

THE GENUS ORTHODONTIUM

BY

W. MEIJER

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CHAPTER I

INTRODUCTION

1. THE PRESENT STATE OF TAXONOMIC BRYOLOGY

At the present day scientists pay relatively little attention to the taxonomy of cryptogams, especially when it concerns such groups with little practical importance as the bryophytes.

Thus we see that special branches of biology are developed in minute details, while others are more neglected than is justified from a purely scientific point of view.

Bryophytes provide most interesting illustrations of morphological phenomena. They offer in their distribution many traits which are valuable in the field of bio-geography. They help us to demonstrate the richness of life, the course of evolution. And there is even a practical side of this part of science, for field knowledge of bryophytes helps us to trace the differences in micro-en general climate and the differences in the composition of soils and rocks.

We should not passively accept the fact of the deplorable state of present day taxonomic bryology. When we develop first of all the systematics of this group, explorations of a wider perspective will be possible. At present the bulk of the work of bryologists consists in naming collections from different parts of the world, giving lists of the new finds and describing new species. It is obvious that only a well trained specialist can do this work with fairly satisfactory result.

But we should earnestly take into consideration the question whether it would not be better to devote more time to elucidate the taxonomy of special groups instead of trying to publish the names of all specimens of new collections.

Bryological floras of great parts of the world are still lacking. VERDOORN (1950) gave a vivid description of the hopeless condition of a botanist in a tropical region, trying to determinate the species collected, even in the neighbourhood of a well equipped botanical institute.

We lack moss floras of South America and of Africa. Outside the well studied European and North American regions we only possess a critical moss flora of Java and surrounding regions by FLEISCHER (1922), one of the Philippines by BARTRAM (1939) and from Middle America one of Guatemala by the same author. Moss floras of Tasmania, New Zealand and Australia are quite out of date. The only complete worldwide survey of the moss genera is that by BROTHERUS (1909) in ENGLER and PRANTL's "Natürliche Pflanzenfamilien". This work is only a tentative survey, by one of the bryologists who were shifting and naming collections of all parts of the world, during their lifetime.

It is becoming obvious to most bryologists that we are handicapped by a great burden of superfluous species names, caused by the lack of coordination in former days.

As VERDOORN (1945) stated: "The terrible status of exotic cryptogamic taxonomy cries for some kind of concentrated attack".

We lack special foundations, special publishing opportunities, as well as stimulation centers, like the former *Annales Bryologici* and *Hedwigia*. Few bryologists are working in special cryptogamic departments of greater botanical institutes. The revision work which has been done during the last four decennia, notwithstanding the difficult circumstances show how much can be done in this field.

The last monograph on a moss genus was MALTA's: "Die Gattung *Zygodon* (1926)". It was shown by this excellent treatise of a genus that approximately half of the c. 160 species names were superfluous.

Other examples are the work done by VERDOORN, HERZOG and

his pupils in Malayan hepatics, by FULFORD in the genus *Bazzania* from South America. Still the words of FLEISCHER (1922) are right when he called monographic work: "die grosse und zugleich auch wichtigste Zukunftsaufgabe der systematischen Bryologie".

2. THE PROBLEM OF NARROWLY RELATED SPECIES

The rapid increase of the number of named species forms a danger for scientific taxonomy in bryophytes. We may not overlook the fact that among bryophytes as in other groups there may exist narrowly related species which can be hardly recognized on a morphological basis, but which have to be considered as separate species. Recent examples of such concealed species from the thoroughly studied European moss floras are *Calliergon megalophyllum* and *Drepanocladus tundrae*, which we have learned to distinguish by the aid of TUOMIKOSKI (1940, 1949).

In this way from time to time we will detect that some narrowly limited species have to be maintained as being separate, because they really behave as such, e.g. by growing together in the same habitat.

These phenomena are less amazing when we bear in mind the results of recent cytogenetical and cytotaxonomical investigations, revealing that one of the causes of species formation is sexual isolation following genetic changes. If we try to explain the taxonomic value of narrowly related species, occurring in the same ecological niche, considerations of that kind cannot be omitted.

3. THE APPLICATION OF GENETIC CONCEPTS IN BRYOLOGY

Until now genetical concepts are often neglected in bryological taxonomy. The following words of VERDOORN (1934) are still applicable here: "Fragen wir uns welche Änderungen die Genetik im Artproblem im Allgemeinen hervorgerufen hat und überlegen dann, ob alle diese Tatsachen, Schlüsse und Hypothesen einen direkten Einfluss auf die Bryologie ausgeübt haben, so finden wir von all dem kaum eine Spur".

In Phanerogamic and Zoological taxonomy these genetic concepts have given much useful explanation, a fruitful use of new terms as 'geographic and ecological subspecies', a better evaluation and investigation of hybrid forms and a theoretical justification of a more general use of a broad species concept (Reviews in E. MAYER 1942, HUXLEY 1940, STEBBINS 1950).

We have a strong suspicion that the same regularities are playing a role among bryophytes, but we are still working too much on orthodox lines, without recognizing subspecies where we certainly have a right to establish them, neglecting the fact that most species are genetically polymorphous and we are unconscious of the possibility that we are dealing partly with hybrid forms.

It is true that we need more experimental work in bryophytes before we can apply terms and concepts which have proved their

usefulness in groups studied by experimental methods. But certain extrapolations seem justified. For example, in the present study *Orthodontium brevicollum* Fleischer, a form which lives on the mountains of Java and Ceylon, in the same habitats as *O. infractum* Dozy & Molkenboer, is no longer considered as a subspecies of the last species. In my opinion we should either treat it as a separate species or as a minor variant.

Among well known European mosses *Eurhynchium striatum* offers a beautiful example of a species divided in geographical subspecies.

This pleurocarp moss is common in our woods. PÉR STØRMER (1942) described a form of this species with more cordate-ovate leaves as a new species: *E. zetterstedtii*. The type of *E. striatum* s.str. possesses acuminate leaves. STØRMER was able to point out that the acuminate type (*E. striatum* s.str.) has a more western distribution in Norway, than the cordate-ovate (*E. zetterstedtii*). Most of the localities of *E. striatum* on the continent of Europe are situated west of a line from Hamburg to Zürich and those of *E. zetterstedtii* occur east of this line. In our opinion this case is quite parallel with that of geographical subspecies among birds and among phanerogams. Therefore it would be more in accordance with modern investigations to call both forms subspecies of *E. striatum* (Hedw.) Schimp.

Until recently so narrow a species concept has been used by European bryologists that differences between species are often considered to consist only of one constant elementary character. In such a way the hepatic *Calypogeia trichomanis* (L.) Corda was considered by most hepaticologists as distinguished from *Calypogeia mülleriana*, because the former possesses blue oil bodies in the cells and the latter translucent ones.¹ The latter form seems to possess a more continental distribution. By my own studies of the genus *Riccia* and of *Lophozia* I am convinced that in such genera the minor species certainly can be arranged in several polytypic major species.

As to the possibility of hybridization, in studying the genus *Orthodontium*, my suspicion has been raised that in a special part of its range the wide variation of forms is partly caused by hybridization. This possibility has never been taken into consideration. As a matter of fact it is very difficult to recognize derivatives of moss hybrids as such and to distinguish them from aberrant forms with only slight variation, caused by mutation (LOTSY, 1928). We may safely accept that hybrids occur among mosses as well as among phanerogams. For further details on this subject we refer to chapter III.

It is obvious that such phenomena are apt to cause great difficulties when we try to draw lines of demarcation between the taxa, in the same way as in some difficult groups of phanerogams.

Matters become even more complicated when the plants are

¹ LINNAEUS must apparently have dealt with the form with translucent oil bodies, because the other is very rare in Sweden, occurring only in the extreme South (ARNELL, in litt.). Thus from a nomenclatorial point of view the names are also wrong.

monoecious as in *Orthodontium*. Then each variant of a variable population may show a certain autonomy, because whole tufts of a special habit can be formed from one single spore. Selffertilisation takes place then and causes the same form with the same habit to be distributed in the neighbourhood. In this way different pure lines next to each other may have come into existence in the same area. Sexual isolation between these forms is only temporarily maintained, until two different forms come to grow intermingled in one tuft. Only twice I found two forms growing intermixed. The consequence of this relation of the sexes and this way of growing is that within each species a high polymorphism may exist and that the demarcation between species and subspecies is rather vague.

All this makes the taxonomy of these groups very difficult.

CHAPTER II

HISTORY OF THE GENUS

1. THE PERIOD OF 1827—1850

SCHWAEGRICHEN (1827) described for the first time the genus *Orthodontium* in the family Bryaceae. It has a double peristome of characteristic construction, not as fully developed as the peristome of *Bryum* and *Pohlia* and quite typical in its teeth, which are straight and erect when moistened, whence the name *Orthodontium*.

The genus was founded on *O. julaceum* and *O. lineare*, the first of which was afterwards placed in *Bryum*, section *Cladodium*, by BRUCH & SCHIMPER (1844). Ten years afterwards (1837) W. J. HOOKER published in his *Icones Plantarum* a new species, *Bryum pellucens*, correctly placed in *Orthodontium* by BRUCH & SCHIMPER (1844). *Orthodontium pellucens* (Hooker) Br. et Schimp. had been found by JAMESON, near Quenca in Colombia (S. America).

It is interesting to note that HOOKER (1837) in the notes following the description of *Bryum pellucens* calls attention to a new find of *Orthodontium* by his English colleague WILSON:

“It is not a little remarkable that about the same time that Professor JAMESON found this beautiful and delicate moss in South America, Mr. W. WILSON detected a species of the same genus in England, so much resembling it that, except its smaller size, narrower and more subulate and not at all glossy leaves, is it hardly to be distinguished from it: *Bryum gracile* Wils. in *Gardn. Musc. Brit.* t. 34 App. (1839)”.

In these words two of the most important differences are indicated between the South American *O. pellucens* and the British *Bryum gracile*, afterwards called *Orthodontium gracile* by BRUCH and SCHIMPER,

viz. smaller leaves, not at all glossy. The minor differences in the peristomes were not observed.

This is possibly one of the reasons why WILSON at first did not think his *Bryum gracile* to be different from *Orthodontium lineare*. He preferred however to place *O. lineare* in the genus *Bryum*, but he had to choose then a new specific epithet, because the name *Bryum lineare* was in use already. He thus gave *Orthodontium lineare* as a synonym of *Bryum gracile*.

BRUCH and SCHIMPER (lit. c.) were the first who dealt with the South African and the European plants as two different species, placed in the genus *Orthodontium*, together with the South American *O. pellucens* (Hook.) Br. et Schimp. WILSON cited in his herbarium the name *Orthodontium gracile* Schwaegr. SCHWAEGRICHEN wrote to him, according to BRUCH and SCHIMPER (1844), that in his opinion *Bryum gracile* and *O. lineare* were different. In this connection it is interesting to make a careful study of WILSON's fine herbarium sheets (in the herbarium of the British Museum, London), fully illustrated with beautiful drawings and long annotations. WILSON was at first inclined to consider all the three forms together as representatives of *O. lineare*, but afterwards he changed his opinion and we read: "Surrucucho, JAMESON, a specimen of *O. pellucens*, is perhaps *O. lineare* Schwaegr.", but he wrote on the annotation: "Differs from *O. lineare* Schwaegr." and he pointed out some differences: "Leaves not so narrow, opercule longer".

As will be shown later these differences will stand the closest examination.

From the fact that in a more recent sheet in WILSON's herbarium we read "*Orthodontium gracile* Schwaegr., Helsby (Cheshire) 1844", instead of "*Bryum gracile*", we can conclude that WILSON afterwards agreed that the English *Orthodontium* was distinct from *O. lineare* Schwaegr. He also investigated another important difference: "This has antheridia with paraphyses in the axils of the perichaetial leaves, unlike what is recorded by SCHWAEGR. (1827) of *O. lineare*, which has terminal male flowers with ovate perigonal leaves". That WILSON had still not seen the original specimen of *O. lineare* and was therefore always somewhat uncertain of its real position, appears from the following. During an expedition into the southern circumpolar regions (1830—1843), Tasmania and New Zealand in H.M. Ships *Erebus* and *Terror*, J. D. HOOKER, the son of W. J. HOOKER, collected another *Orthodontium* in the Falkland Islands, at Hermite Island and in Tasmania. This find was apparently also very carefully studied by WILSON. He pointed out clearly the differences from *Orthodontium gracile*, but wrote in a note on a herbarium sheet: "*O. australe* mihi, *O. lineare* Schwaegr?". It should be stated here that the differences between *O. australe* and *O. lineare* are indeed rather slight (see chapter III).

The collections from Hermite Island and the Falkland Islands were also carefully compared with *O. gracile* from Helsby. Among the differences the most outstanding are the following: "sporular sac

extending nearly $3/4$ of the whole length, of thicker texture, somewhat furrowed when dry. Generally, the outer peristome teeth shorter than the inner, the segments with a central line, leaf nerve more defined. Seta generally longer”.

Up till then the study of *Orthodontium* by well known bryologists such as WILSON, J. D. HOOKER, BRUCH and SCHIMPER had been based on careful study and a broad species concept. In most cases the real differences between the forms studied were described. It was however a misfortune that so little of the type species of the genus, *O. lineare*, had been gathered, that WILSON and HOOKER had no material for comparison and had always to rely upon SCHWAEGRICHEN's description and figure. Another unfortunate fact was that most collections of *O. australe* had young sporogonia which differ from old ones in the very smooth capsules. The same was true of the type specimen of *O. lineare*, as SCHWAEGRICHEN also had before him a specimen with young smooth capsules. Now we know that in both species old capsules can be distinctly furrowed, but in those days they were considered to be smooth or only somewhat furrowed, and this was accepted as an important character. When afterwards JAMES DRUMMOND sent a specimen from Australia of an *Orthodontium* with distinct furrowed capsules, it was described by HOOKER fil. and WILSON (1848) as *O. sulcatum*. A further disadvantage was that out of the whole form complex in Australia, to which this *O. sulcatum* belongs, just this variant, with extremely broad leaves, had been selected for the first description. Thus HOOKER and WILSON wrote (1848): “Allied to *O. lineare* Schwaegr., but different essentially from that and other species in the furrowed capsule. The leaves are shorter and not gradually tapering”.

The consequence of this was that forms from Australia, differing from this type, were described as new species, with no possibility of sharp demarcation, e.g. *O. lanceolatum* Mitten 1856 (now to be considered as a ‘small’ form of *O. sulcatum*) and *O. zetterstedtii* C.M. 1898. I still cannot understand why C. MÜLLER (Halle) described the latter as a new species. Yet it is a curious fact that we find in the herbaria of HOOKER and WILSON specimens from New Holland labelled *Orthodontium lineare*.

This raises the question whether *O. lineare* really occurs in Australia and what is its relation to *O. sulcatum*.

The collections of HOOKER and WILSON were too few to allow a satisfactory classification of this very puzzling and complicate Australian-Subantarctic form complex.

Meanwhile a distinct, more isolated species of the genus was described from Malesia by DOZY and MOLKENBOER (1844): *O. infractum*. Till that date only *O. lineare*, *O. gracile* and *O. pellucens* had been described. DOZY and MOLKENBOER (1844) had made use of the *Bryologia Europaea*, but they had not yet seen HOOKER and WILSON's description of *O. australe*. They pointed out that as to the distribution of antheridia and archegonia *O. infractum* is similar to *O. lineare*, but differs in length and form of the lid. The differences

in the peristome from *O. pellucens* are of great importance. The initial stage in the taxonomy of the genus *Orthodontium*, which occupied the first half of the 19th century, was thus critical and thoughtful.

2. THE PERIOD BETWEEN 1850—1900

Now followed a period during which the creation of new species on a large scale seemed to be the fashion, it is the period of the famous geographical method, by which new finds from different parts of the world were too readily described as new species, without sufficient painstaking investigation. Of course there were some exceptions, but on the whole most superfluous species of *Orthodontium* were described between 1850 and 1900:

1855, *O. aethiopicum* C.M.; 1856, *O. lanceolatum* Mitten; 1857, *O. osculatum* De Not.; 1860, *O. setaceum* W. P. Schimper, nom. nud.; 1865, *O. confine* Hpe; 1869, *O. tenellum* Mitten; 1878, *O. fendleri* Hpe; 1893, *O. ovale* C.M. in litt. ad Broth.; 1898, *O. arenarium* C.M.; 1898, *O. ulei* C.M.; 1898, *O. zetterstedtii* C.M. and 1898, *O. laxirete* Dusen, nom. nud.

On the average, two superfluous species of *Orthodontium* have been described every ten years during this period. Three by HAMPE, four by C. MÜLLER and two by MITTEN, who was the most critical of the above named workers.

We have seen already that his *O. lanceolatum* at first sight comprises a form with narrower leaves than *O. sulcatum*. But from his herbarium we do not get a uniform picture of the species created (see chapter III). He compared his *O. lanceolatum* especially with *O. australe*.

O. tenellum also has at first sight a somewhat different aspect from *O. gracile*, with which it was afterwards joined by LE ROY ANDREWS, in our opinion on good grounds.

The other species created during the geographical period, indicated above, are so clearly identical with species previously described that we shall pay no more attention to them for the present. C. MÜLLER and HAMPE as well as MITTEN however had among their creations some really new forms which deserve to be called separate species:

1880—1881, *O. loreifolium* Besch.; 1881, *O. denticulatum* Geheeb & Hampe; 1885, *Apalodium inflatum* Mitten, and 1863, *O. longisetum* Hampe.

The first two are very closely related to *O. pellucens* and are probably derived from this species. The same may be true of *O. loreifolium* Besch. (1880—1881). *Orthodontium inflatum* (Mitten) is an Australian species, probably related to *O. infractum* Dozy & Molkenb.

3. SUBDIVISION OF THE GENUS

In the meantime some attempts were made to split the genus *Orthodontium*. MITTEN (1869) did this in a rather curious way. He separated the genus *Apalodium* (with *A. pellucens* and *A. australe*) from *Orthodontium sensu stricto* (with *O. tenellum* and *O. gracile*) and placed the former in the family Orthotrichaceae. Consequently (as was clear from his publication of 1885) the type species of the genus

Orthodontium, *O. lineare*, had been put by MITTEN (1869) in Apalodium, contrary to the rules of nomenclature, as these are accepted today.

MITTEN (1885) wrote on p. 198: "*Apalodium lineare*, Schwaegr. t. 188 (Orthodontium), from South Africa, is described and figured with the inner and outer peristome equal in length".

In the meantime LINDBERG (1878) accepted MITTEN's view that *O. gracile* stood sufficiently apart to justify the formation of a genus, containing this species and separate from the other species of Orthodontium. He put things in order when he rejected MITTEN's name Apalodium and created for *O. gracile* a separate genus Stableria. His arguments run as follows:

O. lineare Schwaegr. is the first representative of a separate genus. It belongs to the same group which has been called Apalodium by MITTEN (1869). Then LINDBERG (1878) continues in the following words: "the conclusion from this is that both Orthodontium and Apalodium are synonymous. The European species *O. gracile* has nothing to do with this genus Orthodontium: it belongs to quite a different family and has not any analogy with it. Because it forms thus a distinct separate genus, we feel ourselves obliged to give it another genus name, choosing the name Stableria, after our good friend, the late Mr. G. STABLER, from Westmoreland" (translated by the author).

It is curious to note that MITTEN (1869) as well as LINDBERG (1878) gave no details of what in their opinion were the differences between Orthodontium and Stableria. It seems somewhat strange that they both considered the genera Orthodontium and Stableria to belong to two different families:

1. Orthotrichaceae: Apalodium Mitten = Orthodontium Schwaegr.

2. Bryaceae: Orthodontium Mitten = Stableria Lindb.

BROTHERUS (1909) maintained Stableria as well as Orthodontium and placed both genera in a subfamily of the family Bryaceae. In our opinion they are there in the right position.

REIMERS (1941) and following him MARGADANT & MEIJER (1950), suggested that the creation of Stableria by MITTEN has been caused by a systematic error of LINDBERG:

"Offenbar verhält es sich so, dass MITTEN eine der tropischen Orthodontium-Arten versehentlich als *Apalodium lineare* zu den Orthotrichaceae stellte und S. O. LINDBERG, in der Meinung dass diese Umstellung der Typusart *Orthodontium lineare* galt, für das von ihm als Bryaceae erkannte europäische *O. gracile* den neuen Gattungsnamen Stableria bildete".

In our opinion however LINDBERG was right when he considered Apalodium synonymous with Orthodontium Schwaegr., when reading MITTEN's paper of 1869, and it was quite logical that his taxonomic concept of the whole genus induced the creation of Stableria.

Matters are still more obscured by the fact that MITTEN used the name *Apalodium lineare*, in a paper of 1883 as a synonym of *Weissia*

pallens Hook. & Wils. 1848 and of *Zygodon lineare* Taylor nom. nud. The last name we find also in MITTEN's herbarium on the type sheet of *Orthodontium pallens* (Hook. & Wils.) Broth.

Thus MITTEN's name *Apalodium lineare* (Schwaegr.) Mitten 1885 is a later homonym of *A. lineare* (Taylor) Mitten 1883, and in some herbaria specimens we find even *Orthodontium lineare* Mitten as a synonym of *Orthodontium pallens* (Hook. & Wils.) Broth, sensu BROTHERUS: Nepean River, Blue Mountains, leg. WATTS, Oct. 1899, det. BROTH. (herb. K, NSW, H) and coll. Beaconsfield, Tasm., WEYMOUTH 1133, 1892 (herb. BM, H).

The confusion becomes still greater owing to the fact that these specimens are part of *O. sulcatum*, thus something else than the type of *O. pallens*, from Swan river, coll. DRUMMOND, no. 201. We give this example as an illustration of the disorder in the genus, caused by an insufficient study of types and violations against the rules of nomenclature.

The survey of BROTHERUS (1909) was the first in which the whole genus was considered. Of course BROTHERUS could give only a compilation and in several instances rearrangements, as he dealt with a very comprehensive material and included the moss flora of the whole world. From his compilation and from the use made by others of this work, it appears how confused the taxonomy of exotic mosses is. *Orthodontium* is apparently not the worst example for, in comparison with others it is a rather small genus. The division given by BROTHERUS (1909) is quite artificial. It is based too much on uncertain characters, such as length of peristome teeth and striation of capsules, a common feature of the whole genus, with the exception of *O. gracile*.

The *Orthodontium* species of South America, Africa and Australia were not sufficiently compared. *O. brevifolium* Broth. from Africa and *O. loreifolium* Besch. from Réunion, *O. denticulatum*, *O. ulei* C. M., *O. arenarium* C. M. and *O. confine* Hampe from S. America, belong, according to BROTHERUS' treatment, to a different section as *O. fendleri* C. M. and *O. pellucens* (Hook.) Br. eur., from S. America. In fact the last two species are identical with each other and with the last three of the former group, whereas the others are very closely related to *O. pellucens* and to a species of a third section (*O. longisetum* Hampe).

The same confused state of affairs appears from DIXON's paper on *Orthodontium* in New Zealand (1926), in which he strongly suspected that *O. sulcatum* would have to be reduced to *O. australe* Hook. f. & Wils., but stated furtheron:

"I do not think the problem can be solved satisfactorily except by study in the field."

The naming of Tasmanian *Orthodontiums* was even more difficult than in New Zealand. RODWAY (1913) gave a key with which no *Orthodontium* of that region could be named.

O. lineare and *O. lanceolatum*, both of which have capsules sulcate, when ripe, cannot be separated (as RODWAY does) from *O. australe* and *O. sulcatum* on this character.

4. NEW SPECIES AND THE FIRST LUMPING EFFORTS AFTER 1900

Meanwhile further new species were created: *O. haplohymenium* Dixon et Naveau, Central Africa (1927), *O. brevifolium* Broth. from Central Africa (1914), *O. novae-guineae* Dixon from N. Guinea (1942).

All these species are closely related to some taxa around *O. pellucens*, with greater extensions over tropical regions of the world than was hitherto expected (see chapter III). After C. MÜLLER (1905) had already stated that perhaps not more than 23 species could be described in this genus and the total number had increased by 1932 to thirty-one species, of which only 24 were referred to by BROTHERUS (1925), A. LE ROY ANDREWS (1932, 1935) was one of the first who raised some serious doubts against the treatment of the genus by BROTHERUS (1925). He reviewed some forms occurring in North America and investigated their relations with others. He revealed too that studies had been made by MRS. BRITTON in the herbarium of the New York Botanical Garden, of the South American forms, of which four were considered to be identical with *O. pellucens*. It is regrettable that MRS. BRITTON did not publish this important study. Afterwards (1950) LE ROY ANDREWS also joined *O. tenellum*, *O. osculatianum* and *O. gracile* together. The necessity to have a new modern revision of the whole genus on a monographic basis reached a climax when it appeared more and more clearly that W. WATSON's variety *heterocarpa* of *O. gracile*, published from England (1922), which afterwards was found to have spread to Holland and Germany (there described as *O. germanicum* F. and K. Koppe, 1940), is quite different from *O. gracile* (MARGADANT & MEIJER 1950). It seemed hardly possible that this species had been overlooked during decennia of extensive bryological research in these countries, or had recently arisen by mutation, a hypothesis put forward by BURRELL (1940), in a remarkable review of the whole question.

The history of the extension of this form over Europe (MEIJER 1951, see chapter IV) made it more and more obvious that we have to do here with a species introduced into England from another part of the world. This form appeared to fit in the wide variation of the variable African-Australian species *O. lineare* Schwaegr. Another very puzzling *Orthodontium* was found by GAUME in France and described by ALLORGE and THÉRIOT (1931) as *O. gaumei*. At this point a revision of the whole genus became a necessity, for it soon appeared that all taxonomical problems in *Orthodontium* are closely linked together and only can be solved by a thorough study of the whole complex genus. The search was now for a better subdivision of the genus, a lumping of the many superfluous species and a more accurate picture of the distribution of the species over the world. In the following chapters such a study has been tried.

CHAPTER III

REVISION OF THE GENUS

1. DESCRIPTION OF THE GENUS

Small acrocarpous mosses, 1—2 cm in height, growing in dense tufts (tufts \pm 3 cm), stems densely dichotomous, branching sympodial fastigiate, branches fragile, with many red brown and pale branched rhizoids, with oblique transverse walls, at the base of the stem and from the leaf bases. Stem in cross section with small central cylinder. Chlorophyllous part of protonema sometimes with gemmae (POTIER DE LA VARDE 1950, MEIJER 1951). Gemmae also on rhizoids (Plate II).

Leaves octostichous, erect-patent or recurved, crowded at stem apex, linear-lanceolate, plane or carinate, sometimes twisted, with part of margin reflexed. Length varying considerably on one plant.

