

SOME NOTES ON *ATHROTAXIS*.

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(Sixteen Text-figures.)

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Synopsis.

This paper records some observations on *Athrotaxis* made in Tasmania in 1946-47. The relationships between the three species of the genus are briefly discussed. The pollen of *Athrotaxis* differs from other Taxodiaceae in the absence of a germ pore or germinal papilla. The intine is 2-layered. Female cones often contain larvae of a fly. Some features of the gametophytes described by earlier workers are commented on in the light of more recent work on *Sequoia* and *Sequoiadendron*. *Athrotaxis* differs from all other Taxodiaceae in the absence of cleavage polyembryony. All the embryo initials contribute to a single dicotyledonous embryo. The relationships between *Athrotaxis* and *Sequoia* and *Sequoiadendron* are briefly discussed, but no conclusions reached.

INTRODUCTION.

It is now more than 20 years since Saxton and Doyle (1929) published their fragmentary account of the life history of *Athrotaxis selaginoides*. Since then a description of the stem apex (Cross, 1943) is all that has been published on the morphology of the genus. On the other hand, the life histories of *Sequoia sempervirens* and *Sequoia gigantea* have been worked out (Looby and Doyle, 1937, 1942; Buchholz, 1939a, 1939b). Buchholz considers the two species sufficiently distinct to be placed in different genera, and instead of Lindley's invalid *Wellingtonia* has proposed the genus *Sequoiadendron* for *S. gigantea* (Buchholz, 1939c). While some still consider the two to belong to one genus (Doyle, 1945), many have accepted *Sequoiadendron* (see especially Stebbins, 1948). This, together with the discovery in China of *Metasequoia glyptostroboides*, the morphology and ecology of which are being investigated by a number of botanists,* makes it highly desirable to know something more about *Athrotaxis*. During 1946-47, at the University of Tasmania, I carried out some observations mainly on *A. cupressoides* Don, and though results were far from complete, the following points seem worthy of record.

RELATIONSHIPS BETWEEN THE THREE SPECIES.

No one in Tasmania could agree with Dallimore and Jackson's (1948, p. 207) remark that the three forms "might well be regarded as gradations of one species". The two common species, *A. cupressoides* and *A. selaginoides*, are quite distinct, both in the morphological characters used in taxonomy, such as the shape of the leaves and cone-scales, and ecologically. *A. cupressoides* forms stands or occurs as single trees by the side of tarns and along streams, while *A. selaginoides* is a taller forest tree generally growing on sloping ground. It does sometimes grow beside tarns, but I have not observed it in such habitats when *A. cupressoides* is found there. Where the two species occur near one another, their habitats are distinct, as has been noted by Sutton (1928). *A. laxifolia* is rare, and does not form stands. Many people entertain the possibility that it is a hybrid between the other two species, although there is little substantial evidence for the view at present. However, many more trees than exist in any one locality would be needed to show much segregation of characters.

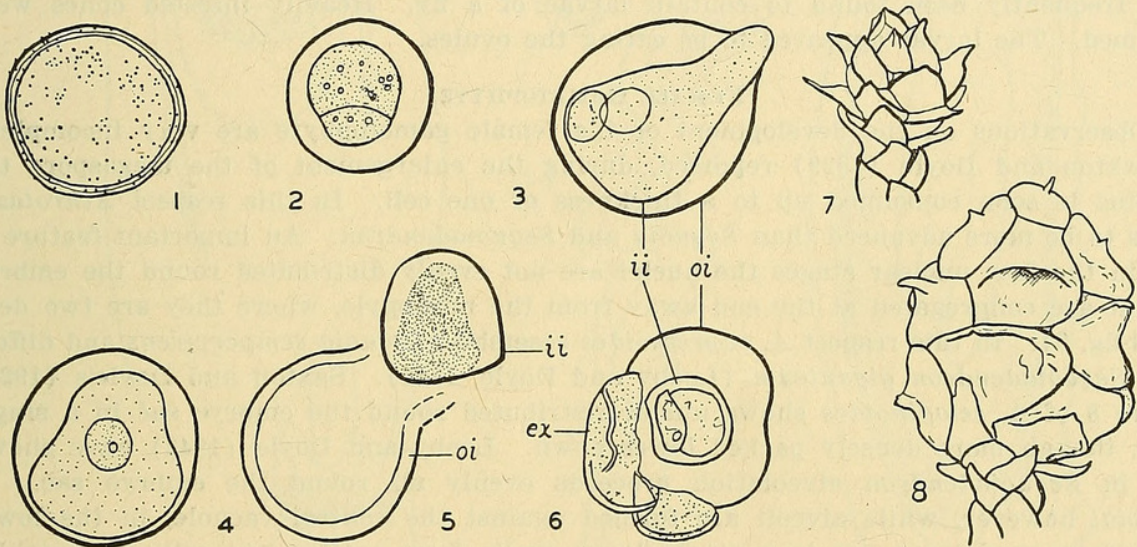
MALE CONES AND POLLEN.

