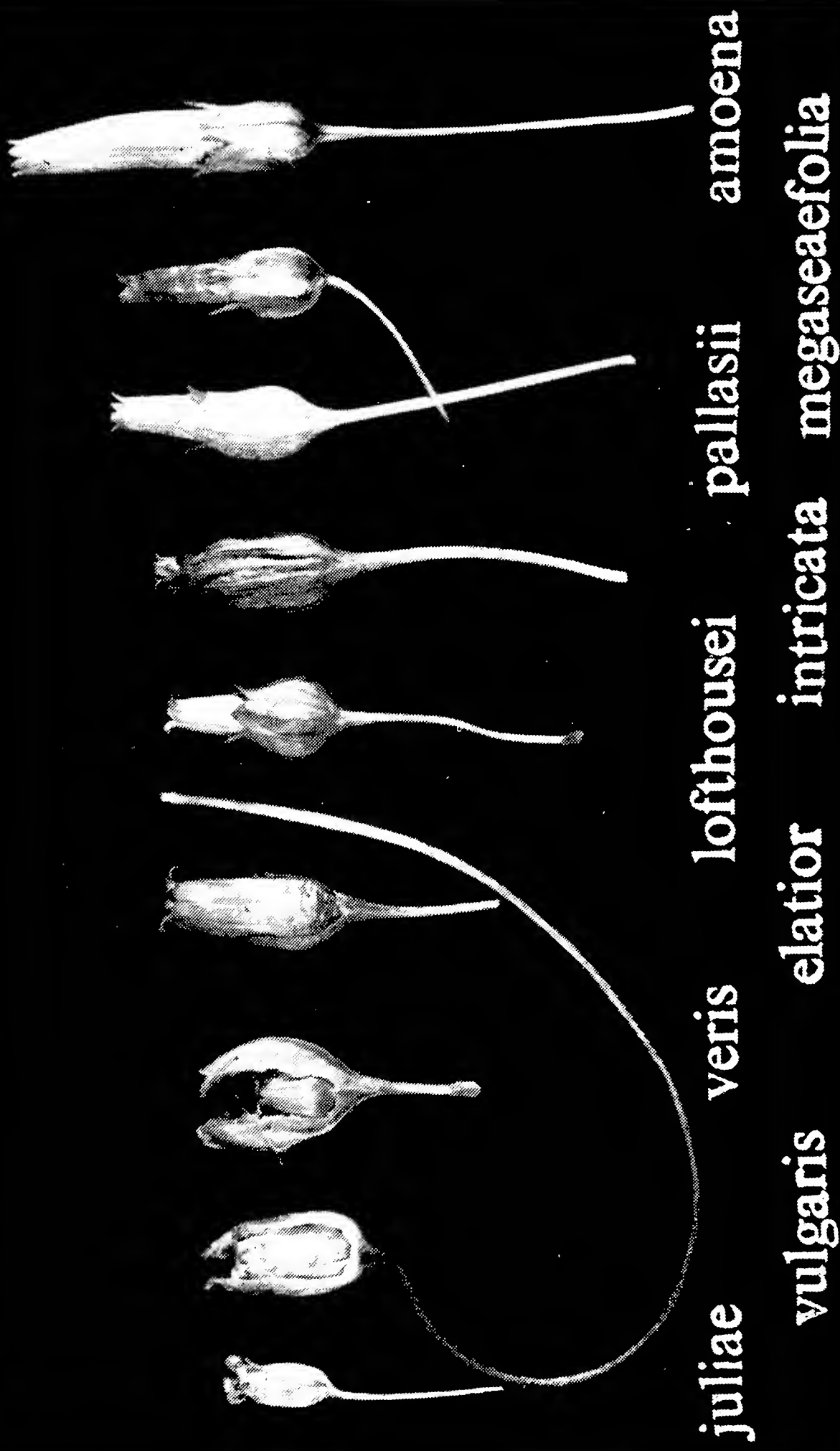


Fig. 5. Capsules of the Vernalis. (Length of *P. amoena* capsule = 27 mm.)
Note the very long stalk of the *P. vulgaris* capsule

- (v) *Capsule length* (Fig. 5). Here one extreme is represented by *amoena*, in which the capsule is extremely long, and the other by *juliae*. The capsule exceeds the calyx in length in all the species except *vulgaris* and *veris*. The fruit-stalk is short in all the species except *vulgaris*.
- (vi) *Inflorescence*. This is pedunculate and umbellate in all species except *vulgaris* and *juliae*, in which the peduncle is lacking, and the flowers arise from the rosette at ground level.
- (vii) *Posture of capsule*. In six species the ripe capsule is erect at maturity; in three (*vulgaris*, *juliae* and *megaseaefolia*) the capsule at maturity is borne more or less horizontally, and in *vulgaris* the seeds are sticky and ant-dispersed.

These characters are summarised in Table 2; quantitative data are not given, but the species are arranged for each character, in order of size. Although by no means all the characters are included in this Table, it does, together with the illustrations, show reasonably well the differences between the species. Thus it indicates the general resemblance between *P. intricata* and *P. lofthousei*; it shows too the numerous resemblances between *P. vulgaris* and *juliae*, which, however, differ so very markedly in leaf-shape.

TABLE 2

Species arranged in order of:—

Corolla diameter (largest first)	1	2	3	4	5	6	7	8	9
Length: breadth of calyx tooth (longest first)	1	6	2	4	3	8	7	5	9
Capsule length (shortest first)	2	1	9	5	8	7	4	6	3
Petiolation of leaf (least petio- late first)	7	1	4	8	9	3	5	2	6
Flower colour	2 3 6 anthocyanin			1 4 5 7 8 9 no anthocyanin					
Posture of capsule	1 2 6 decumbent			3 4 5 7 8 9 erect					
Peduncle	1 2 absent		3 4		5 6 7 8 9 present				
Crossability	9 1		2 5		4 6 3 7 8				

1 = *vulgaris*

2 = *juliae*

3 = *amoena*

4 = *pallasii*

5 = *elatior*

6 = *megaseaefolia*

7 = *intricata*

8 = *lofthousei*

9 = *veris*

We are now in a position to speculate about the adaptive significance of some of these characters. Some, it would appear, are clearly adaptive; thus seed dispersal by censer mechanism from the tough erect capsules of such species as *P. veris*, *P. elatior* and *P. lofthousei* seems to be efficient, as does also the dispersal by ants of the sticky seeds from the soft capsules of *P. vulgaris* which come to lie at the surface of the ground. On the other hand, seed dispersal in *P. juliae* and *P. megaseaefolia*, in which the dry seeds are shaken or fall out of the horizontal capsules appears to be less efficient, and the lack of success of these two very local species may be associated with this fact. The reasons for the variation in shape and size of the dry capsules of the *P. veris* group are obscure; it is not, for example, easy to understand why the capsules of a Swedish stock of *P. veris* should be significantly longer than those of British stocks. The remarkably elongated capsules of *P. amoena*, in which the seeds lie at the base of the capsule and do not come out very easily, are also difficult to interpret. It is tempting to look on capsule length as an orthogenetic character in the Vernales, and to compare the long and apparently overdeveloped capsule of *P. amoena* with the overgrown horns of the Titanotheres or the Irish Elk.

The variations in the size and colour pattern of the flowers are such as might reasonably be expected in a group spread over a wide area and in contact with diverse types of potential insect visitors, though detailed adaptations have not been worked out. It is, however, interesting to note that it is those species which lack a peduncle (*P. vulgaris*, *P. juliae*) which have the largest flowers; it may be inferred that the less conspicuous position of the flowers, close to the ground, is compensated for by their larger size. As with capsule length, there is a good deal of variation between populations of the same species; thus a Bavarian stock of *P. elatior* has a corolla which is significantly smaller than that of British stocks. Again, in *P. vulgaris*, Harrison (1931) has described a form with narrow petals (*P. stenopetala*) which is locally frequent in Britain. It would seem likely that while some of this variation may be adaptive, some of it may be neutral so far as natural selection is concerned, and that a fairly wide variation in characters such as petal size and shape may be tolerated. The same is doubtless true of characters such as the size of the calyx and the dimensions of the calyx teeth. It has always to be remembered that many of the significant differences between the species are physiological and are concerned with their adaptation to conditions of climate (temperature, length of day) and habitat (soil moisture, base status, light intensity). Some of the genes concerned with these characters may well be pleiotropic and affect morphological characters such as we have been discussing. It is noteworthy that in many genera, species differ by characters which are trivial and which appear to have no major adaptive significance.

We turn now to a different line of enquiry, viz., to that of the degree of relationship between the nine species, and of their

phylogeny. In some groups, the occurrence of polyploidy makes it relatively easy to plot the course taken by evolution; but the Vernales are uniformly diploid and chromosome number gives no guide. However, the fact that hybrids can be readily made makes it possible to bring other lines of evidence to bear on the problem of relationship, in addition to the usual comparison of morphological characters. These are based on degree of 'crossability' between the species, and on chromosome pairing in the hybrids; both of these will be discussed, the former in some detail.

Crossability in this group of Primulas depends upon what has been called seed incompatibility. When any pair of species is cross-pollinated (as the group is heterostyled, the cross must be legitimate, i.e. long-styled \times short-styled or vice versa), the pollen grows freely and fertilisation occurs; but there is always some abnormality in the subsequent development of the seeds (e.g. partial or complete failure of the endosperm), so that though the number of seeds produced is not affected, their quality is below normal. Germination of hybrid seed is always less than that of comparable non-hybrid seed. This phenomenon is quite general in interspecific crosses in flowering plants and probably represents the main barrier to crossing between allied species; but in the Vernales there is a feature unusual in homoploid groups. The types of seed produced from reciprocal crosses differ in a constant and easily characterised way; we have called them Type A and Type B. Type A seeds are generally below normal in size, with abnormally thick seed-coat, a small amount of endosperm which may or may not degenerate and a small, often persistent, embryo. Type B seeds have a thinner seed-coat; in less extreme cases, the seeds may be larger than normal, with large embryos and endosperm of varying degrees of imperfection; in the more extreme cases, both endosperm and embryo degenerate soon after fertilisation. The seeds have been more fully described elsewhere (Valentine, 1955).

This phenomenon makes it possible to draw up what may be called a crossability series, in which the species are placed in a definite order. When crosses are made in one direction, seeds of Type A are produced, and in the other direction, Type B. Further, the series can be arranged in such a way that the degree of abnormality of the seeds produced is roughly proportional to the distance apart of the species in the series. This can best be illustrated by discussing the crossability series itself which is shown in Table 3.

Species close to one another in the series can be crossed reciprocally to produce viable hybrids; the proportion of good seed produced drops as the distance between the species increases. The most 'distant' hybrids produced are *P. veris* ♀ \times *elatior* ♂ (very rarely), *P. vulgaris* ♀ \times *lofthousei* ♂ (very low yield) and *P. juliae* ♀ \times *lofthousei* ♂ (very low yield). In each case, the reciprocal cross yields empty seed and no hybrids. It should be added that while most of the species can be definitely placed in the series, some uncertainty still exists at the lower

TABLE 3
The crossability series

	<i>veris</i>	

	<i>vulgaris</i>	

	<i>juliae</i>	

	<i>elator</i>	

	<i>pallasii</i>	

	<i>megaseaeifolia</i>	

	<i>amoena</i>	

	<i>intricata</i>	

	<i>lofthousei</i>	

↑

Crosses made this way give Type A seeds

↓

Crosses made this way give Type B seeds

NOTE.—The “goodness” of the seeds produced is roughly proportional to the distance between the species.

end, as it has not yet been possible to carry out enough crosses with *P. pallasii* and *P. megaseaeifolia*. The series from *P. elator* to *P. lofthousei* is certainly very closely knit, seed-incompatibility between adjacent species being only slight, though in the crosses between the terminal species, *P. elator* and *P. lofthousei*, it is very well marked.

Seed incompatibility is under genetic control. Thus, it has been shown (Valentine, 1956) that the F_1 *P. veris* × *elator* hybrid is intermediate as regards seed incompatibility, between its parent species; and that it will cross readily and reciprocally with *P. vulgaris* which occupies a position about half way between *P. veris* and *P. elator* in the crossability series. In fact the hybrid gives better seed when crossed with *P. vulgaris* than with either of its parent species. Segregation of the seed incompatibility genes has also been demonstrated.

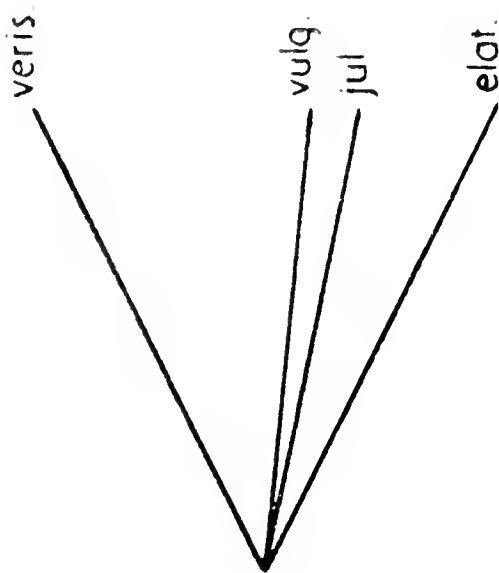
The crossability series gives a very clear lead on the question of the relationship between the species; and it would seem reasonable to utilise it in exploring phylogenetic problems. There is, of course, no doubt that inability to cross is often a very unsafe guide to relationship; as is well known, it is often impossible to cross an artificial tetraploid with the diploid from which it was derived and with which it is undoubtedly closely related. But it does not necessarily follow that the use of crossability in the positive sense is unreliable. In the Vernales, we find a whole series of stages which range from practically complete crossability at one end to practically complete inability to cross at the other; and there is no reason why this ‘character’

should receive any less weight than the customary morphological characters. Both types of character are under genetic control, probably governed in most cases by multiple genes; and both are concerned in isolation, though in different ways. Let us accordingly examine in outline the extent to which the arrangement of the species based on crossability agrees with their arrangement on external morphology.

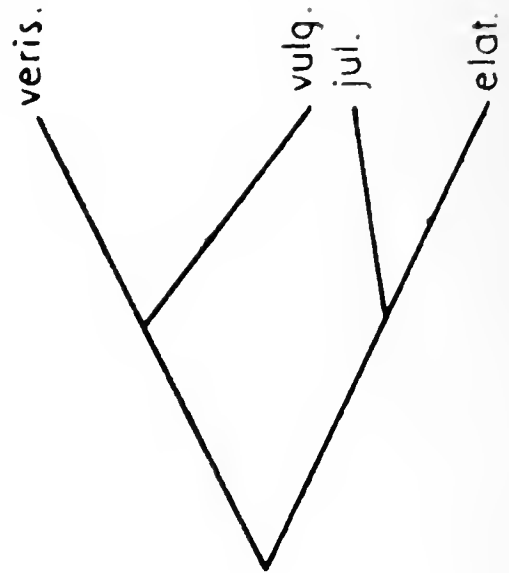
On the basis of morphological characters (Table 2), *P. veris* would appear to have much in common with *P. lofthousei*, which it resembles in many respects, though not in capsule character. On grounds of crossability, however, it is quite remote from *P. lofthousei*; and indeed, it stands apart from all the other species. The difficulty or impossibility of crossing *P. veris* with the *P. elatior-lofthousei* group indeed suggests a divergence of ancient date. The crossability gap between the two groups can be bridged by the *P. vulgaris-juliae* group, which is genetically intermediate in respect of the genes concerned with seed-incompatibility; and this fact presents an interesting problem. As shown in Table 2, *P. vulgaris* and *P. juliae* are alike in habit; both species lack a peduncle and have large flowers arising singly from the rosette of leaves. On the other hand, they differ markedly in leaf-shape, indumentum and mode of seed-dispersal. As regards their crossability genes, they are practically identical; reciprocal crosses give good yields of highly viable seeds. The questions thus arise, are the resemblances between *P. juliae* and *P. vulgaris* due to convergence? What are the phylogenetic possibilities?

There appear to be four possibilities, which are indicated in a simplified way in Fig. 6. In this, the reasonable assumption is made that the Vernales are monophyletic, and the order and spacing of the species is that of the crossability series. The most straightforward explanation of this order is shown in Fig. 6a, in which it is assumed that the species diverged at the beginning of the evolutionary history of the group; and that, as regards the crossability genes, *P. elatior* and its allies diverged steadily from *P. veris*, while *P. vulgaris* and *P. juliae* changed very little and diverged only slightly from one another.

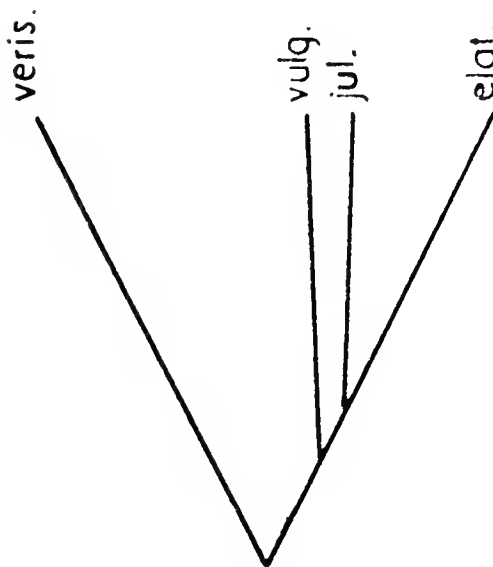
The second explanation is indicated in Fig. 6b; it is that *P. vulgaris* and *P. juliae* arose separately and independently from the *P. veris* and *P. elatior* lines of descent, and, as a result of convergence, became more crossable with time, i.e. mutations of the crossability genes occurred which reversed the former diverging trend. Convergence in characters concerned with adaptation to the environment is of course widespread in evolution, but convergence of the kind postulated here, though it cannot be ruled out, must be regarded as a very unlikely occurrence. An alternative is, however, shown in Fig. 6c. Here it is supposed that *P. vulgaris* and *P. juliae* diverged independently from one of the lines of descent (that of *P. elatior* is selected) and that there was little change in their crossability genes subsequent to their divergence.