Leaf cells hexagonal-linear, oblong, variable in length, but shorter and broader at the brown coloured base, in middle of leaf 10—12 times as long as broad; walls smooth. Leaf margin plane, entire or irregularly dentate near the apex, which is occasionally composed of two cell layers. Costa in most cases ending below the leaf apex, in most cases less than $\frac{1}{4}$ of breadth of leaf. Distribution of sexes variable, autoecious, paroecious or rarely heteroecious. Inner perichaetial leaves in male buds reduced, shorter, more concave, sharp pointed, the nerve rudimentary to wanting, paraphyses longer than the antheridia, numerous, with translucent cells, pale yellow, 1—6 antheridia in each bud. Outer perichaetial leaves longer pointed and with distinct nerve. Perichaetial leaves in female flowers somewhat reduced in size, the outer when the capsules are ripe similar to the ordinary leaves. In paroecious flowers antheridia in the axils of leaves under the archegonia. Sporogonia with red brown vaginula at base, seta 1—25 mm, occasionally somewhat bent near apex, tapering into the neck of the sporogonium. Calyptra shining, cucullate.

Lid conical-rostellate, oblique or straight, annulus not differentiated. Capsule oblong-pyriform, sometimes slightly asymmetric, sometimes striate when ripe, in most instances with some rows of thick-walled cells near the mouth. Neck of sporogonium with planeroporous stomata, cells broadly hexagonal, shorter towards the mouth.

Anatomy of sporogonia as on Plate II 1.

Peristome double, inserted below the mouth of the capsule, basal membrane of inner peristome very short or distinct. In most instances outer peristome more robust than inner, but the 16 processes of the inner peristome may be longer than the 16 alternating teeth of the outer peristome. Teeth of outer peristome with median line at the dorsal surface only, ventral surface with transverse joints, not forming distinct lamellae.

Cuticle of peristome smooth or papillose, rarely inner peristome reduced to the basal membrane. Peristome teeth in general erect when moist and incurved when dry.

Differing from *Pohlia* (*Webera*) and *Bryum* especially in the lanceolate or setaceous leaves, the long cells, the structure and mode of opening of the peristome, the peristome always lacking cilia, even rudimentary and without very distinct lamellae at the inner face of the outer peristome.

2. VARIATION OF CHARACTERS

a. *The leaves*

Having some knowledge of plants of different species, together with their sporogonia, it is very difficult to name a specimen of *Orthodontium* studying the vegetative parts only. In this respect the genus resembles genera such as *Bryum* and *Pohlia*. By a careful study the section to which a specimen belongs can generally be settled if the student is acquainted with the subtle differences in leaf breadth, form of apex, occasionally dentation, width of the cells and dimensions of the leaves. For the last character it is very difficult to give one standard dimension, because on one single plant the leaves can vary considerably. It is better to compare whole plants than single leaves. Further we have to take into account that the dimension of the leaves can vary according to moisture and light conditions of the habitat.

The glossy appearance of *O. pellucens* and the related *O. infractum* seems to be a rather constant character. It occurs only occasionally in some aberrant forms of *O. lineare*. For the dimensions of the cells no constant figures can be given; they are on the average broader in *O. pellucens* than in *O. lineare* and still narrower in *O. inflatum*. It appears that to a certain extent this character fluctuates, according to different habitats, but the notes about this on the herbarium-labels are few and experimental data are almost totally lacking.

b. *Anatomy of the nerves* (Plate II)

The nerves show in *Orthodontium* two different types in cross section. One type is represented by the nerve of *O. gracile*, which lacks definite stereid cells. It is composed of 2—4 layers of cells, of which some may possess a somewhat smaller lumen (fig. 2d). In all the other species we find a definite group of stereid cells in the nerve. At the ventral side of this group two guidecells are found and in some instances a few additional ventral cells and always one row of dorsal cells.

We find in the different forms of *O. lineare* and *O. sulcatum* at the ventral side of the stereid cells one or two cell-layers. This varies accordingly to the extent of development of the leaves. In *O. pellucens* and related forms we only saw one ventral layer.

c. *Distribution of the sexes* (Plate I)

This can vary in such a way that in some species like *O. lineare* and *O. australe*, which are as a rule autoecious, some antheridia are occasionally found between or below the archegonia. In other cases some archegonia occur in buds with antheridia.

That is the reason that we find in literature different statements

about the distribution of the sexes and a great uncertainty about its taxonomic value within the genus.

In our analysis we found always that *O. gracile* is paroecious (antheridia below the archegonia, fig. 4). But this character cannot be used for the discrimination between both sections of *Orthodontium* (*Stableria*, including *O. gracile* and *Orthodontium*, including the other species). In the section *Orthodontium*, which is generally autoecious and heteroecious, there exists one form which is paroecious (Ruahinerange N. Zealand, herbarium Sainsbury).

In the isotype-collection of *O. haplohymenium* Dixon et Naveau, I found buds with one archegonium and five antheridia. DIXON (1942) reported about his *O. novae-guineae*, that it should be polyoecious, but we could not confirm this on the type material. It seemed to be distinctly autoecious.

O. lineare, *O. sulcatum* and *O. australe* offer examples of heteroecious inflorescences, e.g. inflorescences where next to male buds, mixed buds occur. We noted this for example in the type collection of *O. sulcatum*, where we found several buds with antheridia on one plant and one where an antheridium was found between archegonia.

We also observed in the type collection of *O. australe* male buds with one archegonium.

We made the following analysis of *Orthodontium lineare* from Germany:

1. Collection Klövenstein leg. EHRENDORFF, 1948, herb. KOPPE.: On one plant 1 bud with archegonia and 1 antheridium, 1 bud with antheridia, 1 sporogonium with archegonia at its base, together with 1 antheridium. In this connection we could accept that the antheridia near the archegonia were old individuals, arisen in a former growing season, but we found also young antheridia around one non-fertilized archegonium.

2. In another collection (Königsmoor, bei Schmilau) we found one bud with archegonia and two antheridia in the leaf axil below them. We noted in several instances in *O. lineare* that occasionally buds with antheridia are standing quite near the archegonia. Such buds can be strongly reduced. The branch on which they stand may be very short and the number of perichaetial leaves reduced. If this tendency should be strongly developed we should get a paroecious inflorescence. In such a way we discover that in the genus *Orthodontium* we have to do with the following series of types of inflorescence: autoecious → heteroecious → paroecious. Heteroecious inflorescences were also observed on *O. lineare* by WALSH (1951).

It should be very interesting to investigate the genetic structure and the physiology of growth, which causes this different way of distribution of male and female organs on the plants.

d. *Relative length of peristome teeth*

In the peristome the relative length of the inner peristome as compared with the outer is a rather variable character.

In *O. australe* and some forms of *O. lineare* the inner peristome

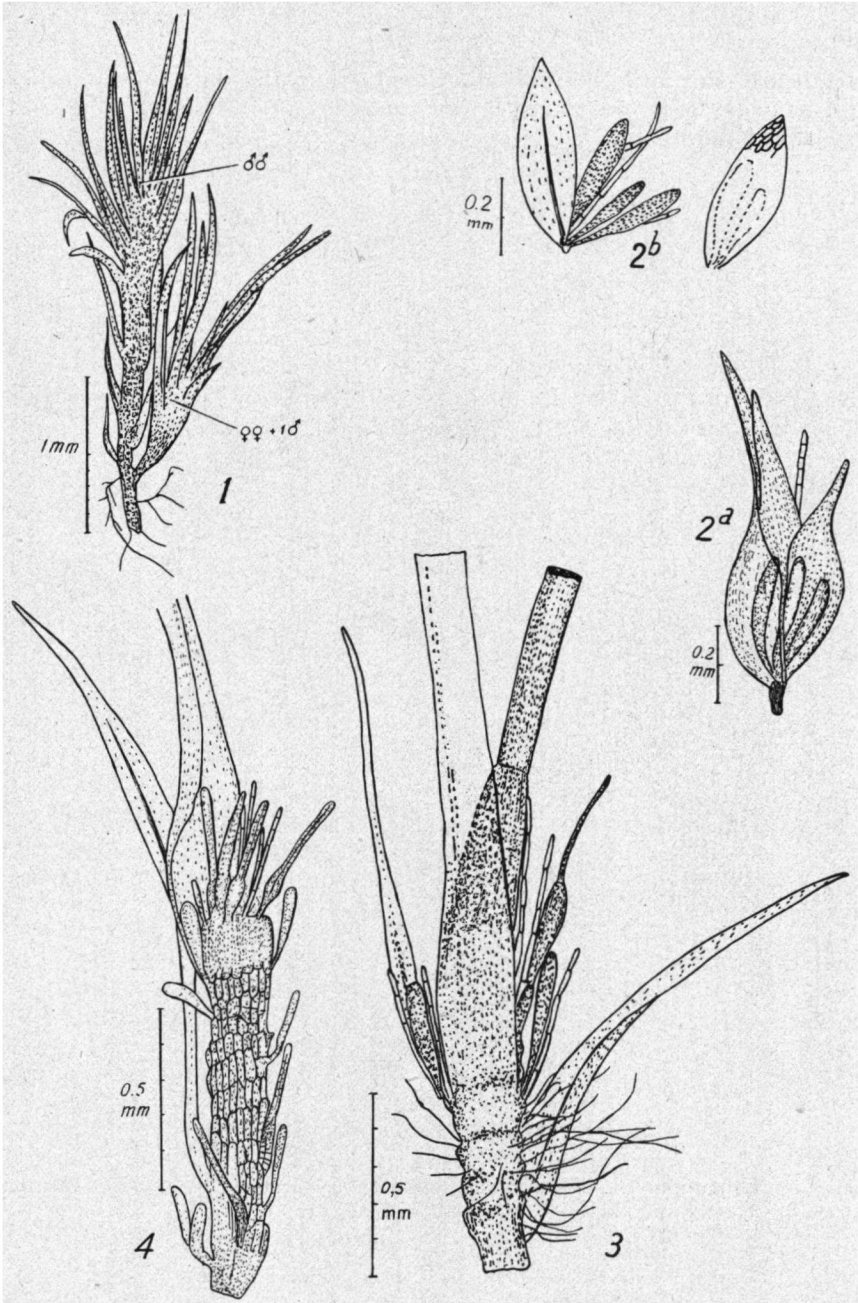


PLATE I

- Fig. 1. Plant of *O. australe*, type collection showing buds with antheridia and archegonia.
 „ 2. Branches with antheridia of *O. australe*, ssp. *robustiusculum*,
 a. leg. WEYMOUTH, Mt. Wellington, Tasm. 3/1893 (NY).
 b. leg. TAYLOR, Tasm. (herb. S).
 „ 3. *O. ruahinense*. Type material (SAINSBURY no. 9197). Paroeocious inflorescence.
 „ 4. *O. gracile*. Tunbridgewells, S. England. leg. WALLACE & MEIJER, 1951. Paroeocious inflorescence.

teeth are constantly considerably longer than the outer, but in other forms of *O. lineare* we found in one and the same capsule longer and shorter inner teeth.

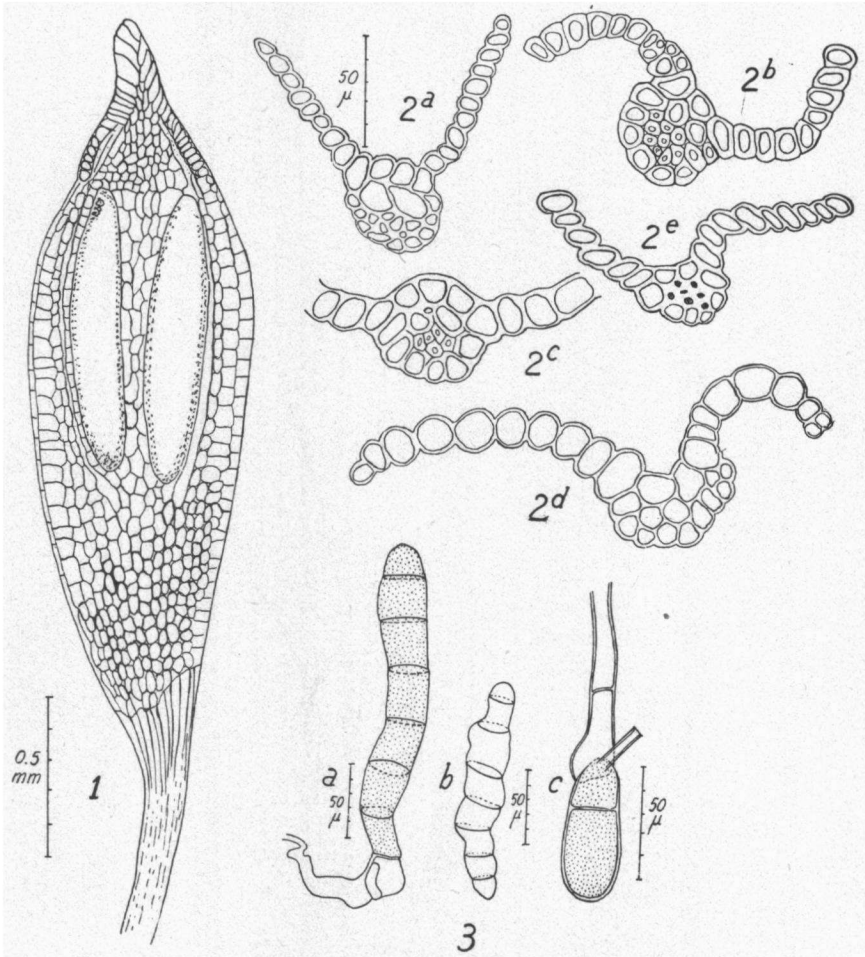


PLATE II

Fig. 1. Longitudinal section of sporogonium of *O. lineare*. Coll. from Doorn, Holland 4—1951.

„ 2. Leaf-sections of

- a. *O. ruahinense* (no. 9196, herb. SAINSB.).
- b. *O. australe* Falkland Isl. Coll. HALLE no. 575 (PC).
- c. *O. lineare* leg. PILLANS, S. Africa.
- d. *O. gracile* Vina del Mar. Musci Sel. no. 245.
- e. *O. infractum*.

„ 3. Gemmae:

- a. *O. lineare* ssp. *sulcatum* (*O. zetterstedtii*, Mt. Williams, Austr.).
- b. *O. novae-guineae*.
- c. *O. australe* ssp. *robustiusculum*.

All observations of the variation of this character show that the discussions on the supposed high taxonomic value of this character were somewhat premature.

The use BROTHERUS (1909, 1925) made of this character for the division of the genus is not justified by the facts. For more details see the discussion of the species.

e. *Dimension and shape of the capsules*

There are several indications that these characters are not of a great taxonomical value. In the first place in one and the same tuft capsules of very different size can be found.

The smaller capsules also have shorter setae. Comparison of forms of *O. australe* and *O. sulcatum* also indicate however that to a certain extent variations of the length of the setae have a genetical basis, because the relations between length of setae and of capsules are different in these species.

In the second place culture experiments show that the ripening of the sporogonia may start approximately at the same time, both in large older and in younger sporogonia, simultaneously with the reduction division of the spore mother cells. From that time all capsules cease to grow in length and breadth.

Now one of the consequences of this is that ripe capsules comprise large as well as small individuals; another is that microclimate and general climate, influencing the interval between first development of sporogonia and date of the reduction division may modify the dimensions of the sporogonia of a whole population. But these phenomena need further investigation by experiment and by observations in the field. It is regrettable that ecological notes are so scarce in herbaria. Several indications of phenotypical variation are to be found in the discussion of the different forms of *O. lineare* in Europe and in Australia.¹

f. *Juvenile states*

Great confusion has been caused in herbaria by the fact that juvenile states of capsules, which resemble the ripe state of other species, are not always recognized as such. The best examples of this are BROTHERUS determinations of *O. pallens* (herb. H). None of this *O. pallens* comprise any specimens of this species. It is an assemblage of young plants of *O. inflatum*, in which the capsules are immature and not yet inflated, together with small forms of *O. lineare*, so called *O. lanceolatum* Mitten.

g. *Over-mature capsules*

Another extreme is that the capsules may be too old and it has sometimes been wrongly supposed that they have a rudimentary inner peristome where in fact it has been broken away (see DIXON's descriptions of *O. haplohymenium* and *O. novae-guineae*).

¹ For Australian forms of *O. lineare* (*O. lineare* ssp *sulcatum*) the name *O. sulcatum* is often used in this paper, as a shortof.

h. Papillosity of peristome

In many instances authors have overlooked the fact that young sporogonia often lack the papillosity, which may be characteristic for the species in question. The same can be true of the small sporogonia ripened in an 'immature' state. Smallness of sporogonia and a smooth peristome can thus be correlated.

If all these phenotypical variations had been born in mind, the greater part of the superfluous species would never have been described, let alone those created only on geographical grounds.

3. HABITAT

The habitats of the different species of the genus are to such an extent similar that it is not necessary to enumerate them under each species.

O. inflatum, *O. pallens*, *O. loreifolium*, *O. denticulatum*, *O. longisetum*, *O. lineare* ssp. *piriformis*, *O. australe* ssp. *robustusculum* and *O. novae-guineae* have only been found on old decaying trunks.

All the other taxa occur also on this substrate, but moreover they are gathered on sandy soil, in crevices of rocks, peaty soil and some forms of *O. lineare* ssp. *sulcatum* even on burnt logs.

O. pellucens is chiefly found on wood, but occasionally on soil (Tennessee, "*O. arenarium*" in S. America).

O. australe ssp. *australe* seems to grow in *Fuegia* on numerous places in bogs and *Nothofagus* woods.

4. SUBDIVISION OF THE GENUS

The interrelations among the species of *Orthodontium* can best be expressed by recognizing a number of subdivisions.

O. gracile, including species of the genus *Stableria* Lindberg, stands apart from every other species in its rather smooth capsule, its paroecious inflorescence, very short basal membrane, and the lack of stereid cells in the costa of the leaves.

A common feature of the *pellucens*-group is that all its species possess glossy leaves. They show a wide variation in peristome structure, forming a series from a simply constructed peristome, with translucent basal membrane and very narrow processes, to a highly papillose robust peristome, with somewhat divided processes. Occasional toothing of the leaves (very pronounced in *O. denticulatum*) and a long beaked lid are other common features of this group. All the species related to *O. lineare* usually possess a more conical lid, and less glossy leaves.

A. In accordance with these considerations the following subdivision of the genus is suggested.

I. Sectio **Stableria** (Lindb., 1878 as genus) Meijer.

Paroecia, foliis setaceis, theca ovato-cuneata, laevissima (*O. gracile*).

II. Sectio **Orthodontium**.

Autoecia vel heteroecia vel paroecia; folia setacea vel ovato-lanceolata; theca ovato-oblonga, sicca plicata.

- a. Subsectio *Pellucens*.
Folia nitida, apice parce denticulato vel integerrimo; operculum rostratum (*O. pellucens* s. l., *O. infractum*, *O. inflatum*).
- b. Subsectio *Linearis*.
Folia opaca, integerrima. Operculum brevirostrum vel conicum (*O. pallens*, *O. lineare* s. l., *O. australe* s. l., *O. ruahinense*).

5. SPECIES DESCRIPTIONS AND KEY TO THE SPECIES

ORTHODONTIUM

Orthodontium Schwaegr. Species Muscorum Suppl. II, Sect. 2, 123, 1827, Hook. Ic. Pl. rar. I, Tab. 34, 1837. Bryi sp. Wils. Engl. Bot. Suppl. 3, t. 2835, t. 1839.

Apalodium Mitten, Musc. austr. amer. p. 238. Journ. Linn. Soc., 1869 (= *Orthodontium* section *Orthodontium*).

Stableria Lindb. Utkast nat. grup., p. 20, 1878 (= *Orthodontium* section *Stableria* (Lindb.) Meijer).

Key to the species

- 1a. Plants paroecious, leaves rather narrow setaceous; costa without stereids; capsule smooth when ripe. 1. **O. gracile**
- b. Plants paroecious, autoecious or heteroecious; capsule in most cases sulcate when ripe, costa with stereids 2
- 2a. Capsule ovate-pyriform, inner peristome on a translucent very thin basal membrane, with very thin and narrow processes 3
- b. Capsule not pyriform, or with a firm inner peristome 4
- 3a. Leaves setaceous, with narrow cells ($\pm 7,5 \mu$), sporogonia distinctly swollen when ripe 6. **O. inflatum**
- b. Leaves broader, lanceolate or ovate-lanceolate, capsules pyriform-ovate, usually not swollen; leaves occasionally toothed near apex 7. **O. infractum**
- 4a. Leaves linear-lanceolate (± 5 mm broad), rather suddenly tapering at apex or more gradually, with a metallic glance, occasionally or regular toothed near apex. Cells at middle of leaf 12—18 μ broad. Lid rather long beaked (0,35—0,95, at average 0,70 mm). 8. **O. pellucens** s.l. (compare 8a—8e)
- b. Leaves usually narrower, more gradually and longer tapering at apex, margin only rarely with some irregular teeth near apex, usually not glossy, cells narrower (± 10 —12 μ) at midst of the leaf. Lid of sporogonium shorter (max. 0,40 mm) 5
- 5a. Inner peristome rudimentary, with high basal membrane, adherent to the outer peristome 5. **O. pallens**
- b. Inner peristome well developed in ripe capsules, in older capsules sometimes broken away 6
- 6a. Plants only paroecious. Several rather short setae on one stem, occasionally the lower reached by the setaceous upper leaves 2. **O. ruahinense**

- b.* Plants generally autoecious, occasionally heteroecious, usually with one sporogonium on one plant 7
- 7*a.* Leaves erect-linear, with strong nerve, in upper part of leaf $1/4$ — $1/3$ of leaf breadth. Capsule oblong-lanceolate, seldom somewhat ovate-pyriform. 4*a.* **O. australe** ssp **australe**
- b.* Leaves erect-spreading, broader; capsule more generally lanceolate-ovate 8
- 8*a.* Robust plants, with long setae (11—25, average 20 mm) and large capsules (length 2,5—3,0 mm). Inner peristome up to $\pm 185 \mu$ in length. 4*b.* **O. australe** ssp **robustiusculum**
- b.* Smaller plants, with shorter setae (5,5—13, average 8 mm) and smaller capsules. Inner peristome up to 280μ in length. 3. **O. lineare** (compare 3*a*, 3*b* and 3*c*)

1. **Orthodontium gracile** Schwaegr. ex Br. et Sch. Bryol. eur. fasc. 3—4, 1844. (in litt. ad Wilson).

Bryum (Pohlia) gracile Wilson, Gardner. Muscol. Brit. T. 34, App. (1839); Suppl. to the English Botany of the late Sir J. E. Smith and Mr. Sowerby 3, t. 2835 (1839); holotype in herb. WILSON (BM).

Orthodontium aethiopicum C. M. Bot. Zeit. 13, Oct. 1855.

Stableria aethiopica (C. M.) Broth. Engler & Prantl. Die Natürliche Pflanzenfam., 10, (1st. ed.), 1909; lectotype in herb. S.¹

Orthodontium laxirete Dusen. nom. nud.; herb. S.

Orthodontium osculatianum De Not. Mem. della Reale Accademia delle Scienze di Torino. Series 2, 18; 444. t. 4, 1857, holotype in herb. Rome.

Orthodontium tenellum Mitt. Musci austro-americi. Journ. of the Linn. Soc. Bot. Vol. 12, 1869; holotype in herb. NY.

Stableria tenella (Mitt.) Broth. Engl. & Prantl., 10 (1st ed.), 1909.

Orthodontium peruvianum Hampe nom. nud.; in herb. BM.

Orthodontium setaceum W. P. Sch. nom. nud., in Mandon Pl. Boliv. n. 1658; type in herb. K.

Orthodontium lineare Schwaegr. p. p. Wilson 1839. Suppl. Eng. Bot.

Description:

Paroecious plants, in dense tufts, variable in height ($1/2$ —7,5 mm), with long pointed, narrow setaceous leaves (1—7 mm), often twisted, or patent. Cells in middle of leaf ± 8 — 12μ broad. Sporogonia sometimes several on 1 plant, seta 2,5—10 mm large. Capsule varying from ovate to narrow lanceolate or wedge shaped, with contracted or wide mouth, extremely variable in dimensions (from $1,2 \times 0,40$ — $2,0 \times 0,80$ mm, $1,8 \times 0,50$ at average). Capsule walls light brownish-yellow. Walls when dry slightly irregular sulcate or smooth. Margin of capsule bordered with 3—4 rows of cells with thin walls and one row of longer cells, forming the transition to the oblong cells beneath them. Colour of the bordercells only slightly darker than the other. Lid conical or shortly rostrate.

Peristome smooth. Outer teeth 6—9, usually with 7 joints,

¹ For abbreviations of herbarium names used see Acknowledgements (p. 77), WM refers to the herbarium of the author.

108—260 μ long, $\pm 40 \mu$ broad at base, margin gradually tapering towards apex. Processi of inner peristome equal, somewhat shorter, or longer in length, much narrower; breadth about 5 μ , for most of their length, $\pm 25 \mu$ at broadened base. Median line only visible in the lower part. Spores 10—18 μ in diameter. (Plate I 4, II 2d, III, IV.)

Discussion:

A variable plant. Variation is however found only in the dimension of the different parts of the plant and in the shape of capsules. The smallest plants (seta 2,5 mm), with the smallest sporogonia are the specimens of *O. laxirete* nom. nud. from South Chile.

Generally more robust are the *O. tenella* forms from W. and Central Africa and from South America. The capsules of this form are usually rather oblong pyriform. Ripened juvenile states however bear much narrower and smaller capsules (Plate III). These are quite comparable with *O. gracile* from England. Some of the English specimens however are more like typical *tenella*-forms (Plate III).

The French specimens and "*O. aethiopicum*" also bear more normal capsules. The same is true of *O. osculatum*, *O. peruvianum* and *O. setaceum*. From several observations it appears that *O. gracile* in England is living near the limit possible for its existence. After severe winters the capsules are damaged, white coloured (Litt. BURRELL, 1940 & herb. WILSON). The small South Chilean form is perhaps also formed under the influence of a colder climate. I have tried honestly to find real differences between the described species of the section *Stableria* (formerly as a genus, LINDB., 1878), but I cannot find any real species limitations in this group.

We should not exclude the possibility that within the series of variation in *O. gracile*, from the equator till northwards and southwards, geographical clines in the sense of HUXLEY (1940) may exist. Without culture experiments it is of course impossible to state to what extent these differences are genetical.

EXAMINED SPECIMENS:

England: Cheshire, Helsby, leg. W. Wilson, 25(—27) March 1833 (BM type; PC, S), March 9, 1836 (W), 1842, 1846 (S); G. E. Hunt, 1868 (S), 1870 (S), W. P. Schimper, 1865 (S); W. Curnow (S, L); Dr Wood (S), Alderley leg. Wood (S); Frodsham, leg. Hund (S).

Alderley Edge, Sandstone rocks, leg. Hurst, 1863, un. itin crypt. W. Ph. Schimper, 1865 (L, PC), W. W., 1896 (K). Peckforton Hill, leg. Armitage, 1916 (K). Yorkshire, V.C. 64, Strid Bolton Abbey., leg. W. H. Burrell, 1923, (Br.), 1927, no. 477 (W), 1830, herb. Baker (U.S.), Bolton Woods, Ingham (PC); Skipton, leg. Lapworth, 1919 (K); Sussex, Rocks at Wakehurst, leg. Hennings, 1854 (U.S.). E. Sussex, V.C. 14, Rocks in Chiddingly Wood, leg. A. Comyn, 1951 (WM. ex herb. F. Rose); Lower Pennrocks, leg. Wallace & Meijer (WM), N.W. of Buxted, Sandstone rocks, leg. F. Rose 1951 (WM). Kent, Eridge rocks, 1844 (Br.), leg. Jameson 1888, 1894 (K), Nicholson, 1913 (U.S.), 1919 (K), Wallace 1946 (WM.), Wallace & Meijer, 1951 (WM.).