The male cones of *Athrotaxis cupressoides* can first be distinguished from vegetative tips about mid-February, and their development proceeds until May, when spore mother cells are found. Cones collected at Lake Dobson (Mt. Field National Park) on 25th

* A bibliography is given by Chu and Cooper (1950).

August, 1946, and fixed in the field, contained microspores, but in some, the uppermost sporangia had quadrinucleate protoplasts with the spindles of the second meiotic division still present. Meiosis thus occurs about the second or third week of August. The pollen is mature about a month later. I have not observed the shedding of pollen in the field, but twigs with male cones collected at Lake Dobson on 9th September, 1946, and placed in jars of water in the laboratory at Hobart shed pollen on 17th September, and cones collected at the Hugel Lakes (Lake St. Clair National Park) on 14th September, 1947, shed pollen in Hobart on 18th September.

The pollen of *Athrotaxis*, in common with that of other Taxodiaceae and Cupressaceae, lacks air bladders, nor are there any male prothallial cells. As in other members of these families, the exine is thin and is thrown off by the swelling of the intine when the mature pollen grain comes into contact with water. The pollen of *A. cupressoides* is spherical or subspherical, and has no trace of any germ pore or germinal papilla. The diameter of acetolysed grains is $27.2 \pm 0.27\mu$. Three of the layers of the exine recognized by Erdtman (1948) can be observed in *Athrotaxis*. The nexine, about 2μ thick, is made up of an endonexine and an ectonexine of approximately equal thickness. The sexine is represented by minute granulae, irregularly scattered, and less than 1μ in diameter (Text-fig. 1).



Text-figures 1-6.—*Athrotaxis cupressoides*.

1. Acetolysed pollen grain. 2. Pollen, mounted in water, from which the exine has come off, showing the protoplast surrounded by a gelatinous "halo". 3, 4. Pollen after four days in water, showing enlargement of the protoplast within the "halo". 5. Pollen after eight days in M/4 sucrose. Protoplast with its wall (ii) emerging from the "halo" (oi). 6. Pollen mounted in potash. ex, exine; ii and oi, inner and outer layers of the intine. Text-figure 1, $\times 640$; all others, $\times 400$.

Text-figures 7-8.—Cones of *Athrotaxis cupressoides*. $\times 2$.

7, about the time of fertilization, 14th December, 1946. 8, with nearly mature seed, 24th February, 1947.

The intine itself consists of two layers. When fresh pollen grains are mounted in water, the grains first become turgid, and the average diameter is 30μ . After the exine is thrown off, the contents of the grain are seen to be surrounded by a spherical gelatinous "halo", the average diameter of the latter being 38μ (Text-fig. 2). The pear-shaped "cell" within the halo is closely surrounded by a wall of its own, especially well seen in dry pollen mounted in potash (Text-fig. 6), which we may call the "endintine" (ii), and the halo then is the "exintine" (oi). After four days in water or sugar solutions the protoplast contained within the endintine has elongated considerably, and although the shape of the protoplast is irregular, the exintine still preserves a spherical form except where it is actually forced out of position (Text-figs. 3, 4). When the cell surrounded by the endintine emerges (Text-fig. 5), the exintine is seen to have a definite thickness. A two-layered intine does not appear to have been

described before in a conifer, but since only the exine is preserved in fossils, it has monopolized the attention of pollen morphologists to the exclusion of the intine.

The pollen of *Athrotaxis* differs markedly from that of *Sequoia*, *Sequoiadendron*, and *Metasequoia*, in all of which there is a prominent germinal papilla, and it likewise differs from *Cryptomeria*, *Taxodium*, and *Glyptostrobus*, which also have a germinal papilla of some sort. It resembles more closely *Cunninghamia* and the Cupressaceae (Wodehouse, 1935; Erdtman, 1943; Sterling, 1949).

FEMALE CONES.

Young female cones have not been distinguished from vegetative tips before mid-September. In some localities production of cones varies from season to season. Cones of *A. cupressoides* were found near Lake St. Clair both in 1946-47 and 1947-48. But in the Mt. Field National Park, near the easterly limit of its distribution, *A. cupressoides* formed no cones in 1946-47, although *A. selaginoides* several miles away did form cones with fertile seeds. The same trees of *A. cupressoides* at Lake Dobson, however, bore cones in 1947-48. Text-figure 7 is a sketch of a cone about the time of fertilization. A fully grown cone is shown in Text-figure 8. Eames (1913, pp. 32, 33) has referred to the arrangement of the vascular bundles in the cone scales. The ovules are in a single row, and have their micropyles directed towards the cone axis. Cones of *A. cupressoides* have frequently been found to contain larvae of a fly. Heavily infested cones were deformed. The larvae appeared to be eating the ovules.