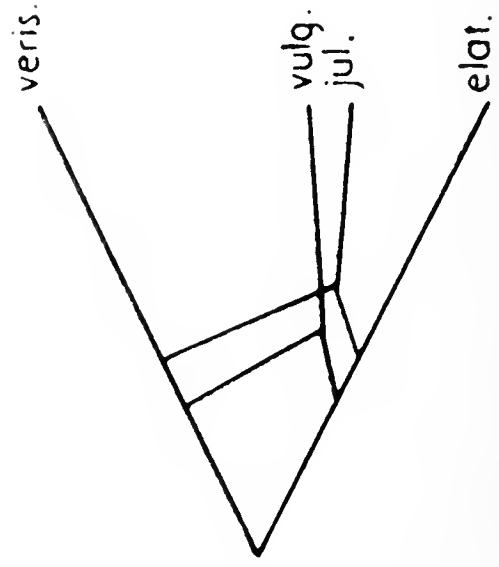
(a) Divergence



(b) Convergence



(c) Parallel Evolution



(d) Hybridization

Fig. 6.

The fourth hypothesis is shown in Fig. 6d, in which it is supposed that interspecific hybridization occurred on two occasions between representatives of the *P. veris* and *P. elatior* lines of descent; and that the hybrids so produced gave rise to new fertile self-perpetuating species, efficiently isolated from their parents. This would account for the intermediate position of *P. vulgaris* and *P. juliae* in the crossability series. The possibility of hybridization of this kind producing new species in a coenospecies such as the Vernales has been put forward by Stebbins (1958), who produces a good deal of evidence in favour of the idea.

On morphological grounds, the last hypothesis, that of hybridization, is difficult to support, and that of convergence has already been dismissed. Of the other two hypotheses, the third seems to be best in line with the morphological evidence. Thus, most members of the genus *Primula* are pedunculate, and it is reasonable to regard the non-pedunculate species as being derived.

The character, as investigated in crosses between *P. elatior* and *P. vulgaris*, is primarily controlled by a major gene (Valentine, 1953) so that it is easy to conceive of non-pedunculate forms arising by mutation and on more than one occasion. The correlated characters of increased flower size and pedicel length, and of specialised methods of seed dispersal (in *P. vulgaris*) could then be envisaged as a response to the new requirements of pollination and dispersal resulting from an inflorescence close to the ground.

It still remains a remarkable fact that two species, which are so distinct morphologically and which must be presumed to have diverged a long time ago, should have remained so highly crossable and interfertile. Such species would be expected not only to originate, but to remain, in distinct geographical areas; or else to occupy such distinct habitats as to be efficiently isolated. *P. vulgaris* subsp. *vulgaris*, which we are discussing here, certainly does not come into contact at present with *P. juliae*, but *P. vulgaris* subsp. *sibthorpii* (Hoffm.) W.W. Sm. et Forr., according to Fedorov (1952), occurs in the same geographical province (E. Transcaucasia) as *P. juliae*. The habitat of *sibthorpii* is given as 'deciduous forest, generally on the forest margins' and that of *P. juliae* as 'wet rocks in the forest zone'. It is not clear what isolating factors are operative, though it is possible that *juliae* is a rock or cliff plant, and *sibthorpii* a plant of the woodland floor. Specimens of *sibthorpii* do not differ greatly in morphology from those of *P. vulgaris* (the main difference appears to be in flower colour), and the two subspecies are said (Fedorov, 1952) to form extensive hybrid swarms along the Black Sea coast. It has not yet been possible to make crosses between *sibthorpii* and *P. juliae*; but should they prove to be highly intercrossable and interfertile, as is likely, they will present an interesting problem in isolation. It may be that the difference in flowering time reported by Fedorov (February-March for *sibthorpii* and April for *P. juliae*) is important.

P. megaseaeifolia is an outstanding example of a species which differs greatly in morphology, and especially in its rather xeromorphic cordate leaves, from the rest of the Vernales. As has been indicated above, there has been some difference of opinion about its relationships; but its crossability with *P. elatior* and other species, and the fact that its hybrids show good meiotic pairing, strongly favour its inclusion. A more detailed discussion of this species will be published elsewhere.

Chromosome pairing in the hybrids has not as yet been fully investigated. Meiosis has been looked at in ten hybrids, and in all these a considerable proportion of the cells shows eleven bivalents. On the other hand, there is always some failure of pairing, and configurations such as 10 bivalents plus 2 univalents are fairly frequent. Polyvalents, such as trivalents and quadrivalents, are generally seen in a small proportion of the cells; and in several hybrids, bridges and fragments have been observed at first anaphase. There is thus evidence that there are structural differences between the chromosomes of the species, and that

both translocations and inversions have occurred in the course of evolution.

It should be possible, by comparing meiosis in different hybrids, to build up a series in which the species would be arranged in order of chromosomal similarity, and a beginning has been made with this. Thus Eaton (1959) has obtained the data of Table 4 for three *P. juliae* hybrids.

TABLE 4
Meiosis in hybrids involving *Primula juliae*

Hybrid	No. of cells examined	No. of cells showing		
		11 bivalents	Some failure of pairing	1 or more polyvalents
<i>elatior</i> × <i>juliae</i>	71	49	21	3
<i>juliae</i> × <i>vulgaris</i>	74	42	31	5
<i>juliae</i> × <i>veris</i>	116	48	67	27

Note.—A cell with 9 (2) + 1 (3) + 1 (1), or some such arrangement, is reckoned as showing *both* failure of pairing *and* a polyvalent.

These data show that, judged by the criterion of chromosome pairing at meiosis, *juliae* is more different from *veris* than it is from either *elatior* or *vulgaris*; and this conclusion is in good agreement with that reached using the criterion of seed incompatibility.

It is perhaps worth making a further comment of a more general nature on these data. Cytologically speaking, it may be said that all the members of the Vernales described in this paper have substantially the same genome, as all their hybrids show good meiotic pairing; yet, as has been shown, their morphological diversity is very considerable. This is a state of affairs which is, of course, not uncommon in homoploid coenospecies. On the other hand, in polyploid complexes, which may often consist of a series of species with only slight morphological diversity, apparent genomic heterogeneity is common. This is well seen in many fern genera, where the species, both diploid and polyploid, show very regular bivalent formation; and in interspecific crosses a sharp meiotic pattern of n bivalents + n univalents, n bivalents + $2n$ univalents, etc., is commonly formed (Manton, 1950). This indicates either that the parents of the allopolyploid species had genomes which were already very sharply differentiated cytologically at the time the polyploids were formed, or that differentiation has occurred, under the influence of selection, in the course of time. The morphological-cytological pattern of groups such as the Vernales suggests that the former hypothesis is unlikely; and the correctness of the latter hypothesis is supported by the observations of Riley and Chapman (1958) on hexaploid wheats, in which it has been shown that the regularity of pairing in the hexaploids is controlled by genes located on specific chromosomes or chromosome segments.

One of the problems arising in groups such as the Vernales is that of taxonomic status, the problem which Darwin raised and settled for *P. vulgaris* and *P. veris*. As we have pointed out, as regards crossability, there is practically every gradation in the Vernales between taxa which cannot be crossed and those which cross with almost complete and full viability of seed; and there is a similar range in hybrid fertility from low (25%) to high (90%). On present evidence, all the taxa described in this paper must be regarded as of ecospecific status, though internal barriers to crossing between some of the ecospecies, e.g. between *P. intricata* and *P. lofthousei*, are very slight. As these two are allopatric, they might be given subspecific rank; yet there are considerable morphological differences between them, and they do not react in the same way when hybridized with other species, such as *P. elatior*. In view of the complete ring of hybrids possible (Fig. 1), it would be possible to rank all the taxa as subspecies; yet though some are allopatric, many are sympatric to varying extents. The habitats of the latter are generally different, and even where species meet and hybridize, and some introgression occurs, as between *P. vulgaris* and *P. elatior*, this introgression is limited in extent, and the species remain substantially distinct. In these circumstances, it seems best to call all the taxa species rather than subspecies; to give some of them specific, and some subspecific, rank could hardly be justified.

Groups of this kind, i.e. coenospecies composed of a group of gradual ecospecies, or homogamic complexes as they have been called by Grant (1953), are not uncommon amongst flowering plants, particularly in long-lived perennials; some of their properties have recently been discussed and analysed by Stebbins (1958). We shall not say any more here about evolution in the Vernales; and we shall conclude this paper by discussing one or two more general aspects of evolution in the genus *Primula*.

Primula is a large genus of some four or five hundred species, closely allied to and apparently grading into the genus *Androsace*. It has been divided, on the basis of such characters as veneration of young leaves, presence or absence of farina, type of capsule, leaf-shape, etc., into some 30 sections, many of which have been investigated cytologically. Bruun (1932) and Wright Smith (1933) have discussed the cytotaxonomy of the genus and have in general found that cytological data support the conclusions of the systematist.

Most sections of *Primula* are found to have a single basic chromosome number, which is generally 8, 9, 10, 11, 12 or 13. Several sections are entirely or predominantly diploid, and in some of these, such as the section Candelabra, fertile inter-specific hybrids have been made (Wright Smith and Fletcher, 1941). Other sections, such as the Farinosae, contain a series of species at various levels of polyploidy; and it is interesting to speculate as to why some groups, such as the Vernales, have not adopted this mechanism of evolution.

It has not been found difficult, by the use of colchicine, to produce autotetraploid stocks of *P. vulgaris*, *veris* and *elatior* which are quite vigorous and fertile; the allotetraploid *P. veris* × *vulgaris* has also been made. There would thus seem to be no reason why tetraploid plants, if they arise in nature, should not survive. They might, however, fail to reproduce. The artificial polyploids so far produced are heterostyled and self-incompatible, like their diploid parents; and the chances of polyploid long and short styled plants arising together under natural conditions are not very high. However, self-compatible plants of some *Primulas* are known, e.g. the homostyle *P. vulgaris*, large populations of which occur in S. England; these have been investigated by Crosby (1949) and are being demonstrated by him at this meeting. Polyploids arising in such populations might well be successful. Alternatively, it is possible that in some groups of *Primula*, polyploidy might induce a breakdown of the heterostyly system and favour the development of homostyles; the experiments of Dowrick (1956) on *Primula obconica* (section *Obconica*) have produced some evidence in favour of this hypothesis. Certainly in the section *Farinosae* subsection *Eu-farinosae*, there is a correlation between polyploidy and homostyly; the diploids are heterostyled and self-incompatible, while the polyploids are homostyled and self-compatible; this was first noticed by Bruun (1938) and has been confirmed by Vogelmann (1955) in the N. American species *P. mistassinica* ($2n=18$) and *P. laurentiana* ($2n=72$).

Another rather remarkable feature of the genus *Primula* is that few or no inter-sectional hybrids are known (unless it be maintained that *P. megaseaefolia* be retained in a section of its own or in the section *Carolinella*). There are various possible explanations; one is that insufficient observations and experiments have been made, and another that the sections represent extremely distinct lines of descent, the links between which have been lost, so that hybridization is no longer possible. The former explanation is, on the face of it, the more likely, and experimental work is clearly needed. In seeking to make new hybrids, as for example, between the *Vernales* and other sections of *Primula*, knowledge of the crossability series may be useful. Thus if a certain species cannot be crossed either with *P. veris*, at one end of the series, or with *P. loftthousei* at the other, it is not likely to be crossable with any of the other species which lie between these two on the series, and there is no need to waste time on the experiments. Further extensions in the application of the series, including the use of artificial polyploids, will be discussed elsewhere.

The *Vernales* may be summed up as a group of species (some of them polytypic) with considerable evolutionary potentialities; these may be developed in the future in several ways, e.g. through polyploidy, through hybridization, or through introgression. Their relationship to other sections of the genus *Primula*, which is based on resemblance in morphological characters, is hardly in

doubt; and we may think of the progenitors of the sections as having arisen, in the past, from some ancestral stock in much the same kind of way as species within the sections have themselves arisen. That is, they arose by the action of natural selection working over a period of time and in a series of changing environments over a wide area; and the genetical mechanisms involved, gene mutation, introgression, chromosome repatterning and polyploidy, were the same as are found within the sections. The fact that hybrids have been produced between *P. megaseaefolia* (formerly placed in other sections) and members of the Vernales helps to convince us that other similar links will be found in time; and it is reasonable to regard the overall process of evolution in the genus as gradual, discontinuities being due to divergencies or extinctions. This idea of gradual descent with modification, as Darwin called it, may be extended beyond the genus to the family and so, step by step, to Angiosperms, the plant kingdom, and all living organisms.

Yet more than one biologist has felt that the morphological gaps between existing genera, families, orders, etc., are often so great that it is difficult to believe that they arose by a process of gradual differentiation. Thus Deyl (1955) distinguishes macro-evolution and micro-evolution; he believes that the genetical processes which lead to the origin of a group such as a family or an order are of a nature fundamentally different from those which are responsible for evolution at the species level. Goldschmidt (1940) has argued in a rather similar way; and he has suggested that the apparently unbridgeable gaps between groups such as sections or genera owe their origin to genetic changes which are qualitatively different from those which lead to speciation in a group such as the Vernales. Geneticists have, in general, been rather resistant to Goldschmidt's ideas, although Waddington (1957), discussing them in the light of recent work on micro-organisms, is inclined to think that the large or 'systemic' mutation is something which may yet have to be taken seriously.

It may well be that experimental evidence on this point will be provided from investigations of wide hybrids in flowering plants as, for example, the hybrids between species of *Fragaria* and *Potentilla* recently reported by Ellis (1958); as indicated above, experiments on hybridization between species of the different sections of *Primula* may likewise produce relevant results. We know very little as yet of the genetic mechanisms involved in crossability, and of their physiological causes. More knowledge of the processes which occur in the interaction between pollen and style, and between embryo, endosperm and maternal parent, may make it possible to make much 'wider' hybrids than is at present possible, and so to extend greatly our understanding of the origins of natural diversity.

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Dr. N. HYLANDER considered that *Primula veris* and *P. juliae* were not as closely related as Professor Valentine had suggested. Mutant plants of *P. veris* lacking the scape had been found twice in Sweden.

Professor BÖCHER stated that the triple hybrid *P. veris* × *vulgaris* × *elatior* occurs in Danish woods.

Professor VALENTINE replied that the triple hybrid was not difficult to synthesise, provided that the hybrid *P. veris* × *elatior* could be obtained; this hybrid could be crossed readily and reciprocally with *P. vulgaris* to give triple hybrids which were healthy and vigorous.

It would undoubtedly be possible, by successive crosses, to obtain hybrids incorporating genetic material from all the species in the section.

SOME TRENDS IN MODERN RESEARCH WORK ON SCANDINAVIAN VASCULAR PLANTS

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Eighty years ago the 11th edition of Hartman's famous *Handbook of the Scandinavian Flora* was published in Stockholm. This edition, a new and original work of Carl Hartman, son of Carl Johan Hartman, who began the work in 1820, has remained a standard work and is still the latest complete scientific flora of Swedish vascular plants, despite later attempts at replacing it by a modern work.

The first of these was made by Thorgny Ossian Bolivar Napoleon Krok, later famous for his excellent bibliography of Swedish botanical literature. In 1889 he published a first part of what was called the 12th edition of Hartman, but these 128 pages were all that ever appeared.

The next attempt also resulted in a fragment. It was made by Otto R. Holmberg of the Botanical Museum in Lund. In 1922 he published a first volume of a flora, including, like that of Krok, also Denmark and east Fennoscandia, i.e. Finland, Russian Karelia and Russian Lapland, and like that appearing as a new edition of Hartman's work. This first part comprised the Pteridophytes, Gymnosperms and part of the Monocotyledons from Helobiae to the first groups of Gramineae according to Engler's system. It was followed in 1926 by a second volume, from which Hartman's name had disappeared and been replaced by that of Holmberg, since the work was—as was stated on the cover—from all points of view a new, independent work. This was undoubtedly true—it was based on thorough original studies in herbaria and in the field by Holmberg and his co-operators.

By the death of Holmberg in December 1930, a sudden end was put to this valuable flora work, except that a volume containing the family Salicaceae was published in 1931; it was written by the *Salix* specialist, Dr. Björn Floderus, and differed rather decidedly from the original plan of the flora.

Despite these discouraging experiences, I started work in the 1940's on a new flora for a still larger area, including also Iceland and the Faeroes. The first volume was published in 1953 and comprised largely the same groups as had already been treated by Holmberg. Nevertheless it was not a copy of Holmberg's work. That was already impossible, because an astonishing wealth of new additions to our flora had appeared in the meantime, not least as regards the grasses. But still more important,

I had during the work found it necessary to treat the matter in another way than has been the rule in floristic handbooks, namely by giving a larger place to discussions of actual problems, especially regarding the delimitation and subdivision of the species.

I think this reflects a considerable change in the mode of approach to the taxonomic questions during this period. More than before the taxonomists were thinking of the species and their subordinate taxa as populations, not as isolated specimens—we may also say, as constituents of different types of vegetation and in their relation to the environment. This means also that variation within the species was now looked upon less as an isolated phenomenon and in the first place in relation to the geographical distribution of the species and the different biotopes where they occur. For this study new methods have been applied, such as comparative transplantation experiments under controlled conditions and investigation of the chromosome numbers, which allow analyses which were not—at least to the same extent—possible with the classical taxonomic methods.

