of numerous trivalents which in many cases are indistinguishable from the bivalents. Olmo was able to count 70 chromosomes in a tapetal cell of one of his "triploids" and considered it likely that this number was characteristic of those having monosomic features. Such plants would not have been derived from fertilization of an unreduced somatic cell (with 47 chromosomes). There has evidently been a doubling of a 23-chromosome nucleus or a fusion of two such nuclei prior to fertilization. It would be of value if a triploid twin could be isolated in a culture suitable for genetic analysis.

In only one instance, among the *Nicotiana* twin seedlings, was there definite evidence of sporophytic polyembryony. A twin pair was obtained from seed of a tetraploid *N. sylvestris* plant which had been pollinated by diploid *N. tomentosa*. One of the resulting individuals was purely maternal, the other clearly a hybrid containing 2 chromosome sets from the female parent and one from the male. The latter must have been of zygotic origin, the former presumably having arisen from nucellar tissue.

SUMMARY

Since this investigation of polyembryony was initiated in 1938, the tobacco cultures have yielded 120 twin and 16 triplet seedlings. The majority of these cultures involved one or other of the 24 monosomic types of *Nicotiana tabacum* var. *Purpurea*. Frequencies of multiple seedlings varied in different years from 0.04–0.25 per cent. Monosomic cultures in general had a higher frequency than those of species, species-hybrids or varietal hybrids. One monosomic line (haplo L) has shown a mean frequency of about 1.0 per cent. Approximately two-thirds of the plural seedlings were made up of more or less closely united members. Considerable variability in extent of the union was expressed in different instances. Diploid and monosomic plants comprised 86.0 per cent of the multiple seedlings studied. The remainder consisted of haploids (7), trisomics (4), triploids (3) and double monosomics (2, from one twin pair). In pairs where both members differed from normal in chromosome number, the number in each member was not always the same. Haploid individuals were conspicuously smaller than their mates during early development. Cytological study of developing ovules has revealed 3 containing multiple embryos; one of these was a triplet. Supernumerary embryo-sacs were not seen but two pollen tubes within a single sac were occasionally observed. One twin pair was the result of sporophytic polyembryony.

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CLUSTERED SPOROPHYTES IN MOSSES [1]

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MANY INSTANCES of abnormal moss sporophytes have been reported. The abnormalities described fall into two main categories: (1) sporophytes with double capsules; (2) clustered sporophytes, when two to several separate sporophytes are produced from a single inflorescence in those species which normally develop only one sporophyte per gametophyte. More or less fusion of the vaginulae may occur and members of the Polytrichaceae may develop what appears to be a common calyptra.

Double capsules are apparently not limited to any family of Musci, since they have been reported in the following genera: *Meesea, Catharinaea, Homalothecium, Orthotrichum,* and *Tetraplodon* (Györffy, 1934a, c, d, e, f, 1936a; Schimper, 1861). The extent of doubleness varies from a condition in which the capsule walls are partially fused to a condition where the capsules are completely separate with the seta branched some distance below them. Double capsules develop as the result of branching of the seta at an early stage in its growth, the degree of doubleness depending upon how early the branching took place. The previously published descriptions are based on mature specimens, so that interpretations of their origin are necessarily difficult and not always reliable.

Clustered sporophytes (referred to in previous papers as twin sporophytes since no more than two associated sporophytes were found) are reported