FEMALE GAMETOPHYTE.

Observations on the development of the female gametophyte are very incomplete. As Saxton and Doyle (1929) reported, during the enlargement of the megaspore the nucellus is soon consumed up to a thickness of one cell. In this respect *Athrotaxis* seems to be more advanced than *Sequoia* and *Sequoiadendron*. An important feature is that in the free nuclear stages the nuclei are not evenly distributed round the embryo sac but are congregated at the end away from the micropyle, where they are two deep (Text-fig. 9). In this respect *A. cupressoides* resembles *Sequoia sempervirens* and differs from *Sequoiadendron giganteum* (Looby and Doyle, 1942). Saxton and Doyle's (1929) Figure 8 of *A. selaginoides* shows nuclei distributed round the embryo sac in a single layer, though more densely packed lower down. Looby and Doyle (1942) have shown that in *Sequoiadendron* alveolation proceeds evenly all round the embryo sac. In *Sequoia*, however, while alveoli are formed against the central vacuole, in the lower part where nuclei are not in a single layer, walls form cutting out cells of irregular arrangement. In *A. selaginoides*, Saxton and Doyle's Figure 18 shows that wall formation takes place by the method in *Sequoia*, with alveoli being formed at the vacuolar edge of the basal portion.

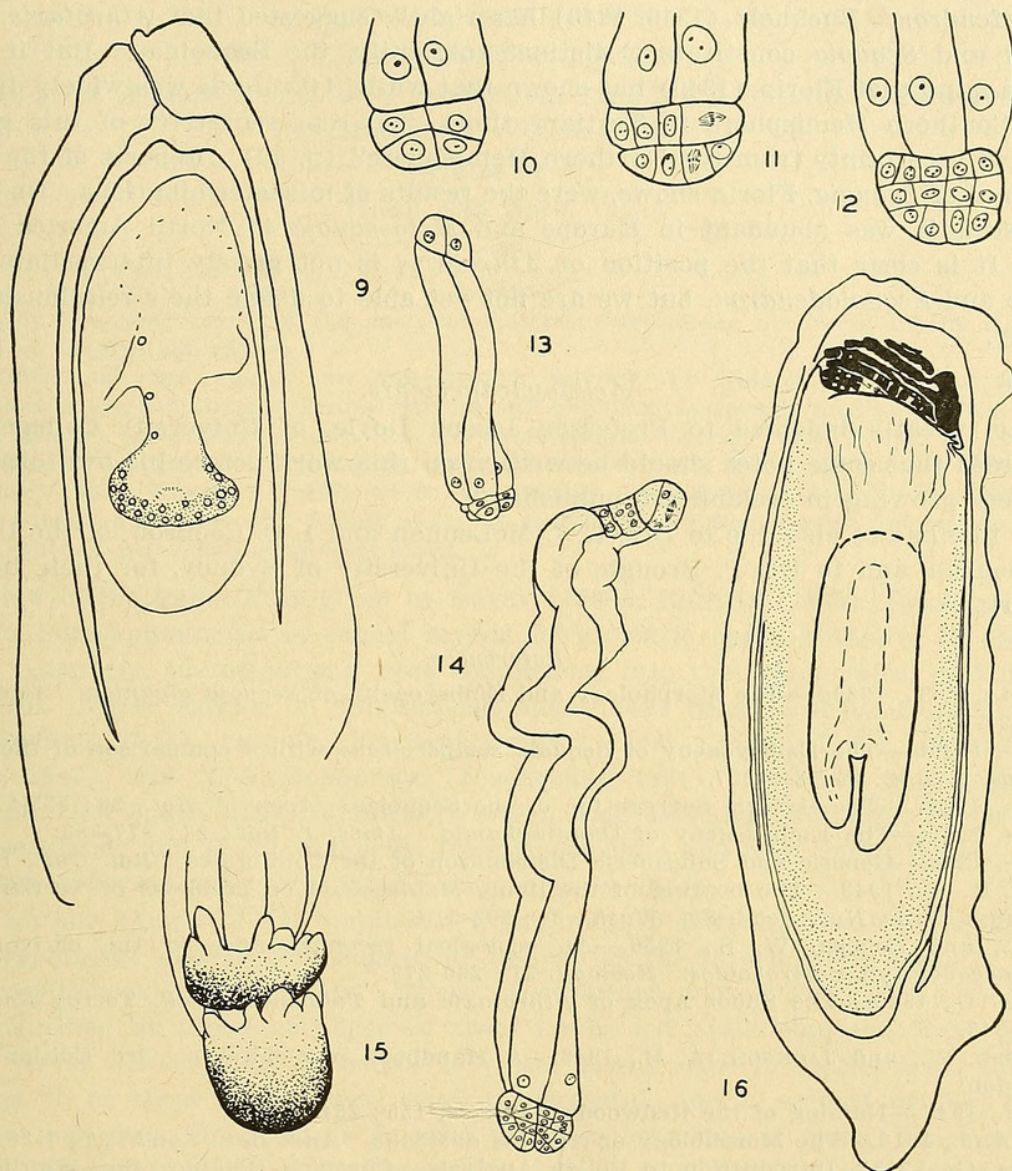
Another feature reported by Saxton and Doyle in which *Athrotaxis* resembles *Sequoia* and not *Sequoiadendron* is that the pollen tube grows over the surface of the nucellus. This is apparently also the case in *Metasequoia* (Sterling, 1949).

