

Remarks on the Organization of the Cones of *Williamsonia gigas* (L. & H.).

BY

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With five Figures in the Text.

AS is well known, the organization of the cones of *Williamsonia gigas* (L. and H.) has remained a palaeobotanical puzzle since the days when Williamson² and Yates³ first attempted that restoration independently in 1849. The memoirs which bear on this matter and have been published since that date must now approach, if they do not exceed, a hundred in number. A detailed account of these researches, with a full and up-to-date bibliography, has recently been given by Professor Seward,⁴ so they need not be enumerated here.

At the present time there is much which is still admittedly obscure in regard to the morphology of the cones of this plant. They have not yet been found with all their organs in continuity, and there seems unfortunately to be little likelihood of such incrustations being obtained in the near future. From analogy with Bennettites, we should expect that the microsporophylls in particular were fleeting, caducous organs, and thus the chance of obtaining specimens fossilized while these structures were mature and before they had been shed appears to be very small indeed. We must look forward rather to the happy discovery of petrified male cones of this or some similar species in the future, a discovery of which we need not despair, seeing that a female petrified cone of *Williamsonia* is now known. Considerable progress has, however, been made in the recognition of what is either the complete or the incomplete female cone, firstly by Lignier,⁵ and more convincingly by Seward⁶ quite recently. It may be well therefore to

¹ Owing to the author's death before this paper was finally revised, the responsibility for any errors which it may contain rests with me. I have to acknowledge a grant from the Royal Society in aid of the preparation of this and other memoirs left by the author in various stages of completion.—AGNES ARBER.

² Williamson (1849).

³ Yates (1849).

⁴ Seward (1917), vol. iii, chapter 37.

⁵ Lignier (1903).

⁶ Seward (1917), vol. iii, pp. 429, &c.

sum up the difficulties which remain in order to see how the position stands at present. This I propose to do briefly here.

The chief uncertainties are as follows:

(1) Were the cones monosporangiate (unisexual) or amphisporangiate (bisexual)?

(2) Where were the male sporophylls attached?

(3) What structure, if any, was borne on the axis of the cone above the female organs (interseminal scales and seeds)?

(4) Was there an infundibular expansion, somewhat similar in form to the united whorl of male sporophylls, but of a sterile nature, and where was it attached?

WERE THE CONES MONOSPORANGIATE OR AMPHISPORANGIATE?

On the question as to whether the cones were monosporangiate or amphisporangiate there will always be differences of opinion until the perfect male cone has been discovered. It is, at present, a case merely of the balance of probability. On the amphisporangiate side, the older view, we find ranged the opinions of Lignier,¹ Wieland,² and quite recently Seward,³ who says (1917) 'they may have been bisporangiate—a view that seems to me the more probable—but this has not been demonstrated'.

That the cone of *Williamsonia* was monosporangiate, and that there were separate male and female cones, was first advocated by Nathorst,⁴ and more recently has been supported by Thomas.⁵ The present writer supports the Monosporangiate theory on the following grounds.

He believes that all the parts of the two cones, male and female, were figured by Williamson⁶ as far back as 1870, and that it is merely a matter of piecing the parts together correctly. The illustrations in question are Figs. 1, 2, 4, and 5 of Williamson's Pl. 52, and Figs. 6–8 of the same author's Plate 53. The latter set of specimens are now known to represent the apex of the axis still bearing interseminal scales, probably sterile. More complete specimens of the lower parts of the same cones were figured by Saporta⁷ from British specimens in 1891. The only doubt then as regards the female cone is whether any organ was borne at the tip of the axis of that cone at the region of the terminal mamilla, termed by Williamson the corona, a point to be further discussed presently.

As particularly pertinent to this inquiry, emphasis may be laid on a fact, which appears to have been overlooked in recent years. The cones of *Williamsonia* had two quite different axes, exactly as Williamson first figured them, and despite Lignier's⁸ opinion that the staminal whorl

¹ Lignier (1907).