Wales: Nant y Ffrith, Flintshire, V.C. 51; leg. Jones and Rhodes, *Bauer Musci europ.* 1775 (S, Br.). Ffrith, Flintsh. leg. Watson, 1913 (S).

Scotland: Rosslyn Glen, Edinburgh, leg. W. Evans, 1900 (K).

France: Bretagne, leg. Husnot. *Musc. gall.* no. 665. Finistère (Bannalec, Scaer).

Central Africa, Congo: E. de Nirraganga, 2900 m, Lebrun 8737 (Br.), Shahu, Lebrun 9356 (Br.), versant N. d. Karisimbi 3900 m, alpage à bruyères et Senecios arboresc, epiphyte s. Philippia, Louis 5350 (Br.) Karisimbi Louis 1347B; entre Kabara et Rakumi versant N. du Karasimbi, Lebrun 7393, 1937 (WM ex Br.).

Cameroon: Montane forest, above Ukile, Cameroon Mountain, Br. Cameroons, ca. 8500 ft, leg. P. W. Richards no. 4298, 1948 (WM).

Abyssinia: leg. W. Schimper, Cosso Berri: 11200 ft (L; S lectotype of *O. aethiopicum* C.M.; MEL).

America, California: Buxham Ranch. Sonoma, L. J. Koch, 1939 (herb. Bartram); Mendocina, leg. Howe 1896. (herb. Le Roy Andrews).

Guatemala: Chiquiral, Quetzaltenango, 8200 ft, leg. Sharp, 2135, 1945 (herb. Bartram, det. as *O. pellucens*), East of Totouicapan, 10.500 ft, 12618, 1945, coll. Sharp (herb. Bartram det. as *O. pellucens*).

Colombia: ad Mt. Napi, leg. Osculatis, *O. osculationum* de Not., (isotype in herb. L.); Andes Quintensis, [herb. Hooker (K), isotype of *O. tenellum*, Mitten].

Peru: Gay no. 2044, 1839—1840 (PC; BM, type of *O. peruvianum*).

Bolivia: Vicinus Sorata, Prov. Larecacha, 3200 m, 1858. Manson, *Plantae Andium Bolivienae* no. 1658; as *O. setaceum* W.P. Sch., nom. nud., (herb. PC, type in herb. K.); Sorata, 2500 m, leg. Williams, no. 1706, 1902 (K).

Chile: Chile australis, insula Quiriquina, leg. P. Dusen, 1896, type of *O. laxirete* Dusen, nom. nud. (in herb. S, NY, PC, FH). Vina del Mar, Salto, leg. Bertho; 1934; det. Thériot as *O. tenellum* Mitten, *Musc. Sel. et Crit. ed. Fr. Verdoorn*, V (1938). (L, herb. Amsterdam).

2. *Orthodontium ruahinense* Meijer, nov. spec.

Latin diagnosis:

Paroecum. Plantae humiles, cum tomento fusco in basi; folia gradatim setacea, siccata crispata; nervus modice distinctus, cum cellulis stereidis, evanescens ante folii apicem; aliquot sporogonia superposita in uno caule, aliquando sporogonio infimo paulum folio oculo. Capsulae atque setae longitudine diversae; capsulae forma ovata-cylindrica; capsula laevis vel paulum sulcata, cum collenchymateis cellulis ad marginem. Peristomium in explorato specimine non distincte papillosum. Operculum et sporae nondum inventa.

Description:

Paroecious. Small plants, at base with brownish tomentum. Leaves gradually setaceous, 2—7 mm, somewhat curled when dry. Costa rather distinct, with stereid cells, ending before the leaf-apex.

EXPLANATION OF PLATE III

Capsules of *O. gracile* from different parts of the world.

- a. Leg. P. W. RICHARDS, Br. Cameroon. 1948, no. 4298. Both capsules of this collection!
- b. Leg. HUNT, Cheshire, England, 1868 (S).
- c. Leg. W. SCHIMPER, Abyssinia C.M.
Isotype of *O. aethiopicum* (S).
- d. *O. peruvianum* Hampe nom. nud. Peru, (isotype PC).
- e. Coll. SHARP no. 2618, Guatemala (herb. BARTRAM).
- f. Coll. LOUIS, no. 5350. Congo Belg. (Br).
- g. and h: coll. LEBRUN, no. 9356. Congo Belg. (Br).
- i. Pennrocks, Tunbridgewells, S. England. Leg. WALLACE & MEIJER, 12-4-51.
- j. Eridergerocks, Kent. S. England, 1844 (Br).
- k. Bolivia type of *O. setaceum* W. P. Sch. nom. nud., type in herb. K.
- l. and m. Guatemala. Coll. SHARP, no. 2135 (herb. BARTRAM).

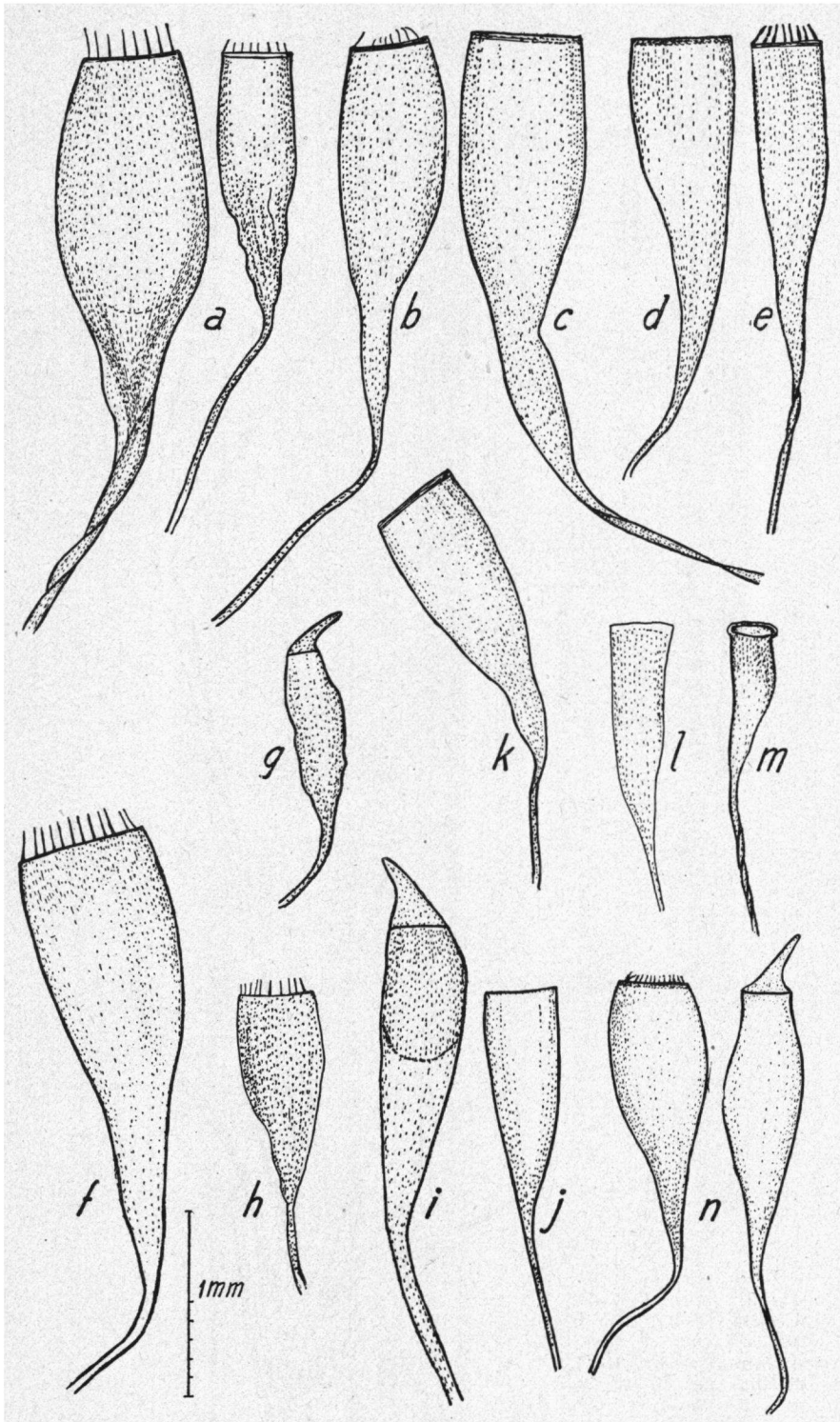


PLATE III

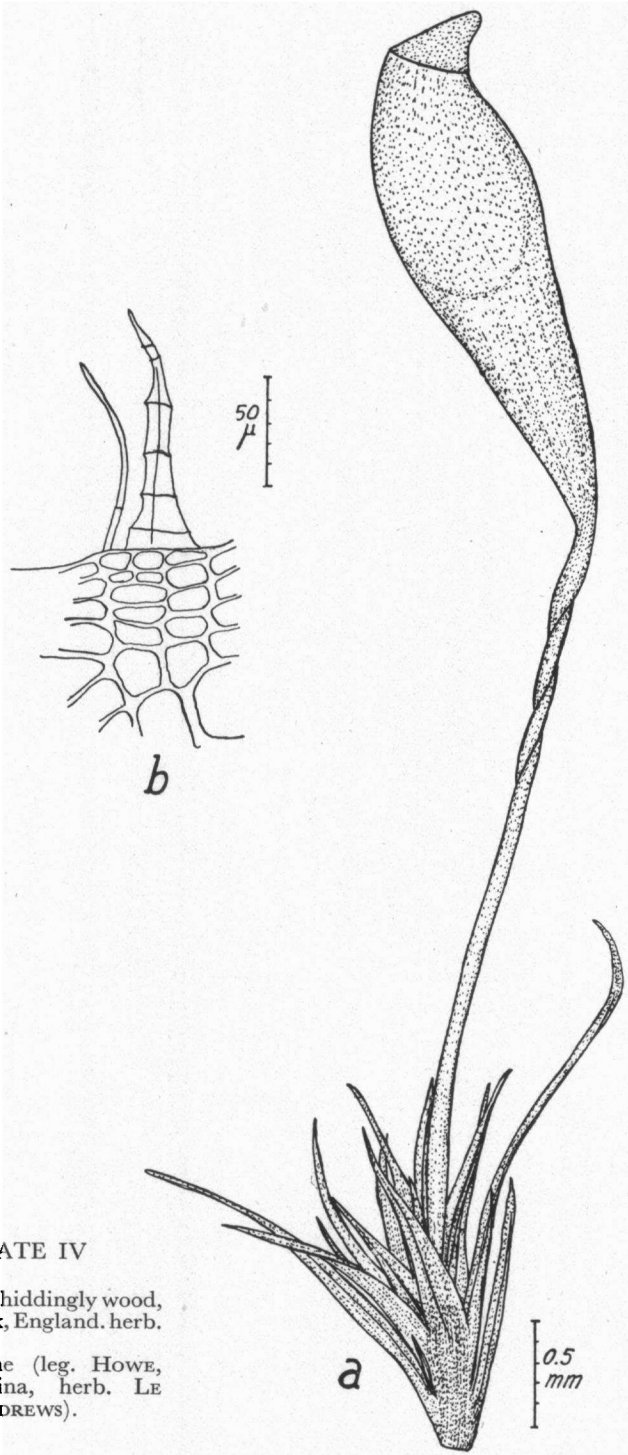


PLATE IV

O. gracile:

a. Habit. Chiddingly wood,
E. Sussex, England. herb.
ROSE.

b. Peristome (leg. HOWE,
Mendocina, herb. LE
ROY ANDREWS).

Sporogonia several above each other on one stem, occasionally the lowest somewhat hidden by the leaves. Capsules as well as setae of different length. Shape of the capsule ovate-cylindrical. Capsule wall smooth or slightly sulcate; with collenchymatous cells near the margin. Peristome rather simply constructed, not distinctly papillose in the examined specimen. Lid and spores unknown (Plate I 3, II 2a, V).

Discussion:

Closely related to narrow-leaved forms of *O. lineare* ssp *sulcatum*. Different from that in its paroecious inflorescence, the somewhat longer setaceous leaves and the rather small peristome.

In habit strongly resembling *O. gracile*, because the leaves are narrow and long, the plants bear several setae, situated on the same stem and the form of the capsules is rather similar.

I first supposed that it should belong to that species, because it has the same habit. A more detailed investigation revealed however, that it possesses the following characters of section *Orthodontium*: collenchymatous cells near the margin of the capsule mouth and stereid cells in the costa. The peristome resembles that of *O. gracile* in its dimensions and its smoothness, but the processes are broader.

The leaf-type is similar to that of narrow-leaved forms of *O. sulcatum*, but even more setaceous. While the difference autoecious (or heteroecious) against paroecious is in general a good distinguishing character between the species of the section *Orthodontium* and *O. gracile* (section *Stableria*), its great usefulness in the subdivision of the genus breaks down here.

Of course it should be possible to minimize the importance of the sex relations totally and to consider this form as a variant of *O. lineare* ssp *sulcatum*. But then we should neglect the fact that it differs also in the other respects, indicated above, from that taxon. Nevertheless the distribution of this peculiar form, which has been gathered only twice on approximately the same place in New Zealand, deserves a further study.

Especially its relation to the narrow-leaved forms of *O. sulcatum* should be further investigated. We accept here that it has its own position as an endemic species in New Zealand.

EXAMINED SPECIMENS:

Type: N.W. Ruahine Ranges, N. Island, N.Z., leg. A. P. Druce Jan. 1948, herb. G. O. K. Sainsbury no. 9197.

Other collection, same locality, collector and date: herb. G. O. K. Sainsbury no. 9196.

Mr. SAINSBURY kindly informed me that these specimens are growing on a very rugged place in the island, not easily accessible.

3. ***Orthodontium lineare*** Schwaegr, *Species Muscorum*, Suppl. 2, Sect. 2: 123—125, Plate 138. Holotype in herb. Geneva.

Apalodium lineare (Schwaegr.) Mitten. Voy. H. M. S. Challenger, Bot. IV, p. 198, in adn., 1885, non *Apalodium lineare* (Taylor) Mitten. Trans and Proc. Royal Soc. of Victoria, vol. 19, 1883.

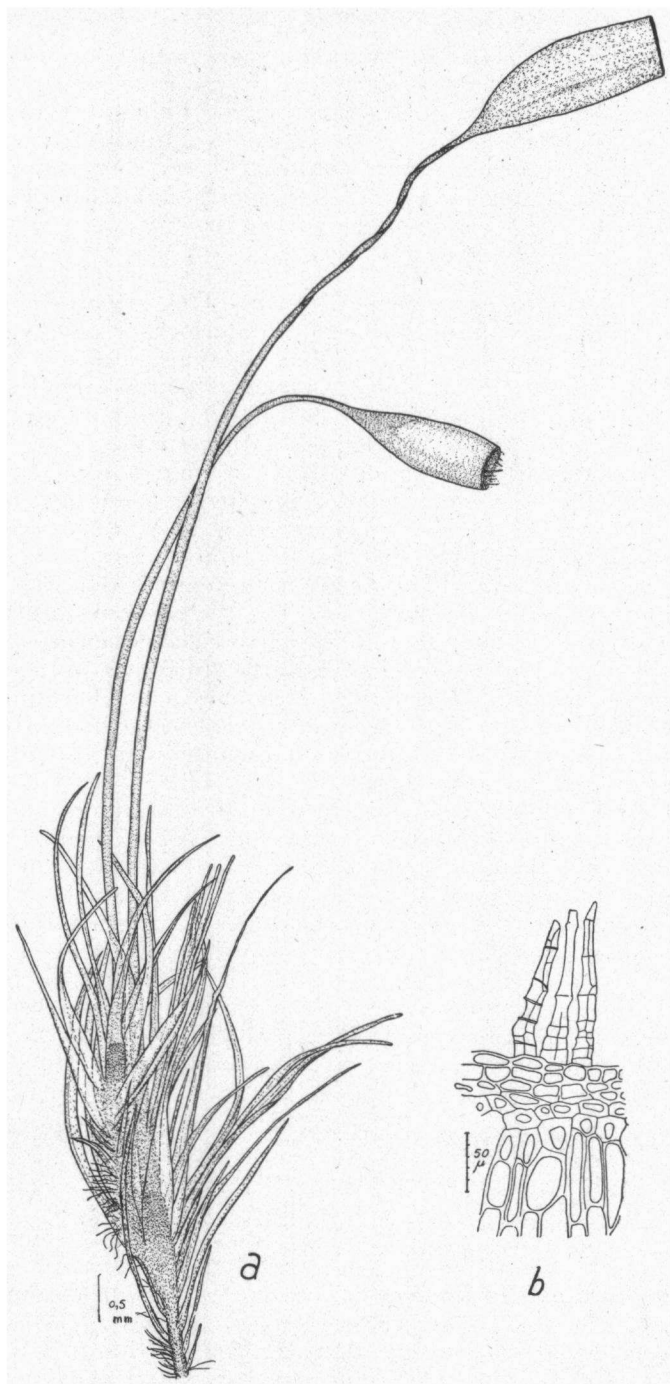


PLATE V

O. ruahinense:

a. Habit of type mat., N. Zealand. (herb. SAINSBURY no. 9196).

b. Peristome (New Zealand, leg. DRUCE, herb. SAINSBURY no. 9196).

Orthodontium gracile Schwaegr. ex Br. et Sch. var. *heterocarpum* Watson, Journal of Bot. 60: 139—41, 1922.

Orthodontium germanicum F. et K. Koppe. Fedde Repert., Beiheft CXXI: 40—47, 1940.

a. ***Orthodontium lineare* Schwaegr. ssp *lineare*.**

Description:

Autoecious plants, with crowded, dull green, gradually tapering, rather narrow, erect and recurved leaves (max. breadth c. 0,4 mm, max. length 2—6 mm). Cells in middle of leaf at the average 12 μ broad, thin walled. Seta 6—13 (av. 8) mm long. Capsule erect or somewhat bent, globose-ovate, rather short neck, before ripeness contracted at the mouth, which is bordered with thin-walled cells, above some red brown collenchymatous rows.

Lid conical or rostellate. Capsules variable in dimension (0,8—2,5 mm) \times (0,4—0,9 mm), sulcate or smooth when dry. Peristome varying in length, accordingly to the dimensions of the capsules; outer teeth somewhat papillose, 75—150 μ in length, 25—35 μ broad at base; segments in inner peristome 70—220 μ in length, 10—15 μ broad at base, papillose, especially near the summit, composed of 6—8 joints. Basal membrane of inner peristome some cells high, with distinct median line, finely papillose. The whole peristome pale coloured. Relative length of outer peristome and segments of the inner variable even within one capsule, equal in length, or the inner segments considerably longer. Spores 15—20 μ . (Plate II 2, VI).

Discussion:

Very closely related to *O. lineare* ssp *sulcatum*, but distinguished from that by a narrower variation of gametophyte characters. The leaves have a more uniform character; they are always narrow acuminate.

The peristome type of *O. australe* resembles that of *O. lineare* ssp *lineare*. The differential characters of *O. australe* ssp *australe* are: seta generally longer, capsule usually more oblong, peristome with a stronger tendency to an equal length of inner and outer teeth, leaves with broader nerve.

O. australe ssp *australe* has a more robust peristome (max. length of teeth 280 μ) and the leaves are somewhat longer and broader. *O. lineare* ssp *piriformis* has a more pyriform capsule, smaller and more glossy leaves and a more rostellate lid.

For a further illustration of these differences we give here our measurements of various characters in *O. australe* ssp *australe*, *O. australe* ssp *robustusculum*, *O. lineare* ssp *lineare* and *O. lineare* ssp *sulcatum*.

From a study of this table it will be evident that *O. australe* ssp *australe* and *O. australe* ssp *robustusculum* differ from *O. lineare* ssp *sulcatum* and *O. lineare* ssp *lineare*, in the somewhat smaller maxima of leaf-length and in higher maxima of length of seta.

The maximum dimensions of the peristome and the spores in

O. australe are considerably greater than in *O. lineare* and the minima differ even more widely.

Between *O. lineare* ssp *sulcatum* and *O. lineare* ssp *lineare* the differences in these dimensions are very slight. The minimum size of the capsules of *O. sulcatum* may be somewhat smaller than of *O. lineare*.

TABLE I
Comparison of some taxa

Taxon:	australe	robustus- culum	sulcatum	lineare
1. Max. length of leaves in mm	4,5	5	6	6
2. Breadth of cells at middle of leaves in μ	8—11	10—12	9—14	12
3. Length of seta in mm	5—20	11—26	4—13	5—13
4. Dimensions of capsules in mm:				
length	1,9—2,5	2,5—3,2	0,8—2,5	1,1—2,4
breadth	0,5—0,6	0,7—1,0	0,4—0,9	0,45—0,90
5. Length of outer peristome in μ	130—195	110—250	100—170	70—150
Length of processes in μ	180—290	160—280	100—230	70—220
6. Diameter of spores in μ	12—23	15—24	15—20	15—20
7. Length of lid in mm	0,4—0,5	0,7—	0,5	0,5

It ought to be stressed that these figures give only an impression of the range of variation of the characters. The material which is available is too small (c. 160 specimens of the whole subsection *Linearis*), to give any reliable figures of the variation. Only some tendencies can be shown. Moreover the differences between *O. lineare* ssp *sulcatum* and *O. lineare* ssp *lineare* are somewhat greater than appears from the figures given in above table, because *O. sulcatum* shows a greater variation of leaf types and of peristome characters. The outer peristome especially has a tendency to remain smooth, while the inner is usually papillose.

O. lineare ssp *lineare* and *O. lineare* ssp *sulcatum* possess so many characters in common, that they partly cannot always be separated; they are thus typical examples of geographical subspecies. Of these two subspecies the Australian ssp *sulcatum* is the richest in characters, as will be shown below.

EXAMINED SPECIMENS:

S. Africa: Cape, leg. Menzies, holotype, herb. Hedwig-Schwaegrichen (Geneva); George, Cape Colony, leg. H. A. Wager, 1906, no. 542 (BM); South of Great Kop, Cape Peninsula, leg. N.S. Pillans, 4271, 14 Jan. 1923 (BM, PRET).

EXPLANATION OF PLATE VI

O. lineare ssp *lineare*:

- a. Habit (coll. PILLANS no. 4271, herb. PRET).
- b. older sporogonium (coll. WAGER, George, Cape Colony, BM).
- c. Young sporogonium (coll. Naardermeer, Holland).
- d. Leaf apex. 1. *O. lineare* (coll. BURRELL 1923, England) PC.
- e. Base of leaf (same coll.).
- f. Peristome (Doorn, Holland, leg. W.M.).

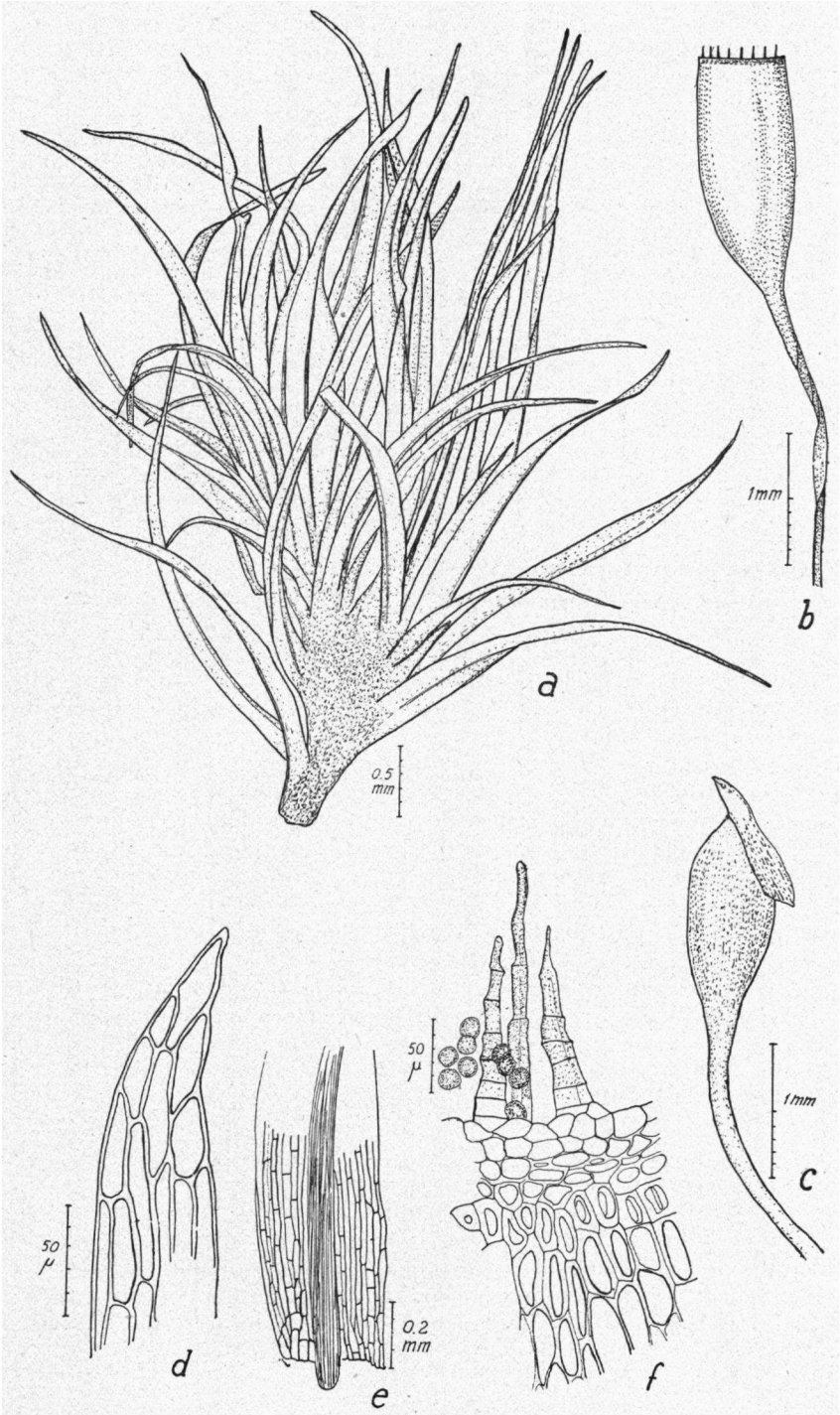


PLATE VI

England: V.C. 11, Wood N.E. of Bagshot, leg. F. Rose, 1951 (WM); V.C. 12, Blackmoor, Golfcourse nr. Borden, 300ft, leg. F. Rose & E. C. Wallace, 1951 (WM); VC 14, (Sussex), Lower Pennrocks, leg. F. Rose, 1951 (WM); The Rocks, Uckfield, E. Sussex, leg. F. Rose, 1951 (WM); V.C. 16, Pettswood, leg. F. Rose, 1949 (WM); V.C. 24, Black Park, Hangley, leg. F. Rose, 1950, (WM); V.C. 58 (Cheshire), Gritstone rocks, Crowden, leg. Broome & W. Watson 1920, type coll. of var. *heterocarpum*; Watson (K) Overton Hills, leg. E. A. Richards, 1911 (BM, earliest collection, as hitherto known); Laddow rocks, leg. W. Watson, 1927 (BM). V.C. 54, Laceyby, leg. G. H. Allison, 1934 (K); Yorkshire. Yearsly moor, leg. E. C. Wallace, 1946 (WM); Harrogate, herb. Stevens (K); Midhope moor, leg. Burrell, 1923 (K, PC, BM); V.C. 61, E. Yorkshire, Shipwith common, 50 ft, leg. Burrell, 1935 (herb. Bartram, U.S.); V.C. 62, W. Yorkshire, Brewham, Sandstone rocks, leg. E. C. Wallace 542, 1943 (WM); N. E. Yorkshire Buttercrambe Moor, leg. F. Rose, 1948 (WM); V.C. 63 Ramsdon rocks, Holmfirth, leg. Milson, 1924 (K); V.C. 67, E. Ebington, nr. Hayden Bridge, 1939, leg. E. M. Lobby, (herb. Bartram 374).