On the other hand, this does not at all mean that the classical methods have lost their value. On the contrary, there will, as before, be no good taxonomy without that special gift which we in Sweden call “systematisk blick”, let us say “the taxonomic eye”—the ability to find, so to say, by intuition which parts of a plant material belong together taxonomically.

In some cases, namely in the study of apomictic microspecies, these methods are still the only possible means for a correct delimitation and determination of the units—although, of course, modern cytological and embryological methods are necessary for the understanding of the mechanisms which are the basis for the constancy of these “small” taxa. I shall return to this question later but should like to mention first, quite briefly, some results of the floristic-taxonomic work of “classical” type in Sweden during these decades, namely the detection of some “good” species as novelties in the indigenous Swedish flora. I have given a more comprehensive survey of such novelties in *Botaniska Notiser* for 1954, and must, for the species mentioned below, refer to the bibliography given there.

Some of these species were known before from adjacent parts of Scandinavia, partly seashore plants such as *Atriplex sabulosa* and *Rumex pseudonatronatus*, partly high mountain plants from the Northern Scandes: *Carex holostoma*, *Gentianella aurea*, *Ranunculus sulphureus*, *Draba crassifolia*, *Stellaria longipes*, and *Armeria scabra* (*sibirica*). In other cases, the finds have been more surprising since they meant a most considerable disjunction from the nearest extra-Scandinavian occurrences. Examples are southern coast plants, such as *Oenanthe lachenalii* in Blekinge and *Scutellaria minor* in Scania, and mountain plants such as the highly interesting *Potentilla hyparctica* (*emarginata*), and furthermore two species from Gotland—that island of botanical surprises—namely the small fern *Ceterach officinarum* and an

orchid, *Orchis spitzelii*—as a matter of fact not at all rare in Gotland but otherwise a Central and South European, and West Asiatic species.

It should be observed that all these “novelties”—which have, at least mainly, grown for hundreds or thousands of years in Sweden—were described as species long ago—in most cases more than 100 years ago. This also holds true for another group of species which are also novelties in the Swedish flora, although in another sense. I mean such species, of which there has long since existed herbarium material, although never correctly determined but hidden among some common related species. A good example is *Poa supina*, in fact quite a common plant in many parts of Sweden and now also found in adjacent parts of Denmark, Norway and Finland but not distinguished from *P. annua* until Nannfeldt's studies in 1935. In this case, the species had on the whole been quite forgotten; described in 1806, it was not “resurrected” until 1932 by Lindberg fil. on the basis of Spanish and Moroccan material. It is thus analogous to the resurrection of *Glyceria declinata*, as a Swedish plant first distinguished by Max Walters in 1948. Oddly enough, it was quite correctly described in Holmberg's flora, although as an insignificant variety of *G. fluitans*.

In some other similar cases, the new species had in the same way remained unknown in Sweden but were kept as distinct species in south Europe, and thought to be more or less endemic there. Examples of this kind are *Apera interrupta* and *Aphanes microcarpa*—*inter se* very different ecologically but both offering great interest from a phytogeographical point of view.

A case of special interest is that of *Geranium lanuginosum*. In 1916 Erik Almquist described, as subsp. *deprehensum* of *G. bohemicum*, a plant which had been found as a single specimen growing together with the latter species, from which it differed, *inter alia*, in the form of the leaves and cotyledons. Thanks to a thorough study, including crossing experiments, by Professor O. Dahlgren in Uppsala, it soon became clear that it was an independent species, and in 1926 Lindman raised it to specific rank as *G. deprehensum*. However, nothing was known about its distribution outside Sweden until I showed it in 1933 to be identical with *G. perreymondii* Shuttlew., which had in its turn already been identified by Burnat in 1896 as *G. lanuginosum*, described by Lamarck from Numidia (i.e. North Africa) as early as 1786. With the exception of Sweden, this species is still known exclusively from the Mediterranean region with its northernmost locality in southern France. The most puzzling facts, however, are that *G. lanuginosum* and *G. bohemicum* have exactly the same, extremely specialised ecology, confined as they are almost exclusively to burnt soil, and that *G. lanuginosum* in most of its Swedish localities—they are still very few—has been found together with the much more common *G. bohemicum*; and the latter species has outside Sweden a totally different, eastern European distribution. (cf. Dahlgren, 1943.)

But species described long ago from our own country may also sometimes be forgotten and resurrected, as is shown by the following case. In 1934 Professor Rolf Nordhagen of Oslo found in northernmost Norway—indeed in the vicinity of Nordkap—an *Arenaria* which was new to him but which he, after his return to Oslo, was able to identify with *A. cylindrocarpa*, a species described by Fernald from North America in 1914. Looking for this species in the earlier herbarium material, Nordhagen found, however, that it was also identical with a species described more than 100 years ago, namely *A. humifusa*, found by Göran Wahlenberg in Swedish Lapland and published by him in 1812. (cf. Nordhagen, 1935.) It had later been misunderstood as a form of the *A. ciliata* complex and thought to be identical with *A. norvegica* of Gunnerus; in fact, it is very well distinguished from the whole *A. ciliata* group and has during the last years been found in many new localities in Sweden and Norway and sometimes in some quantity. The circumstance that it is more or less exclusively bound to a very special type of rock, namely serpentine, may partly be the reason for its having been so neglected.

But there are also some Scandinavian plants which have been described as new species during this period. In few (if any) cases, however, have they been generally accepted as independent species. Some of them belong to intricate polymorphic groups, others form, so to speak, a pair with a well-known species, from which the new species may be distinguished morphologically only with difficulty and not always with certainty, but from which it differs by having another chromosome number. It may also show a \pm distinct difference in its distribution or ecology. Good examples of the last type are "species" like *Empetrum hermaphroditum* (Hagerup, 1927) and *Anthoxanthum alpinum* (Løve & Løve, 1948). In these cases the "new" species has a wide distribution outside Scandinavia also. On the other hand, we have an endemic taxon that has also been raised to specific rank during this period, namely *Primula scandinavica* (Bruun, 1938). Earlier Scandinavian authors had considered it identical with *P. scotica*, but Bruun showed that it had another chromosome number and differed in some morphological details. These are, however, very slight and partly not constant, so it seems best to treat *scandinavica* merely as a variety of *scotica*—the more so since Miss Davies has shown the existence of different chromosome numbers within Swedish *P. farinosa* s.str.

Among the representatives of polymorphic groups, *Valeriana salina* may be mentioned. It is known from the seashores of Norway, Sweden and Finland, but its independence may be disputed or should at least be reconsidered, since recent cytological studies of the *Valeriana officinalis* group, to which it belongs, have shown that the taxonomy of this group is much more complex than was known in 1924 when *V. salina* was described (Pleijel, 1924).

It is, of course, no mere chance that there are so few endemics within the Scandinavian vascular flora and that the

endemic taxa are so little marked morphologically. On the contrary, this is quite natural when we remember that this flora is very young, due to the fact that the whole area was covered by inland ice during the quaternary period. There has been a very lively discussion during the last 40 years whether the glaciation in Scandinavia was total or whether there were, at least during the last ice age, some restricted areas left like the nunataks which rise above the inland ice of Greenland. In fact, the most renowned cases of endemic taxa described during the last decades from Scandinavia have awakened an immense interest just because they have been considered as proofs of the existence of survivors from inter-glacial times. The group in question is that of *Papaver radicum*, which became famous through the investigations of Nordhagen published in 1932. By these, it was shown that the polymorphy of the group, which had been to some extent studied before by Lundström and Tolmatchew, was considerably greater than these authors had known, and that some of the new taxa, which Nordhagen described as subspecies of *P. radicum* or as independent species, had a very restricted area in Scandinavia. According to Nordhagen some of these areas coincided surprisingly well with such districts as could for geological reasons be considered as probably unglaciated during the last ice age.

Soon afterwards it was shown that the morphological diversity was combined with a variation in chromosome number; all of these taxa were polyploid, but the somatic number was in some 56, in others 70 (Horn, 1938). Further investigations mainly by Mrs. Knaben in Oslo, have shown that the polymorphy is still greater than was thought even by Nordhagen; it has become clear that there are additional, very local races to be distinguished but also that some of the morphological characters used by Nordhagen, such as the colour of the milk sap, have a more restricted taxonomic value than he supposed. These new data make it, in my opinion, necessary to reconsider the whole question of the *radicum* group as interglacial relics, taking the possibility of neoendemism into consideration.

There are, however, still many cases of plant distribution within the Scandinavian mountains—or the Scandes, as we now prefer to say—which are most difficult to explain without the aid of the “over-wintering hypothesis”, and this has, during the last decades, been almost unanimously accepted by Scandinavian botanists. On the other hand, geologists have, on the whole, especially in Norway, taken a sceptical attitude, and recently there seems to have arisen a certain opposition even among younger botanists. This may, in part, be due to the tendency during late years to add more and more species to the list of survivors so that the supposed refugia have begun to give the impression of over-population, the more so since this list now shows the most diverse elements, from high alpine species to species of the sub-alpine belt, including even the spruce. It is also remarkable that the type of distribution of mountain plants in

Scandinavia, called the bicentric group, which has been much used as an argument in favour of the relic hypothesis, occurs also among species of sub-alpine and lower habitats, as shown by Gunnar Björkman (1939) for *Luzula parviflora*. In addition, it must be pointed out that such a differentiation of a rare northern \pm montane species, with a few scattered occurrences, in a small number of morphologically distinct local populations does not *per se* prove that the species is a relic. As an example may be mentioned *Potentilla multifida*, which seems to be represented in two of its 4 localities in Swedish Lapland by a race very similar to those in Spitzbergen and the Alps, while it occurs in the two other Swedish localities in a very different form; this, on the other hand, comes near the peculiar var. *lapponica* known from a single locality in the Kola Peninsula. None of these populations grow in the alpine belt, nor in the vicinity of an area which anybody can reasonably interpret as having been a refugium.

Under such circumstances it is, of course, of the utmost interest to study the Scandinavian taxa in their relation to the extra-Scandinavian representatives of the same species, in other words, to study the whole distribution of the species in question and its differentiation into geographical races. A considerable number of Scandinavian species have been mapped, mainly according to the dot method, by various investigators, as regards both the Scandinavian and the total distribution. The leading authority in this field is Professor Eric Hultén in Stockholm, and he is also the Swedish botanist who has more than anybody else studied the differentiation of the species in geographical races within their total area.

As regards the geographical differentiation within Scandinavia, several species have been studied from this point of view by Professor Jaakko Jalas in Helsingfors. In some of these cases, e.g., *Oxytropis campestris* and *Thymus serpyllum*, it was possible (Jalas, 1950) to divide the Scandinavian population into a few geographically isolated subspecies; in other cases a separation could be made into a number of subspecies possessing distribution areas that are markedly different but fairly often overlapping (constantly or accidentally) and then connected by a more or less well-developed intermediate population. An example of this type is *Anthyllis vulneraria*. In still another case, such as *Lotus corniculatus*, the main biotype mass cannot be subdivided in this way, but it is possible, as Jalas did, to distinguish local races—called varieties by him as well as by me—which can be morphologically characterised and which more or less exclusively represent the species in a special type of habitat within a certain region.

In the two last-mentioned cases, the delimitation between the races is often obscured by the occurrence within new areas of foreign synanthropic races which hybridise with the indigenous, otherwise distinct race. On the other hand, a closer analysis of the geographical races of an alien species may sometimes give a

greater interest to that flora element, especially in species which have been relatively recently introduced but are now established and spreading further by seeds. Except for some apomictic composites, I think no plant subjects give such good opportunities for direct observation of the ways and mode of expansion as these races, but unfortunately too little attention was paid to these things, while there was still time. As a good example should be mentioned *Thlaspi alpestre* (Hylander, 1943b), which is a synanthropic newcomer in Scandinavia on the whole, but widely distributed and naturalised in Sweden in two main races, one of which includes several taxa of lower rank; the distributions of these taxa are widely different, and they have evidently been introduced at different times and with different seeds.

Returning to the races of *Lotus corniculatus*, it is clear that they are not merely geographical races but also ecological ones, some of them being restricted to the shores of the Baltic, others, e.g., to the sandy soils of the oases. They are thus examples of ecotypes, in the same way as some of Jalas' subspecies, e.g., *Oxytropis campestris* subsp. *typica* in Öland, or the two subspecies of *Anthyllis vulneraria*: *fennica* in Finland and *lapponica* in Norway and northernmost Sweden. In other cases, too, it is possible to treat an ecotype as a subspecies or a variety, especially in cases where the ecotype consists of a morphologically uniform population in a habitat of very specialised character, where the biotype mass has become much reduced, due to long isolation. An extreme case of such a reduction and selection process is that of the serpenticolous races studied by Kotilainen in Finland and treated monographically by the Swede Olof Rune (1953) in the Scandes.

The best examples of such ecotypes are otherwise, I think, from the lime-rock heath (the "alvar") of Öland, in some cases, as in *Aster linosyris*, solely representing their species in Scandinavia, in other cases representing only a part of the whole Scandinavian population, such as *Allium schoenoprasum* var. *alvarensense* and *Viscaria alpina* var. *oelandica*. Similar but not such clear cases are the prostrate seashore races of *Atriplex patula* and *Hieracium umbellatum* studied by Turesson, the father of the ecotype concept.

As with the term species, it is not easy to give a good and unequivocal definition of the term ecotype. Sjörs (1956) has characterised an ecotype as a group of biotypes within a species which are adapted to a relatively distinct milieu, thanks to similar ecologically important interior and exterior qualities. In many, or perhaps most, cases, the exterior morphological differences between different ecotypes of one and the same species are not distinct enough to make it possible to treat them with the aid of the classical descriptive methods, nor to arrange them in one of the usual taxonomic ranks. To a great extent, the ecological differentiation is not so much a differentiation into races of different habitats as a regional differentiation, and its

expression more a variation as regards time of flowering and seed setting, light response and similar physiological reactions.

The introduction of the ecotype concept (Turesson, 1922, 1925) has had a most important influence on taxonomic thought in Scandinavia. Species after species has been studied from this point of view by experimental methods, but also research workers using herbarium material and classical taxonomic methods have paid more and more attention to this aspect. At present, many polymorphous Scandinavian species are being studied by scholars in Lund under the direction of Professor Weimarck, but the most thorough studies of Scandinavian plants from this point of view are those made by Professor Böcher and his co-operators in Copenhagen.

These modern studies have, however, a character that differs from the original ones by Turesson, since ecological variation has been more and more connected with the variation in chromosome number. As an example of such an investigation in Sweden may be mentioned Lövkvist's studies (1956) of the *Cardamine pratensis* group.

It is most interesting that there seems to be at least a tendency to an ecotypical variation even within some apomictic microspecies, as shown by Turesson's most interesting experiments with Scandinavian *Alchemillas* of the *vulgaris* group (Turesson, 1943, 1956, 1957). In any case, these comparative cultivation experiments showed clearly that the postulation of Heribert Nilsson (1947) that an apomictic microspecies is identical with one single biotype is, at least in these cases, totally wrong, that, on the contrary, there is, within all the widespread lowland microspecies, a considerable variation in such characters as flowering time, ratio leaf/flowers, resistance to mildew, etc. But this variation, the constancy of which was shown by raising new generations from seed, did not in the least affect the distinct limits between the microspecies. The existence of a certain variation within Swedish *Alchemilla* microspecies had been observed also by Samuelsson, according to his monographic work on the Scandinavian distribution of *Alchemillas* (1943). Thanks to Samuelsson's field work, interest was again directed to this genus, where nothing remarkably new had happened or had even been expected to happen after the pioneer works of Westerlund and Lindberg, but where Samuelsson (1940) was able to reveal as well-established and rather widespread Swedish taxa no less than 3 species earlier described from Russia or the Baltic states.

In 1943 Samuelsson published his monograph on the distribution of the microspecies of the *Alchemilla vulgaris* group in north Europe. For this he had studied the whole Scandinavian material of all Nordic herbaria, but he was never able to complete his research work—the main part of the *acutidens* complex, the taxa more or less restricted to the mountains, was only partly and preliminarily dealt with. These taxa seem to offer difficulties of quite another kind than our other *Alchemillas*, which is true

even as regards the cytology; according to Turesson's work (1957) on the chromosome numbers in the *Alchemilla vulgaris* group, which were shown to be very high, normally between (101-)102 and 110, these obscure types definitely show still higher numbers, which in his material fell into three classes: 130-144, c. 150, and 165-168. I have studied this group in north Sweden and Norway during the past three summers, and the impression I have got is that of a group where the differentiation is not yet finished. If it becomes possible to divide this group also into well-defined microspecies, these will in any case be many more than has hitherto been realised, and the distinguishing morphological characters much "smaller" than in the microspecies hitherto described. (cf. also Lundh-Almestrand, 1958.) What makes the analysis of this complex still more difficult is the circumstance that they often occur only in very small colonies and therefore are more difficult to recognise in the field than is the case with most of our *Alchemilla* microspecies.

Within some of our lowland *Alchemillas* there is, in addition to the variation just mentioned, also another type of variation which is a rare phenomenon in nature and which must be ascribed to mutation. In these cases, the pilosity is not, as in the normal type of the species, patent but appressed. Such *adpressepilosa* forms were first described by Lindberg fil. from Finland (in *A. acutiloba*) and by Baltic authors (in *A. glaucescens* and *A. micans*); the two latter forms are now known also from Sweden, from where Samuelsson could, in addition, report the same phenomenon in *A. pastoralis* in a few Northern localities.

This is of a special interest since we know now similar phenomena within two other groups of apomicts, namely the *Ranunculus auricomus* complex and, more clearly, *Taraxacum*. Here Gustaf Haglund (1946) was able to show some cases of parallel mutations within a few microspecies of the *Erythrosperma* group, in the form of some specimens differing by straw-coloured fruits from the type, where these are reddish. The cytological background of this phenomenon is not known, but thanks to the Danish research team of Sörensen & Gudjónson we have a very good knowledge of another unusually interesting type of parallel aberrations in *Taraxacum*.