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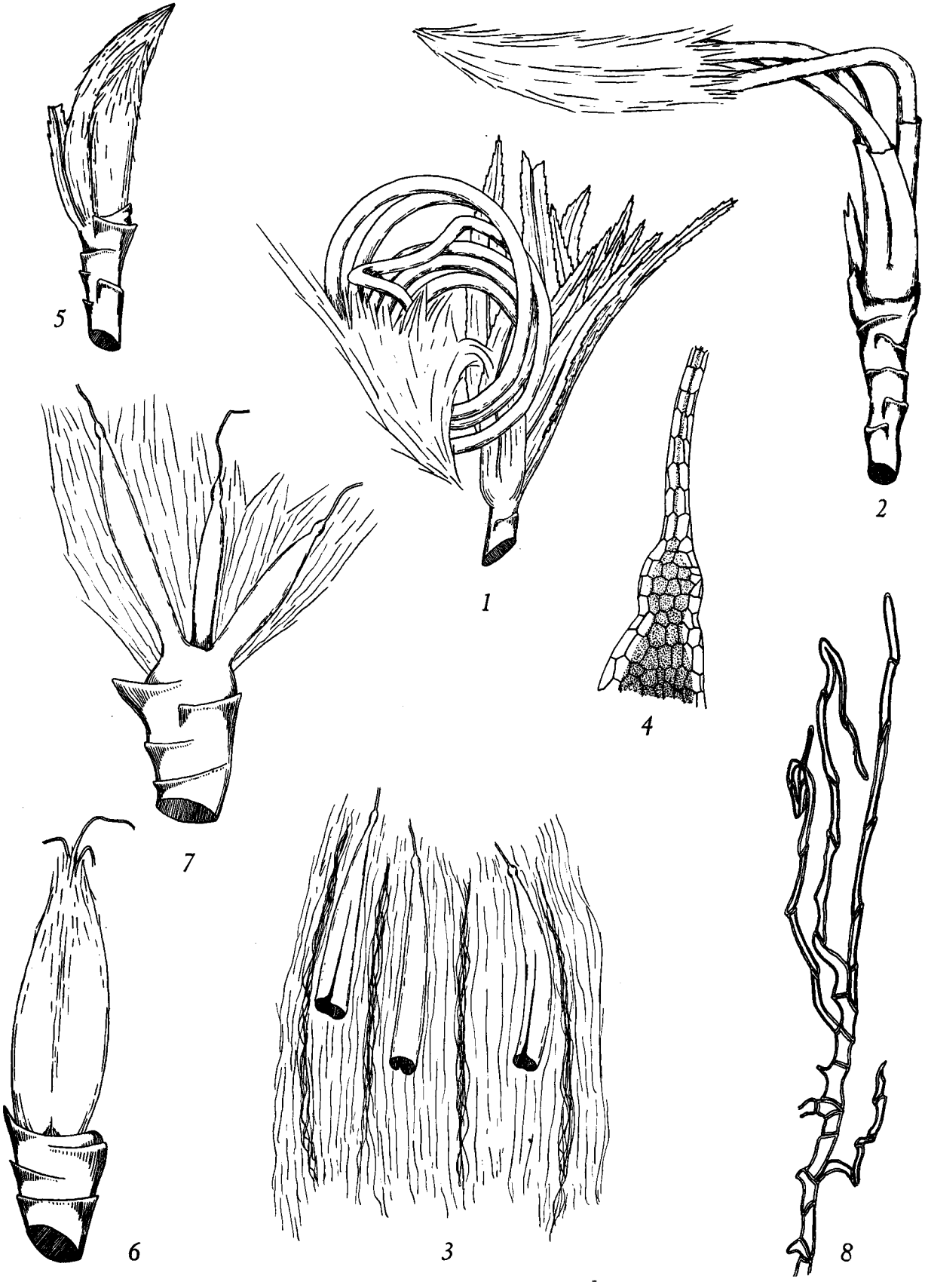
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for *Grimmia, Catharinaea, Polytrichum, Sphagnum,* and *Bartramia* (Györffy, 1931, 1934b, f, 1936a, b; Lyon, 1905; Tobler, 1902; Andrews, 1939). In all the above examples the sporophytes were completely separate and apparently normally developed, although often of unequal size and with some fusion of the associated vaginulae. In *Polytrichum,* Tobler and Györffy described a common or fused calyptra covering the two capsules of the cluster. Andrews' specimen of *Polytrichum commune* had what appeared to be a common calyptra which he showed to be a compound structure.

Several suggestions have been advanced to explain the development of double capsules as well as clustered sporophytes. Schimper pointed out the possibility that two eggs were present in a single archegonium which were subsequently fertilized and during their early development fused to a greater or less degree, giving rise to a sporophyte with a double capsule. Two young *Sphagnum* sporophytes within a common archegonium were found by Lyon and seem to illustrate the above mode of development. Györffy described and illustrated two *Sphagnum* specimens having double sporophytes. The remaining gametophytic tissue around their bases strongly suggests that they developed within a single archegonium. The possible division, or partial division, of the embryo into two parts at an early stage must not be overlooked, however.

The origin of twin or clustered sporophytes has been ascribed to the fusion of separate archegonia during their development subsequent to fertilization. The common calyptra which often occurs in the Polytrichaceae and which seems to represent a single archegonium has been shown by Andrews to be composed, in reality, of separate true calyptras enclosed in a common hairy covering. He explained the development of his specimen as follows: "two adjacent archegonia became superficially fused in the region of their venters; as the setae elongated and began to carry aloft their respective archegonial necks or calyptras the latter remained sufficiently close together to be enclosed by a common hairy covering." The specimens to be described in this paper have similar calyptras. Tobler believed that two archegonia fused to produce the common calyptra described by him.

The most interesting point concerning the formation of twin or clustered sporophytes is the fact that a moss plant that normally produces only one sporophyte may occasionally produce two or more. This behavior is apparently genetic and the occasional plant producing such sporophytes must therefore represent a mutant form. The author feels that this is the situation in the *Pogonatum* material reported here.

All previous reports of clustered sporophytes have been based on mature specimens with the result that their interpretation has been only indirect. In this respect the author was very fortunate in having at his disposal an excellent collection of *Pogonatum tortile* with clustered sporophytes in all stages of development.

MATERIAL AND METHODS.—*1.*—The material of *Pogonatum tortile* (Sw.) Brid. was collected by Professor William C. Steere, March 20, 1940, on a rocky bank along the trail from the Toro Negro Reservoir to Jayuya, Cordillera Central, Puerto Rico (W. C. S. 6903). A remarkable collection! There are over a hundred plants with clustered sporophytes (two–five sporophytes per cluster) in all stages of development. Plants of this collection were used for the dissections and drawings for this paper. The collection is now in the Herbarium of the University of Michigan.