Holland: Thijssesbos, Naardermeer leg. W. Vergouw & W. Meijer, 1943, leg. WM, 1949 (WM); Zonneheuvel, Doorn, 1949, 1951. leg. WM (WM). Schovenhorst, Putten 1950. leg. Bryol. Werkgr. (WM); Heelsumse beekdal, Heelsum leg. E. Nannenga-Bremekamp, 1950, 1951 (WM).

Germany: Ex. herb. F. Koppe, in herb. WM: Eberswalde, Brandenburg, Kreis Oberbarmin, leg. K. Koppe, 1939, type of *O. germanicum* F. & K. Koppe; Lauenburg, Königsmoor bei Schmilau Elmendorff, 1950; Klövenstein Jg. 12, 1948, leg. Elmendorff.

b. *Orthodontium lineare* Schwaegr.

nov. subspec. **piriforme** Meijer.

Latin diagnosis:

foliis breviter subulatis, parce nitidis; seta 6—7 mm; theca piriiformis; operculo rostellato; peristomium internum papillosum, externum laeve; sporae 15—25 μ .

Description:

Differs from *O. lineare* Schwaegr. subsp. *lineare* in its more glossy leaves, in the typical pyriform sporogonia and the rostellate lid. The peristome is papillose on the endostome only, the dimensions of the spores are rather large (15—25 μ). Type no. 16629, coll. L. J. BRASS. Vernay Nyasaland Expedition 1946 — Lucheny plateau. Lower part of trunk of a *Widdringtonia* tree, 2000 m alt., July 3, 1946.

Other collections from the same region and the same expedition, collected by BRASS are: no. 16540. Small patch on trunk of a forest tree in deep shade, 1890 m alt., June 30, 1946 and no. 1645: exposed crown of a tall *Widdringtonia* tree, 1890 m. alt. June 30, 1946 (all herb. BARTRAM). (Plate VII).

Discussion:

This peculiar form has been determined by Dr BARTRAM as *O. lineare* Schwaegr. I agree with him, but in my opinion the above named differences from *O. lineare* Schwaegr. from the Cape indicate that it may be named a geographical variation of that species. The glossiness of the leaves give it an appearance of a member of the subsection *Linearis*. It seems however to me to be too closely related to *O. lineare* Schwaegr. to describe it as a new species.

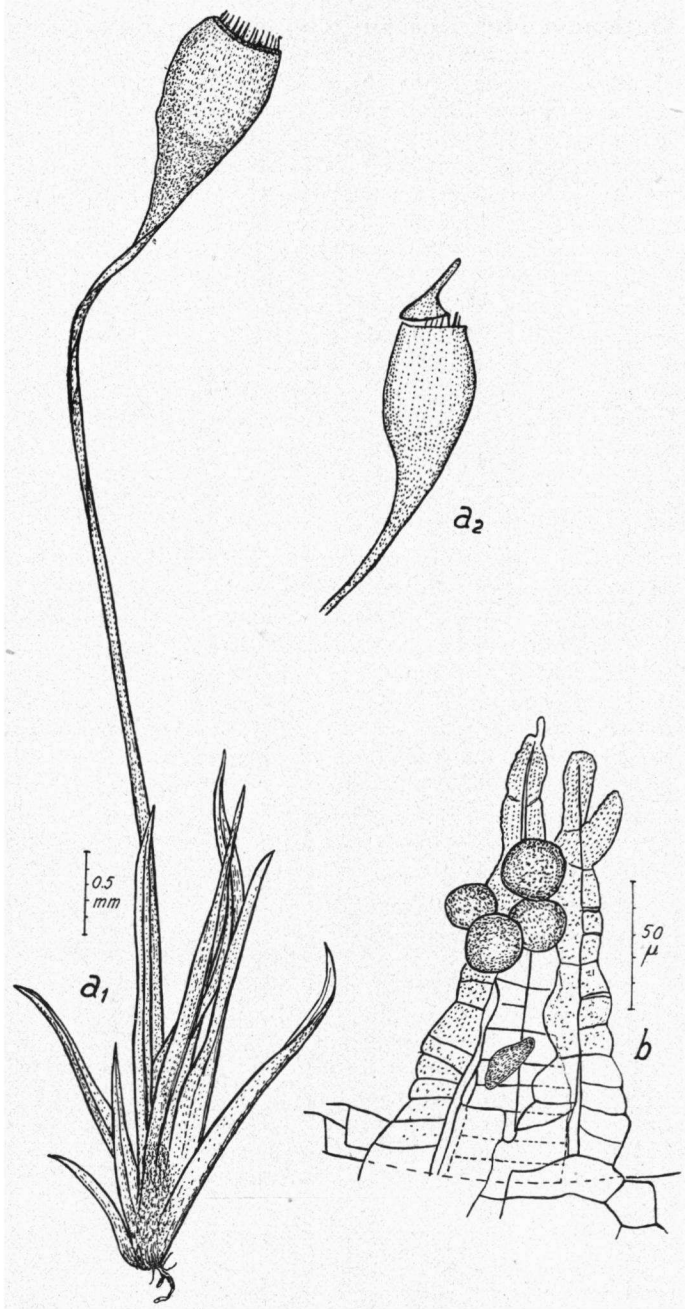


PLATE VII

O. lineare ssp. *piriforme*:

*a*₁ Habit, Nyasaland, coll. BRASS. no. 16545 (herb. BARTRAM).

*a*₂ Capsule, coll. BRASS. no. 16540, (herb. BARTRAM).

b. Peristome, coll. BRASS. no. 16629 (herb. BARTRAM).

c. **Orthodontium lineare** Schwaegr. ssp **sulcatum** (Hook.f. et Wils.) Meijer, comb. nov.

Orthodontium sulcatum Hook. fil et Wils. Hooker Icones Plantarum, Vol. IV, New Series 1848. Tab. 739 B; type in herb. Wils. (BM)

Apalodium sulcatum (Hook. f. et Wils.) Mitten. Austr. Mosses. Trans. & Proc. of Royal Soc. of Vict. 19: 49—96, 1883.

Orthodontium lanceolatum Mitten. Hookers Journ. of Bot. and Kew Garden Mescallany. 8, 1856; type in herb. NY.

Apalodium lanceolatum (Mitten) Mitten; Trans. & Proc. Royal Soc. of Vict. 19: 49—96, 1883.

Orthodontium zetterstedtii C. M. Symb. ad Bryol. Austr. Hedwigia 37: 76—171, 1898; type in herb. MEL.

Based on erroneous determinations are:

Apalodium lineare Auct. non (Taylor) Mitten; Watts & Whitelegge 1905, Census musc. Austr. Proc. Linn. Soc. of N.S. Wales. Suppl.

Orthodontium pallens Auct. non Hook. fil. et Wils; Watts & Whitelegge 1905, lit. cit.

Description:

In habit and dimensions of gametophyte and sporophyte similar to *O. lineare* ssp *lineare*. Autoecious or heteroecious.

In the typical common form the leaves are somewhat shorter pointed than in ssp *lineare*. But forms with narrow pointed leaves or even broader leaves also occur. The last have approximately the leaf type of the subsection *Pellucens*. The apex of those leaves can also be toothed occasionally. Peristome smooth, or only the inner processes papillose, or sometimes both the processes and the teeth of the outer peristome papillose. Processes on distinct basal membrane, texture and dimensions of the peristome as in ssp *lineare*. Lid of sporogonium conical or shortly rostellate. Form, margin and sulcation of the sporogonium similar to *O. l. lineare*. (Plate II 3a; VIII, IX and X.)

Discussion:

HOOKE & WILSON (1848) wrote after the original description: "Allied to *O. lineare* Schwaegr., but differing essentially from that and the other species in the furrowed capsule. The leaves also are shorter and not gradually tapering".

We have shown however that the capsules of *O. lineare* and of *O. australe* may be sulcate too when ripe. HOOKE & WILSON saw only a drawing of *O. lineare* and specimens of *O. australe* with young smooth capsules. Later bryologists followed in the steps of HOOKE & WILSON,

EXPLANATION OF PLATE VIII

O. lineare ssp *sulcatum*:

a. Narrow leaved form. (Coll. BELL. N. Zealand, Jan. 1887, H).

b., c. and d. type of *O. lanceolatum* Mitten (NY).

b. habit.

c. capsule.

d. peristome.

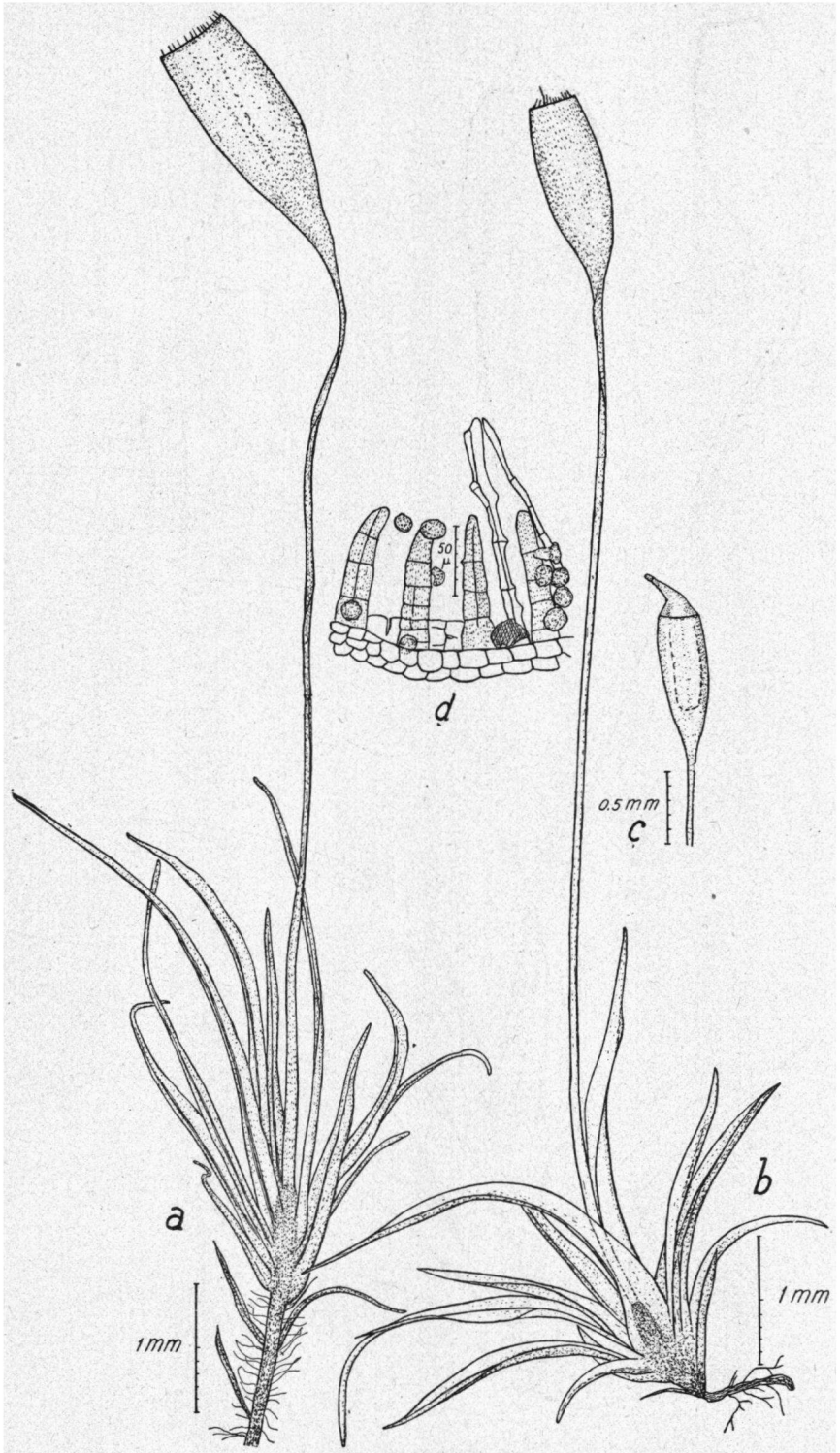


PLATE VIII

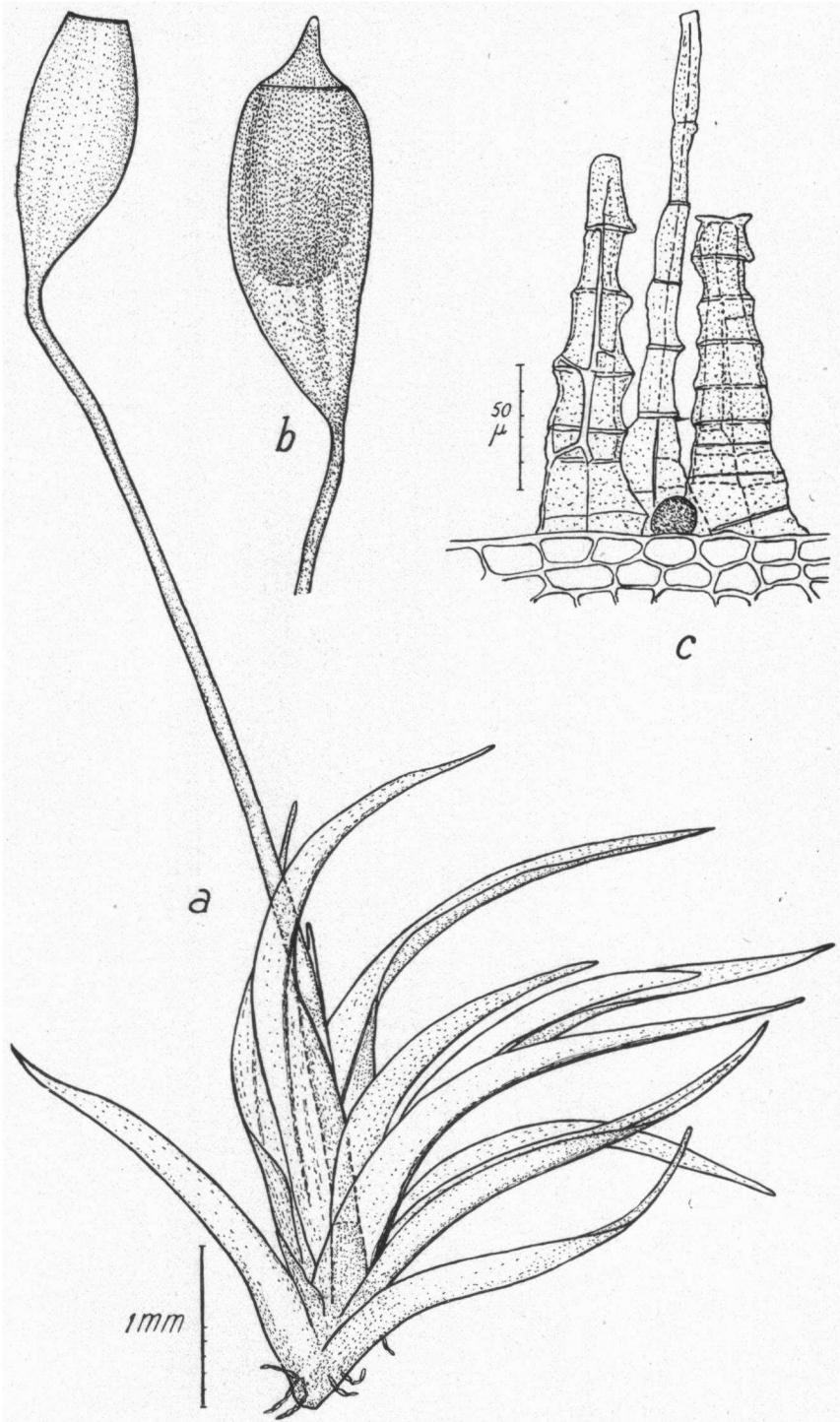


PLATE IX
Explanation on page 38



PLATE IX (Continued)
Explanation see next page

using the misleading specific epithet "sulcatum" as a clue for their determinations.

When we compare the type specimens of *O. sulcatum* with *O. lanceolatum* we should think them quite different, *O. lanceolatum* having short setae and a relatively small capsule (Plate VIII). Further study might support this view, because we found again and again in the collections a bigger and a smaller form. In several richer collections our suspicion has been raised, for we found there the bigger and the smaller sporogonia intermixed in the same tuft (*O. sulcatum* coll. BELL).

These specimens show that the dimensions of the sporogonia are to a certain extent dependent on conditions of local climate and changing weather conditions. The same phenomena is seen in the supposedly homogeneous *O. l. lineare*, in its recent European stations.

The form of the leaves and the breadth of the cells is probably also much influenced by growing conditions. It could not be by accident, that the plants from Masons Falls in Australia have the broadest leaves, but when we compare the type of *O. l. sulcatum* with *O. l. lineare*, *O. australe* ssp *australe* and *O. australe* ssp *robustusculum* we get the impression that the differences in leaf form are to a certain extent also genotypical.

For a further elucidation of this complex taxon we need culture experiments and ecological observations, in order to investigate if there exist special biotypes with constantly smooth peristome, in contrast with the highly papillose and for a better evaluation of the different leaf types: setaceous (coll. BELL. Plate VIIIa), narrow lanceolate leaves (type of *O. lanceolatum*) and somewhat broader leaves.

EXAMINED SPECIMENS:

Australia: New Holland, herb. Hooker & herb. Wilson (K & BM).

W. Australia: Swan river, James Drummond no. 263 (BM, holotype; K and NY isotype); Karriforest, 4 miles E. of Pemberton, leg. J. H. Willis, 1947, no. 722, (ex herb. Willis. WM).

N. S. Wales: Port Jackson district, Tempe near Sydney, leg. Hamilton, 1898 (S, NWS, H); Woronora River, leg. E. Cheel, 1901 (NSW, H); Kerosine Bay, 1884, no. 108 (NSW); Double Bay, leg. Whitelegge, 1884 (NSW, H); Ball's Head Bay, Sydney, leg. Whitelegge, 1884 (MEL, isotype of *O. zetterstedtii* C.M.); Wollongang, leg. Watts, 1895 (NSW; H; K as *O. zetterstedtii*); Nellius Glen, Katoomba, Blue Mountains, leg. Whitelegge, 1891 (H, NSW, as *O. zetterstedtii*); Nepean river, leg. W. W. Watts, 1899 [K, H; det. as *O. pallens* (Hook.f. et Wils.) Broth. by Brotherus]; Gosford, leg. Whitelegge, 1891, no. 446 (NSW; H, det. as *O. pallens* by Brotherus); Mt. Duval, leg. Watts., 1903 (NSW; H, det. *O. pallens* by Brotherus); Lilyvale, leg. Forsyth, 1900, no. 456 (S, NSW).

EXPLANATION OF PLATE IX

O. lineare ssp *sulcatum*:

- a. habit (Australia Worona river, leg. CHEEL, NSW).
- b. capsule, Australia (Mt. Lofty, leg. OPHEL, herb. BARTRAM).
- c. peristome (*O. sulcatum*, Karriforest, Pemberton, W. Australia, leg. J. H. WILLIS, 8-9-1947).
- d. *O. australe* ssp *robustusculum* Tasm. leg. WEYMOUTH, no. 2336 Mt. Wellington. St. Crispus, 2000 ft. 28-12-1908, det. BROTH. as *O. sulcatum* Hook.f. et Wils. (NY); habit and capsule.
- e. *O. australe* ssp *robustusculum*, peristome (leg. TAYLOR herb. S).

Victoria: leg. Flora M. Campbell, no. 754 (H); Old Grampians, leg. F. Müller, 1881 (BM), leg. Sullivan, 1887 (MEL & NSW; H), leg. Jos. Tilden, Dec. 1912 (herb. Bartram; NSW); Healesville, leg. Mardock, 1903 (BM); Mason's fall, Kinglake Nat. Park, leg. Willis, 1951 (herb. Willis, MEL); Russell's Dam, Creswick, leg. Willis, 1951 (herb. Willis, MEL); Mt. William leg. Sullivan, 1883 (PC, det. by C. Müller as *O. zetterstedtii* C.M.); Mt. Wellington, Gippsland, leg. F. v. Müller, no. 61, 1855 (type of *O. lanceolatum* Mitten, NY; isotype MEL).

South-Australia: Mt. Lofty, leg. Ophel, 32B, 1948 (herb. Bartram); Blewits Spring, Clarendon, leg. Tepper (herb. Willis, MEL).

Tasmania: ?¹ Coll. Archer, W. End rivulet (K, NY); Hobart rivulet 550 ft, leg. Weymouth, 1898 (BM); Huton, Glaciers Bay, leg. Weymouth no. 2928, 1892 (BM); Lady Edeline Falls, leg. Weymouth no. 2320 (det. Broth., H) Hobart rivulet, Track on wood., leg. Weymouth, no. 208, 1890 (NY, no. 298; H). Near Watson's Skye, leg. Weymouth, no. 1296, 1892 (H); Mt. Faulkner, leg. Weymouth 1892 (S, BM, NSW); N. W. Coast, on rocky bank, Castra Road, leg. Weymouth, no. 2289, 1907 (H); Beaconsfield, leg. Weymouth, no. 1133, 1892 (BM, H, det. as *O. pallens* by Brotherus).

New Zealand: Hokitika, Westland, 1938, leg. Martin no. 318.2 (WM); Riverton rocks, leg. Martin 318.18, 1950 (WM ex herb. M); Port Williams, NZ, Dr Lyall (NY, BM).

N. Island: S. end of S. Rotorua, leg. Allison & Sainsbury, no. 659 (BM); Rotorua, near edge of lake, leg. Allison no. 433, 1930 (herb. Sainsbury), 1929 (WELT); Hawkes Bay, Ohu, security mile Bush, leg. Naylor Beckett, no. 886, 1899 (PC, S, H, K), Rotomabana, leg. Berggren, 1874 (S); Whakapapa, Mt. Ruapeku, 3700 ft, leg. Sainsbury, no. 4066, 1929 (herb. Sainsb.); Eastbourne, Wellington, leg. Martin no. 318.17, 1945 (WM ex herb. Martin).

S. Island: Ravensbourne, Dunedin, leg. Martin, 1880 no. 54 (BM); Pine Hill leg. Bell, collections from Oct. 1886, no. 280, 280b; Dec. 1886, no. 1400, 30b; Jan. 1887, no. 1000; Febr. 1888 (H); Pine Hill leg. Martin, no. 659, 1948 (herb. Sainsb. no. 11835); Signal Hill, Dunedin, Otago, leg. K. W. Allison no. 94, 1944 (herb. Sainsb. no. 11044); Track to Coverham, Kaikoura ranges, Marlborough, leg. Sainsbury, no. 4067 (herb. Sainsb.); Leith valley, nr. Dunedin, leg. Naylor Beckett, no. 525 (H, herb. Wellington, special form, narrowly related to *O. australe*).

Stewart Island: Collections made by W. M. Martin in herb. Martin and herb. WM: Thale, 1946 (herb. Sainsb. no. 11047), Kaipipitrack, Paterson's Inlet, 1946, no. 318.5; stream, Ferndale, 1946, 318.6; Pt. Pegasus, Wilson's Bay, peaty coastal bank, no. 318.10, 1949; South of Pt. Pegasus, in Forest, no. 318.11, 1949; Bathing Beach, Oban, no.'s 318.12, 318.15, 1946; seaward Bush, Invercargill, 318.14, 1946, Coastal bank, Big Glory, 316.16, 1948.

4. ***Orthodontium australe*** J. D. Hooker & W. Wilson. Musci antarctici, London Journ. of Bot. Vol. III, 1844; type in herb. Wilson (BM).

Apalodium australe (Hooker, fil. et Wils.) Mitten. Musci austro-americi. Journ. Linn. Soc. Bot. 12, 1869.

a. ***O. australe* ssp. *australe*.**

Description:

Autoecious or heteroecious. Growing in dense tufts, with crowded leaves, somewhat curled when dry, erect when wet, gradually pointed, rather small setaceous, with stout nerve. Sporogonia generally on a longer seta (6—20 mm), capsules variable in length and form, the general form is oblong (3.5—4 times as long as broad), but sometimes pyriform. (Plate X). Length of capsule from 1.5 to 2.5 mm. Lid of the same length as in *O. lineare* (0.4—0.5 mm), but somewhat more rostellate.

Peristome generally showing great differences in length of outer peristome teeth and segments of the inner peristome. (segments

¹) This puzzling specimen bears a distinct papillose peristome.

1.5—2 times longer than the teeth). Outer peristome 130—145 μ in length, inner 180—290 μ , both generally pale coloured, both or only the processes papillose.

Spores varying from 12—23 μ . (Plate I 1; II 2b; X).

Discussion:

See under *O. australe* ssp *robustusculum* and *O. lineare* ssp *sulcatum*.

EXAMINED SPECIMENS:

Falkland Islands: Antarct. Exp., 1839—1843, leg. J. D. Hooker (K, holotype; BM; L; S); W. Point Island, leg. Halle 1907, no. 575 (PC, S).

Hermite Island, Cape Horn: Antarctic Exp., 1839—1843, leg. J. D. Hooker, 1841 (K, BM, L, paratype).

Fuegia: Exp. Fennica, leg. Roivainen, 1928—1929 (herb. Bartram). From the following localities: Estanção Carmen, Puesto Millaldeo (139); Estanção Cameron (874); Puesto Artaso (918); Rio Bueno; Lago Linch (1405); Lago Fagnano (254); Rio Rusfin. Expedition Suecia, 1907—1909, leg. Halle & Skottsberg, in herb. S. et herb. PC (det. Cardot): Vallée du Rio Azopardo, 300 m.s.m. (493); Same place, Rio mascarella (494); Almirantazza, Puesto Gomez (495); Cami et Descado (var. *brevisetum* Cardot) no. 496; canal Jeronimo, var. *sinuosi-folium* Card. nov. var. (497).