The microspecies studied by them, all belonging to the *Vulgaria* group, are normally triploid with a chromosome number of 24, i.e. with 3 identical sets of 8 chromosomes. Now, Sörensen, in his extensive cultivation experiments, fairly often found aberrations from the normal type in leaf form, etc.; to be exact, 8 different types of aberrations, some of which were found in quite a number of microspecies, in some cases also in nature. In one case, all these 8 aberrations were found in one and the same microspecies, in another microspecies 7 of them were found, while only 1 of the aberrations was observed in one single microspecies.

Since each of the 8 chromosomes of a set has a characteristic form, Gudjónson was able to show, that each of these aberrations

was due to the loss of one special chromosome; thus the aberration called *elegans*, which had been found in 8 microspecies in cultivation, was in all cases caused by the loss of chromosome A, and aberration *pygmaea*, seen in no less than 10 microspecies, by loss of chromosome E, etc.

In a few cases, individuals were found with only 22 chromosomes; in these cases, two aberrations were combined, due to the loss of two different chromosomes; in no case, however, could a loss of two homologous chromosomes be shown.

In a few microspecies, *gigas* individuals were also found; they showed the chromosome number of 48—or in some cases 46, which meant that a doubling of the number had occurred in a 23-chromosome aberrant too.

The death of Dr. Gustaf Haglund meant a very heavy loss to European taxonomy, where he was the leading authority on *Taraxacum*. Through his own field work and his determinations of other collectors' herbarium material we have a good knowledge of the *Taraxacum* flora of many Swedish provinces, but his new revision of the *Erythrosperma* group was never completed, nor was anything published of his most interesting studies on the ways and modes of dispersal of the microspecies of the *Vulgaria* group. In this field there is certainly much to be done since this group evidently contains quite different elements as regards their age within our area and the provenance of the different neosynanthropic microspecies. It is, for instance, very instructive to note that the microspecies that occur as really noxious weeds seem all to belong to a relatively very recently introduced group, while the old indigenous or archeosynanthropic species, which belong to natural habitats or to the near vicinity of old habitations, do not seem capable of tolerating competition, for instance in a clover field.

The mode and speed of dispersal of the various microspecies, their different ability to colonise new habitats and the variation as regards competition were studied in another apomictic group, namely the *Vulgata* group of the genus *Hieracium*, by Karl Johansson, who published two papers on these questions in 1923 and 1926. Unfortunately these papers, so unusually rich in observations as well as ideas for further research work, were only published in Swedish with a short German summary and so have remained largely unknown internationally. They also included maps—partly schematic—for most of our *Vulgata* microspecies; a selection of microspecies representing all the main Scandinavian groups of the genus was later mapped by Samuelsson and after his death completed and published by Erik Almquist in 1954.

In the second of the papers mentioned, Johansson also critically revised the cases of Swedish microspecies that had been said to occur outside Scandinavia. Such an occurrence could be proved only for half a dozen of our most widespread microspecies, all other reports being false—with one exception. But this exception was *H. grandidens*, a representative of the so-called park *Hieracia* within the group *Silvaticiformia*. These park

Hieracia are native to central Europe but have been unintentionally introduced into Sweden with foreign grass seeds and are now \pm established in and around old-fashioned parks and gardens. Only 6 of these "difficult" species, as Johansson called them, were known from Sweden at that time. As a result of my studies in this element, in connection with an analysis of the characteristic adventive park flora, with which they are intimately allied, no less than about 140 microspecies could be distinguished from Sweden. Only one of them, however, has been able to escape outside the parks and become really naturalised as a neophyte, namely the *H. grandidens* just mentioned, which was described already in 1892 by Dahlstedt. In some regions, for instance, around Uppsala, this is now perhaps the most common of all *Silvaticiformia* and occurs in some localities in tens of thousands of individuals. It is very characteristic of the whole group of these park species that they occur in most localities in masses, at least partly due to their habit of reflowering in the autumn. The only indigenous microspecies of this group, where such an autumnal flowering occurs more regularly, is the south Swedish *H. subulatidens*, and it is most noteworthy that this species, as pointed out by Johansson, is the only one which has been able, during recent times, to take possession of new more or less man-made localities and grow in immense quantities. But it is also worth mentioning that *H. grandidens* is a species of very wide distribution as an indigenous plant and seems to be the only one of all these adventive microspecies which is common within its original area.

It has, unfortunately, not been possible to study this group in its original home, which cannot therefore yet be located more exactly. This would otherwise be of great interest, not only for the determination of the provenance of the seeds. Most of these alien microspecies could, as I found, be arranged in a few subgroups which I named after a typical representative, but all of them belong very close together if compared with at least the majority of the indigenous Swedish microspecies—in fact, the first two described from Sweden, *grandidens* and *torticeps*, were placed by their author, H. Dahlstedt, as subspecies under one and the same species, although they belong to different subgroups in my system. Now, it is interesting to note that, especially within one of these subgroups, that of *H. strengnense*, there are a few species of apparently very close relationship which in a most remarkable way occur together in the Swedish localities, so that one or more of them accompany *strengnense*—the only one that is known from a more considerable number of localities—or that two or more of the rarer species occur together. This must, in my opinion, be interpreted so that we have within a very limited area in central Europe a centre for the development of this group of constant microspecies, which must thus be of a fairly recent origin.

Such centres of origin seem to occur, within other complexes of *Hieracium* microspecies, also in Sweden, judging from some

examples given by K. Johansson, who also discussed the question of the age of various Swedish microspecies. On this point we have in Sweden perhaps a unique case in which this can be established with rather great exactitude, namely a series of microspecies endemic to Gotland, where they are restricted to a narrow border along the sea which was not above water until after the Littorina period, i.e. in rather late postglacial time.

Samuelsson was also very interested in the question of the age of our apomictic microspecies, *inter alia* in *Alchemilla*, where he pointed out that, judging from the present distribution, such a species as *A. wichurae* must have originated before the last glaciation; he also stressed the rôle of such a species in the discussion of the age of the Scandinavian flora. In some other cases also apomictic taxa have been used as arguments in favour of the "over-wintering" hypothesis, recently, e.g., the interesting race of *Poa arctica* described by Nannfeldt (1940) as var. *caespitans*, and known outside Scandinavia from such a faraway region as Ellesmere Island in Arctic North America.

Poa arctica may be chosen as a representative of one of the many genera in which we have a mixture of sexual and asexual seed formation within one and the same collective species or species group. These groups present a most difficult problem to the taxonomists. In many cases, such as *Poa arctica*, it seems only possible to distinguish as varieties some small isolated populations, perhaps consisting each of one single biotype, leaving the large unsorted mass of biotypes undivided—in the same way as in a sexual species such as *Lotus corniculatus*. In other cases, no such small units seem to have been established, and then it will, as in *Poa pratensis*, at the most be possible to make a more or less schematic grouping in polymorphous biotype groups, which have, however, in common not only some morphological characters but also ecological properties and to some extent also the chromosome number.

Poa is a genus that has been most intensely studied by modern Swedish botanists as regards cytology and embryology. Also some other genera with more or less obligate apomictic seed formation have been the subject of a similar, partly monographic treatment, e.g. *Calamagrostis* (Nygren, 1946) and *Rubus* (Gustafsson, 1943), in which we now know the cytological and embryological processes in connection with the embryo formation rather well and thus have a better basis for the taxonomic treatment.

The last genus which has been the subject of a monograph in this respect is *Sorbus*. A taxonomic monograph was written by Hedlund as early as 1901, and for decades this fine research worker studied the intricate microspecies endemic to Scandinavia which he found by his isolation and crossing experiments to be apomictic, to be more exact, pseudogamous. Little of these studies was published except for a small paper in 1948 on the formation of new biotypes in connection with some new finds

of the very rare hybrids between the sexual *S. aucuparia* and the asexual *S. intermedia (suecica)*. These studies were completed by the cytological and embryological studies of Alf Liljefors (1953, 1955), who arranged these endemic taxa in different groups according to their chromosome number and also proposed a genome formula by which these groups could be explained as well as the genesis of the various units.

Pseudogamy seems to be very common within apomictic groups and has recently been found also in the last group, where it seems possible to establish well delimited and, as it appears, obligately apomictic microspecies, namely the group of *Ranunculus auricomus*. In Scandinavia this group has been the subject of very intense research work by Dr. Gunnar Marklund in Helsingfors during the last 10 years. Until now he has been able to distinguish from Finland about 250 microspecies, but as yet he has only published a preliminary survey (Marklund, 1954). According to this, these microspecies represent four main groups, of which the typical *auricomus* group comprises about 200 microspecies in Finland. Of the three small groups, one is north-eastern (Siberian) and two south-eastern, the *fallax* group and the *cassubicus* group. In Finland there are about ten microspecies of the last-mentioned complex; in Scandinavia it is otherwise only represented in Sweden and here only by one single taxon, *cassubicus* s.str. The *fallax* group, too, which is represented in Finland by about forty or fifty microspecies, is in Scandinavia otherwise restricted to Sweden, where it has perhaps half a dozen representatives in the eastern parts of middle Sweden. This region falls only slightly outside the Swedish area of *cassubicus*, and it is therefore natural that the members of this group were in Sweden earlier regarded as hybrids between *auricomus* and the latter species. The microspecies of the typical *auricomus* group behave very differently as regards their distribution within Finland—some of them being very widespread but often only occurring very scattered, others having a very restricted area, where they, however, may occur in large quantities. Astonishingly few seem to be common to Finland and Sweden; even microspecies with a maximum frequency in south-westernmost Finland do not, as a rule, occur in Sweden. Here, it is true, the study of this interesting group has only begun, but the province of Uppland, which lies so near the Åland archipelago, is—as a matter of fact—fairly well known in this respect; here Professor Nannfeldt and some co-operators among the Uppsala botanists have made extensive collections, although nothing has yet been published about them, nor about the Swedish *auricomi* at all.

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- , 1956, Variation in the apomictic microspecies of Alchemilla vulgaris L. II. Progeny tests in agamotypes with regard to morphological characters, *Ibid.*, **1956**, 400-404.
- , 1957, Variation in the apomictic microspecies of Alchemilla vulgaris L. III. Geographical distribution and chromosome number, *Ibid.*, **1957**, 413-422.

Mr. DANDY said that Dr. Hylander had given an excellent survey of work which had been carried out on the Scandinavian flora with which the British Isles were so closely connected and he had at the same time shown us that Scandinavian botanists are still very active in these lines of research.

Professor VALENTINE said he was sorry to hear that we have lost one of our few endemic species, *Primula scotica*. He asked whether Müntzing's genetical work on *Potentilla* had been related to taxonomy.

Dr. HYLANDER. In Scandinavia, according to Müntzing (1958), "diploid and hexaploid *argentea* types (with $2n = 14$ and 42 resp.) are predominating and morphologically fairly easy to distinguish. They correspond rather well to the taxonomical sub-units *P. argentea* s. str. (L.) and *P. impolita* Wg. distinguished by Marklund However, the taxonomy of the collective species is complicated, not only by the occurrence of sexual, diploid strains in the Mediterranean region but also by octoploid apomicts in middle Europe and tetraploid and pentaploid apomicts in Sweden".

Mr. F. R. HORNE asked if there was much polyploidy recorded in *Sorbus discolor*, as he had found that *S. aucuparia* planted around it had not produced berries. He also wished to know the natural distribution of *Sorbus intermedia*, a beautiful tree which ought to be planted more often.

Dr. HYLANDER said that *Sorbus intermedia*, which is a tetraploid and according to Liljefors (1955) may have arisen from *S. aria* × *torminalis*, is confined to south Sweden (mainly along the Baltic coast), southwesternmost Finland, Bornholm and the East Baltic countries. It is not indigenous in Norway. The apomictic Scandinavian microspecies are partly triploids, partly tetraploids.

Professor BÖCHER wanted to know if there was a triploid in the *Ranunculus auricomus* complex of microspecies.

Dr. HYLANDER replied that, according to the researches by Rousi (1956) on a considerable number of Marklund's microspecies from Finland, the majority were tetraploid ($2n = 32$), while two were pentaploid; in one specimen of a normally tetraploid species some roots showed $2n = 48$. The high-arctic *R. auricomus* var. *glabratus* from Nova Zemlya, Greenland and a few places in northernmost Scandinavia with $2n = 16$ seemed to be worth the rank of an independent species, since it also looks very distinct morphologically; it has in fact been called *R. lyngei* H. Smith although this name has not yet been validly published. Professor BÖCHER remarked that meiosis in the Greenland plant was apparently similar to that observed in the tetraploid.

Professor CAMP asked whether Hylander took into account the Post-Pleistocene xerothermic period when considering nunataks? Professor Fernald did not do so in N. America and this made his conclusions debatable, especially in view of the cold period which followed the xerothermic optimum. It was also difficult to explain the erratic boulders found on long cherished nunataks! Dr. HYLANDER said that this and several other problems concerning the "overwintering hypothesis" had recently been discussed in the year book of the Swedish Natural Science Research Council.

For the postglacial time in Scandinavia, Sernander had suggested that there had been an alternation of dry and humid, as well as warm and cold periods.

EVOLUTION IN THE PTERIDOPHYTA

I. MANTON

(University of Leeds)

INTRODUCTION

Evolution in the Pteridophyta, even in the cytological sense, is now a subject too large to be discussed fully in one hour and it will therefore be necessary to select a limited slice of it, ignoring the rest until some later occasion or occasions. Hybridity in ferns is one such convenient slice and I propose to limit my remarks on this occasion to it.

In the current number of the *Journal of the Torrey Botanical Club* the statement is made (Knoblock, 1959) that there are 158 reported fern hybrids; a statement about which the author promises to write a separate paper. This number, at first sight, is rather a peculiar one and it will be a matter of great interest to hear more of this author's views upon it. One must suppose for the time being that it is based on herbarium records thought to be hybrids by one or more taxonomists, since in any other relation the number is either too large to refer to experimentally authenticated hybrids or too small to be any guide to the number of hybrid ferns which must actually exist in nature. Among 10,000 odd named species, many of which are undoubtedly species-complexes, something between 5,000 and 50,000 species-hybrids must exist. Not all of these will ever be found but many more have in fact been collected than have been recognised, and one effect of the present communication may perhaps be to suggest why this has come about and why an attempt to rectify it might be rewarding.

SOME CONSEQUENCES OF THE FERN LIFE-HISTORY

It may perhaps assist at the outset to draw attention to some commonly held misconceptions which in this particular group have contributed greatly to prevailing uncertainties. The facts of life history of a fern are of course well known, but not all the consequences following on these facts. Thus the hermaphrodite potentialities possessed by all prothalli from homosporous ferns (i.e. the great majority of all ferns) does NOT mean that these are habitually self-fertilised. In certain cases, of which the bracken (*Pteridium*) is the best known, self-fertilisation is actively prevented by means of a physiological incompatibility mechanism; self-sterile clones can then be set up horticulturally by subdividing single prothalli. Far more commonly self-fertilisation is discouraged if not prevented by a marked difference in the age

or state of maturity at which the organs of the two sexes are developed. A young prothallus will always produce antheridia long before it is mature enough to bear archegonia and if impeded in its growth by being overshadowed by its neighbours or in other ways it may never reach the female condition. Such stunted prothalli may be exceptionally vigorous in production of male cells and it is very often these which in fact are responsible for fertilisations, since by the time that a gametophyte has become fully female its own production of spermatozoids may have ceased. This is true not only in culture but also in nature where niches suitable for prothallial growth (cracks between stones or under fallen logs) are commonly crowded with prothalli from wind-blown spores in very different developmental states. The resulting population of sporophytes is therefore always a mixture in which some individuals are doubtless from self-fertilisations of single prothalli but the great majority are from cross fertilisations between an egg and a spermatozoid from a different prothallus which, in a certain proportion of cases will have belonged to a different species of fern.

Fern cultivators, especially during the 19th century when ferns enjoyed a considerable vogue as ornamental plants, were familiar with the practice of sowing mixed spores of different species together in the hope of securing hybrids. In some cases this did, and still does (for a good example, see Darling, 1957) have this effect through far less commonly than has sometimes been supposed. Some measure of incompatibility between the gametes of different species is very common and even in well-known hybrids such as *Asplenium germanicum* (auct.) which has frequently been recorded in nature the intrinsic incompatibility between the 2 parents can, under cultural conditions, only be overcome by inseminating an average of 50 prothalli for every hybrid successfully achieved. Very large populations of prothalli must therefore be used if reliance is to be placed on random matings in mixed cultures and it is probable that in nature a special circumstance favouring the production of even difficult hybrids is a mixture of prothalli of such a kind that those of one species very greatly outnumber those of the other.

Under other conditions the mixing of prothalli of different species may actually encourage selfing, merely by reducing the frequency of individuals of the same species at different stages within easy reach of each other. In that case the cultivator may be seriously misled by the operation of simple genetical laws. Every prothallus is descended from a different spore the production of which has been preceded by meiosis, the cytological process responsible for genetical segregation. A prothallus which becomes self fertilised gives rise at once to a sporophyte which is *homozygous* for every character no matter how heterozygous may have been the sporophyte from which the spore came. A prothallus which is cross fertilised produces a sporophyte which is *heterozygous* for any characters in which the two prothalli

involved as gamete donors differ. In many cases this will not make any detectable morphological difference but sometimes the effects can be very startling.