EMBRYO.

Proembryo stages were not found. The earliest stage observed showed eight cells in two tiers of four cells below the four-celled prosuspensor (Text-figs. 10, 13). The early growth of these embryo cells (Text-figs. 11, 12) gives rise to a single embryonic mass which may show some lobing (Text-fig. 14) and whose origin from four primary cells is generally apparent for some time. However, cleavage of this embryo, such as occurs in *Sequoiadendron* and *Taxodium*, was found never to take place.

There is no primary suspensor. A massive secondary suspensor is produced by the single embryo. An early stage of development of embryonal tubes is seen in Text-figure 15. As the suspensor elongates and its upper part becomes folded, the nucellus and rather indefinite prothallial tissue are included in the folds, and all together form a compact mass at the micropylar end of the mature seed (Text-fig. 16). The embryo has two cotyledons. Rosette cells are present in the early stages (Text-figs. 13, 14). Nuclear divisions are numerous in the chalazal part of the gametophyte, but unfortunately in no case could the chromosome number be counted; however, it does not

appear to be large. Embryo systems are frequently found in pairs, the result presumably of the fertilization of two adjacent archegonia by the two male cells (Text-fig. 15). Thus *Athrotaxis* exhibits only Simple Polyembryony as defined by Buchholz. In this respect it is unique in the Taxodiaceae.



Text-figures 9-16.—*Athrotaxis cupressoides*.

9. Longitudinal section of ovule at free nuclear stage, showing micropyle, integument, etc. Embryo sac badly shrunken, but it shows nuclei congregated at lower end in two layers, 14th December, 1946. $\times 60$. 10. 8-celled embryo, 27th January, 1947. $\times 168$. 11. Embryo with two tiers of cells each of more than four cells, 27th January, 1947. $\times 168$. 12. Three-tiered embryo, 27th January, 1947. $\times 168$. 13. Embryo system with two rosette cells, 4-celled prosuspensor, and 8-celled embryo, similar to Text-figure 10. 27th January, 1947. $\times 72$. 14. Embryo system with rosette cells and lobed multicellular embryo, 19th January, 1947. $\times 72$. 15. Embryos of two different systems showing early stage in development of embryonal tubes, 26th January, 1947, $\times 72$. (Material from which Text-figures 10-13 is taken is from a more exposed locality at a higher altitude than those which gave Text-figures 14-15, hence the earlier dates of the latter. Text-figures 10-15 from dissected embryos.) 16. Longitudinal section of nearly mature seed, 24th February, 1947. $\times 24$.

Free nuclear stages in the gametophyte were found in mid-December, and nearly mature embryos late in February.

DISCUSSION.

Athrotaxis shows some significant differences from both *Sequoia* and *Sequoiadendron* in its morphological features—in its pollen grain, simple polyembryony; also in its one-cell-thick nucellus. It agrees with *Sequoia* in the method of wall formation in the

embryo sac, thin megaspore membrane, and two cotyledons. It resembles *Sequoiadendron* in its mature leaves being of one type only, in the presence of a prosuspensor and rosette cells, and one might expect in general features of proembryo development. It is clearly impossible to derive the *Athrotaxis* type of embryogeny with its prosuspensor from the *Sequoia* type which has none; but it may have been derived from that in *Sequoiadendron*. Buchholz (1940, 1948) has rightly suggested that *Athrotaxis*, *Sequoiadendron* and *Sequoia* constitute a distinct subfamily, the Sequoidae. But it must be borne in mind that Florin (1940) has shown that while *Athrotaxis* was widely distributed in the Southern Hemisphere in Tertiary times, "no representatives of this genus are known with certainty from the Northern Hemisphere" (p. 90). Reports of the southern occurrence of *Sequoia*, Florin shows, were the results of misdeterminations. On the other hand, *Sequoia* was abundant in Europe and *Metasequoia* in North America (Chaney, 1948). It is clear that the position of *Athrotaxis* is not merely intermediate between *Sequoia* and *Sequoiadendron*, but we are not yet able to define their relationships more precisely.

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