² Wieland (1911), p. 462.

³ Seward (1917), vol. iii, pp. 423–4.

⁴ Nathorst, (1909) p. 30, (1911) p. 26.

⁵ Thomas (1915), p. 137.

⁶ Williamson (1870).

⁷ Saporta (1891), vol. iv, Pl. 18, Fig. 2; Pl. 19, Fig. 2; Pl. 20, Fig. 2.

⁸ Lignier (1907).

occurred on the same axis as the female organs. The cones which we now know to have been partly or wholly female had a long *conical* axis, the best illustrations of which are those of Saporta already referred to above. The shape of these axes is also shown in the restoration of the female cone given here in Figs. 1 and 2. Other cones, however, possessed a flask-shaped or urn-shaped axis as figured on Williamson's Pl. 52, Fig. 4 (refigured in outline here as Fig. 5, p. 177). The writer has also seen more than one other example of the same structures among the specimens of *Williamsonia* at Cambridge. The shape of this axis is entirely different from that of the female flower, and thus there are certainly grounds for very strong suspicion

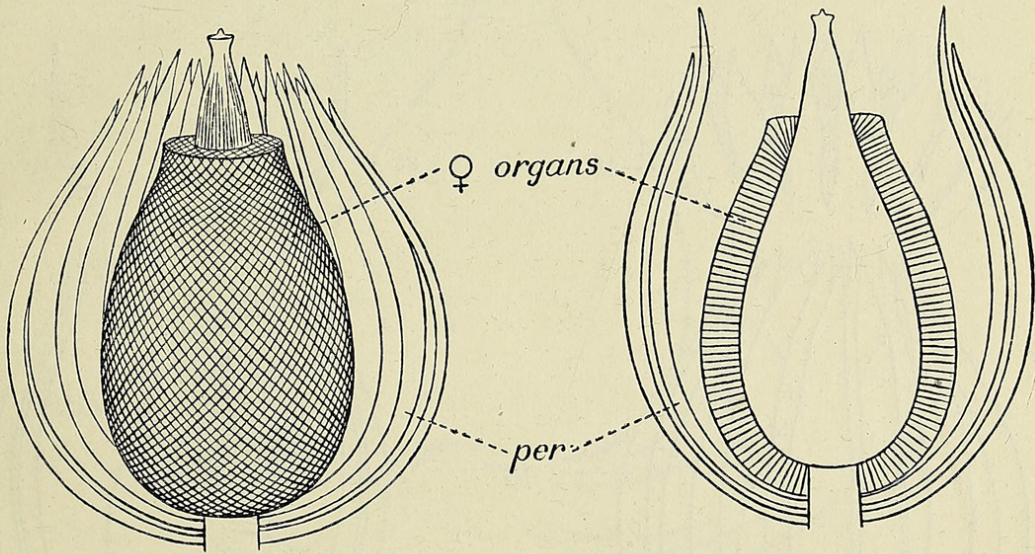


FIG. 1. Restoration of female cone of *Williamsonia gigas* with the front bracts (*per.*) removed (half natural size). FIG. 2. The same in section; ♀ organs = interseminal scales or seeds.

that this plant possessed two cones. None of the urn-shaped axes, regarded by the writer as male, ever show any trace of interseminal scales such as are almost always persistent at the base or apex or both regions of the female flower. Any organs which they bore were clearly attached apically, and it is difficult to imagine that they could have been other than the microsporophylls.

WHERE WERE THE MALE SPOROPHYLLS ATTACHED?