SEGREGATION AS A SOURCE OF CONFUSION

Genic mutation is an ultimate source of genetical diversity in ferns as in other plants and animals, and here, as elsewhere, undesirable mutations, if recessive, do no harm as long as the individuals carrying them are heterozygous, in which state even a potentially lethal mutation may escape detection. Every recessive character in the homozygous condition is, however, at once revealed and there can be no doubt that in the horticulture of ferns many of the morphological monstrosities so beloved of 19th century collectors are, in fact, recessive mutants which have suddenly become visible either in the wild or in culture in consequence of an occasional self-fertilisation in a normally outbreeding but heterozygous fern population. The amateur literature is full of instances in which certain localities are recorded as notoriously good for "finds" of this kind and anyone who has had occasion to raise spores gathered from wild plants as frequently as I have will have personal experience of the sudden arrival of unexpected monstrosities in the progeny of specimens of perfectly normal appearance. If such monstrosities arise in cultures which have been subjected to experimental treatment of any kind it is only too easy to mistake their origin and attribute them to the treatment. To quote an actual example from my own experience, I once tried to obtain an autopolyploid from the species of *Dryopteris* from Cyprus which yielded the spermatozoid on the frontispiece of my book. The spores had been gathered from a wild plant and the prothalli at an early age were subjected to colchicine treatment and then left to mature. As they did so a proportion of manifestly peculiar young sporophytes appeared which were carefully segregated and watched with eagerness in anticipation of a successful experiment. Fortunately, an untreated control culture had also been kept, in which similar plants began to appear with a frequency bearing a suspicious resemblance to 1:3. As the plants grew older it became apparent that in both cultures the peculiar plants were of similar character, having parsley-like leaves wholly unlike those of the parent plant which must therefore have been heterozygous for this particular mutant character in the wild condition in Cyprus, from which island, however, no previous or subsequent herbarium evidence exists to indicate that local populations are of this nature.

It is quite certain, from the many occasions on which I have examined monstrosities thought to have been produced in horticulture as hybrids from sowings of mixed spores and found them to be cytologically in complete conflict with such an origin, that many mistakes have in fact been recorded in the horticulture of ferns by which segregation has been mistaken for signs of successful hybridity.

The herbarium botanist dealing with dried specimens of unknown parentage collected in nature can readily be pardoned for making the same mistake and I have little doubt that some at least of the 158 recorded fern hybrids will turn out to be peculiar mutants.

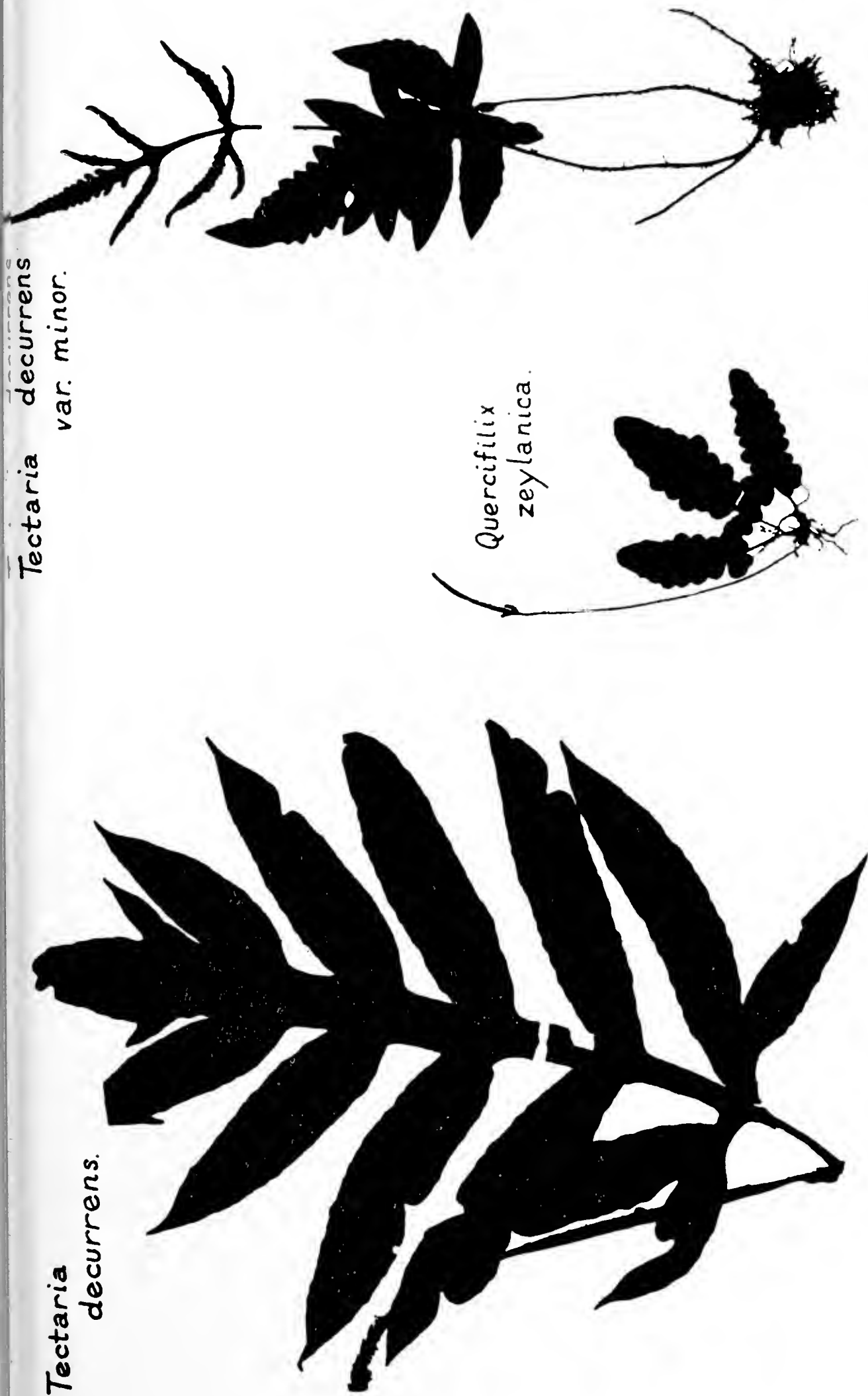
HYBRIDS MISTAKEN FOR SPECIES OR VARIETIES

The great majority of actual hybrids which survive for long enough to be collected are not peculiar at all. Some of them when first encountered are mistaken for good taxonomic species or varieties. This has been done in every flora which I have closely analysed. In the European flora the binomial treatment of hybrids such as *Asplenium germanicum*, *Polystichum illyricum*, etc., records a past uncertainty as to their specific nature which is no longer felt. In the flora of Ceylon there was *Tectaria decurrens* var. *minor* of Beddome (see text-fig. 1) which we now believe to be *Tectaria decurrens* × *Quercifilix zeylanica* (Manton and Sledge, 1954). In the flora of Malaya there was *Egenolfia singaporensis* Holttum which is undoubtedly (as Holttum himself suggested as possible) *Egenolfia appendiculata* × *Bolbitis diversifolia*; there is also *Athyrium cordatum*, a sterile hybrid of entirely uncertain parentage. In the African flora there is *Asplenium akimense*, a hybrid probably involving *A. variabile* with some other as yet unidentified species. These cases have all caught the eye of the collector by possessing morphological characters different from those of other described species in the area, and since more than one specimen has in each case been found a hybrid origin has not been seriously considered. There are, however, several ways of obtaining multiple specimens of hybrid ferns in nature of which repeated resynthesis is only one. (For further discussion see p. 111). That these are not good species is at once clear from their cytological behaviour.

It cannot be too frequently stressed that chromosomes under some conditions are a great deal more sensitive to taxonomic boundaries than are the eye and intuition of a human taxonomist, and had they been consulted earlier there need have been no uncertainty about the true nature of any of the cases listed in the last paragraph and of innumerable others of comparable kind. Since these remarks are addressed to the B.S.B.I. and not merely to the professional botanists in it, an explanatory digression may perhaps be permitted here for the benefit of the non-professional members of my audience.

A CYTOLOGICAL DIGRESSION

The first thing that a cytologist needs to find out with respect to an unknown plant is its chromosome number and in many cases this will suffice to confirm or refute an interpretation of its nature (i.e., whether hybrid or otherwise) based on other evidence. When fertilisation occurs in an archegonium, the



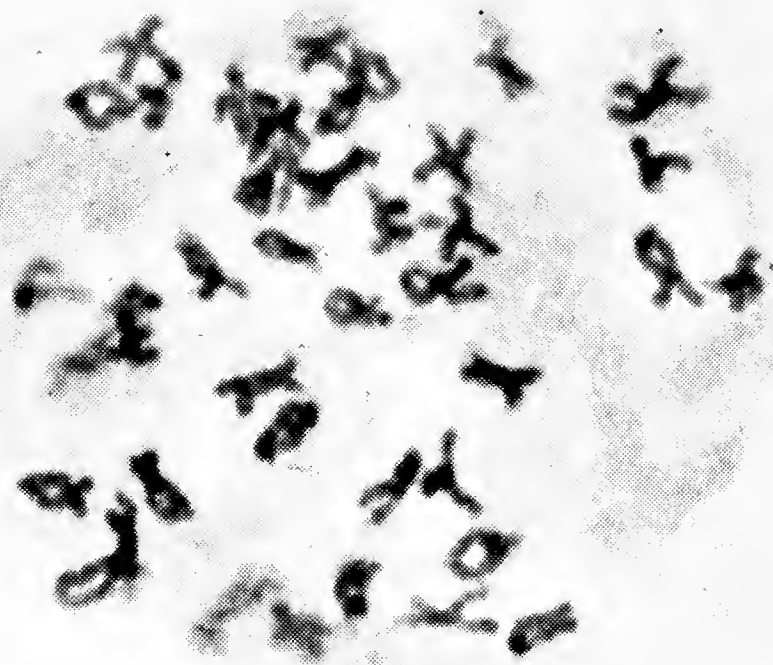
Text-fig. 1. An example of a hybrid mistaken for a variety of one of the parent species. *Tectaria decurrens* (left) and *Quercifilix zeylanica* (centre) are widespread in Ceylon. "*Tectaria decurrens* var. *minor*" (right) is an undoubted hybrid found as single plants in close association with *Quercifilix* populations but much larger. It is almost certainly the hybrid between these two species though it has not yet been artificially synthesised. Silhouettes of wild plants from the collection of Dr. W. A. Sledge all reduced to approximately $\frac{1}{2}$ natural size; the fertile fronds of the very large *T. decurrens* are similar to the sterile frond depicted although with slightly narrower segments; the extreme dimorphism shown by *Quercifilix* is also present in the hybrid which is quite sterile.

nucleus of a spermatozoid fuses with that of the egg and therefore every cell in the vegetative parts of the fern plant which results must necessarily have the sum of the nuclear contributions from the two parents unless something abnormal has occurred. The chromosomes may be counted either in the vegetative or reproductive tissues. If the number found is in agreement with expectation from previous knowledge of the chromosome numbers of the putative parents this does not in itself prove hybridity except in particular circumstances, but if the number found disagrees with expectation then an error of some kind has to be looked for. In the special circumstances in which the chromosome numbers of the two putative parents differ then the discovery of a third number which is the sum of these is very strong evidence indeed for the hybrid constitution of the plant under investigation.

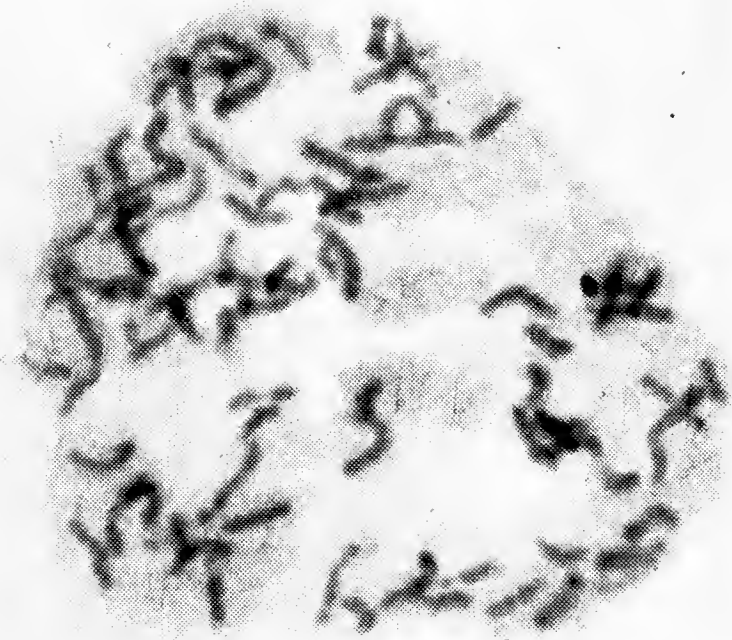
A considerably more powerful technique, since it can give unequivocal evidence even in cases in which no numerical difference exists between the parents of a putative hybrid is the analysis of chromosome pairing at meiosis. The chromosomes do not pair individually at the time of nuclear fusion but only at a much later stage, namely, in the young sporangia as part of the developmental sequence by which spore mother cells give rise to tetrads of spores. At the stage of meiosis at which chromosome pairing normally takes place, one of three different things may be found by which a hybrid differs from a true species. If the chromosomes of the two parents are very different qualitatively no pairing may occur at all even though the chromosome numbers may be the same in both parents and hybrid. *Bolbitis singaporensis* (Plate 6b) is an example of this and the very different appearance of the hybrid compared with *Egenolfia appendiculata* (Plate 6a) at exactly the same stage is very striking. At the other extreme is triploid *Osmunda regalis* obtained by crossing a normal with a horticulturally induced form with doubled chromosome number (for further details see Manton, 1950). Meiosis here reveals numerous groups in threes known as trivalents and though trivalent pairing is never complete in this material which is undoubtedly "autopolyploid" from its mode of origin the pairing is always sufficiently nearly complete to lead to recognition of autopolyploidy even if encountered in the wild in an unknown plant. A third alternative which is encountered in very many artificially synthesised species hybrids is for a combination of pairs and univalents of such a kind as to give important information on the nature of the relationship between the two species which have been crossed. An example of this is illustrated in Plate 7 and others will be discussed below.

Determination of chromosome number and chromosome pairing absolutely requires living material in a healthy state; herbarium specimens cannot be used. On the other hand, one consequence of any of these types of irregular meiotic behaviour is readily ascertainable on dried material, namely abortive or mis-shapen spores. Hybrids with meiotic irregularities of any

PLATE VI.



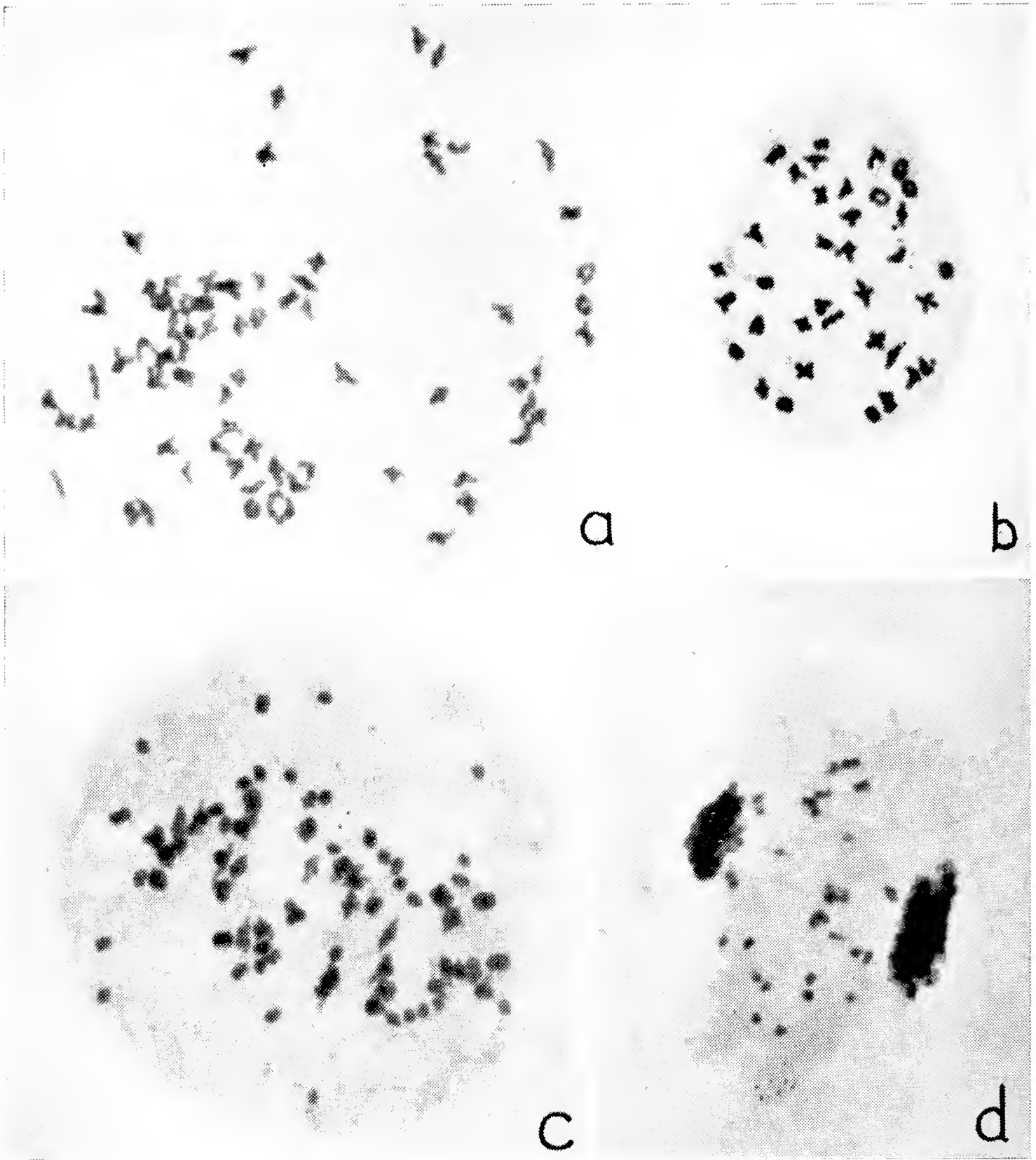
a



b

Example of meiosis in a hybrid between two species which are not closely related although possessing identical chromosome numbers; photographs of spore mother cells at the stage of meiosis in which chromosome pairing is most clearly displayed, magnified $\times 1000$. Fig. (a), one of the parent species, *Egenolfia appendiculata* with 82 chromosomes arranged as 41 pairs (after Manton and Sledge, 1954). Fig. (b), the same stage in *Bolbilis singaporensis* from Malaya a sterile hybrid almost certainly involving *E. appendiculata* and *Bolbilis diversifolia*, showing 82 unpaired chromosomes

PLATE VII.