2.—A single specimen of *Polytrichum juniperinum* L. with a cluster of two immature sporophytes and a common calyptra was found by Professor Bradley M. Davis in class material at the University of Michigan.

3.—A single specimen of *Polytrichum piliferum* L., similar to the above, was collected by Ernest E. Dale in open woods at Schenectady, New York, April 29, 1933.

Dissections were made under a binocular dissecting microscope and the drawings were prepared with the aid of a camera lucida.

OBSERVATIONS.—The *Pogonatum tortile* collection of 118 individuals with clustered sporophytes had the following composition: 81 plants had 2 sporophytes, 77 with a common calyptra and 4 with separate calyptras; 32 plants had 3 sporophytes, 26 with a common calyptra, 5 with 2 sporophytes united by a common calyptra and 1 separate sporophyte, and 1 plant with 3 separate sporophytes; 4 plants had 4 sporophytes, 1 with a common calyptra, 1 with 2 pair of sporophytes each united by a common calyptra, and 2 plants with 3 sporophytes under a common calyptra and 1 separate; there was 1 plant with 5 sporophytes united by a common calyptra.

The common calyptras were found to consist of separate true calyptras enclosed by the felt-like hairy covering (fig. 3). A situation nearly identical with that found by Andrews in his *Polytrichum* specimen. This difference was noted however: Andrews states that the true calyptra is a modification of the archegonium neck. In *Pogonatum tortile*

Fig. 1–8.—Fig. 1. *Pogonatum tortile,* a cluster of three mature sporophytes showing the curved condition of the setae and the common calyptra, ×10.—Fig. 2. *P. tortile,* a cluster of three immature sporophytes with a common calyptra, perichaetial leaves removed to show the separate vaginulae, ×10.—Fig. 3. *P. tortile,* a common calyptra opened to show the three true calyptras and hairy covering, ×15.—Fig. 4. *P. tortile,* apical portion of a true calyptra showing the archegonium neck and venter at its tip, ×70.—Fig. 5. *P. tortile,* a cluster of very young sporophytes, enclosed by the calyptral hairs, ×10.—Fig. 6. *P. tortile,* a cluster of three very young sporophytes, the archegonial necks may be seen protruding from the hairy covering, ×15.—Fig. 7. *P. tortile,* a dissected view of a very young sporophyte cluster, ×15.—Fig. 8. *P. tortile,* a calyptral hair, ×70.

it is a modification of the most basal part of the archegonium, the neck and venter were found, unmodified, at the tip of the calyptra (fig. 3 and enlarged in fig. 4). A similar structure was found in the specimens of *Polytrichum juniperinum* and *P. piliferum*. In these two species the lower half of the venter, as well as the archegonium base, is slightly involved in calyptra formation.

The hairy covering of the calyptras was found to be well developed very early during the growth of the embryo sporophytes (fig. 5). Many very young sporophytes, still within their unruptured calyptras, in groups of two or three in a cluster were found firmly bound together by the felted hairs produced by their separate true calyptras. The number of sporophytes involved in a cluster could, at this early stage, be determined by counting the archegonial necks which protrude from the tip of the mass of enveloping hairs (fig. 6). No evidence of any tissue fusion was discovered between adjacent calyptras in a cluster (fig. 7). The calyptral hairs develop in a short region immediately below the archegonium venter. Their many branches and contortions are conducive to felting (fig. 8).

As the sporophytes of a cluster mature the setae elongate and when they are held together at their tips by a common calyptra they become curved due to unequal elongation (fig. 2). Setae of mature sporophytes in such a cluster often form a helical spiral of from one to two turns (fig. 1). No instances of vaginulae fusion were found in clusters of mature sporophytes. The capsules of clustered sporophytes develop normally, with the exception of being somewhat smaller than single specimens. All mature capsules examined contained spores.

No significant differences were found between the specimens of *Polytrichum juniperinum* and *P. piliferum* and the *Pogonatum* material of comparable age, thus demonstrating a similar development for the clustered sporophytes of these two species.

SUMMARY

The origin of clustered sporophytes in *Pogonatum tortile* is due to environmental influences of an unknown nature, or, as seems more reasonable to the author, a genetic change. In either case several zygotes are able to continue a simultaneous growth and development in the same perichaetium. As the embryos develop, the gametophytic tissue surrounding them (bases of the archegonia) enlarges and becomes closely crowded together. At the same time the hairy covering begins to develop on each calyptra and, due to their close proximity, eventually encloses and firmly binds them together in a common felt-like tangle of hairs. The hairy covering, containing the true calyptras, firmly holds the tips of the sporophytes together during their subsequent growth. The unequal elongation of the setae naturally results in their irregular curvature. The capsules, although smaller than single specimens, are normal and produce spores. Clustered sporophytes of *Polytrichum juniperinum* and *P. piliferum* develop in a fashion similar to those of *Pogonatum tortile*. No evidence of tissue fusion between the vaginulae in either the *Pogonatum* or *Polytrichum* specimens was found and in this respect they differ from examples previously reported by other authors.

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