Patagonia: Princeton Sc. Exp. 1896—97 leg. Hatcher (NY; herb. Bartram).

Chile: Punta Arenas, leg. Thaxter, 1905—06, no. 124 (US, FH) and no. 127 (US).

Tasmania: Kangaroo bottom, Sept. 3, 1840, leg. J. D. Hooker (K, BM); Oldfield 330, Brown river; Oldfield 225, 134b, Back river (K, BM); Mt. Wellington 2000 ft. leg. J. D. Hooker 1328 (K), St. Crispus track, leg. Weymouth, no. 1149, 1888 (H somewhat intermediate between *O. sulcatum* and *O. australe*), no. 776, 1891 (H, PC); Bush, N.W. of new reservoir, Hobart, leg. Weymouth (MEL); Guy Hawkes Rivulet near Hobart, leg. Weymouth, no. 387, 1890, (H); Batess Creek, Peppermint Bay, leg. Weymouth no. 232, 1889 (H); Balfes Hill, Crador, Huon, leg. Weymouth, no. 157, 1889 (H).

b. *Orthodontium australe* Hook.f. et Wils. ssp *robustusculum* (C.M.) Meijer comb. nov.

Orthodontium robustiusculum C. M. Symbolae ad Bryol. Australiae II, Hedwigia, 37: 76—171, 1898; Lectotype in herb. H.

Description:

Autoecious or heteroecious. Tufts of a somewhat looser texture than in *O. australe* ssp *australe*, leaves somewhat broader. Seta in many cases much larger (till 26 mm) as well as the capsules (3.2×1.0 , maximum).

Outer peristome teeth more generally as long as the inner, usually brownish coloured, slightly papillose, inner peristome lighter coloured, more distinctly papillose, segments on a distinct basal membrane, of 2—3 cells in height, sometimes slightly split at their base.

Lid longer than in *O. australe* ssp *australe* (ca. 0.7 mm). (Plate I 2; II 3c; IX).

Discussion:

This form can be distinguished from *O. lineare* ssp *sulcatum* by its generally larger sporogonia, longer setae (10—26 mm) and larger

capsules. The maximum dimensions of sporogonium of *O. sulcatum* are the minimum dimension in *O. robustiusculum*. The maximum length of the peristome teeth is somewhat larger, but the whole structure is rather similar in both. It is this form which has caused very much confusion among bryologists. We find specimens belonging to *O. australe* ssp *robustiusculum* named as *O. sulcatum*, *O. lanceolatum* and *O. australe*, by BROTHERUS and WEYMOUTH and when we compare them, we cannot see any real differences. CARL MÜLLER (1898) selected one of them and described it as his new species: *O. robustiusculum*. This was totally neglected by other bryologists, perhaps because they had the suspicion that this was yet another of CARL MÜLLER's species without any real existence in nature.

A good illustration of the difficulties in a preliminary study in this group is given by the following extract from DIXON's generally praised "Studies in the Bryology of New Zealand" (1926) p. 197:

"*Orthodontium sulcatum* Hook. f. et Wils.

The only species. Recognized at once by the long narrow linear setaceous leaves, erect, elliptic capsule, sulcate when dry and empty, the rostellate lid, and delicate peristome.

I have it from two or three stations in the South Island, but it would seem to be rare. It is also found in Australia and Tasmania. I strongly suspect that *O. sulcatum* will have to be reduced to *O. australe* H. f. & W. Lond. Journ. Bot. iii, 545 (1844), from the Falkland Islands, Hermite Island and Tasmania. The authors of the two species did not think it necessary to compare them with another, no doubt since in their view *O. sulcatum* differs from all the other species in the furrowed capsule while *O. australe* is figured (and described by implication) as with smooth capsule. I have examined the types of both species and if the matter could rest on these alone the two might well stand, but the matter is quite altered when other specimens are examined. In the original specimens of *O. australe* from the Falkland Islands, the young capsules are quite smooth, while the old ones are irregularly plicate, but do not show any trace of the regular ribbing that is characteristic of *O. sulcatum*. There are however, few or no capsules in good condition."

We have seen that the ribbing of the mature sporogonia occurs in all the species of the subsection *Linearis* and that it therefore cannot be used for distinguishing species within this section. Juvenile states differ from mature. DIXON proceeds as follows:

"Tasmanian specimens in HOOKER's collection are very puzzling, and perhaps the best comment on the distinctness of the two plants is to be found in the fact that in herb. HOOKER there are certain specimens labelled *O. sulcatum* which certainly belong to *O. australe* and others labelled *O. australe*, which if the two are to be kept separate must as certainly be referred to *O. sulcatum*. The capsules in fact seem to show all gradations from a smooth

surface to a very regularly ribbed and sulcate one. The bulk of the specimens however lack capsules in good mature condition and I do not think the problem can be solved satisfactorily except by study of good material in the field”.

From this it appears that DIXON was not quite sure about the worth of the ribbing as a character and from the last sentence we conclude that he was not quite sure of his own concept of both species. That he did not succeed in finding the real differences, owing to lack of material, appears from what follows:

“*O. sulcatum* is described and figured as with short only slightly tapering leaves, but this is not a constant character. Tasmanian specimens of ARCHER’s collecting with highly ribbed capsules, have the leaves very narrowly and long tapering, which is the case also with New Zealand specimens in herb. Kew, coll. NORKETT”.

These observations are right, as will be shown later. MITTEN brought ARCHER’s collection in his *O. lanceolatum*. DIXON continues:

“RODWAY, (Tasmanian Bryophyta, Mosses) described both *O. australe* and *O. sulcatum* as with sulcate capsules, separating them by the form of the fruit, oblong in the former, pyriform in the latter, but there is no difference in the form of the capsule, either as figured by HOOKER or as exhibited by the original specimens, except in as much as is produced by different stages of maturity”.

To a certain extent we agree with this opinion, but our observations revealed a slight tendency for more oblong capsules among *O. australe* and showed that all old sporogonia may be distinctly furrowed.

So much for the earlier difficulties in recognizing *O. australe* ssp *robustusculum*. The differences between *O. lineare* ssp *sulcatum* and *O. australe* *robustusculum* are mainly in the dimensions of the sporogonia, setae etc. as we showed earlier. The question then arises whether the former taxon cannot be a haploid state of the latter. The dimensions of the sporogonia suggested investigation of this possibility. It turned out then that the real differences in size of the sporogonia are not correlated with considerable difference in the diameter of the spores. They measure 11—20 μ at *O. lineare* ssp *sulcatum* and 15—24 μ at *O. australe* ssp *robustusculum*.

Moreover the leaf cells do not differ considerably: average breadth of cells in the middle of the leaf in *O. l. sulcatum* 9—14 μ , in *O. robustusculum* 10—12 μ .

Another explanation, at first sight more fantastic, but after longer consideration more likely, is that hybridization of *O. australe* and *O. lineare* ssp *sulcatum* has taken place in Tasmania. In these autoecious groups of mosses one cross is enough to give rise to quite a new homozygous “race” (LOTSY 1928).

We remember in this connection the rather robust, small-leaved

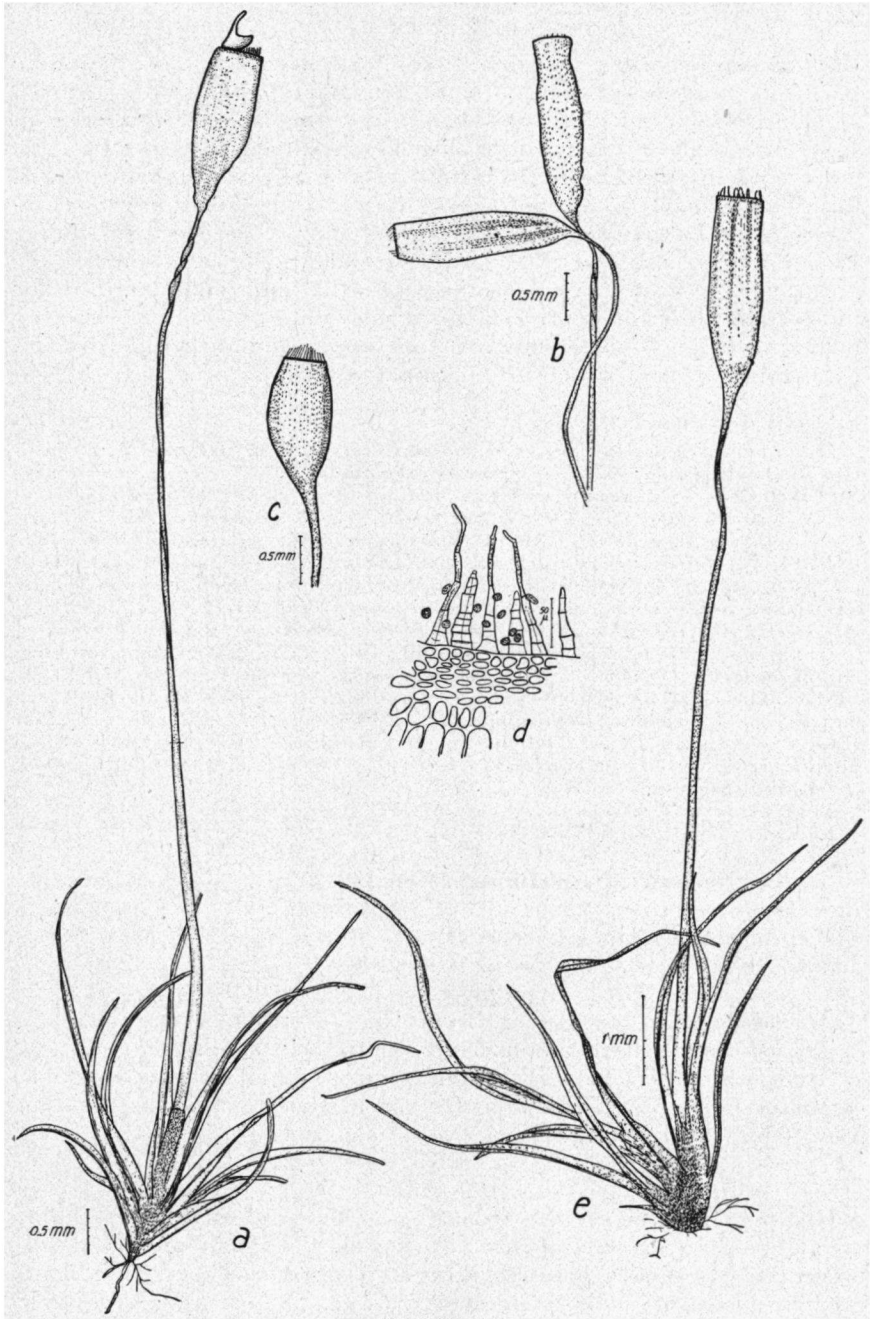


PLATE X

- a. *O. australe*. Isotype (NY).
 b. *O. australe*, old sulcate capsules. Patagonia. Princeton Exp. coll. HATCHER (NY).
 c. *O. australe*. Leg. ROIVANEN, Fuegia media; Estancia Carmen 18-1-1929. (More or less pyriformous capsule, herb. BARTRAM).
 d. Peristome, *O. australe* (isotype; NY).
 e. *O. australe* × *O. sulcatum*? Leg. ARCHER, Tasm. (NY).

"*O. lanceolatum*" from Tasmania (coll. ARCHER). Its more papillose peristome and longer setae might be characters introduced from *O. a. australe* into *O. lineare sulcatum* and the lack of difference in spore size and cell size would thus be explained.

By such hybridization the origin of the puzzling narrow-leaved forms with short small sporogonia, formerly included in *O. lanceolatum*, from Lady Edeline Falls, Tasm. and *O. sulcatum* coll. BELL. Pine Hill Nw Zealand, Plate VIII, could also be explained.

It appears from these considerations that our chief need is for more collections and more ecological information, in short, for more field knowledge. Our taxonomical conclusions should then be checked by cytological and genetical investigations.

EXAMINED SPECIMENS:

Tasmania: Eagle Hawk Neck Hill, East Coast, 1889, leg. Weymouth (H, lectotype of *O. robustiusculum* C.M.; S); Forestiers Peninsula, leg. Weym. no. 257 (NSW); Mt. Wellington St. Crispus well leg. Bastow, 1886 (NSW), St. Crispus track, leg. Weymouth 1890, no. 320 (NY, H), 1891 (H, PC) 1908 no. 2336 (NY, H, det. Broth. as *O. sulcatum*); Mt. Wellington, leg. Weymouth, no. 1498, 1893 (NY, S, H), Hobart rivulet track, no. 298, 1890, (NY, H), Shady banks 2400 ft, no. 2566, 1896 (H), New track, Vinger Post, no. 1166, 1890 (H, intermediate form between ssp *australe* and ssp *robustusculum*), Deep Creek, no. 2168, 1897 (H), Derby, 1000 ft, leg. Weymouth, no. 2716, 1913 (H, K); South Coast Recherche, near Leprena, 200 ft, leg. Weym., no. 13, 1911; Gully Mt. Dromedary, leg. Bastow no. 649, 1886 (BM); Hobart water works, leg. Weym., no. 2926, 1891 (BM); Recherche bay, leg. Weymouth, no. 2882, 1911 (H), Recherche, Catamassan, leg. Cockayne & Weymouth, no. 2579, 1911 (H, both with somewhat glossy leaves); East Coast, 1400 ft, leg. Weymouth no. 2477, 1911 (H); Lady Edeline Falls, leg. Weymouth no. 2346, 19-1—1909, (H, no. 2320, 19-1—1909, *O. sulcatum*, from same locality!).

Australia: Vict. Erskine River, leg. W. W. Watts, no. 1077 (H).

New Zealand: Bluff, herb. Bell. (H).

5. *Orthodontium pallens* (Hook.f. et Wils.) Broth. Engler & Prantl.

Weissia pallens (Hook.f. et Wils.). Ic. Plant. Vol. IV, New Series Tab. 739A, 1848; holotype in herb. BM.

Seligeria pallens C.M. Syn. musc., p. 423, 1849.

Microdus pallens Par. Index bryol., p. 805 (1896).

Zygodon lineare Taylor nom. nud. (herb. Mitten, NY).

Apalodium lineare (Taylor) Mitten. Transact. and Proc. Royal Soc. of Victoria, Vol. 19, 1883, non *Apalodium lineare* (Schwaegr.) Mitten, Voy. Challenger Exp. 1885.

Description:

Growing in tufts, or intermixed with other mosses. General habit of gametophyt as *O. sulcatum*. Autoecious. Leaves rather glossy, lanceolate, gradually pointed, upright standing, or somewhat bent, greatest breadth ca. 0,3 mm, length ca. 2—3 mm, cells at middle of leaf ca. 10 μ in breadth.

Seta rather short (ca. 3—4 mm). Capsule somewhat bent, slightly pyriform, with short neck, collenchymatous cells near the margin of the mouth very distinct. Lid oblique rostellate. Peristome rather

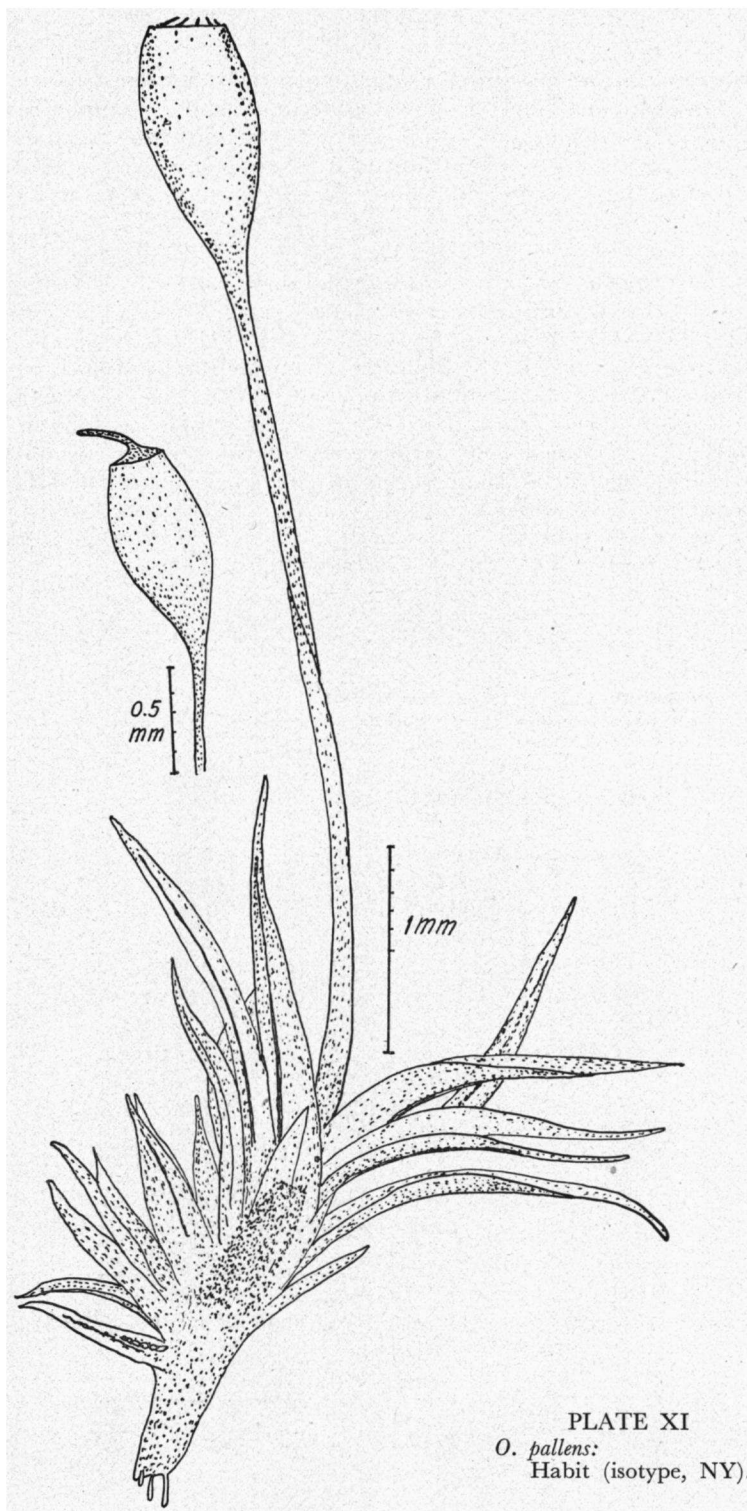


PLATE XI
O. pallens:
Habit (isotype, NY).

rudimentary developed. Outer peristome teeth ca. 110—120 μ long, totally smooth, light yellow, sometimes with irregular sculptures; inner peristome mainly composed of a very undistinct basal membrane, very fragile and thin, translucent, split between the outer teeth. Processes not developed. Spores 20—25 μ , finely punctate (Plate XI).

Discussion:

This species is difficult to distinguish, without sporogonia, from rather broad leaved forms of *O. sulcatum*. It is not surprising that bryologists confused it with juvenile states of *O. sulcatum* and *O. inflatum*, for in both such forms the inner peristome is only slightly developed; in the last named it remains thin and translucent even in the mature state. It is fairly certain that *O. pallens* is narrowly related to *O. inflatum* and to *O. sulcatum*. The large size of its spores is a common feature with *O. inflatum* and the shape of the leaves with *O. sulcatum*. The tendency to produce reduced or rudimentary inner peristomes can be traced within the series leading from *O. pallens* over *O. inflatum* to *O. infractum*. *O. pallens* forms a bridge between subsection *Linearis* and subsection *Pellucens*.

EXAMINED SPECIMENS:

S. W. Australia: Swan River, leg. Drummond, no. 201 (BM type; K; NY, mixed with the type of *O. sulcatum* Hook.f. et Wils.!).

Tasmania: South Coast Recherche, forest near Deprena, 200 ft., leg. Weymouth, 1911 (NY, mixed with *O. robustiusculum*).

6. *Orthodontium inflatum* (Mitt.) Par. Index bryol. 1894—1900.

Apalodium inflatum Mitten. Voy. H. M. S. Challenger, 1885; holotype in herb. NY.

Orthodontium ovale C.M. ex Broth. Some new species of Australian mosses described. II, Öfersigt af Finska, Vetenskaps-Soc. Förhandl. 35, 1892—1893, Helsingf. 1893; lectotype in herb. H.

Wilsoniella compacta Geheeb, nom. nud. Watts & Whitelegge 1905. Cens. Musc. Austral. Proc. Linn. Soc. of NSW.

O. pallens (Hook.f. et Wils.) Broth. sensu Brotherus, Engler & Prantl., is partly *O. inflatum*, partly *O. lineare* ssp. *sulcatum*, according to the specimens and determinations of Brotherus in herb. H.

Description:

Autoecious. Very densely growing in tufts. Plants with many rhizoids at their bases. Leaves somewhat glossy, very narrow lance-

EXPLANATION OF PLATE XII

O. inflatum:

- a. Habit (type mat.; NY).
- b. Young capsule with calyptra (type mat. of *O. ovale* C.M., NSW).
- c. Capsule with lid.
- d. Peristome (type mat. of *O. ovale*; NSW).

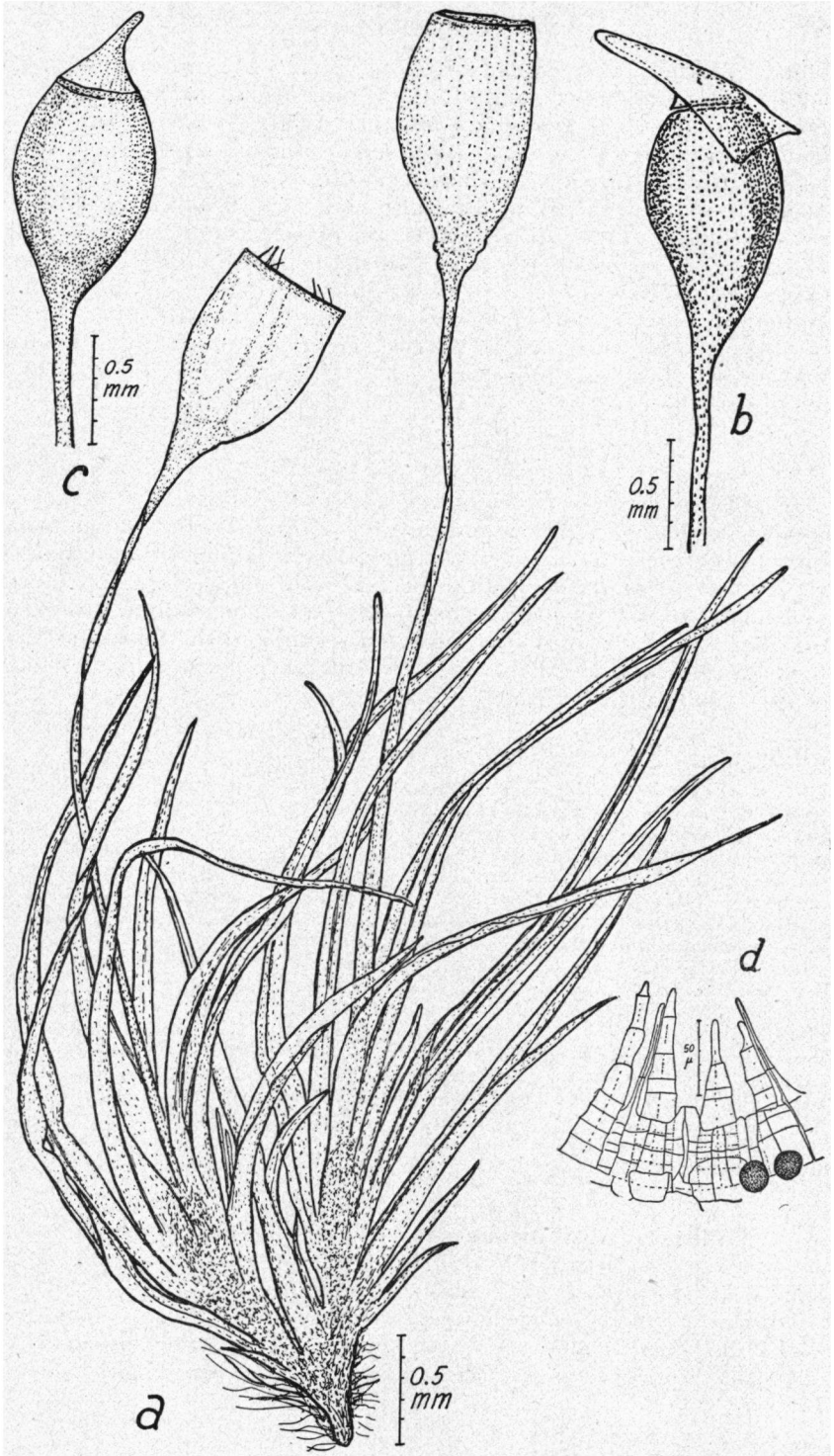


PLATE XII

olate, gradually acuminate in a long point. Maximal breadth ca. 0,20—0,30 mm, max. length 3—5 mm. Cells prosenchymatous, breadth c. 8—10 μ , nerve very distinct, relatively broad, till 1/4 of leaf breadth. Seta 4—5 mm, capsule erect or only slightly bent, when ripe distinctly broadly pyriform (swollen), c. 1—1,2 mm long and 0,6—0,7 mm broad, occasionally with some broad furrows. Neck relatively short. Lid rostrate, length one third of total capsule length. Calyptra longer than the lid, cucullate. Outer peristome well developed, yellow-brown coloured. Inner peristome with a rather high thin and translucent basal membrane, composed of 3—4 cells in height, with very fragile narrow processes and with a median line, which becomes indistinct below the apex. Spores 20—30 μ , in diam. (Plate XII).

Discussion :

O. inflatum is very easy to recognize by its combination of narrow leaves, swollen sporogonia, long lid, big spores and the rather translucent inner peristome. Juvenile states are sometimes wrongly named *O. sulcatum* or *O. pallens*. This species is the closest relative of the indo-malayan *O. infractum*. They possess the long lid in common, together with the translucent inner peristome and the more pyriform shape of the capsules. Their greatest difference consists in the shape of their leaves.