Examples of chromosome behaviour in a wild hybrid between two closely related parent species possessing different chromosome numbers in a polyploid series. All magnified $\times 1000$. Fig. (a), Meiosis in *Asplenium adullerinum* from Austria, a tetraploid with 72 pairs of chromosomes. Fig. (b), *Asplenium viride* from Austria, a diploid with 36 pairs of chromosomes (after Lovis, 1958, unpub.). Figs. (c) and (d), *Asplenium proskarskianum*, from Austria, the wild triploid hybrid between these two species, showing approximately 36 pairs and 36 univalents in Fig. (c), and an array of lagging chromosomes scattered on the spindle in Fig. (d); the pairs are *A. viride* chromosomes, the laggards are from the unpaired set derived from *A. adullerinum* but originally belonging to a different diploid species (in this case believed to be diploid *A. trichomanes*). The parentage of the wild *A. proskarskianum* has been confirmed by artificial synthesis of this hybrid which is also important for confirming the genetical affinities of the tetraploid species *A. adullerinum*.

kind show a considerable amount of, and often complete, sterility from spores and had ripe sporangia been present at the time of gathering and had the spores been routinely examined under a low power of the microscope none of the hybrids listed above could possibly have been mistaken for species.

SPORE IMPERFECTIONS

Defective spore production is actually the most powerful as well as the most easily observed sign that something is wrong with a particular plant of the kind which should preclude its use as the type of a species. Had this been understood earlier some classic mistakes even by the great Linnaeus would have been avoided. A particularly unfortunate Linnean "species" is *Polypodium cambricum* included in the *Species Plantarum* as if on a level with *Polypodium vulgare* L. *Polypodium cambricum* however bears neither spores nor sporangia and has been noted for their absence for nearly two centuries. Its leaves are of the monstrous type beloved of collectors who have treasured it in culture. It is undoubtedly a monstrosity of the type already discussed.

Had spores been examined in either *Bolbitis singaporensis*, *Athyrium cordifolium*, *Tectaria decurrens* var. *minor* or *Asplenium akimense* their defective nature would at once have been detected in spite of a booby trap specially prepared by Nature for unwary taxonomists, namely, that some very successful hybrids may not only show extra hybrid vigour but possess accessory means of vegetative propagation by means of which local multiplication of individuals can occur in spite of defective sporulation. This is so in both *Bolbitis singaporensis* and *Athyrium cordatum* both of which can reproduce quite vigorously by means of adventitious buds at the bases of the leaf lamina. In such a case the distinction between the sterile hybrid existing as a clone and the local population of sufficient size to justify binomial recognition is a narrow one which nevertheless is generally fairly easy to resolve provided that the facts are known.

THE SPECIAL CASE OF APOMIXIS

Obligate apomicts are, however, a special category which must often be treated differently. These can reproduce and form local populations on a scale exactly comparable with that of sexual species, by means of diplospores which, in varying proportions, are produced amongst the abortive spores which have attempted normal development. Such species are always hybrids, as far as present evidence goes, and they are more often triploid than at any other level of nuclear complexity. In all floras so far investigated on a statistical scale (Europe, Madeira, Ceylon, Malaya, Africa) they represent from 5-10% of the described species. Table 1 lists the cytologically authenticated cases investigated up to 1954 when the table was prepared for the Paris Congress; more have been added since without changing the

TABLE I
POLYPLOIDY IN APOGAMOUS FERNS

$2n$	$3n$	$4n$	$5n$
2	15	3	3

Summary of 23 cases of apogamous ferns investigated up to 1954 and compiled from Manton 1950, Manton and Sledge 1954 and Manton 1954.

Note the great preponderance of triploids

general pattern and in any case these are only a tiny fraction of the apogamous species which exist. They are valid species in every vegetational sense but woe betide the splitter who tackles them in ignorance of their life history. Where every local mutant can become a population and where further hybrids with sexual species can also occur, each with the capacity for local multiplication by virtue of the apogamous tendencies transmitted by its male parent, too narrow a concept of species will produce an uninterpretable forest of names, though if this pitfall is avoided, the great majority of apogamous specimens can be referred with certainty to well defined populations which can usefully be named.

MORE ORDINARY CHARACTERS OF HYBRIDS

Where interpretation is not complicated by apogamy a range of morphological expressions of hybridity is to be expected. True species hybrids tend to occur as single plants among populations of other species. As such they may attract attention by being different from other members of the fern populations among which they grow, by being intermediate in character between two very dissimilar species, or by having a mixture of characters which is unusual. This is, however, by no means the only possible form. In extensive programmes of artificially synthesised hybrids which have been carried out by numerous workers in Leeds during the last ten years we have frequently encountered cases in which the more conspicuous morphological criteria of one species may behave as complete recessives in hybrids involving another species. In such a case the hybrid may resemble one of its two parents so much that it may be difficult or impossible to decide except on cytological criteria that hybridisation has occurred at all. The best case of the kind to have been placed on record is G. Panigrahi's work on *Cyclosorus* (Panigrahi and Manton, 1958) in which a very distinct diploid species having an erect versus a creeping rhizome, no anthocyanin pigment versus copious pigment, conspicuously decrescent fronds versus non-decrescent fronds proved to be recessive in all these three characters with the result that morphologically the F_1 hybrid could scarcely be distinguished from the other parent.

There is not the slightest doubt that very many hybrids have been collected and placed unrecognised in herbarium covers belonging to otherwise perfectly good species for this reason. Further, it is probably a valid generalisation that in any closely

knit species-complex of several components, the herbarium botanist is likely to detect first those representatives having well-marked recessive characters and to give precedence to these in the designation of species owing to the ease with which they can be picked out of a crowd.

It should not be forgotten that fern spores are very efficient propagules, in every sense of the word. They are both the principal means of building up populations in the great majority of ferns and they are almost the sole means of dispersal to new areas. Owing to their small size, wind dispersal is very effective, and ferns in consequence play a conspicuous part as early colonisers of areas as diverse as bombed sites in London (Bracken) or the devastated volcanic surface of an oceanic island such as Krakatoa. In these circumstances the genetical implications of their capacity for self-fertilisation already discussed may be of paramount importance. With long-range dispersals, the spore of any particular species must almost always arrive singly and if the species is to become established the prothallus in the first instance must necessarily be self-fertilised if not apogamous. The resulting homozygous population will thereafter breed true and show all the characters which the original spore may have carried no matter whether these were dominant or recessive in the previous population. In the extreme case, dispersal from a heterozygous population in one area can lead to establishment of many morphologically different (but true-breeding) populations in other areas merely by this process. Whether such populations will deserve or require taxonomic recognition will depend upon the usual criteria of population size, degree of distinctness, capacity for effective competition, etc. Only a tiny fraction, it must be supposed, of populations which owe their initiation to such single-spore introductions to new areas will, in fact, become sufficiently differentiated to be treated as species, though it cannot be doubted that some will and that many have done so. In flowering plants on the other hand the propagule is the seed, a diploid and not a haploid structure. A single seed derived from a normally out-breeding population will almost certainly be heterozygous to some extent and though the population to which it can give rise will doubtless be poorer in biotypes than that in the parent area, the immediate establishment of a local pure line can scarcely occur. There is, therefore, perhaps a real difference between ferns and flowering plants in the ease with which groups of recessive characters can occur together, which may have had an effect on herbarium botany.

Whether this is the explanation or not, there can be no doubt that the degree of morphological difference between two related species is a most uncertain guide to the probable appearance of a hybrid between them. We have numerous cases comparable to that of *Cyclosorus* mentioned above in which the F_1 hybrid is so like one of two very dissimilar parents that the participation of the other is virtually undetectable except by the chromosomes

and breeding behaviour. At other times, when specific differences prove to be quantitative and multifactorial, the F_1 hybrid may be thoroughly intermediate in appearance. It may nevertheless again escape detection in the wild condition if it is mistaken for a link bridging the gap between the two species which are then commonly misinterpreted as only the extremes of a continuous range of variation. That this has occurred many times is shown by the vast number of species-complexes which cytological work has revealed, and in a few cases resolved, in the fern floras of temperate and tropical countries (for further literature see Manton, 1959, etc.). *Polypodium* is a well known example in which an extremely distinct south European diploid (*P. australe* Fée) would long ago have been generally recognised as a good species had the intermediates which bridge the gaps towards the other European taxa been recognised for the hybrids which they undoubtedly are. Routine examination of spores wherever a wide range of morphological diversity is thought to exist within a species would not only add to the list of recognised hybrids but in so doing would undoubtedly remove some of the difficulties of the herbarium botanist who always wants, if he can, to find natural boundaries before naming his specimens.

Spore examination alone is, however, not always enough. Some sexually reproducing species hybrids are fertile and in that case the only test of hybridity possible is either to sow the spores and detect genetical segregation or to resynthesise the hybrid after discovering its parents. The best recorded instance among ferns in which both these things have been done is the now classic work of Trevor Walker (1958) who was able to show that some very vigorous and polymorphic populations of *Pteris* in Ceylon, to which the specific name of *P. otaria* had been given by Beddome, are in fact of hybrid origin and incapable of breeding true. In this case the genetical (mutational) diversity between the parent species (*P. multiaurita* and *P. quadriaurita*) has far outstripped their cytological diversity and vigorous 'hybrid' but not true-breeding populations are produced when the ecological and geographical barriers are breached by human interference. In such a case the herbarium botanist with only dead plants to study is almost helpless, and although our experience with several floras now suggests that this is a somewhat extreme case of a relatively uncommon kind there can be no doubt that some fern hybrids, unable to breed true, but not unable to breed, constitute a definite if small proportion of the taxonomists' named species.

NUMERICAL ASSESSMENT

There are, therefore, many obstacles to an accurate numerical assessment of fern species-hybrids and the only reliable method is indeed the experimental one, though this, unfortunately, can only be applied on a very small scale. If one considers the British flora, however, as a sample of one of the most intensively studied areas from this point of view, we have the following list of species

hybrids, each fully attested as such by cytological or experimental methods or both. There are some 20 items in a flora of little over 40 species. Extrapolating from this to a world population of some 10,000 species we reach the number of 5,000 which was quoted as a probable minimum in the opening paragraph.

TABLE II
CYTOLOGICALLY AUTHENTICATED EUROPEAN HYBRID FERNS*

	<i>Wild</i>	<i>Synthesised</i>
<i>Dryopteris filix-mas</i> × <i>D. abbreviata</i>	—	3n
<i>D. dilatata</i> × diploid <i>D. dilatata</i>	3n	3n
<i>D. spinulosa</i> × diploid <i>D. dilatata</i>	—	3n
<i>D. cristata</i> × diploid <i>D. dilatata</i>	—	3n
<i>D. spinulosa</i> × <i>D. dilatata</i>	4n	—
<i>D. spinulosa</i> × <i>D. cristata</i>	4n	—
<i>Polystichum aculeatum</i> × <i>P. lonchitis</i>	3n	—
„ „ × <i>P. setiferum</i>	3n	3n
„ <i>braunii</i> × <i>P. setiferum</i>	3n	—
„ „ × <i>P. aculeatum</i>	4n	—
<i>Woodsia ilvensis</i> × <i>W. alpina</i>	3n	—
<i>C. fragilis</i> 4n × <i>C. dickieana</i>	4n	—
<i>Polypodium interjectum</i> × <i>P. vulgare</i>	5n	5n
„ „ × <i>P. australe</i>	4n	4n
„ <i>vulgare</i> × <i>P. australe</i>	3n	3n
<i>Asplenium adiantum-nigrum</i> × <i>A. onopteris</i>	—	3n
„ „ × <i>A. cuneifolium</i>	—	3n
„ <i>obovatum</i> × <i>A. onopteris</i>	—	3n
„ <i>adiantum-nigrum</i> × <i>A. obovatum</i>	—	4n
„ <i>trichomanes</i> 2n × <i>A. septentrionale</i>	3n	3n
„ <i>trichomanes</i> 2n × <i>A. adulterinum</i>	3n	3n
„ <i>adulterinum</i> × <i>A. viride</i>	3n	—
<i>Scolopendrium hybridum</i> × <i>S. hemionitis</i>	—	3n

*This list includes only such cases as can be quoted from my own personal experience of the cytology. Some additions could be made within *Asplenium* from the publications of D. E. Meyer.

NEW SPECIES OF HYBRID ORIGIN

Even this is, however, not the whole story. An F_1 species-hybrid such as *Egenolfia singaporensis*, completely unable to pair its chromosomes at meiosis and, therefore, limited to local clone formation by purely vegetative means if it is to reproduce at all, is clearly not a species in any generally accepted sense of the word. It is, nevertheless, the raw material out of which a species

can be made. Given long enough or, alternatively, if this hybrid is resynthesised sufficiently often under the varying circumstances in which the parental species may meet, sooner or later an accidental misdivision at a critical moment may produce a local chromosome doubling. If this takes place in the path of the fertile tissues, quite suddenly partners will be found for every chromosome. Meiosis will be regular instead of irregular and spores will be formed with twice the chromosome number that would otherwise have been expected. Such spores are not only viable but will perform their full life history without ever again being embarrassed by reproductive irregularities. They can build up local populations and disperse to new areas like any other sexual species, but since the morphological or physiological characteristics present in the original sterile F_1 are retained without segregating, such populations can either resemble one of the parent species very closely (except for cytology) or be strictly intermediate between the two parent species, or display some apparently new combination of attributes.

There is active controversy at the present time whether in all these cases a new specific name is needed or whether a new name should be limited to the last type only. There is no simple answer to this question though I have discussed it and made recommendations about it elsewhere (Manton, 1958). The facts, nevertheless, indicate that provided such a doubled F_1 (generally called an amphidiploid) is sufficiently vigorous to be able to extend its range, without which the question of species will normally not arise, it will usually do so by virtue of possessing some attribute or attributes different from those of either parent and by virtue of which it can take possession of an ecological or geographical niche of its own. It will necessarily also display a sterility barrier with both its parents, since hybrids with them will have an intermediate chromosome number and only partial chromosome pairing. In all biological senses it is a true species, no matter what its morphology may be and irrespective of what the herbarium botanist may think.

TEMPERATURE AND TROPICAL FLORAS

But are such species important? It may perhaps be of interest to assemble the ascertained facts for the ferns in the British flora, obtained from the evidence of chromosome pairing in species hybrids and in other ways (e.g., induced apogamy, Manton and Walker, 1954). Out of 40 odd species at least half, and these not the least familiar, undoubtedly originated in this way as amphidiploids. In several cases, e.g., *Dryopteris filix-mas* and *Woodsia alpina*, one of the parents seems to be actually another species still in our flora. In a few cases we still possess both parental types. The hexaploid *Polypodium interjectum* is the best known example of this. Occasionally we have neither of the parent species in our own flora but can detect an ancestor of a common British species as a common or rare species in some

other country. The most extreme example of this is the recent detection on unequivocal evidence, that a common diploid *Polypodium* of eastern North America, *P. virginianum*, is in fact one of the ancestors of tetraploid *Polypodium vulgare* of Europe.

TABLE III
EUROPEAN FERNS WITH POSITIVE EVIDENCE FOR A HYBRID
(AMPHIDIPOID) ORIGIN

Dryopteris	felix-mas (= D. abbreviata × unknown)
„	dilatata (= diploid D. dilatata × unknown X)
„	spinulosa (= diploid D. dilatata × unknown Y)
„	cristata (= unknown Y × unknown Z)
„	villarsii (= diploid D. villarsii × unknown)
Polystichum	aculeatum (= probably P. setiferum × P. lonchitis)
Woodsia	alpina (= W. ilvensis × unknown, possibly W. glabella)
C. fragilis	6n (= C. fragilis 4n × unknown)
Polypodium	interjectum (= P. australe × P. vulgare)
„	vulgare (= P. virginianum × unknown)
Asplenium	adiantum-nigrum (= A. cuneifolium × A. onopteris)
„	adulterinum (= A. viride × diploid A. trichomanes)
„	obovatum (= A. onopteris × unknown)
Scolopendrium	hybridum (= S. hemionitis × unknown)

Such information is not confined to temperate regions. We have numerous investigations completed or partly completed on selected groups of species from tropical countries and we find the same thing on, if anything, an even bigger scale. The work on *Cyclosorus* begun by Panigrahi as previously mentioned (Panigrahi and Manton, 1958) has been continued by Ghatak whose work is about to be published. The diploid ancestor of *Cyclosorus parasiticus* and several other related tetraploid species, originally gathered in Ceylon and traced with difficulty in a few herbarium specimens from Malaya and Borneo, has, under another specific name turned up in Africa. It is the same species to judge by its genetical behaviour in both areas and we are now advising systematists to ignore the minor morphological differences in the different geographical areas and to call them all by the oldest name attributed to any, which is *Cyclosorus contiguus*. It is interesting to compile a map of the distribution of this species as it is at present known, though this will doubtless be incomplete. As we may see in Text-Fig. 2, we have a row of isolated occurrences lying almost in a straight line close to the Equator.