Perhaps the greatest difficulty in regard to the Williamsonian cone is to decide where the male sporophylls were attached. These organs are of course now exceedingly well known as detached objects. It should be remembered in this connexion that Nathorst,¹ to whom we owe our knowledge of these organs in particular, has shown that they were borne *terminally* on something. The axis bearing them was not produced beyond the cup of united sporophylls. That fact is incontestable. The male sporophylls

¹ Nathorst, (1909) pp. 11, 12, (1911) p. 20.

were thus certainly not attached below the interseminal scales. It follows therefore that they were borne either at the apex (corona) of the female conical axes, or on the urn-shaped axis distinguished above. My own view is that the latter possibility is almost certainly correct. If the urn-shaped axes did not bear the microsporophylls, what did they bear? They must have borne some organ beyond doubt. They certainly did not bear interseminal scales, unless in some other more distal region, now missing, and even in that case one would have to admit that the cones of *Williamsonia* were dimorphic.

My view is that Williamson's Plate 52, Fig. 1, was seated on the apex of the axes seen in Figs. 4 and 5 of the same plate, and that his Fig. 2 is

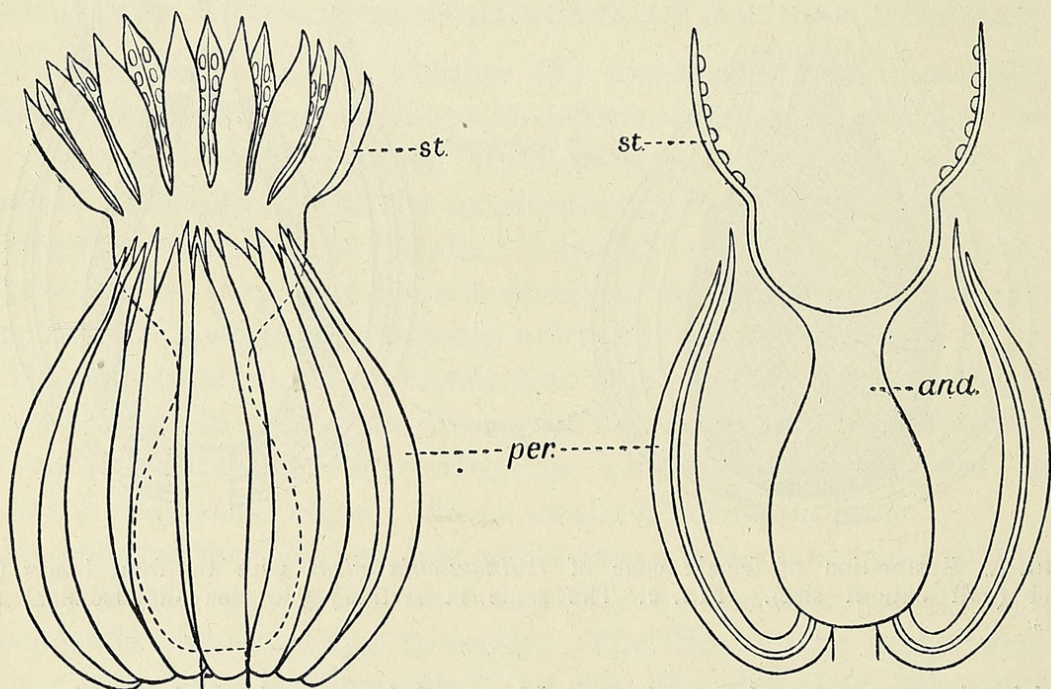


FIG. 3. Restoration of male cone of *Williamsonia gigas* (half natural size). FIG. 4. The same in section. *st.* = whorl of microsporophylls; *per.* = bracts; *and.* = androphore.

simply the lower surface of the cup of united microsporophylls. I therefore restore provisionally the male cone of *Williamsonia* as shown in Figs. 3 and 4.

If this is correct the male strobilus in this species had a distinct gonophore, or more strictly speaking androphore (*and.* in Figs. 3 and 4), whereas the female cone had none. That is to say, there was a considerable elongation of the internode or internodes between the perianth bearing nodes at the base of the cone, and the node bearing the whorl of microsporophylls. Such a gonophore occurs in the case of several Angiospermous amphisporangiate flowers, though somewhat rarely. The genus *Gynandropsis* (family Capparidaceae), of South America and elsewhere, furnishes a well-known example. In *Williamsonia*, the object of the gonophore no doubt was to elevate the microsporophylls when mature out

of the circumscribed space enclosed by the perianth members when the cone was immature.

