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The Morphology of the Pine Cone

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THE MORPHOLOGY OF THE PINE CONE.⁴

(WITH PLATE VIII)

SO MUCH has been said in regard to the morphology of the cone of the pine and its near allies that it would seem impossible as well as unnecessary to suggest anything further. However, the recent excellent summary in Coulter and Chamberlain's "Morphology of the Spermatophytes" of the many theories hitherto advanced to clear up the matter, and the conclusions reached by the authors named, show that it is by no means settled, and perhaps warrant me in presenting an interpretation which I have used in lectures before my own classes for half a dozen years or more.

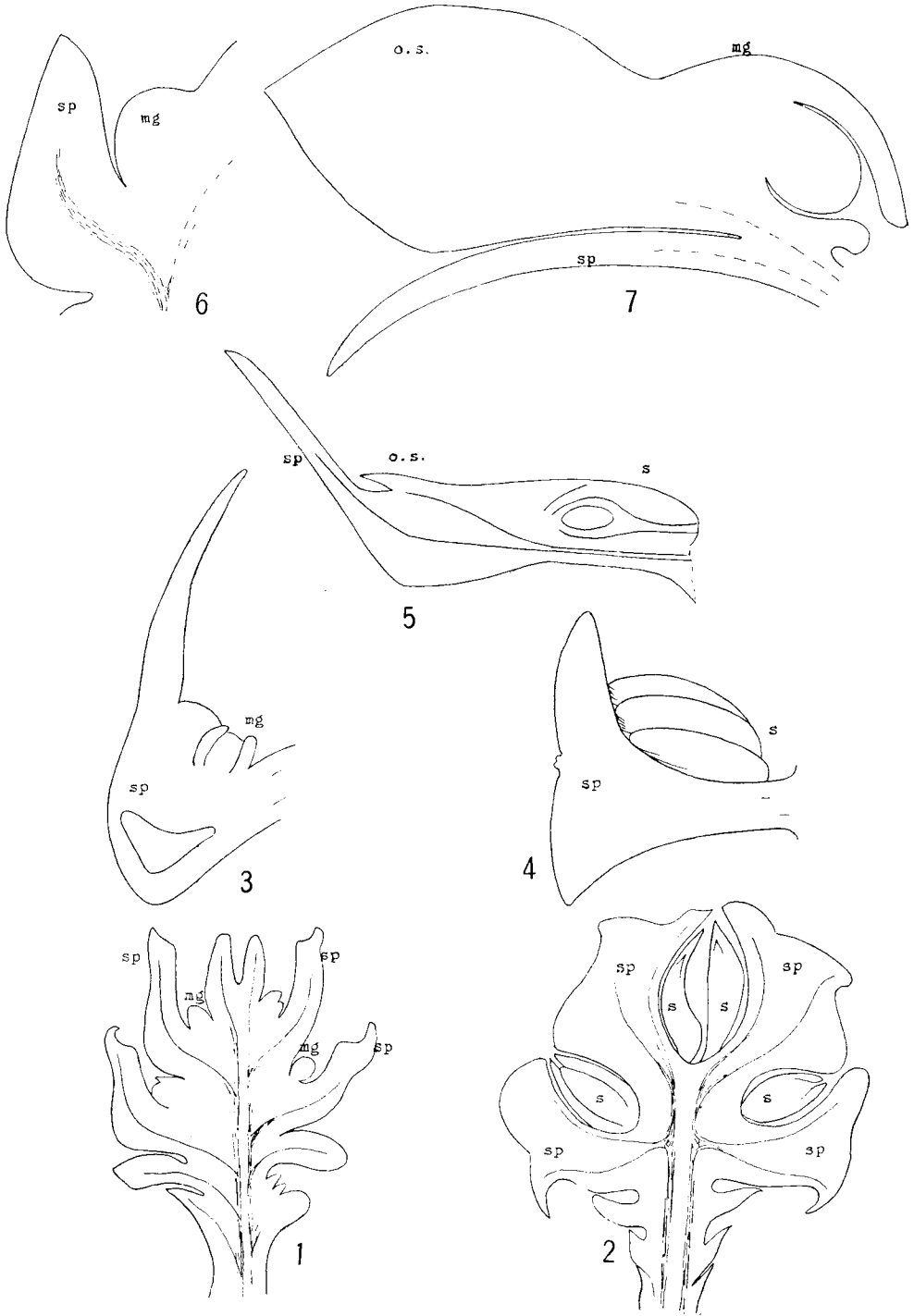
The point at issue is, in short, the morphological nature of the so-called "ovuliferous scale," a structure present in the cones of the Abietineae, but rudimentary or wholly wanting in the other tribes of the Pinaceae. In a pine cone the axis bears bracts which are the homologues of the stamens in the staminate cones, and in addition to these bracts there are thick, woody scales (one immediately above each bract) which bear the seeds. In such a seed-bearing cone the woody

⁴ Read before Section G, Botany, of the A. A. A. S., Denver meeting, August, 1901.

scales constitute the bulk of the cone, the bracts always remaining relatively small and inconspicuous. On the other hand, in the cone of a *Sequoia*, *Taxodium*, or *Cupressus*, the whole structure is composed of the enlarged bracts borne upon the axis. On *à priori* grounds there should be no question as to the morphological equivalence of the seed-bearing cones of pines and cypresses, and yet the added structure in the pines—the ovuliferous scale—has brought about a most uncomfortable confusion.