The discovery of one ancestral type is a key to only a small part of the evolutionary history of the group to which it belongs since tetraploids are many and there must likewise have been many more diploids than we at present know. The first to be detected owes this distinction almost certainly to its possession



Text-fig. 2. Distribution of known samples of the only diploid so far discovered in the *Cyclosorus parasiticus* complex; black spots are sources of cytogenetically investigated living specimens, circles are localities inferred from herbarium citations, redrawn after Ghatak, 1958 (thesis, unpub.).

of conspicuous recessive characters as already explained. The diploid bearers of dominant characters may, for all we know, be lying unrecognised within the herbarium covers labelled with the names of the tetraploid descendants or they may grow in other areas not yet adequately sampled or they may be extinct. Until we know more, the analysis of any one individual case can proceed no further. Nevertheless, in spite of incomplete knowledge the collective evidence is overwhelmingly clear that in tropical and temperate zones alike an endless succession of reproduction and hybridisation, with occasional chromosome doubling has been continually at work in the ferns as in other groups, to provide the raw material for the waxing and waning of populations and of species through the shifting climatic, geographic and ecological conditions of our changing world.

CONCLUSION

The topic of hybridisation in ferns is thus clearly not a minor or a trivial slice of the rather grandiose subject on which I was asked to speak, but a major component of the evolutionary history of all fern floras. It is, of course, not the whole story. On some future occasion it may be possible to enquire usefully into the general question of how chromosome numbers change in ways other than by mere multiplication of complete sets. Perhaps this also involves hybridisation, but, if so, how? Population genetics is another evolutionary topic about which evidence is accumulating in ferns as in other groups.

Perhaps I have said enough, however, to suggest that the Pteridophyta in general, and the ferns in particular, are not all fossils, living or otherwise, but are a very lively element in the

vegetation of to-day. They are evolving actively all over the world, and hybridisation is a major, though not the only, component factor in this process.

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Professor VALENTINE enquired why, since so much hybridisation was involved in the origin of the numerous amphidiploid species of ferns, introgressive hybridisation was almost absent? Was this in part due to the widespread sterility of triploid hybrids?

Professor MANTON said that the tetraploid species *Dryopteris spinulosa* and *D. dilatata* share one common ancestor and at least one population resembling a hybrid swarm is known to occur. An occasional prothallus may be backcrossed.

Dr. STANLEY WALKER said that there was no proof at present of introgression between these two species but if there is it is on the *D. dilatata* side. In Europe *D. dilatata* is very variable while *D. spinulosa* is very constant. In N. America the reverse was true, for *D. campylotrapa* (which is equivalent to *D. dilata*) is constant and *D. spinulosa* is variable, especially in leaf shape. Sowing spores of the hybrid has not yet given any indication of introgression.

Professor BÖCHER wondered whether the various base numbers of chromosomes in the fern genera was derived by fusion or loss?

Professor MANTON replied that in some few instances the chromosome number had fallen but in many it had risen. Only rarely is there any clue as to the mechanism.

Dr. GOODWAY enquired how important a rôle in fern evolution was played by autopolyploidy? He also suggested that it was unlikely that introgression would occur where the genomes are so distinct.

Professor MANTON said that she had realised that taxonomists had tended to stress autopolyploidy as a mechanism for evolution, but cytological studies have shown repeatedly that this is not the case. Dr. Lovis has obtained some evidence in *Trichomanes* for autopolyploidy together with some for amphidiploidy but there is no unequivocal evidence for it alone. Odd sporangia on a plant, it was true, may be autopolyploid but this is as far as we can be certain at the moment.

Dr. GOODWAY stated that while half the genomes of *Woodsia alpina* may have come from *W. ilvensis* this does not necessarily imply that the morphology of the ancestral form was identical with *W. ilvensis*.

Professor MANTON said that this was true and was something which required stressing.

Dr. S. WALKER pointed out in this connection that *Dryopteris dilatata* has diploid taxa on Madeira and on the Continent. They carry the same genome as one of the ancestors of *D. dilatata* but are themselves morphologically distinct. The ancestral diploid may or may not have resembled these in morphology.

Professor CAMP said that he was particularly delighted to have heard Professor Manton's lecture as he had missed her lectures which were given recently in Montreal and Scandinavia. Especially interesting, he felt, was the prevalence of polyploidy in tropical ferns. He felt that this disproved the hypothesis of Løve [that polyploidy increased towards the Poles.—Ed.]. The evidence presented in Darlington and Janaki-Ammal's *Atlas* and that of *Solanum* bore this out; while the data Løve quotes from island floras is obviously not typical, nor would we expect it to be, as island floras are usually derived from the nearest land mass and are especially atypical in the Arctic. In addition, many diploid plants may yet be discovered in the Arctic. He went on to say that the loss of the flora in Europe during the Pleistocene was a very important factor in understanding present distributions.

In *Vaccinium oxycoccus* (where diploid, tetraploid and hexaploid series are known) the diploid species occur in the Arctic and in the mountains of N. America (but not Europe) and the allotetraploid is circumboreal. The same was found to be the case in *V. uliginosus*.

PHYLOGENY, GENETIC VARIATION AND PLANT BREEDING

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On considering the content of my contribution to this symposium I thought first that I should deal with the more academic approach to the origin of cultivated plants and, of course, give due consideration to that aspect of Darwin's work that is particularly pertinent to my theme, namely, the variation of plants under domestication. I concluded, however, that if I did this I should not be able to talk about the position as it exists to-day regarding the plant breeder's approach to the exploitation of genetic variability in the improvement of crop plants. This is really the reason for my being included in this symposium, and consequently I must concentrate on these matters which are fundamental to the breeder's work and tasks. Nevertheless, I trust you will not feel that I am not paying due and adequate acknowledgment to Charles Darwin, whose contributions to botanical thought you are honouring.

As a botanist who gravitated very early to the study of the botany of agricultural plants in general, and to the improvement of crop plants in particular, I have naturally had reason to consider Darwin's views, and especially those expounded in his *Variation of Animals and Plants under Domestication*. It is interesting for us to note how in Volume I he devotes such a small proportion of his book to cultivated plants and in his preliminary remarks he says, on page 322, "I shall not enter into so much detail on the variability of cultivated plants, as in the case of domestic animals. The subject is involved in much difficulty. Botanists have generally neglected cultivated varieties as beneath their notice Not a few botanists believe that several of our ancient cultivated plants have become so profoundly modified that it is not possible now to recognise their aboriginal parent forms. Equally perplexing are the doubts whether some of them are descended from one species or from several inextricably commingled by crossing and variation". We can be more definite than this with our present knowledge of some cultivated plants, although there are others which are still incompletely understood, and great contributions have been made by researches on phylogeny, cytology and genetic variation that can be used in plant breeding.

The improvement of plants must surely be one of the most ancient arts and experiments practised by man in his efforts to ensure that he can feed himself effectively and economically, and

it is to crop plants that this talk will be devoted because they provide some of the most illuminating examples of the scientific theses that we are considering. You will appreciate that, because plant breeding seeks to exploit genetic variation and direct it into desired combinations for particular purposes, a great deal of information has become available in some taxonomic groups in relation to evolutionary trends, phylogeny, taxonomy, cytology and genetics, and the use to which this knowledge is put is really the background of all plant breeding methods and techniques. The study of cultivated plants, and the problems concerned with their improvement, have naturally provided a great deal of evidence on theories of selection in different kinds of genetic populations, on adaptation and on evolutionary trends as they affect the relationship between plants and their environment. Of particular interest are the origins of cultivated plants, the source and extent of their genetic variability, and their capacity for further variation under domestication in the hands of the cultivator and the breeder. Indeed, we find ourselves immersed in the fundamentals of biology which so attracted Darwin, and which formed the background to so much of his thinking, experimentation, philosophy and ultimate statements on biological phenomena.

It is obvious that the origin of the cultivated forms of the plant group in which a breeder is interested in his attempts at improvement must be of vital interest as is the means by which the genetic variability which is available has arisen. The breeder must study the methods which operate without his interference, and see whether he can utilise these to concentrate genetic variation into the genotypes and the phenotypes which he considers will be improvements. The techniques by which he can achieve this in the most efficient way are, of course, the basis of the experimental biology which is plant breeding, and they embrace the teaching and methods of the scientific disciplines I have mentioned, and others such as physiology, pathology and statistics. These are the tools with which he strives to improve the cultivated forms of plants which have come into being in some cases over many thousands of years. The breeder tries to hasten the gentle pace of natural evolution, and to bring about changes that it is most unlikely will occur without any interference.

In his introduction to the *Variation of Animals and Plants under Domestication* Darwin says: "If organic beings had not possessed an inherent tendency to vary, man could have done nothing No doubt man selects varying individuals, sows their seeds, and again selects their varying offspring. But the initial variation on which man works, and without which he can do nothing, is caused by slight changes in the conditions of life, which must often have occurred under nature. Man, therefore, can be said to have been trying an experiment on a large scale; and it is an experiment which nature during the long lapse of time has incessantly tried". Scientific plant breeding is

certainly engaged in a gigantic experiment, and of course to-day we have a great deal more knowledge and more exact methods of experimentation than Darwin enjoyed a hundred years ago. Indeed, we are infinitely better placed to exploit this variability, to create new recombinants, to select more efficiently, and to do all of this more rapidly. We have replaced natural selection by systems of artificial selection, and have introduced controlled hybridisation as a potent means of creating variation.

It is in this substitution of the concept of merely using the natural genetic variation that offers in cultivation by the creation of a directed genetic variation, followed by controlled and objective selection, that the big change in plant breeding has taken place in the last 100 years. Darwin emphasised the importance of natural variation arising on which natural selection operated, in order to produce the great range of variation on which a plant breeder could work, and concluded that there was little else to be done for further improvement. Admittedly he recognised that plants have varied greatly under domestication, but he contended that man could not cause variability, and although Darwin admitted that man "has effected wonderful changes and improvements", he sees these only as the result of "adding up variations, often so slight as to be imperceptible by an uneducated eye". Nevertheless, Darwin recognised, as far as selection is concerned, that it can be either methodical and intentional, or unconscious and unintentional.

The realisation and exploitation of the effectiveness and possibilities of controlled and directed selection, as opposed to a more haphazard approach, and of the potentialities of creating genetic variability in terms of new genotypes by hybridisation, led to radical changes in plant breeding methods and to great improvements in many crops. On the other hand, it must be appreciated that the selection of some cultivated plants had been carried on for some hundreds of years before the beginning of the 18th century, and the first recorded artificial hybridisation of a plant (*Dianthus*) was effected in 1719. In the late 18th and early 19th centuries the early hybridists in crop plants embarked on improving plants by this means in this country, but it was the late 19th century that really ushered in the era of hybridisation for the improvement of crops, and this, of course, coincided with the analytical approach in experimentation founded on the new knowledge in many fields of biological science.

It is not possible to trace the changes in thought underlying the approach to plant breeding and in the techniques being used during the last 60 years. The overriding difference, however, is that the methods are now analytical and synthetic because the emphasis is on the manipulation of genetic variation in terms of genotypic constitution and phenotypic expression. Characters of economic importance are now recognised heritable entities, some of which are susceptible to genetic analysis and therefore of predictable behaviour. Agricultural varieties are definable in

terms of their genetic status, and improvement can be reduced to genetic change in terms of individual characters. The means by which such genetic changes may be brought about are better understood, even if the effort is not always successful, and the creation of suitable genetic variation by hybridisation is a purposeful experiment which is predictable within limits. But of even greater significance, perhaps, is the realisation of the power of directed selection and how this should be carried out, whether within populations that have been produced by controlled hybridisation, or in those occurring naturally. There has been a concentration of effort on narrower ranges of genetic variation accompanied by orderly synthesis in the breeding of new varieties which are for the most part genetically much more homogeneous than were the older varieties.

However, almost as a consequence of this tendency to concentrate on a narrow botanical basis, with the danger of restricting genetic variability, there has been a healthy and valuable corrective to try and ensure that the full available genetic variation is known and can be made available in breeding. Varietal collections are exchanged on an international basis, and most breeding work has a cosmopolitan aspect in an effort to ensure that valuable genes are not being omitted. Land varieties and unimproved stocks are being searched for neglected characters of value, while indigenous plant material growing in the wild is being collected and studied. The centres of origin and genetic variation have been explored in many crops and primitive forms not only studied for useful characters, but subjected to genetic analysis. This has resulted in very detailed studies of the taxonomy and phylogeny of families, genera and species and has led to new ideas on how to exploit the natural evolutionary sequence that has taken place in the synthesis of most advanced cultivated forms. There are several outstanding examples of this in important agricultural plants, as in cotton, bananas, potatoes, wheat, barley and oats where classical work on taxonomy and phylogeny has led to a much clearer picture of how best to exploit the available material, and has resulted in the development of entirely new and more potent breeding techniques. Much of this work emanated from Vavilov's monumental studies on the centres of genetic variation of cultivated plants which indicated that these centres, if not demonstrating the centres of origin, at least showed that they were the centres where the crops had been established for the longest time. Vavilov concluded from this aggregation of genetic variability in these ancient centres that genetic variability in the old established plants is primitive, and not the result of recent hybridisation. On the other hand, Vavilov recognised that valuable cultivated forms do occur far removed from the primary centres of origin, and that some of these are the result of plant breeding of long standing.

The taxonomy of cultivated plants is notorious for its difficulties, but the intensive study of some groups has done a

great deal towards a better understanding of the origin of genetic variation, of the concept of species, and the evolutionary significance of taxonomic groupings, as well as being helpful in understanding such important biological principles as the significance of polyploidy and the nature of genetic variability in natural and cultivated plant populations. Here one has the convergence and identification of ideas and scientific knowledge on the behaviour of uncultivated and cultivated plants with a unification of thought which helps the plant breeder enormously in learning how to handle his material and exploit it in the most efficient manner. Studies of this kind also emphasise the implications and consequence of the domestication and cultivation of a plant with particular reference to the size and genetic status of plant populations and the effect of various kinds of selection.

It is, therefore, essential to have a full appreciation of the cultivated forms of a crop with regard to their botanical origins, affinities, ecology, method of development in terms of hybridity and chromosomal complements including the occurrence of polyploidy. All these help to provide the breeder with the necessary knowledge on the biological and genetic status of the crop, and the nature of the ultimate taxonomic unit in which he is primarily interested, i.e. the agricultural variety. It is possible, by using this knowledge, not only to decide at what level to establish a breeding programme in terms of the taxonomic units that it will be necessary to use, but decisions can be reached regarding the utilisation of the various forms of breeding techniques, with particular reference to exploiting hybridisation. For example, the method of evolution and the taxonomic relationships based on genome differentiation and the genetic status of the taxonomic units, including agricultural varieties, gives the general pattern of genetic differentiation and character distribution. Decisions can be made whether to confine a breeding programme to agricultural varieties, and if so to particular groups of these, or whether it is necessary to go outside the narrower taxonomic groups and use the variation in other species or genera. Finally, it can be decided whether, for certain purposes, it is necessary to go back to primitive forms or wild progenitors to seek special characters, and whether repeating the early stages of evolutionary development offers possibilities.

All the major biological principles and concepts that I have so far mentioned imply a considerable amount of genetic and cytological research, and this has provided the basic knowledge on hereditary behaviour which is fundamental to all plant breeding work. The genetic architecture and status of a particular crop with particular regard to its agricultural varieties, and how these have arisen or have been developed, give a good guide to what has been called the "evolutionary prospects" of the crop. One can judge what is likely to happen to a crop in cultivation if left to its own devices, what it is possible to do for its improvement, and how this can be done by developing new cultivated

forms that can be handled agriculturally. Ultimately, therefore, the building up of a body of information on character heritability and gene control becomes necessary, and the manipulation and exploitation of genetic variation depend on the method and kind of genetic control.

It has only been possible for me to speak in the most generalised terms on the applications of these fundamental biological principles to the improvement of agricultural plants, but I should like to conclude by illustrating some of my remarks with reference to wheat breeding. I have chosen this crop because not only is it one of world-wide importance and therefore familiar to you, but it exemplifies the utilisation and application of all the branches of study that I have considered. Few groups of plants have been studied so intensively as wheat, and the study has been most rewarding from the point of view of phylogeny, taxonomy and cytogenetics, and this is reflected in the most recent ideas on the breeding of this crop.

The genus *Triticum* is one of several important genera that occur within the sub-group Triticinae of the Hordeae. Like some of the genera of the Triticinae it exists in the diploid, tetraploid and hexaploid forms and therefore shows a polyploid series. The primary centres of genetic variation are in the Mediterranean area and in Asia Minor, and it is interesting to see how, with the development of polyploidy in this genus, the distribution extends from the primary concentration which is also the centre of primitive forms in related genera. In the diploid forms there are wild and cultivated species, and the genetic variability is restricted when one compares it with most of the tetraploid species. In addition to the wider range and distribution of the tetraploids there is also a greater variability with a larger number of recognised species, and among these species there are some important and widely distributed and extensively cultivated forms, whereas in the diploids the cultivated forms are almost in the nature of relicts. Finally, among the hexaploid species we have one with a considerably wider range and distribution—*Triticum vulgare* (= *aestivum*)—the most widely grown and successful species. This species also has a great range of variability in terms of cultivated forms while the number of agricultural varieties runs into many thousands. It is interesting, however, that there are hexaploid forms which do not show either a wide range of cultivation or the evolution of many botanical types, and for the most part the highest-yielding agricultural varieties occur in *T. vulgare* which is the most productive wheat cultivated to-day, contributing as it does the bulk of the world's crop.

The genus *Triticum* illustrates very clearly the concept of genomes and the occurrence of the A, B, G and D genomes is fairly easily discernible from the ear morphology, while it is interesting to note that wild forms occur only at the diploid and tetraploid levels with genome structure A A or A A B B. The cultivated tetraploids have either the A and B, or the A and G genomes, and the hexaploids have the constitution of AABBDD.