EXAMINED SPECIMENS:

Australia, N. S. Wales: Blue Mountains, leg. Rev. R. Collie, 1885, holotype (NY); Botany Bay, La Perouse, leg. Whitelegge 1885 (MEL, det. as *O. ovale* by Brotherus, in herb. H, under the name *Wilsoniella compacta* Geheeb nom. nud., no. 211, leg. Whitelegge no. 297); La Perouse leg. Forsyth 1898 no. 3960 (NSW, det. as *O. pallens* (Hook.f. et Wils.) Broth. by Brotherus in herb. S), 1899 (H, no. 644, det. as *O. ovale* by Broth; PC), 1900. [H, PC, as *O. lineare* (Mitt.), herb. Cardot = *O. pallens* comm. Broth]. *It is very probable that Forsyth made these collections all at the same locality. They obtained four different wrong names! Watts and Whitelegge (1905) wrote already "may be O. inflatum"; Pennshurt, leg. Forsyth, no. 954 (NSW, det. Broth: O. pallens); Gosford, leg. Whitelegge no. 445, 1891. The type coll. of O. ovale C.M. ex Broth (NSW; H, lectotype; PC); Tempe near Sydney, leg. Forsyth, no. 541, 1899 (det. Broth: O. ovale, NSW, H); Port Jackson district, leg. Forsyth 1898 (comm. Brotherus O. ovale C.M., S, H); Bollina, Sydney, Cook's river, leg. W. W. Watts, no. 128, 1896 (det. Broth: O. ovale, H, PC); Park Grays Island, leg. Watts, 1896 (H, det. Broth: O. ovale; BM; WM ex MEL); Watsons Bay, leg. Hamilton, leg. Watts. no. 128 (H).*

S. E. Vict: Stanley Creek, leg. J. H. Willis, 1951, (det. G. O. K. Sainsbury as *O. sulcatum*, WM ex herb. MEL).

7. **Orthodontium infractum** Dozy & Molkenboer. Musci frond. Arch. Ind. Ann. Sciences, Nat. 1844, p. 313; Musci frond. ex Arch. Ind. 1844. With plate; type in herb. L.

Orthodontium brevicollum Fleischer. Die Musci der Flora von Buitenzorg II Bd.: 495, 1902—1904. With figure; type in herb. Fleischer, FH.

O. sulcatum (Hook.f.) et Wils. p.p. C. M. Synopsis Muscorum, 1849, p. 239.

Description:

Autoecious, growing in tufts. Plants densely leaved; leaves with the same metallic gloss as the leaves of *O. pellucens*, dry somewhat curled, wet curved, gradually pointed, keeled, variable in breadth (0,35—0,45 mm) and in length (2—5 mm); margin undulated on some places, occasionally slightly denticulate near apex. Cells narrow prosenchymatous, c. 6—10 μ in breadth and 10—15 times as long as broad, towards the basis wider (as in all *Orthodontium* species). Nerve possessing stereid cells. Seta 5—12 mm in length. Capsules erect or somewhat bent, ovato-oblong or pyriform, c. 1 mm long; cells near margin of capsule of the ordinary collenchymatous type; lid rostrate, $\frac{2}{3}$ of total capsule length. Outer peristome yellow ochre, smooth, inner with translucent basal membrane, some cells high. Processes narrow, generally darker coloured than the basal membrane, median line not fully developed. Spores minutely punctate, 14—18 μ in diam. (Plate II e; XIII.)

Discussion:

O. infractum is standing at the borderline of the group of species which are closely related with *O. pellucens*.

It differs from that species in its smaller dimensions, narrower cells and its less developed inner peristome. Pyriformous capsules, with long lids occur also within the range of *O. pellucens*. *O. infractum* is not so very easy to distinguish from *O. novae-guineae*. The last species possesses however longer setae, somewhat greater leaves, and a less pyriform capsule. It has a well developed peristome, inner and outer are papillose at maturity. FLEISCHER described *O. brevicollum* as a subspecies from the same area as *O. infractum*. The types of both differ indeed as regards shape of the capsules and of the leaves, the capsules being more pyriformous and the leaves broader in *O. brevicollum*. The other collections show however that these are not constant differences. In some instances, forms with the typical characters of both intergrade within one tuft. That's why we put together here such minor variants in one species.

EXAMINED SPECIMENS:

Java: Type collection, leg. Zippelius Sederatoc, Java (L); coll. Horsfield 73 and 13, herb. Mitten (NY); Pangerango leg. Nyman, 1898 (L); Pangerango, 2700 m, leg. Fleischer 1898 (type coll. of *O. brevicollum*, L; PC, H); Dieengplateau, Praoe, 2500 m, leg. Fleischer, 1898 (S, L, H), 1901 (S, L, NY) Papandajan, leg. Verdoorn 1930, det. Dixon (BM), leg. Wichura, no. 2496, 1861 (H); Pancoban Prau, leg. Wichura, no. 2498, 1861 (H); Pangerango, leg. Wichura 24976 and 249760, 1861 (H).

Ceylon: Hotton-plaines, 2500 m, leg. Fleischer, det. as *O. brevicollum* (L); leg. Binstead, 1913 (BM); Central Province leg. Thwaites, no. 102 (NY, BM, MEL); Ambewelle-Pattipola, 1900 m, leg. Herzog, 1906 (H).

Borneo: leg. Korthals (L, S).

8a. ***Orthodontium pellucens*** (Hooker) Br. & Sch. Bryol. Eur. fasc. 3—4, 1844.

Bryum pellucens Hook. Ic. pl. rar. 1, t. 34, 1837; holotype in herb. K.

Apalodium pellucens (Hook.) Mitt. J. Linn. Soc. Bot. Vol. 12, p. 238, 1869.

Orthodontium confine Hampe. Ann. Sc. Nat. 5. ser. 4: 338, 1865; holotype in herb. BM.

Apalodium confine (Hampe) Mitt. Voy. H. M. S. Challenger, 1885.

Orthodontium fendleri C. M. Linnaea 42: 473, 1878—79; (N.F. Bd. VIII, no. 33); lectotype in herb. N.Y.

Orthodontium ulei C.M. Bull. Herb. Boissier 6: 29, 1898; lectotype in herb. NY.

Orthodontium pycnoblustum C.M. nom. nud. (herb. name of the type of *O. ulei* C.M.).

Orthodontium arenarium C.M. Bull. Herb. Boissier 6: 29, 1898; lectotype in herb. NY.

Stableria gracilis (Schwaegr.) Lindb. var. *californica* Howe, Erythea Vol. 5: 92, 1897; type in herb. US.

Orthodontium gaumei Allorge et Thériot. Rev. Bryol. 1931: T. IV: 194—196.

Description:

Autoecious, growing in loose or very dense tufts, sometimes strongly interwoven with tomentum. Plants 0,5—5 cm high, with a metallic sheen; leaves broader than in most specimens of *O. lineare* and *O. gracile*, 0,3—0,5 mm broad and 3—6 mm long, twisted when dry, acute or acuminate, usually rather short compared with other species, with occasional teeth near the apex, cell walls rather thick, cells in the midst of the leaf 13—18 μ broad, linear oblong.

Sporogonia with red setae, 5—8 (7—14) mm long, capsule red-brown, erect-flexed, gradually tapering into the neck, at mouth rather broad (0,50—0,65 mm), 2—3 times as long as broad, (max. length 1,85 mm min. 0,80 mm). Older capsules regularly furrowed when dry, with distinct dark border of collenchymatous cells near the margin.

Peristome rather robust but variable, outer teeth 200—290 μ , segments of the inner peristome 150—300 μ , the latter with splits at base, along the median line. Outer teeth somewhat broader at base than the processes (\pm 30 and 20 μ respectively), outer teeth of 8—12 joints, (*O. gracile* 6—9), processes 6—7. In fully developed peristome the outer teeth are reddish brown in colour and densely papillose, papillae sometimes in indistinct rows, the inner teeth are lighter coloured. In unripe capsules the peristome is almost smooth and paler coloured, segments on thin basal membrane, 3—4 cells high.

EXPLANATION OF PLATE XIII

O. infractum:

a. Habit (isotype material of *O. brevicollum* Fleisch; L).

b. Young capsule (coll. FLEISCHER, 363, Dieeng plateau, Praoc, herb. L.).

c. Pyriformous and lanceolate capsule from coll. HERZOG, Ceylon. Pattipola-Ambevelle (herb. H).

d. Peristome (coll. FLEISCHER, Dieeng, Praoc, Java (L)).

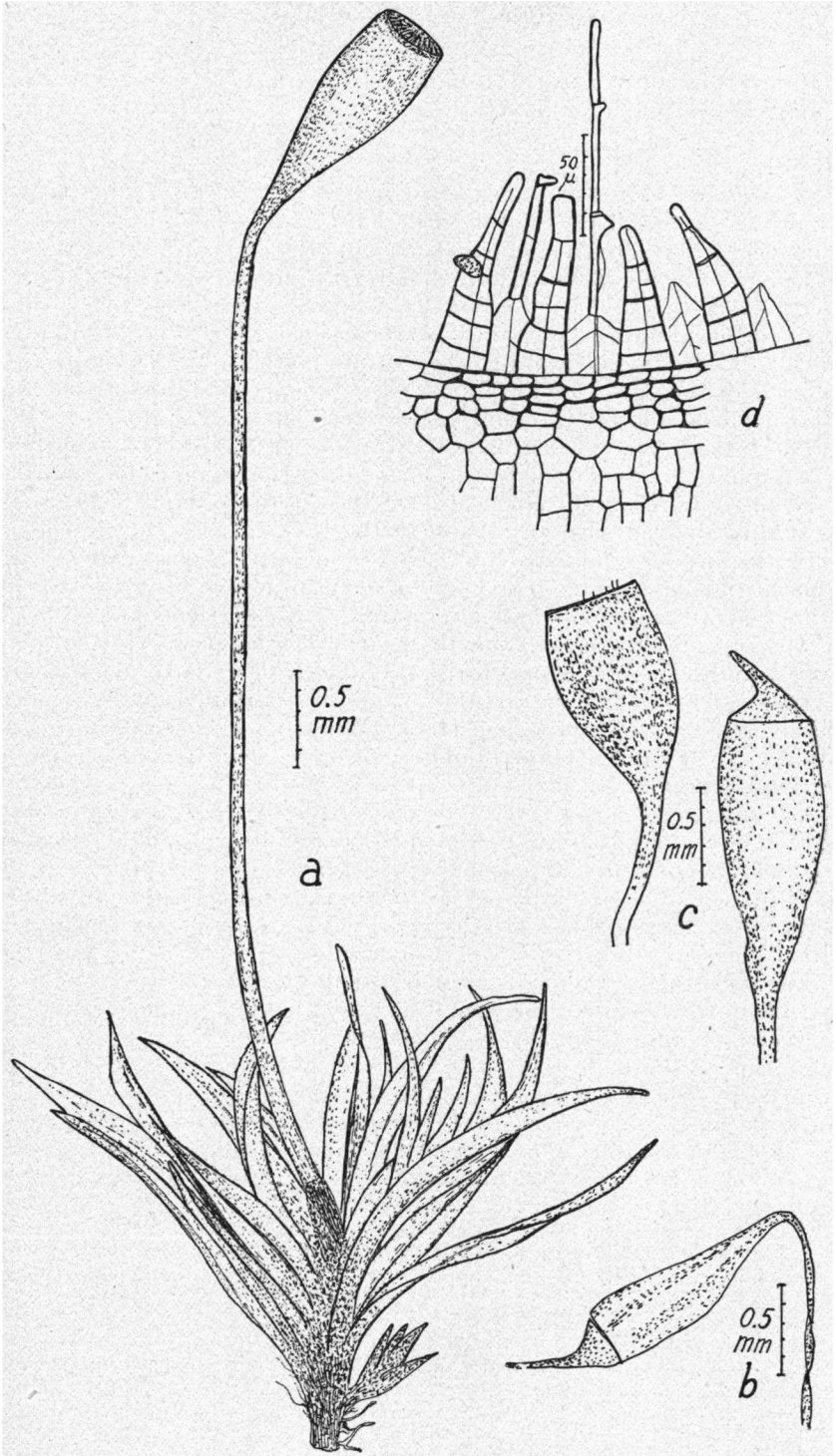


PLATE XIII

Lid rostrate, often oblique, usually $\pm 0,75$ mm long, rarely 0,80 mm. Spores finely punctate dark brown, 15—20 μ . (Plate II 2e; XIV).

Discussion:

O. pellucens s.s. is a widely distributed species along the South American Andes. Very slightly different, or quite identical forms of this species have been described as separate species: *O. confine*, *O. fendleri*, *O. ulei*, *O. arenarium*. Mrs. BRITTON indicated already on the sheets of the New York herbarium that her studies on this group resulted in a putting together of these forms. LE ROY ANDREWS (1932, 1935) paid attention to these studies. I have tried to find any differences of which I could suppose that they were not due to phaenotypical variation, but I could not succeed in finding them.

There exists however one remarkable form, which is not described as a separate taxon, namely the form from Jamaica. It has shorter setae and a more pyriformous capsule. Most of the Jamaica collections have this aberrant aspect. (Table XIVc).

In the list of synonyms has also been put *O. gaumei* Allorge & Thériot. Some twenty years ago that form has been detected in France (GAUME, 1932), and afterwards in Spain (ALLORGE, 1934). It was repeatedly compared with *O. infractum* Dozy & Molkenboer, by the authors, by MARGADANT & MEIJER (1950) and previously by REIMERS (1941). The last author supposed that it could be more closely related to *O. pellucens* (Hook.) Br. eur., but MARGADANT & MEIJER (1950) uttered some doubts against the geographical argument used by REIMERS for his statement.

A closer comparison showed me distinctly that REIMERS was right. The leaf types are just the same. I made drawings of *O. pellucens* (*O. confine* type) and *O. gaumei* type, which showed the very great resemblance. The resemblance with *O. infractum* is only apparent, because the sporogonia were young. In such a state the lid can be rather long in comparison with the theca.

The peristome fragments which I saw were smooth, but Mr. POTIER DE LA VARDE kindly informed me that he had a sample for study which had them distinctly papillose.

In this way the words of ALLORGE & THÉRIOT (1931) become even more true: "La présence d'un Orthodontium à Fontainebleau constitue un fait bryogéographique tout à fait intéressant; elle ajoute un cas remarquable aux disjonctions déjà connues dans la flore muscinale de l'Europe (ALLORGE 1931)."

EXPLANATION OF PLATE XIV

O. bellucens:

- a. Habit. Coll. LINDIG, Nova Granata. Monte de Moro (L).
- b. Capsule (isotype of *O. confine* Hampe, L).
- c. Pyriformous capsule, Jamaica, herb. MITTEN (NY).
- d. Peristome. Jamaica, Coll. E. G. BRITTON, New Haven Gap, no. 65 (NY).
- e. Apex of leaf (type material of *O. gaumei*; PC).

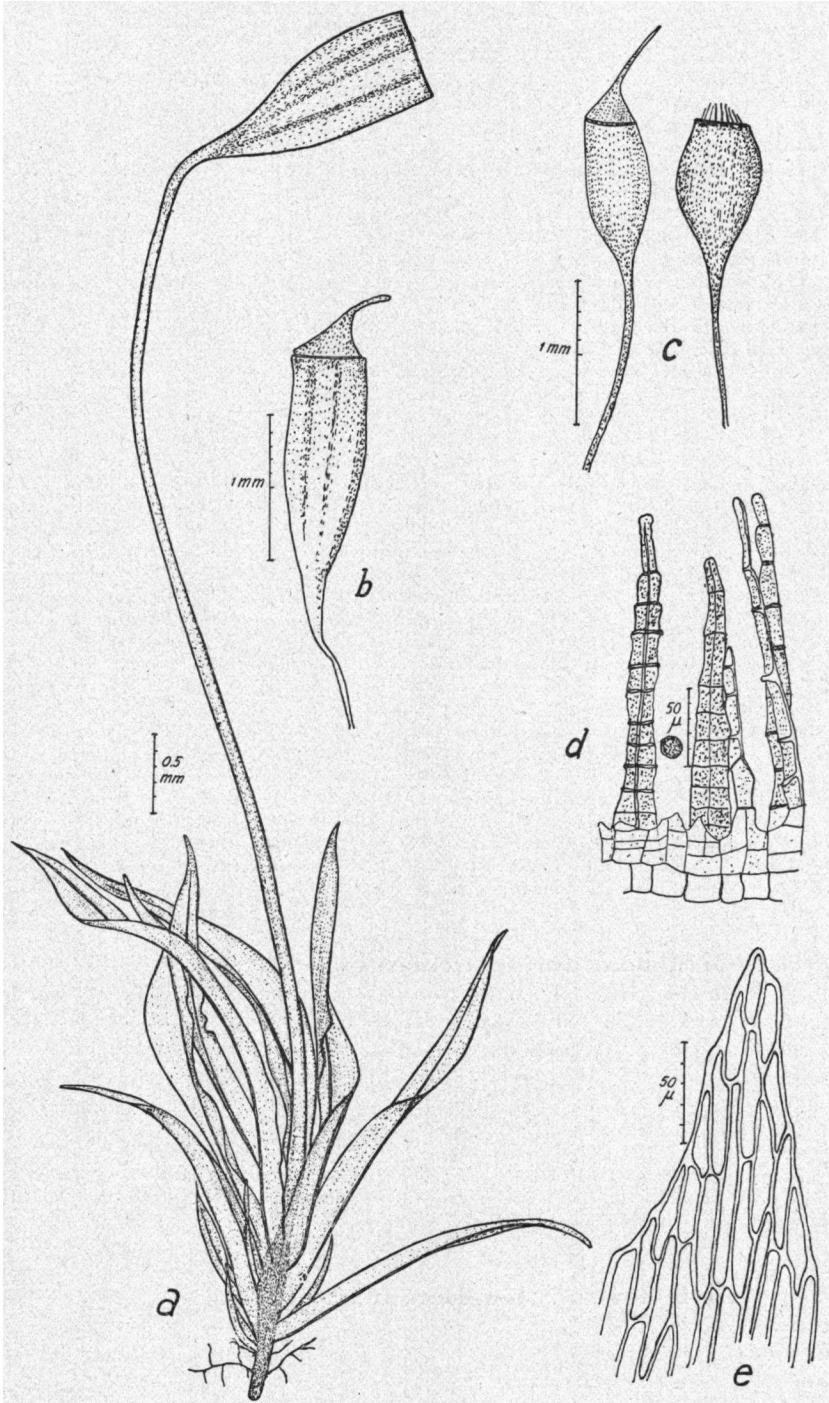


PLATE XIV

EXAMINED SPECIMENS:

California: Eureka, on redwood stumps, leg. Howe, 1896 (U.S.).

Tennessee: Sevier Co., 3800 ft, leg. A. J. Sharp, no. 34713, 1934 (NY, same place 1937, herb. Bartram).

Cuba: Loma del Gato, leg. Clement. (NY; PC, det. as *O. arenarium* C.M. by Thériot).

Haiti: Mornes de la Hotte, leg. Ekman, 1918, no. 565, det. Thériot as *O. osculatianum* (BM; NSW; U.S.).

Jamaica: Vicinity of Cinchoma, New Haven Gap, leg. E. G. Britton, 1906 (NY); Hark 1883, herb. Mitten (NY); Morces Gap, leg. G. E. Nichols, no. 44, 1906 (NY, S).

Guatemala: Dept. Quezaltenango, Volcan Zunil, 2500—3800 m, leg. Steyermark, 1940 (herb. Bartram).

Costarica: La Palma, 1500 m, leg. Valerio, no. 137, no. 138, 1928 (NY, herb. Bartram); La Fuente, Peratta, 1200 m, leg. Alfaro, no. 22, 1934 (herb. Bartram); Volcan de Barba, 2400 m, 1926 (herb. Bartram); El Silencio de San Remon, leg. Breues, 1933 (herb. Bartram); El Gallito, Prov. of Heredia, 2000 m, leg. Valerio, no. 197, 1928, (herb. Bartram; U.S.).

Venezuela: Tovar, leg. Fendler 1854—55, Musci Ven. det. C. Muller, no. 33 (lectotype of *O. fendleri*, NY; S; PC).

Colombia: Surrucucho near Cuenca, leg. Jameson (BM, holotype; NY); Andes Bogotensis, leg. Weir, 6800 m, no. 314 (NY, PC); Dept. Cundinamarca, Parama de Guarca, ca. 3250 m, leg. E. P. Killip, no. 36060, 1939 (herb. Bartram; FH; U.S.); Dept. Tolima, Quindio Highway, 3300—3600 m, leg. Killip, no. 34599, 1939 (herb. Bartram; U.S.); leg. J. C. Mutis, 1760—1808, no. 3383, det. Bartram (U.S.); Bogota, 2500 m, leg. Lindig, 1863, Tequendama) BM, holotype of *O. confine* Hpe; NY; U.S.; PC; S); Guadalupe, 2900 m, 3100 m, Monte del Moro, 2200 m, leg. Lindig (NY, L).

Galapagos Islands: James Island, leg. Stewart, no. 6000, 1905—1906 (NY).

Peru: Dept. Cuzco, Prov. Pavcartambo, Janamayo, 2000 m, herb. Vargas (herb. Bartram).

Bolivia: Between Tolapampa and Mapiri, 2300 m, leg. Williams, 1901 (NY, H); on decayed wood near Mapiri, leg. Williams 1902 (NY).

Brazil: Rio grande do Sul, Bon Jesus, 900 m, leg. Sehuern, 1942 (herb. Bartram); Prov. S. Catharina, Serra Geral, leg. Ule, 1891, Bryoth. bras. no. 132, (NY, lectotype of *O. ulei* C.M.; L; S; PC; H); Caraça, leg. Ule (NY, lectotype of *O. arenarium* C.M.; PC).

Hawaii: Kauai, Kohua ridge, C. 3500 ft, leg. Cranwell, Selling & Skottsberg, no. 4091, 1938 (herb. Bartram).

8b. *Orthodontium denticulatum* Geh. et Hampe. En. Musc. hact. in prov. Bras. Rio de Janeiro et Sao Paulo dect. Flora 64, no. 24: 374, 1881, holotype in herb. BM.

Differing from *O. pellucens* in the smooth peristome, the translucent segments and the regular dentate leaf apex. (Plate XV).

EXAMINED SPECIMENS:

Brazil: Prope Apiahy, S. Paulo; leg. Louis Puiggari, no. 902, 1879 (BM, type; NY; L; H); Parana, Rio negro, leg. P. Dusen, 1908, det. Broth. (H); Rio Janeiro, leg. Gardner no. 54 (herb. Bartram).

8c. *Orthodontium longisetum* Hampe. Linn. 32: 129, 1863, type in herb. BM.

Apalodium pellucens (Hook.) Mitten p.p., in Mitten, Journ. of Linn. Soc. 12, 1869.

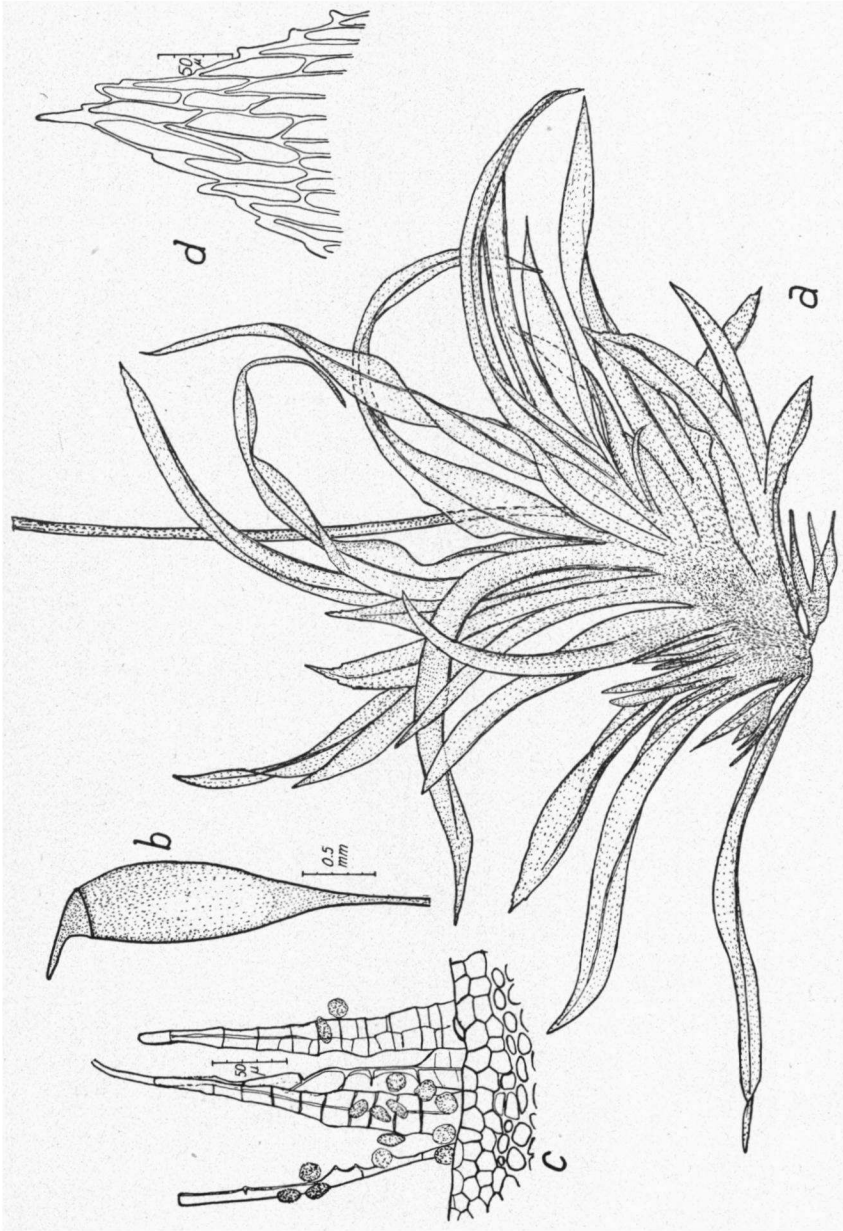


PLATE XV. *O. penicillatum*: a. Habit. b. Capsule. c. Peristome (isotype, L). d. Apex of leaf (isotype, L).

Differing from *O. pellucens*, in the somewhat more pointed leaves and the more robust peristome (Table II).

Seta generally longer (14 mm). (Plate XVI).

EXAMINED SPECIMENS:

Colombia: Nova granata, sylvis Manzanos, 2700 m, leg. Lindig, no. 2111. (BM, type; NY; PC; U.S.; L; MEL).

Bolivia: Bergwald Rio Tacorani, 2600 m leg. Herzog no. 4054, 1911 (L, S, H, NY, PC); San Mateo-Sunchal, 2000 m, 1911, leg. Herzog, no. 4480 (L, S).