What is this structure? Is it a second leaf, as Robert Brown thought; a flattened axillary stem, as Schleiden thought; a single leaf of a short axillary shoot, as von Mohl suggested; or a fusion of two such leaves, as suggested by Alexander Braun, and accepted by many botanists? Is it a ligular growth as Sachs would have us believe; or is it a vestigial structure resulting from the modification and partial suppression of the axillary stem, as Celakovsky holds? This is not the place for a critical discussion of these views, but I may say in passing that they all fail to homologize the staminate and seminiferous cones.

Many years' study of the young cones of the pines has impressed me more and more with the essential identity of the cones bearing the two sexual cells, and at the same time has suggested an explanation of the origin of the ovuliferous scale which has for several years been helpful to my students. It is noticed that when the megasporangia first appear they are rounded masses of cells pushing up from the axillary region at the base of the bract of the young cone; later, this differentiates into scale and ovule. For a long time the scale portion is composed of chlorophyll-bearing parenchyma, and it is only much later that it becomes brown and woody. At all times there is no line of demarcation between scale and ovule, but the tissues are continuous and pass insensibly from one to the other. These facts led to the suggestion that the scale in the pine cone is a backward extension of the chalazal tissues of the ovules. The scale according to this view is ovular in nature, *i. e.*, it is not a new structure, but merely an enlargement and modification of a structure already present. The cones in the Cupressineae and Taxodieae are normal, *i. e.*, the megasporangia are borne by the bracts (carpels) which later become enlarged. In the Araucarieae the same structural conditions prevail, but while there is a slight backward ovular growth, the bract is still so large as to greatly overshadow it. In the Abietineae the megasporangia, which at first are secondary



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to the bracts, soon make so great a backward (chalazal) growth as to greatly overshadow the bracts. With the enlargement of the ovular tissue there has been a decreased development of the bract. As the ovular tissue has enlarged it has assumed more and more the photosynthetic and nutritive functions elsewhere discharged by the bract (carpel), until now the latter is practically functionless.

Concisely stated this view may be formulated as follows: The microsporangial and megasporangial cones are strictly homologous, and in the latter the sporophyll enlarges or remains small just as the chalazal development of the megasporangium into a scale is less or more pronounced.

In accordance with this view the tribes of the family Pinaceae should be rearranged so as to place the Abietineae at the summit of the group. Probably the sequence would be something like the following:

Tribe I. CUPRESSINEAE.—With *Callitris*, *Thuya*, and *Cupressus* leading to *Taxodieae*, *Juniperus* leading off in a side line.

Tribe II. TAXODIEAE.—Leading through *Taxodium*, *Sequoia*, and *Cunninghamia* to the two tribes *Araucarieae* and *Abietineae*.

Tribe III. ARAUCARIEAE.—With *Agathis* lower than *Araucaria*.

Tribe IV. ABIETINEAE.—With *Picea*, *Tsuga*, *Abies*, etc., lower, and *Larix*, *Cedrus*, and *Pinus* higher.—CHARLES E. BESSEY, *The University of Nebraska*.

EXPLANATION OF PLATE VIII.

FIGS. 1, 2, 5, 7, are from Strasburger's *Die Coniferen und Gnetaceen*; *fig. 3* from Shaw's *Life history of Sequoia sempervirens* (BOT. GAZ. 21: 332. 1896); *fig. 7* from Coulter and Chamberlain's *Morphology of Spermatophytes*; *fig. 4* is original. In all the figures *mg* is the megasporangium; *o. s.*, ovuliferous scale; *s*, seed; *sp*, sporophyll.

FIGS. 1, 2. *Cupressus funebris*; 1, longitudinal section of a young megasporangial cone; 2, longitudinal section of a seed-bearing cone, the seeds nearly mature.

FIGS. 3, 4. *Sequoia sempervirens*; 3, vertical section of a young sporophyll and a single megasporangium; 4, longitudinal section of a sporophyll with seeds at maturity.

FIG. 5. *Araucaria excelsa*; longitudinal section of a young sporophyll, with seed and rudimentary ovuliferous scale.

FIGS 6, 7. *Pinus Pumilio*; 6, longitudinal section of a young sporophyll with rudimentary megasporangium; 7, longitudinal section of an older sporophyll, with megasporangium grown backward as an ovuliferous scale.