There is considerable intergeneric fertility between the genera in the *Hordeae*, although for the most part hybrids can only be obtained by artificial crossing. It is obvious that there must have been evolution in the group through spontaneous hybridisation followed by chromosome doubling, and although the most primitive forms are not known which were involved in this hybridisation, nevertheless it has been possible to determine with fair certainty that the hexaploid wheats have been built up through two separate intergeneric allopolyploids, with of course speciation taking place at the tetraploid and hexaploid levels. At one time it was considered that the genus *Agropyron* was probably concerned with one of these hybridisations, but more recent views are that the genus *Aegilops* has contributed the B and D genomes. It is significant that this genus *Aegilops* occurs in the same centre as the primitive *Triticum* species, while *Aegilops* has also developed a polyploid series of its own.

The breeding of wheat is normally conducted within particular species, as for example in *T. vulgare* which contributes the greatest number of cultivated forms in the world, while also in a species like *T. durum*—the hard or macaroni wheats—improvement of agricultural varieties is largely carried out by exploiting the genetic variation within that one species. However, everything depends on the range of genetic variation that is available and the type of improvement that is being sought, and breeders are for the most part content with creating new genetic variability by hybridisation between groups of varieties which are particularly suitable to their conditions and objectives. Such inter-varietal hybridisation can be conducted in many ways and by using varying numbers of parental forms, and a wide range of characters of agricultural importance, such as yield, straw height and strength, winter hardiness, earliness, disease resistance and grain quality, can be handled in this way and new forms synthesized.

Although inter-varietal crossing, leading to the very detailed synthesis of desirable genotypes, is by far the most important method of breeding used in the genus, nevertheless there are examples where interspecies crossing, even between chromosome races, has been practised with some success. In particular, crosses between hexaploid and tetraploid species have been used, and a wide range of segregation can be obtained in this way. However, unless it is desired to obtain the transfer of some particular character from a tetraploid species to a hexaploid species, this type of hybridisation is not used. There are also examples where breeding programmes have been based on the direct use of valuable characters occurring in the G genome, and the species *T. timopheevi* has been utilised in this way.

There is still an infinite amount of genetic variability within the species *T. vulgare* which can be used and exploited for the improvement of cultivated varieties, but there are certain problems which do not seem to be soluble, or possibilities which need to be tested, by bringing in genetic variability from outside

the genus *Triticum*. If the hexaploid wheats have evolved through spontaneous hybridisation followed by chromosome doubling, and involved forms which, although perhaps not at present in existence, are represented by what are now regarded as distinct genera, there is the possibility that evolution can be retraced to some degree by recreating artificially such allopolyploids. It was for this reason that some 10 years ago we started creating interspecific and intergeneric allopolyploids involving different *Triticum* species and also species of *Aegilops* and forms from *Secale cereale*. We created a very large number of these forms, and it was largely as a result of this investigation that the new concept of the evolution of *T. vulgare* was proposed. These synthetic allopolyploids do not promise to have any direct agricultural value of their own, and it is most unlikely that it will be possible to produce an agricultural variety of any worth by this means. Nevertheless, it is possible to use these allopolyploids as bridging forms to bring in genetic characters from otherwise inaccessible sources.

Hybrids have therefore been made between some of these artificial allopolyploids and *T. vulgare*, and in particular we have been working with *T. durum* × *aegilopoides* and *T. pyramidalis* × *aegilopoides*. Interesting new forms have been selected from these crosses, and it is undoubtedly possible to synthesize new genotypes by means of the segregation of characters coming from the amphidiploid, and therefore originally from their parental species. Nevertheless, the most highly developed method of utilising genetic variability outside the genus is concerned with the use of *Secale cereale*, the common rye. It is quite simple to hybridise rye with wheat and produce an allopolyploid with 56 chromosomes, and the type of allopolyploid that is produced depends very much on the wheat variety that is used as a parent. The so-called Triticale forms in themselves are of no great agricultural interest, but the genetic variation of rye can be exploited in another way. By backcrossing the Triticale form to *T. vulgare* it is possible to select forms which have individual rye chromosomes added to the wheat complement, either in the monosomic or disomic condition. It is also possible to substitute wheat chromosomes by rye chromosomes and in this way to transfer the characters carried on those particular chromosomes. Finally, as a more refined technique, the long arm or the short arm of a particular rye chromosome can be transferred to wheat, and with it some valuable characters. In many ways this breeding work involving the manipulation of whole alien chromosomes, or parts of chromosomes, is unique in agricultural plant breeding, and is a most interesting example of the utilisation of the detailed knowledge which has been developed from the phylogenetic study of this group of plants. The basis of such work is of course the cytological analysis of the material, and such research utilises directly the cytological concepts of species and genera relationships and the chromosomal basis of evolution. There are not many groups of cultivated plants which provide such an interest-

ing picture, but there are many examples of the use to which breeders are putting the valuable knowledge accumulated by intensive studies of the patterns of genetic variation in taxonomic groups of plants.

Dr. HAWKES referred to the circumscription of the genera *Triticum* and *Aegilops*, and wondered about the assigning of the tetraploids (which were $\frac{1}{2}$ *Aegilops*) and the hexaploids (which are $\frac{1}{3}$ *Aegilops*) to the genus *Triticum*.

Dr. BELL replied that this was a problem but he has over 200 synthetic taxa, what should he call them?

Dr. W. T. STEARN said that the type-species of the genus *Triticum* is the bread wheat, which is hexaploid. If *Aegilops* is divided into two groups and those species which have contributed to the tetraploid and hexaploid wheats are put in to *Triticum* and the other species left in *Aegilops sensu stricto* it would make a more natural system. No wild hexaploid exists and it was thought that lethal strains were saved from extinction in the wild by man and cultivated. The original collection of *T. dicoccoides* was made in Palestine and had a great inherent variability to begin with.

Professor CAMP said that he had taken a lot out of his paper when he heard that Dr. Bell was speaking at the Conference and one example was the interesting case of *Vaccinium* subgenus *Cyanococcus*. In N. America the same type of background occurs in these blueberries as Dr. Bell has described for the wheats. Taxonomists regard the groups of different ploidy as intersterile, but they are not always. After 10,000 trial crosses one berry with 25 seeds had been obtained. Of these three germinated, but two subsequently perished. The remaining plant proved to be an amphihexaploid which was completely fertile with every naturally occurring hexaploid blueberry in the world!

Dr. S. M. WALTERS commented from the Chair that this was a most suitable triumphant note on which to end the discussion.

CLOSING REMARKS BY THE PRESIDENT

Professor Tutin said that everyone deserved our thanks and congratulations for a most successful conference. Success was assured from the moment that a plane named 'Charles Darwin' flew from Denmark with Professor Böcher. A vast amount of information had been exchanged without overwhelming those present as the speakers had made it so palatable and easily digested. Climbing plants were one of the few topics which had been omitted of those to which Darwin had paid special attention. This was understandable, for we knew no more now about them than he did a hundred years ago.

EXHIBITS ILLUSTRATING RECENT RESEARCH ON THE SUBJECTS OF DARWIN'S BOTANICAL MONOGRAPHS

RECENT RESEARCH WORK ON THE PRIMROSE

The electronic computer has been used to investigate the effects of random fluctuations on evolution towards homostyly in the primrose, and on gene flow between populations. An imaginary map of homostyle distribution was shown which was produced by simulating evolution and gene flow (both subjected to random fluctuations) by means of such a computer. It was compared with a real map of homostyle distribution in Somerset.

J. L. CROSBY (Durham).

VARIATION AND SPECIATION IN *TRIFOLIUM REPENS*

Much of the great variability of *Trifolium repens* L. is not amenable to orthodox taxonomic treatment, but on the coasts of West Cornwall and the Channel Isles there are, on warm, dry, rocky or sandy slopes, very uniform plants which appear sufficiently distinct to warrant taxonomic recognition, and which might be regarded as a separate species. These plants have persistently hairy petioles; small, thick, completely unmarked leaves with a papillose upper epidermis; few-flowered, scentless heads; and they flower from late March to early July. They appear to be self-compatible, and are more drought-resistant and salt-tolerant than typical *T. repens*. They may be related to the Mediterranean *T. biasoletianum* Steud. & Hochst.

D. E. COOMBE (Cambridge).

VARIATION, PHYLOGENY AND PLANT BREEDING IN THE TRITICINAE

The Triticinae includes the important agricultural genera, *Triticum* and *Secale*, as well as the grass genera, *Aegilops* and *Agropyron*. The genus *Triticum*, to which belong the cultivated wheats, exists in a polyploid series of diploid, tetraploid and hexaploid species, the most important economic species being *Triticum vulgare* (= *aestivum*) which is a hexaploid. This species has arisen as a result of natural allopolyploidy, and in wheat breeding use can be made of species at different chromosome levels, while intergeneric hybrids and chromosome substitution and addition were being investigated.

G. D. H. BELL and R. RILEY.

CROSS AND SELF FERTILIZATION IN PLANTS

Barriers preventing self fertilization are of many kinds in the Plant Kingdom. Some are accompanied by differences in form as for instance in *Melandrium* where the sexes are separate or in *Primula* with pin and thrum flowers. Other equally effective and

more widespread barriers provide no morphological clue to their presence, for example in *Prunus* and *Petunia*. The breakdown of these compulsory outbreeding devices has shown the structural complexity of the genes which govern the breeding system. Physiological studies have shown how the controlling genes act and breeding experiments have demonstrated the vital rôle of these same genes in plant survival and evolution.

LESLIE K. CROWE (Oxford).

DARWIN'S VASCULUM

This vasculum accompanied Darwin during his voyage with the "Beagle" in 1831-36. It subsequently passed into the possession of one of his sister's gardeners and eventually into that of the Linnean Society of London, by whose permission it was exhibited.

So far as is known, it is the oldest vasculum still in existence. Measuring 16 in. \times 7½ in. \times 5 in., and weighing only 2 lb. 10 oz., it is a good example of the modern standard type which came into being about 1800. On typological grounds (the rather cylindrical shape, hasp instead of a bolt, etc.) it resembles French and German examples rather than the type which was already standard equipment for the field classes in botany at Edinburgh at the time when Darwin was a student there. This would appear to strengthen the impression that Darwin had little to do with botany or botanists before his departure in the *Beagle*. It is not known whether Henslow used a vasculum, but it seems likely that it was he who suggested the usefulness of one on the voyage and Darwin doubtless procured the first he could find, or perhaps had one made to rather vague specifications.

The possession of this vasculum emphasises Darwin's essential modernity. Together with his geological hammer (which in South America he even used on occasions to bring down birds) it represented the new, well-proven and now standardised equipment of an age, no longer of dilettantism, but of intensive scientific investigation. It is a link, not with the past, but with the present.

D. E. ALLEN.

FRAGMENTS OF THE DARWIN-BABINGTON CORRESPONDENCE

In the correspondence of C. C. Babington, preserved in the Cambridge University Herbarium, are several Darwin letters which seem to have escaped notice and are not referred to in any of the published Darwiniana. Although these letters do not materially add to our knowledge of Darwin's work, two were exhibited as being of some interest, a request by Darwin for seed of *Lythrum hyssopifolia* (to which Babington's reply is available), and a fragment of the Darwin correspondence on the subject of sizes and variability of genera (to which, unfortunately, Babington's replies are unknown).

S. M. WALTERS (Cambridge).

DARWIN'S GALAPAGOS PLANTS

A small exhibit was made of a selection of the plants collected by Darwin in the Galapagos Islands and preserved in the Cambridge University Herbarium. Though it was understandably the giant tortoises and lizards and the endemic land-birds which impressed Darwin, he discharged his promise to his teacher Henslow to collect the plants, and his material was worked on by J. D. Hooker for the 'Enumeration of the plants of the Galapagos Archipelago' (*Trans. Linn. Soc.*, **20**, pt. II, 163, 1847) in which more than 100 new species were described.

S. M. WALTERS (Cambridge).

RESEARCH ON THE GENUS *UTRICULARIA*

Darwin's work on *Utricularia* was mainly concerned with the traps or bladders of the European species, all of which are very similar. The traps of the tropical species are, however, of many very different kinds and their morphology is of great importance in the classification of the genus. Drawings of *Utricularia* traps, made from pickled material in the Kew herbarium of various tropical species, were shown.

P. TAYLOR (Kew).

PITCHER PLANTS FROM SARAWAK

A collection of *Nepenthes* species made in Sarawak in 1954-1955 and dried in their natural shape, included *Nepenthes rafflesiana*, *N. ampullaria* and *N. gracilis*. The two diverse forms in *N. rafflesiana* were shown, pitchers that rest on the ground and those that hang from a climbing stem.

Miss W. M. A. BROOKE.

CLIMBING PLANTS

Two plants which twine in opposite directions were demonstrated, and it was pointed out that very little experimental work on climbing plants had been carried out since Darwin's monograph.

H. J. M. BOWEN.

SENSITIVE PLANTS

Recent research has given us more insight into the anatomy of the movements of sensitive plants like *Mimosa pudica*, but the physiology of the movement remains obscure.

H. J. M. BOWEN.

PLANT MOVEMENTS

A series of diagrams was used to illustrate how Darwin's observation that the tip of a coleoptile is the only part sensitive to light, led to the discovery of plant growth hormones, which are now the basis of a large industry.

H. J. M. BOWEN.

THE VARIOUS CONTRIVANCES BY WHICH ORCHIDS ARE FERTILISED
BY INSECTS

By means of living plants, photographs, drawings and both living and preserved specimens, the following methods of pollination in orchids were illustrated.

In the majority of our British species, e.g. *Dactylorhiza* spp., an insect on entering the flower knocks against the viscid base of the pollen-mass stalks. These become detached from the plant and attached to the body of the insect by means of a rapidly setting natural cement and soon afterwards reorientate themselves in a forward position so that they make contact with the stigmatic surface when next the insect visits another flower.

Special mechanisms are developed to ensure that the insect touches the pollen masses. The lip of the orchid flower is delicately hinged in some, e.g. *Bulbophyllum* spp., and the weight of the insect's body tilts the insect forward so that it contacts the viscid base.

The columns of some tropical species are very sensitive and the stimulus of the insect's body causes a mechanism to shoot the pollen-masses and their stalks forward with considerable velocity thus attaching them to the insect's body. *Catasetum* and *Cycnoches* spp. were shown to illustrate this.

The lips of the flowers of the *Cypripedium* tribe and of *Coryantees* spp. are modified into buckets which contain an attractive fluid. The insect falls into this bucket and its only means of escape is through small apertures where its body contacts pollinia and stigmatic surfaces.

Many species have long spurs, and moths, which sip the nectar at the end of these spurs, unavoidably contact the pollinia stalks. The classic example of this is *Angraecum sesquipedale* Thou. pollinated by *Xanthopan morgani* var. *praedicta* and specimens of both moth and orchid were shown.

Carrion flies are attracted by the lurid colours and foetid smells of some exotic species and thus become the pollinating agents. A painting of the deep scarlet *Bulbophyllum fletcherianum* Rolfe was exhibited here.

The lips of *Ophrys* spp. mimic the bodies of certain female insects. These attract the males of the species who attempt to copulate with the flower. These pseudo-copulatory movements serve to force the insect's head on to the correct part of the flower. Hymenoptera concerned with some species, including the British *O. sphegodes* Mill., *O. fuciflora* (Crantz) Moench, and *O. insectifera* L. were shown. If not successfully cross-pollinated in this way some species of *Ophrys* become self-pollinated by the pollinia stalks bending down and round until they contact the stigmatic surfaces, as in *O. apifera* Huds.

The plant specimens and drawings were kindly lent by the Director, Royal Botanic Gardens, Kew, and the insects were exhibited by kind permission of the Keeper of Entomology, British Museum (Natural History).

P. F. HUNT and A. C. JERMY.

EVOLUTION IN RELATION TO SOIL FACTORS

Darwin clearly maintained that evolution was a process not only of the past but also of the present, and that this process, whose occurrence in the past had given rise to the species of the present, was also operating at the present within species.

Experimental studies on plant species have disclosed a wealth of examples of this. It is now an accepted fact that species are often split up into populations (or ecotypes) adapted to local conditions. Most of the work on such intra-specific evolution has been concerned with morphological and developmental differences. But since it is clear that there are often profound nutritional differences between species it is reasonable to suppose that such differences are to be found within species. Investigations in three quite unrelated species show that this is true.

- (i) *Festuca ovina*. Populations from calcareous downland soil and peaty soil have completely contrasting soil preferences, which can be shown by reciprocal transplant into the two types of soil, and in sand cultures where calcium level is varied. In the latter experiment, the calcareous population has a reaction similar to that of *Lolium perenne*, while the peat population has a reaction similar to that of *Nardus stricta*.
- (ii) *Trifolium repens*. The differences between populations shown in this species are similar to those in *Festuca ovina* but slightly less marked. However, differences can be shown not only in relation to calcium level, but also phosphate, magnesium and iron, in populations coming from calcareous, neutral, and base deficient soils.
- (iii) *Agrostis tenuis*. Populations of this species can be found growing on the waste heaps of old lead, copper and other metal mines, on soils containing toxic amounts of these metals. Such populations can be shown to be tolerant of much higher concentrations of the metal than normal populations. Populations have been found which are separately tolerant of copper, lead, zinc and nickel.

“I see no limit to this power in slowly and beautifully adapting each form to the complex relations of life”.—*The Origin of Species*, Chapter XV.

A. D. BRADSHAW, R. W. SNAYDON and D. JOWETT
(Bangor).

DARWIN'S BOTANICAL MONOGRAPHS

First editions of all these were exhibited.

NORA BARLOW.

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