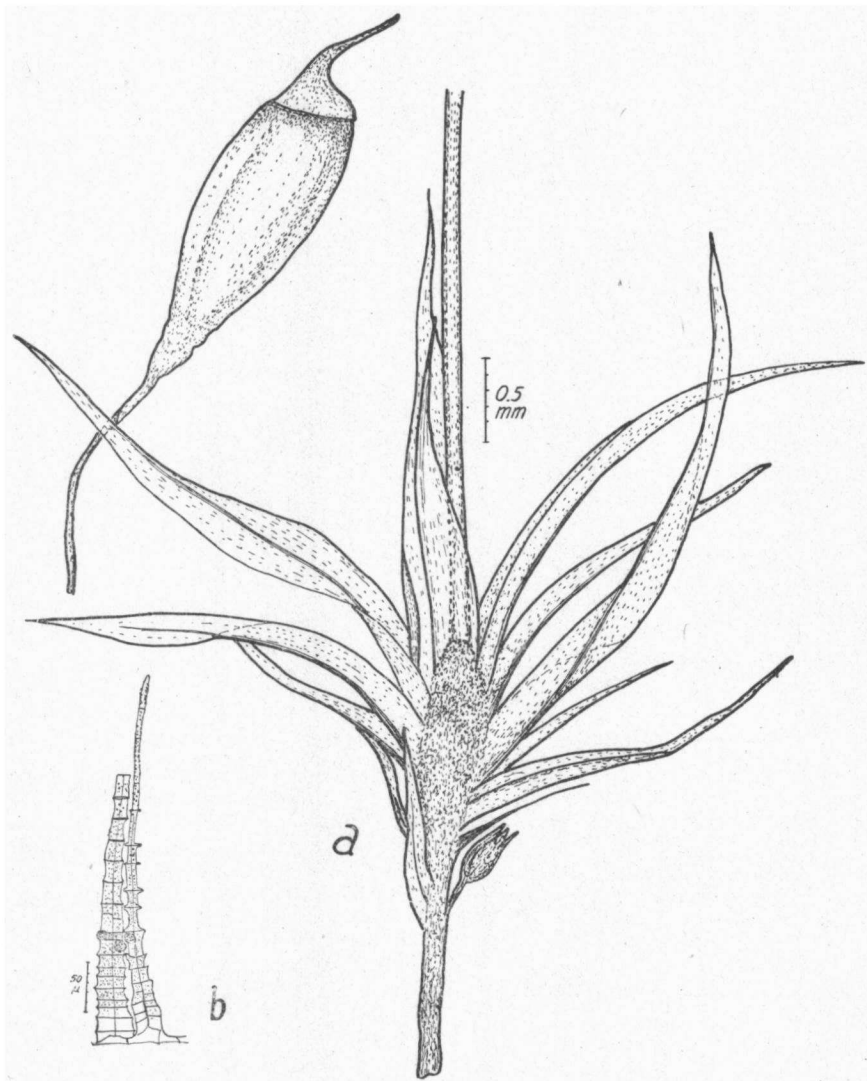


PLATE XVI

O. longisetum: a. Habit. b. Peristome (leg. HERZOG, Bolivia no. 4054, L).

8d. **Orthodontium loreifolium** Besch. Fl. bryol. Reunion, 1880—1881; holotype in herb. PC.

Orthodontium brevifolium Broth. in Mildbread. Wiss. Erg. Deutsch Zentr. Afrika Exp. 1907—08, II: 153, 1914, with fig.; holotype in herb. H.

Orthodontium haplohymenium Dixon et Naveau. Naveau Musci Bequarti I, Bull. Soc. Royale Bot. Belg. LX: 35, 1928; holotype in herb. BM.

Description:

Generally a robust seta like *O. longisetum*.

Cell texture of the *pellucens* type, leaves at average longer and more pointed. Seta longer (10—20 mm). Maximal dimension of capsule somewhat larger (See Table II). Peristome pale, only the apex of the processes slightly papillose, in the examined specimens. (Plate XVII).

Discussion:

The delimitation of *O. denticulatum*, *O. longisetum*, *O. loreifolium*, *O. novae-guineae* and other related forms, which are described as separate species (*O. haplohymenium*, *O. brevifolium*, *O. emodi*), is rather difficult.

When we compare the different specimens we waver between the distinction of five or eight very slightly different species or the recognition of one species: *O. pellucens* sensu lato. When all local populations of this group were replacing each other geographically, we would be right in calling them all subspecies. But two of them are overlapping in South America with *O. pellucens*, namely *O. longisetum* and *O. denticulatum*. So they are probably no eco-geographical races of *O. pellucens*. There are no indications that they represent ecological subspecies. The only plausible hypothesis is, that they represent real species, isolated in their reproduction from *O. pellucens* sensu stricto. As the differences of the other more remote distributed forms are of the same degree as between *O. pellucens*, *O. denticulatum* and *O. longisetum*, the consequence of all these facts is in our opinion that they also cannot be lumped with *O. pellucens*.

Apparently they were isolated in the remote past from the main stock of *O. pellucens* and they developed gradually to special species, losing their geographical and genetical contact with *O. pellucens* sensu stricto. We have to do here in our opinion with one of the difficult cases of a transition between species and subspecies. The whole group can be called a superspecies in the sense of E. MAYR (1942), "Artenkreis" in the German language.

In the manner in which we have resolved the problem here there still exist rather big disjunctions in the ranges of several of the taxa. *O. loreifolium*, originally described from Réunion, is lumped here with *O. brevifolium* and *O. haplohymenium* from Central Africa (both possessing a double peristome). This is done because the morphological differences between these local forms are so slight that specimens of these forms could not be named without knowing their locality.

With the exception of matured small sporogonia we have to do here with comparatively robust capsules with rather long setae. It is sometimes not possible to distinguish the leaves from those of *O. pellucens* sensu stricto, but some individuals show a tendency to develop acuminate leaves, a character which is more pronounced in *O. novae-guineae* and *O. emodi*, nom. nud. We find the same character indicated at *O. longisetum*, a species differing however in its more robust, distinctly papillose and dark coloured peristome. *O. novae-guineae* is

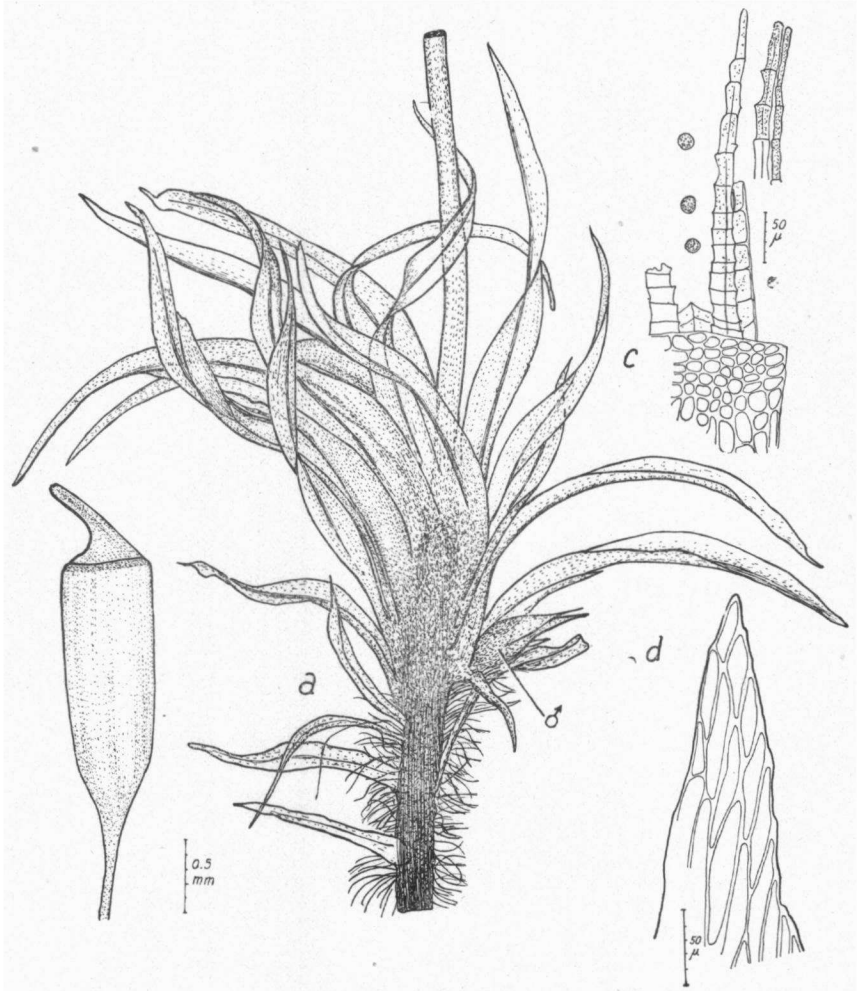


PLATE XVII

O. loreifolium:

- a. Habit (type of *O. brevifolium* Broth, H).
- b. Capsule (type material, PC).
- c. Peristome (Réunion, Lepervauche, K).
- d. Apex of leaf (type material, PC).

taken together with *O. emodi* on analogous grounds. This species represents a variation of *O. pellucens* with somewhat shorter setae than *O. longisetum* and *O. loreifolium*, a pale peristome, more like that of *O. denticulatum* and rather acute leaves, compared with *O. pellucens* sensu stricto.

TABLE II
Variation of some characters in the superspecies *Orthodontium pellucens*

Species	<i>O. pellucens</i>	<i>O. denticulatum</i>	<i>O. longisetum</i>	<i>O. loreifolium</i>	<i>O. novae-guineae</i>
seta-length in mm. . . .	5—17	7—14	14—16	9—20 (1,3)	7—15
capsule, length	1,30—1,85	1,6—1,8	1,8	1,65—2,2	1,2—1,8
capsule, breadth in mm.	0,50—0,65	0,60—0,80	0,60—0,65	0,60—1,00	0,50—0,60
length outer peristome in μ	200—290	160—220	320	185—320	180—240
length inner peristome in μ	150—300	160—225	370—400	250—300	250—290
diam. of spores in μ . . .	15—20	15	15	15—20	15—20
length of the lid in mm	0,35—0,75	0,50	0,80	0,60—0,95	0,40—0,65
leaf apex bl. or acute . . .	bl.	bl.	ac.	ac.	ac.
peristome papillose or smooth	pap.	sm.	pap.	sm.	sm. + pap.

EXAMINED SPECIMENS:

Type collection:

La Reunion: G. de L'Isle, no. 209, 1875 (PC); other coll.: leg. Lepervauche, 1880, (K, herb. Bescherelle).

Type of *O. brevifolium* Broth:

E. Africa: Ruwenzori Butagn-Tal, Ericaceen-wald, 3300 m, leg. Mildbread, 1908 (H); other coll.: Kilimandscharo, unterer Raganwald leg. A. Engler 2600 m, no. 1735, 1902 (H).

Type of *O. haplohymenium* Dixon et Naveau:

Central Africa: Ruwenzori Butagn. ca. 3000 m, leg. Bequaert, 1914 (PC, BM); other coll.: Mohanga, 3310 m, leg. Le Roy (Br); Ruwenzori, Uganda, Bujaka Valley near Bigocamp, 3300 m, leg. Olov Hedberg, 1948, no. 376 and 454 (herb. Uppsala & Potier de la Varde); Kenya, Aberdare Range, Kinangop, 3050 m, leg. O. Hedberg no. 1637, 1948, (herb. Uppsala, WM):

8e. ***Orthodontium novae-guineae*** Dixon. Papuan Mosses, Journ. of Bot. 1942.

Orthodontium emodi Hampe nom. nud., in herb. BM.

Description:

Growing in short tufts. Autoecious or heteroecious (the latter accordingly to DIXON lit. cit.).

Leaves glossy, yellowish green, length 2,3—3,3 mm. Shape variable; one collection (BRASS 12480) showing rather broad shortly acuminate leaves and some leaves blunt and toothed near apex, another collection (BRASS no. 12334) possesses narrower leaves, more longly sharply acuminate, just like the type collection (Carr).

Vegetative parts much resembling *O. pellucens* and *O. loreifolium*, but somewhat smaller.

Seta 9—15 mm, capsules of very different dimensions (length 1,2—1,8 mm), longly ovate, regular plicate when ripe, lid 0,6—0,7 mm, rostrate.

Peristome light yellow coloured or translucent, at maturity distinctly papillose, the inner as well as the outer. Inner peristome somewhat translucent and slightly narrower than the outer, outer peristome and processes rather long (till 290 μ). Spores 15—20 μ . (Plate II 3b, XVIII).

Discussion :

Very narrowly related is *O. emodi* Hampe nom. nud., from the Sikkim Himalaya. The collection of this form seems to me to be practically identical with *O. novae-guineae* and also very difficult to separate from *O. loreifolium*. It bears also glossy leaves, gradually pointed, it is autoecious, it bears gemmae (of 6—8 cells), the leaves are sometimes slightly dentate at apex. The capsules are regular ribbed when dry, their setae have approximately the same length (8—15 mm), the peristome is rather stout.

It is only preliminarily that *O. novae-guineae* is maintained here as a separate species and *O. emodi* nom. nud. as part of it. More collections from the Himalaya and Malaya mountains ought to reveal their real status.

The concepts which different bryologists have about *O. novae-guineae* differ extremely. DIXON stated after his type description (1942): “*O. infractum*, *O. sulcatum* and *O. australe* have shorter seta, less developed outer teeth and well-developed processes”.

Comparison with the descriptions, given in this revision of the above named species, will show that real differences in seta length don't occur and that well-developed processes are a feature which these three species have in common with *O. novae-guineae*. BARTRAM determined in his herbarium the collection of BRASS as *O. sulcatum* (Hook.) f. et Wils. In our opinion *O. sulcatum* is such a variable species that it should not be totally impossible to include *O. novae-guineae* in it. Some collections of *O. sulcatum* show fairly glossy leaves, a rostrate lid and a seta length of 11—14 mm, for example Weymouth's collections of Recherche bay, Tasmania.

In our opinion the resemblance between *O. novae-guineae* and some forms of *O. sulcatum* is only apparently. The differences in length of capsule lid, in the dimensions of the peristome and the tothing of the leaves are enough to consider it as more narrowly related to *O. loreifolium* and *O. pellucens*. The ripe peristome of *O. novae-guineae* is too much papillose, sporogonia and leaves show too great dimensions, to make it possible to put this species together with *O. infractum*.

It is not impossible that the existence of this New Guinean-Himalayan species indicate that *O. pellucens* as a superspecies (*O. pellucens*, *O. loreifolium* and *O. novae-guineae*) took his origin somewhere in the Australian region.

EXPLANATION OF PLATE XVIII

O. novae-guineae:

- a. Habit (type, BM).
- b. Capsule (isotype, L).
- c. Peristome (type coll., BM).

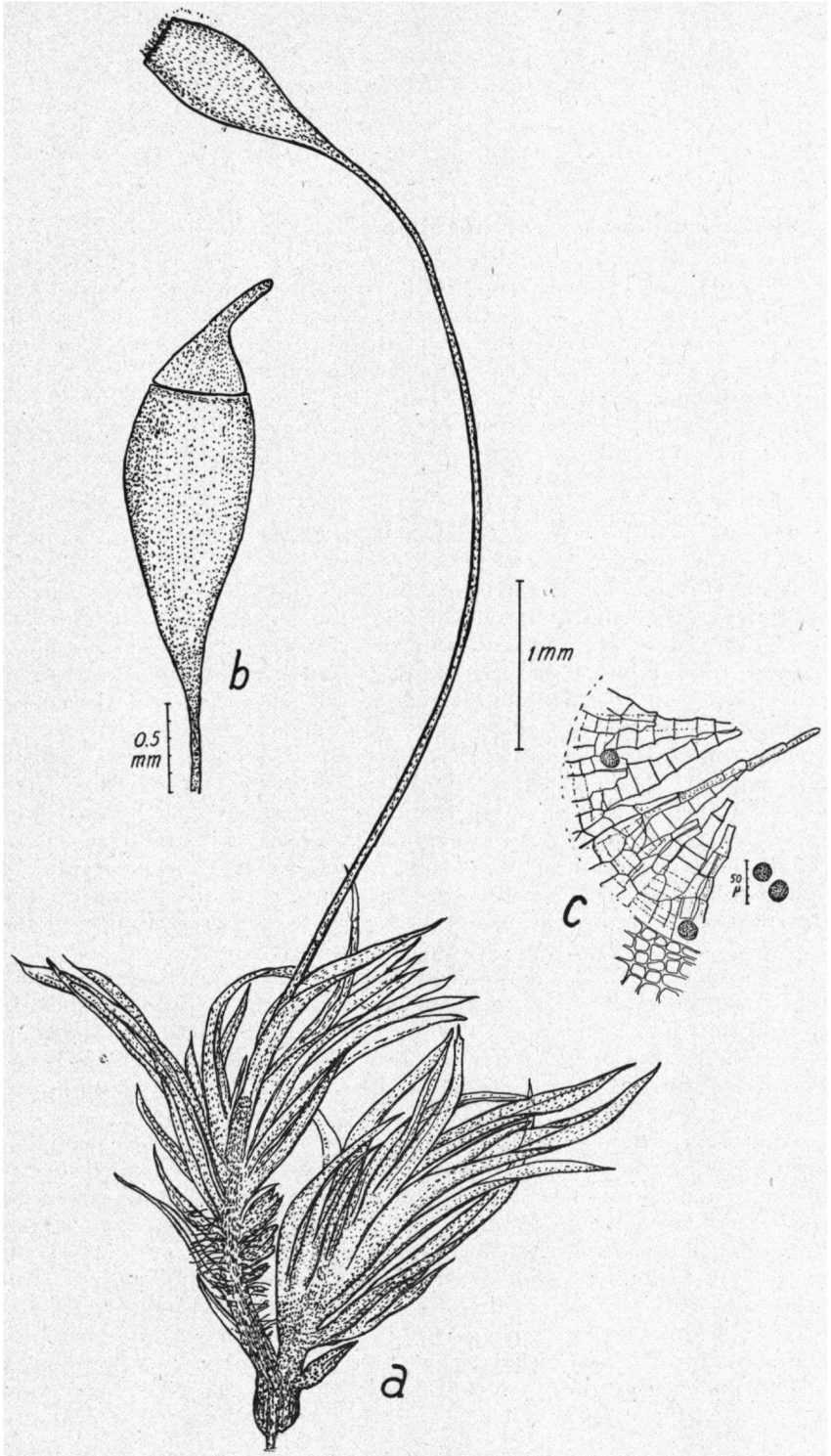


PLATE XVIII

N. Guinea. The Gap, Forest, 7200 ft, leg. Carr, 1936 (BM, type; L); Mossy forest, 18 km S.W. of Bernard Camp, Idenburg River, 2150 m, leg. L. J. Brass, no. 12480, 1939 (herb. Bartram); Mossy forest, 13 km S.W. of Bernard Camp, Idenburg River, 1800 m, leg. Brass no. 12334, 1948 (herb. Bartram).

Sikkim Himalaya, 7000 ft, J. Kurz. 2934 (BM, type *O. emodi* Hampe, nom. nud.; NY).

Species dubiae et excludendae.

Stableria(?) *ruwensorensis* Thér. et Naveau.

Naveau, Musci Bequarti: Bull. de la Soc. Royale de Bot. de Belgique. Tome LX (Dixième Serie, Tome X), fasc. I, 1927, p. 34. Sterile specimen in herb. Br. Certainly no representative of section *Stableria* or any species of section *Orthodontium*.

Orthodontium itacolumitis C.M. Bull. Herb. Boissier, 1898, p. 30; in herb. PC and H. The type material is for me too scanty and it bears too young sporogonia to settle the position of this form.

6. SUMMARY

The chief results of the taxonomic study of the genus *Orthodontium* are the following.

A close study of the different characters used in the taxonomy of the genus reveals that many of them are to a certain extent so variable that they cannot be used without reserve for the delimitation of taxa, namely dimension of the sporogonia, relative length of the teeth of inner and outer peristomes, papillosity or smoothness of peristome and sulcation of the capsules.

The consequence of this is that BROTHÉRUS' sections (1909), which were chiefly based on these characters, must be considered as artificial. A more natural arrangement of the genus is achieved after recognizing the slight variability of the following characters: length of the lids, reduction of inner peristome, the lack or possession of collenchymatous cell walls near the margin of the capsules, the distribution of the sexes (to a certain extent), the cross section of the leaf nerves, and even the glossiness of the leaves.

The following characters can probably be modified by mutations: the length of setae, the breadth of the leaves, the papillosity and the dimensions of the peristome, the size of the spores and the toothing of the leaves. But these characters also vary according to the habitat. We must thus be very careful in using them in our taxonomical considerations.

After revealing more of the real affinities between the species, a better subdivision of the genus could be tried. All the described species of the genus *Stableria* are to be considered as representatives of one species which possesses in different climates and habitats somewhat different modifications. This species, *Orthodontium gracile* Schwaegr. ex Br. et Schimper, possesses so many characters in common with other species of *Orthodontium*, for example the cell texture of the leaves and the type of the peristome (key characters for the whole genus, within the family Bryaceae), that it can be only a member of a separate section, the section *Stableria* (Lindb.) W. M. This section

is different from the other section (Sect. *Orthodontium*) in the type of the nerve, and in some details of the structure of the sporogonia.

Within the section *Orthodontium* there can be distinguished two groups of species, though there cannot be drawn a sharp line of demarcation between these groups. They can be arranged around two highly polymorphous species: *O. pellucens* (subject. *Pellucens*) and *O. lineare* (subject. *Linearis*).

A further consequence of the morphological study of the genus is that many species names are considered to be superfluous. Of 33 names, 12 remain as names of species or subspecies and among the more recent collections two new taxa have been described. It has been pointed out that *O. pellucens* s.l. must be considered as a superspecies, a species which is represented in tropical America, Africa and Asia by different closely related forms (*O. pellucens* s.s., *O. loreifolium*, *O. novae-guineae*). The type of species formation within the subsection *Pellucens* in South America, reveals that the most adequate treatment of this complex is a treatment as a superspecies (*Artenkreis*). The members of the subsection *Linearis* are the most variable and accordingly the most difficult. Totally satisfactory results could not yet be reached here. It is not impossible that hybridization played a role. Nevertheless, in this subsection several species names are to be considered superfluous, after careful study.

An interesting result of this study is that there exists no sharp line of demarcation between the South African *O. lineare* Schwaegr. and the Australian *O. sulcatum* Hook. fil. et Wilson.

They differ chiefly in their range of variation. That's why they are both considered as subspecies of *O. lineare* Schwaegr.

The problems in European bryology, about the real status of *O. gracile* var. *heterocarpum* Watson and *O. gaumei* Allorge et Thériot, are resolved in the following way.

The first must be considered as a part of *O. lineare* Schwaegr. and of the second it is very probably that it belongs to *O. pellucens* (Hook.) Br. eur.

In this way the picture of the taxonomy of this genus is totally changed. Several taxa appear to have a much greater range than has been supposed in former days.

CHAPTER IV

ORTHODONTIUM LINEARE IN EUROPE

In the year 1927 the British bryologist W. WATSON distributed under the name *Orthodontium gracile* Schwaegr. a specimen of *Orthodontium*, collected by him and by H. C. BROOME on gritstone rocks, which were surrounded by peat, near Crowden (Cheshire).

We read the following about this find in the Moss Exchange Club Report:

"A remarkable form, perhaps a distinct species, and certainly a good variety. From all my samples it differs in being more rigid, in its sub-falcate, secund leaves, which are less flexuose and shorter and have mostly much shorter and broader points; and in its shorter, broader, often sub-pyriform capsule, which in age is sometimes markedly asymmetrical. The processes of the endostome show under a high power minute punctate markings, which I could not see in any of my ordinary gatherings with which I compared it, and there are other differences in the processes. The spores are as in the typical plant. It could be passed in the field very easily as a *Dicranella*".

In the next year W. WATSON published this new discovery as variety *heterocarpa* (more correctly spelt *heterocarpum*) of *Orthodontium gracile* Schwaegr. ex. Br. & Schimp. (WATSON 1922). He gave the following description of this variety:

"Differs from the type in the shorter broader often more or less gibbous capsule, which may be smooth or deeply sulcate, straight or curved (sometimes very strongly so). Teeth of inner peristome minutely punctate. Antheridia usually in separate gemmiform groups".

Of course this new find came also under notice of H. N. DIXON, in those days the leading man of British bryology. He made the following notations on the herbarium sheet of the Crowden collections:

"Autoecious, paroecious and perhaps dioecious. D. A. JONES in litt. On this account and the rather large turgid somewhat gibbous short necked capsule it seems well worth a var. name.

H.N.D. 3.21.

Later described as var. *heterocarpa* Watson. I am almost inclined to think it specifically distinct — I cannot separate it from *O. lineare* Schwaegr. H.N.D."

These notes, now in herb. Kew, were somewhat amended in DIXON'S Handbook (1924) where we read: "Recent investigations indicate that it may prove to be a distinct species".

Certainly DIXON had in mind then the work of W. H. BURRELL, who had this peculiar moss in close observation. We learn that from his letter of July 23d 1923 to Dixon, kept in the Kew herbarium. This letter is such a vivid report on the first dissemination of the so called var. *heterocarpum* in England, that I'll cite it here.

"Will you kindly tell me what value should be placed on BROTHERUS' treatment of *Orthodontium* in ENGLER? If striation of capsule, texture of inner peristome, state of inflorescence and habitat, taken collectively, are of specific value, there should be two plants in Yorkshire as suggested in WATSON'S paper J. of Bot. 1922. At any rate I may tell you my experience with the plant, with the hope that it may ultimately lead to another of your nice little reviews of a genus from a worldwide standpoint. At Bolton Abbey (Strid) and at Plumpton by Knaresborough it

grows on perpendicular faces of massive gritstone rocks, and is so limited in its distribution that the rock at Bolton where I know it, is probably the spot where SPRUCE knew it, and it appeared to be restricted to a similar small place at Plumpton.

Le J. COCKS gathered it at Birk Crag Harrowgate in 1912, a millstone grit area; he would probably have specially noted the fact had it not been on a rock.

The gatherings from these three stations in my herbarium were gathered during the winterhalf of the year, Sept. to March and are not in good condition, but the slides enclosed show they are paroecious as fig. 405 D. ENGLER, and the old capsules present are smooth.

Gatherings made during the past 18 months near Huddersfield, Ingleton and Penistone were growing on peat (partly on Birch boles at Raikes Dyke); the capsules are striated and the male inflorescence gemmiform, autoecious. All the antheridia are axillary in the rock plant and I have no definite evidence that any are axillary in the peat plants.

The statement in WATSON's paper that the inflorescence is variable has not been overlooked, but in the only case of that kind that came under notice I suspected two seasons growths were involved, young male organs showing above old archegonia; this however needs further elucidation.

Recently the Y.N.U. held a weekend meeting at Penistone; on the Friday evening, during an after supperstroll, *Orthodontium* turned up within 2 miles of the town, on a small piece of moorland, associated with *Calluna*, *Vaccinium* and *Aira flexuosa*, on peat.

Saturday was spent in the Little Don Valley above Langsell Reservoir; the plant turned up early and was seen repeatedly during the day. On Sunday Midhope Moor was visited and again *Orthodontium* was the outstanding moss from the start about 750 ft. to the deep peat bogs at 1600 ft. under Cloudberry.

In one place the side of a peat pool had an area of 3 sq.ft. covered with capsules like that enclosed in the box. I saw none on rock; although there was a good deal of variation in the capsule, both in apparant texture, shape and sulcation, this appeared to be at least partly due to state of development; where striation was hardly evident, the microscope shows traces. I do not understand how the plant in such profusion can have been overlooked. Is it possibly a new comer, now in the rampant stage, like *Matricaria suaveolens*?

The points that impress me are:

- the habitat
- the inflorescence
- the striated capsule
- the papillose processes (about 0.15 mm long)"

The most striking item in this letter is the passage: "Is it possibly a new comer?"

Seventeen years later BURRELL devoted a special extensive paper to the whole problem (BURRELL 1940). He stated that all gatherings of *Orthodontium* before 1900 in England belong to WILSON's *Bryum gracile* (= *O. gracile* Schwaegr. ex Br. et Schimp.). The earliest known gathering of the so called variety *heterocarpum* Watson is made by E. A. RICHARDS, from Overton Hills, Cheshire, May 1911, according to BURRELL's examination of the most important British collections. BURRELL (1940) gave a map showing that till 1940 the variety had spread over an area of approximately 160 miles in length in the central parts of England, centered round Cheshire and Yorkshire.

Of course several questions arose around the so called variety *heterocarpum*. Was it a real variety of *O. gracile*, or was it a separate species? What was its origin?

All the known facts indicate that it had only recently been on the moors. Two possibilities exist for its origin there, either it arose by introduction, or by mutation from *O. gracile* Schwaegr.

The last named species is rather frequent in the same area where the variety had been found first, but it occurs also farther away, in Sussex, Devon and Southern Scotland (map in BURRELL 1940).

While BURRELL only touched the first possibility in his letter to DIXON (deposed in Dixon's herbarium, Kew) he gave in his publication of 1940 preference to the second hypothesis. His conclusion was:

"WATSON's variety *heterocarpum* appears to be a true breeding, very fertile, fixed mutation, that has established itself in Cheshire and the adjacent countries, during the past fifty years, and is still spreading".

Now it is true that var. *heterocarpum* is more robust, more hardish, and more fertile than *O. gracile* Schwaegr., at least in England. While *O. gracile* Schwaegr. has a very constant area, the so called variety is still spreading. Nowadays it has already reached Eire and Scotland. But we shall see that all these facts are no proof that it is a mutation, as BURRELL suggested, or to be more specific a polyploid form of *O. gracile*. We should investigate as well the other possibility, and perhaps with a better result, namely introduction of the var. into England. The last supposition is for example more probable, because the differences with *O. gracile* are quite on the scale of species differences in the genus *Orthodontium*. We have seen that they can even be treated as differences between two sections of the whole genus.

So BURRELL's hypothesis means no less than a macromutation, performing itself under our eyes. Perhaps the few lines which BURRELL devoted to the possibility of introduction into England offer the real solution of the problem. We read on page 298 of his paper: "TRAVIS reported the introduction of mosses to the Mersey with timber; *Orthodontium* grows on living and dead wood as well as on peat and rock, but there is no evidence in support of alien immigration."

New investigations on this problem started after the spreading of the so called var. *heterocarpum* to the continent. It was collected by the author on an excursion with his friend W. VERGOUW in the nature-reserve Naardermeer, Holland, on the 22nd of March 1943.

Sporogonia were in such a young state that the sample could be named only after some difficulty (MEIJER 1948, MARGADANT and MEIJER in AGSTERIBBE c.s. 1950).

Starting from this find, MARGADANT and MEIJER (1950) published a study of all known species of *Orthodontium* in Europe, in which they stated that this so called variety had to be named identical with *O. lineare* Schwaegr. and that *O. germanicum* F. & K. Koppe belongs to the same species. REIMERS (1941) had previously stated that the var. is identical with *O. germanicum*.

We did not know anything about DIXON's suggestion that he could see no difference with *O. lineare*. Apparently nobody noticed that. In a preliminary study of the whole genus it seemed probable that the variety had nothing to do with *O. gracile*. It became gradually apparent that its distribution over Western Europe was amazing and the insight grew that it could be an immigrant, introduced by human influence (MEIJER 1951). It was a pity however that attempts to establish the chromosomenumbers of both forms had no success in England and no more in Holland, because the plants are very difficult objects for cytological studies. Polyploidy is not very evident however on theoretical grounds, though it should not be excluded in our minds. It is not likely that we should get by autopolyploidy from *O. gracile* a species that is autoecious or heteroecious instead of paroecious, and which has quite another structure of peristome, papillose instead of smooth, with broad processes instead of narrow, with a band of collenchymatous cells near the mouth on the capsule instead of parenchymatous and with approximately the same size of the spores and the same cell dimensions.

Analogous to the result of WETTSTEIN (1932) we could only await plants with greater cells, more robust habit and with reduced fertility, at least in the first generations.

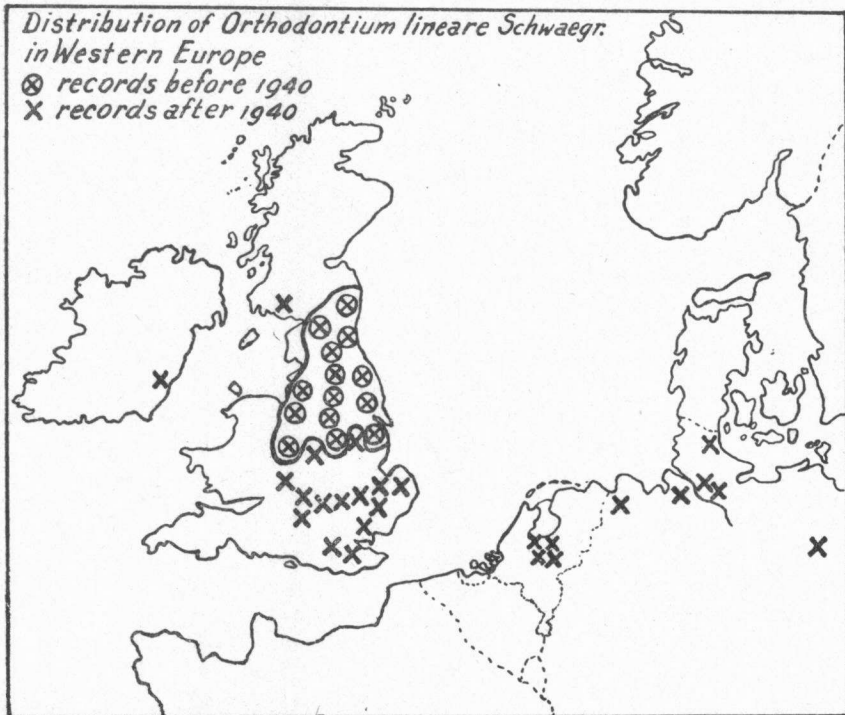
What evidence exists in support of alien immigration of *O. lineare* into England? TRAVIS reported the introduction of mosses with timber along the Mersey. Now this is the river near Liverpool. It is here that *Orthodontium* could be introduced from the Cape Colony. The place where it first had been collected is just south of Liverpool in Cheshire and another locality is situated 50 miles (80 km) to the N. East. Afterwards the spores must have been carried 300 km and more, before they found suitable habitats in Holland. The study of plants from England, Holland and Germany revealed such a great mutual resemblance that it is in our opinion not impossible to assume that they all are derivatives of one tuft.

Mr. W. G. TRAVIS was so kind to give us the following valuable information about imports of timber with mosses near Liverpool.

“The sentence in BURRELL's paper in the *Naturalist* (1940) which you quote, is evidently based on the fact that in 1920 and some subsequent years I sent some moss specimens to the Moss Exchange Club, collected from the bark of timber imported into Liverpool.

In the years 1920—1924, my brother, who was in a firm of hardwood timber merchants in Liverpool, used occasionally to give me tufts of mosses and hepatics, which he scraped off the bark of tree trunks imported by the firm from abroad. These included, at different times, samples of mossgrowths that he happened to notice on the bark of logs or trunks, e.g. from the Caucasus region, Asia minor, on boxwood (*Buxus sempervirens*); Kamerun (West-Africa); Cape Colony (South Africa), and from the U.S.A.

It is about the specimens from South Africa that will be of interest to you. The mosses were named for me by Mr. H. N. Dixon; and I contributed some packets of specimens to the Moss Exchange Club. The timber came from Cape Colony, Knysna and East London, or was shipped from those ports. The mosses were all barkgrowing plants. There was no *Orthodontium lineare* among them,”



MAP 1

So far Mr. TRAVIS.

It is of course not impossible that *Orthodontium* was at least once among the mosses imported in this way. We should stress the fact in this connection that Knysna is laying only some 80 km from George where *O. lineare* has been collected by PILLANS in a form which

is almost identical with the European. Sub-tropical rainwoods are or were found there.

About the stations near Liverpool Mr. TRAVIS wrote me:

“The Crowden locality of Watson is about 10 miles S.E. of Oldham and is in Yorkshire. This locality is fully 40 miles distant from Liverpool. The nearest station to Liverpool that I know of *O. lineare* is on peaty heathy ground at Thurstoston Hill, about 6 miles S.W. of Birkenhead, Cheshire, (bank of the Mersey, opposite to Liverpool, W.M.), where it was discovered a few years ago (about 1944 or 1945), long after the date of WATSON'S paper (1922). It may of course have been long present in that station, but passed over by local bryologists as *Dicranella heteromalla*.”

In our opinion we are now not far from the truth when we state that all known facts justify the conclusion that *Orthodontium lineare* is an immigrant in Europe, just like *Elodea canadensis*, *Vaccinium macrocarpon*, *Aronia melanocarpa*, etc.

It is quite understandable that not all samples from S. Africa are to the same extent identical with the European. Only one tuft out of a variable population could be the ancestor of the more uniform European populations. (Map 1).

Map 1 gives an impression of the present known distribution of *O. lineare* in Europe, compared with its known range up till 1940.

We thank the new dates of the distribution in England to Mr. E. F. WARBURG, the recorder of the British Bryological Society and from Germany we got them from Dr F. KOPPE (Bielefeld). In Germany till May 1951 twelve stations were known.

CHAPTER V

GEOGRAPHICAL CONSIDERATIONS

1. DISTRIBUTION OF THE TAXA OVER THE WORLD

The distribution of the genus *Orthodontium* over the world is rather discontinuous. The greatest range possesses *Orthodontium gracile*: California, Central and South America, Central Africa and Abyssinia, N.W. Europe (Map 2).

O. pellucens has numerous stations in South and Central America. Moreover it occurs on some islands in the Caribbean Sea¹, in California, Tennessee, Galapagos Islands and Hawaii. In South America it is not restricted to the Western part as is *O. gracile* (Map 3).

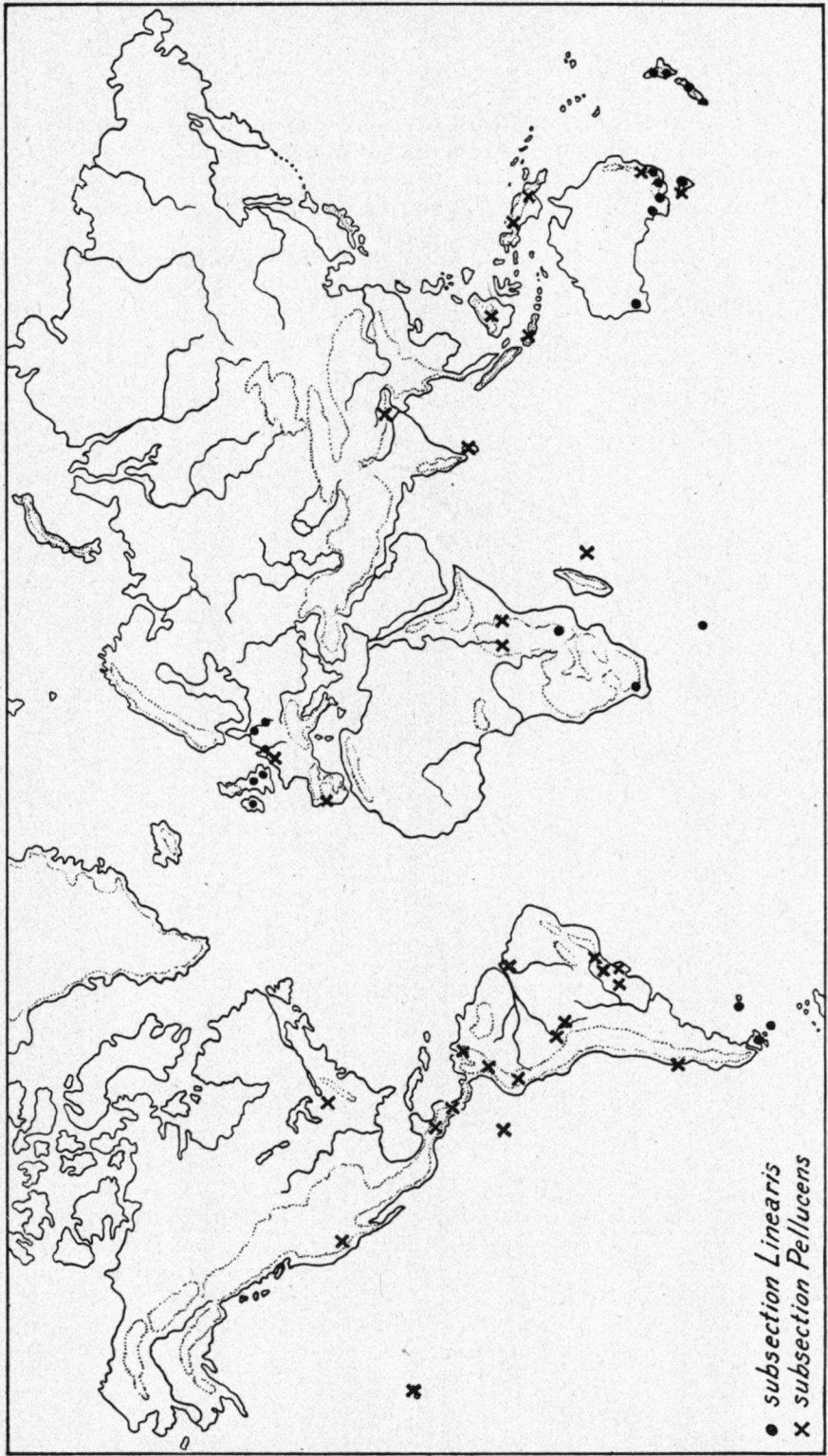
The closely related species *O. loreifolium* is scattered over Africa and Asia: Réunion, Ruwenzori, Kilimandscharo and Mt. Kenya.

Sikkim Himalaya and New Guinea are the ranges of *O. novae-*

¹ Omitted on Map 3.



MAP 2 Distribution of *Orthodontium gracile* Schwaegr. ex Br. Schimp. over the world

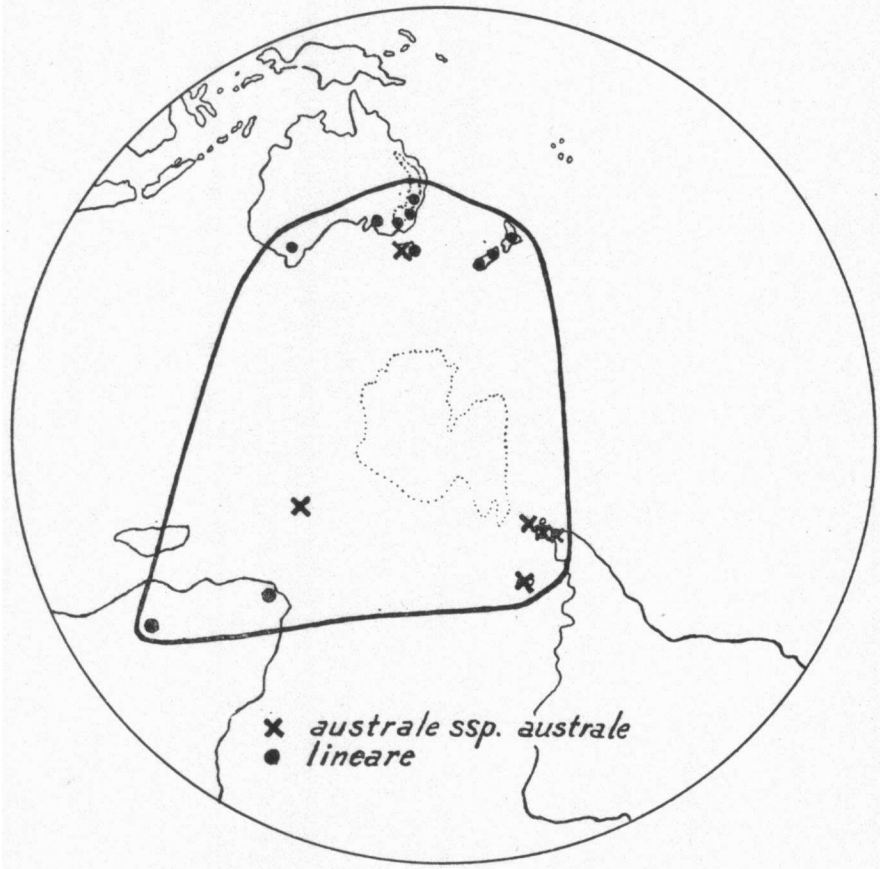


MAP 3 Distribution of Orthodontium Section Orthodontium over the world.

guineae. *O. infractum* is restricted to Ceylon, Borneo and Java. The related *O. inflatum* occurs in South East Australia.

The last region together with South West Australia, Tasmania and New Zealand forms the range of *O. sulcatum*. This species is closely related to the South African *O. lineare*, which possesses an outpost in Nyasaland.

O. australe, the most southern species, is restricted to Fuegia, Falkland Islands, Hermite Island, Marion Island and Tasmania (Map 4).



MAP 4

Distribution of *O. australe ssp. australe* and *O. lineare* on the Southern hemisphere.

It is evident that the genus occurs chiefly on the southern hemisphere. Thereby it is interesting to note that the subsections *Pellucens* and *Linearis* are partly overlapping, *Linearis* being confined to more southern latitudes than *Pellucens*.

The relative frequency of taxa in certain regions of the world appears from the following table.

TABLE I
The number of species and subspecies of *Orthodontium* in different regions of the world

	Austr.	N. Am.	S. Am.	Africa	N.W. Europe	S.E. Asia
whole genus	6	2	4	4	2(3)	2
section <i>Orthodontium</i> (section <i>Stableria</i> excluded)	6	1	3	3	1(2)	1

We have to take into consideration that one species, occurring in N.W. Europe, is probably a rather recent immigrant, brought there by human influence (chapter IV).

It appears from the above table that the Australian region, including Tasmania and New Zealand, is the richest for *Orthodontium*. This is strengthened by the fact that also the frequency of localities of the separate species according to the collections made, appears to be greatest there. When we compare the frequency of characters in these separate regions we get the following picture:

TABLE 2
Frequency of some differential characters in different parts of the world

	Austr.	N. Am.	S. Am.	Africa	N.W. Europe	S.E. Asia
pyriform capsule	×			×		×
paroecious infl.	×	(×)	(×)	(×)	(×)	
leaves without stereid cells inner peristome rudimentary	×	(×)	(×)	(×)	(×)	
extremely long setae (20 mm)	×		×			
distinctly dentate leaves conical lid	×	(×)	(×)	×	×	×
long beaked lid	×	×	×	×	×	×
Total	6	4	6	5	4	3
<i>Orthodontium gracile</i> excluded	6	1	3	3	2	3

The figures are not very high. We cannot conclude from them that Australia should be the centre of variation of the whole genus.

When we exclude *O. gracile*, which is by some authors considered as a separate genus (*Stableria*), we get another sum total of differential characters. For this reason, characters represented in a certain region only by *O. gracile* are put between brackets. From this it appears that within the section *Orthodontium*, Australia is not only the region with the greatest number of different species, but also the richest in characters. The different characters are rather widely distributed over the whole range of the genus. Perhaps this phenomenon indicates a rather high age of the genus. In this connection it is a remarkable fact that the Australian-Asian region is not reached by the section *Stableria* and that the subsection *Linearis* is lacking in Asia.

2. HABITAT PREFERENCES

When we compare all the ecological notes, brought together from the stations where species have been collected, we discover that the whole genus is rather homogeneous in its habitat adaptations.

All species of *Orthodontium* favour moist habitats. They cannot stand long desiccations, though a rather dry season is not unfavourable for *O. lineare*, during the fruiting stage. As far as we know all species are growing on acid substrates: peat, poor soil, dead tree stumps, sandstone rocks, etc. The ecological specialisation of the species does not show great differences. In tropical regions they only occur in the higher zones of mountains, in forests or in shrubs near the tree limit. *Orthodontium* avoids all dry tropical and continental regions of the world.

Now it is a well known fact that the general climate of oceanic regions in the temperate zones has much in common with the local climate on mountains in the tropics. Both are wet climates with a rather small amplitude of temperature during the year. Epiphytes, among them mosses, grow luxuriant in such climates. The life forms of plants of tropical mountains and of the oceanic islands on the southern hemisphere have many features in common (TROLL 1948), a natural consequence of the similarity of the climate.

When we study, from the ecological point of view, the regions where species of *Orthodontium* are growing, we discover that all taxa are adapted to this mountainous or oceanic climate. This preference is partly the reason for the fact that the genus is chiefly distributed over the southern hemisphere and over the antarctic regions, where these climates are predominant.

We find species of our genus on the Andes of South America, through the Cordilleras of Middle America, on the islands in the Caribbean Sea, but always in damp mossy forests in wet mountainous climates. The same is true of the Central African Highlands, where it has been collected in the ericaceous shrubs and the vegetations with giant *Senecio*'s, of Ruwenzori, Kilimandscharo, Mt. Kenya and the Highlands of Abyssinia. In the southern part of Africa *Orthodontium* is found in sub-tropical and wet temperature forests. In Australia the range comprises the mountainous parts of the southern temperate zone (S. of Queensland): the Australian Alps and the Blue Mountains. In Tasmania and New Zealand damp mountain forests as well as lowland stations are the localities of *Orthodontium*. In southern Chile, on Fuegia, Falkland Islands and Marion Island the sealevel is reached, just as in the atlantic parts of Europe and the redwood areas of California.

In the Asian region only the mossy forests on the vulcanos of Java, the mountains of New Guinea and the Sikkim Himalaya are the localities hitherto known. (Map 3).

These facts are sufficient to illustrate the preference of the whole genus for oceanic or temperate mountain climates.

From the foregoing paragraphs it will be clear that two special aspects play a role in the history of the genus:

1. the migration from some centre of dispersion.
2. the preference for oceanic mountainous climates.

It is very difficult to reveal the general trends in migration and evolution of the genus, in connection with the distribution of the different species and with their affinities. We might suppose that the distribution of the genus over the world has been determined by its ecological preferences only, assuming that the spores could spread all over the world. In this case the present areas would give information only about the ecological preferences, without any further data in connection with historic biogeography.

This assumption can be checked from two sides:

1. by direct knowledge of the probability or improbability of random distribution by wind drift of spores.
2. by a careful study of the types of the areas.

We consider the distribution of the species within those parts of the world, of which we may assume that they form the potential area of the genus: all oceanic and wet mountainous regions together. Then we discover that within this area not all the species are distributed in the same way. We can distinguish different types of distribution:

- a. The *gracile*-type
Area comprising America, Europe and Africa. *O. gracile*, *O. pellucens*.
- b. The *lineare*-type
Area comprising S. Africa and Australia. *O. lineare*.
- c. The *australe*-type
Area comprising S. America, Marion and Tasmania. *O. australe*.

The other species-areas are of a more endemic type. The above named types of distribution (*a*, *b*, and *c*) relate to species which belong probably to the oldest in the genus, because they are highly polymorphous, while *b* and *c* may be considered from a taxonomic point of view as the centra around which the other species can be grouped.

These different types of area and the probability that the age of the area plays a role in their extent, are in accordance with the hypothesis that the distribution of species of *Orthodontium* is not merely a case of random spread of spores all over the world. It must be a distribution along certain lines of migration which is strongly influenced by the geographical history of the globe.

Why should *Orthodontium gracile* be missing in Asia and Australia when it could be easily distributed everywhere by its spores? Why should *O. lineare* be lacking in South America? The evidence for the above stated hypothesis becomes even stronger when we take into account that the same distribution types *a*, *b*, and *c* occur among phanerogams (IRMSCHER 1923, CAIN 1944, WULFF 1943).

3. ANALOGOUS DISTRIBUTION PATTERNS IN OTHER GROUPS OF PLANTS

a. *O. gracile*-type.

There are many taxa of musci which are restricted to America and Europe-Africa, namely two families, 36 genera, 8 subgenera and sections, 144 species, totalling 190. In phanerogams there are relatively more genera, but less species of this type of distribution.

b. *O. lineare*-type (S. Africa-Australia).

This disjunction is paralleled by some mosses like *Gigaspermum repens*, *Campylopus bicolor* and *Pleuridium nervosum*. Among phanerogams this is paralleled by two genera of the Restionaceae: *Restio* and *Hypolaena*.

c. *O. australe*-type (S. America, Marion, Tasmania).

IRMSCHER (1923) gives examples of several other taxa (genera and species) with analogous distribution in the southern hemisphere, in total 1 family, 8 genera, 3 sections and 18 species. Among mosses and hepatics this is a rather common type of distribution. Parallel cases among phanerogams are the genera *Acaena* (Rosaceae) and *Weinmannia* (Cunoniaceae). They belong to the so called *Azorella*-type. Examples among mosses are *Ptychomnium müllerella* and *Blindia magellanica*.

In this way we can understand that HERZOG (1925, 1926) as well as IRMSCHER (1923) and WULFF (1943) make use of distribution areas of special taxa of mosses as additional support for the theory of continental drift.

But without exact direct knowledge of the effect of spread by spores, all our considerations remain very speculative.

We must admit that we know very little about this topic.

An illustrative example is the discussion of PERSSON (1944) with PETERSON (1940), about the occurrence of spores of the mosses *Aloina brevirostris* (Hook. & Grev.) Kindb. and *A. rigida* (Hedw.) Dixon, in rainwater in Finland. Both species are lacking in Finland. PETERSON accepted the hypothesis that these spores came from Siberia, but PERSSON made evident that they might originate from stations nearer by.

Fortunately we have some exact direct indications now of the spread of *O. lineare* from England to the continent. At least some hundreds of kilometers between the Middle-England stations and suitable places on the diluvial parts of Holland have been bridged by the spores. Within a few decennia this species has spread from Middle England to Schleswig-Holstein, at the Danish-German border.

Such a spread is more rapid than in the cases of phanerogams as e.g. *Anthoxanthum aristatum* and *Galinsoga parviflora* in Holland.

On the other hand, when we take the genus *Orthodontium* as a whole, it is likely that the wide and disjunct distribution of several of its species cannot be accounted for, without assuming a formerly, more extended, antarctic continent, though it is not inevitably

necessary to assume simultaneous landconnections between the exact recent areas in S. America, Tasmania and New Zealand.

4. CONCLUSION

From the foregoing considerations we draw the following conclusions:

1. The genus *Orthodontium* is especially distributed in temperate oceanic and tropical mountainous climates, consequently the chief part of its area is situated on the southern hemisphere.
2. Distribution of species within this area cannot be a result of unlimited airborne spread of spores, but it is certainly influenced by the distribution of seas and continents in former ages.
3. Spread by means of spores is possible within a favourable climate, at least over distances of some hundreds of kilometers.
4. It is not unlikely that the species with the greatest ranges are the oldest.
5. The relatively small differentiation in ecological preferences between the species gives an indication that the causes of speciation in the genus *Orthodontium* should be sought in phenomena other than in adaptation to different habitats.

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