The male cone of *Williamsonia* is probably not the only strobilus of this group possessing a gonophore. In *Williamsoniella coronata*, recently instituted by Thomas,¹ we find both the male and female organs of this amphisporangiate cone borne on a long stalk. It is true that perianth segments (so-called bracts) are not known to occur at the base of this stalk,

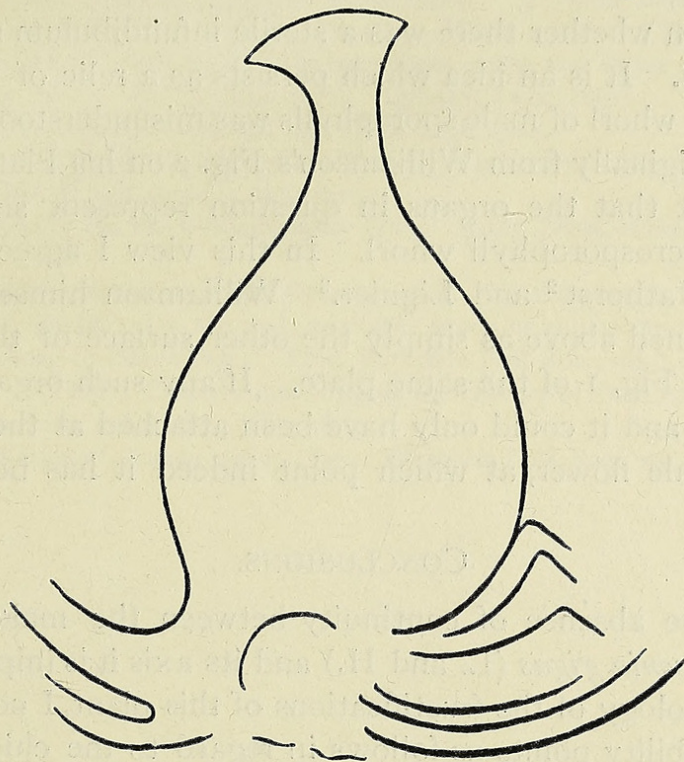


FIG. 5. Outline of the 'pyriform axis' (androphore) of a male cone of *Williamsonia gigas* (after Williamson, W. C., 1870, Pl. 52, Fig. 4), natural size.

but at the same time this organ may be at least provisionally interpreted as being of the nature of a gonophore.

WERE ANY STRUCTURES BORNE AT THE APEX OF THE FEMALE CONE?

The question as to whether any structure was borne at the 'corona' of the female axis must be left open. In *Williamsoniella coronata*, mentioned above, the axis is also prolonged somewhat beyond the region of the inter-seminal scales, though to a much less degree than in the female *Williamsonia* cone. There is no evidence, however, that it bore any other structure above the female organs.

In the case of *Williamsonia*, I think it is very unlikely that anything was attached in that region. Certainly the male sporophylls were not borne here, and if anything was attached in this region it must have been some other organ. It should also be recalled that many other examples of

¹ Thomas (1915), Text-fig. 1.

female cones of other species of *Williamsonia* are known as impressions, and in one case as a petrification. In none of these is there any evidence that the axis projected beyond the zone of the interseminal scales. The female cone of *Williamsonia gigas* appears to be quite exceptional in this respect. It is therefore extremely improbable that any organ at all was attached at the corona.

WAS THERE A STERILE INFUNDIBULUM?

The question whether there was a sterile infundibulum may, I think, be almost dismissed. It is an idea which persists as a relic of the times when the nature of the whorl of male sporophylls was misunderstood, and probably the idea arose originally from Williamson's Fig. 2 on his Plate 52. There is very little doubt that the organs in question represent simply the lower surface of the microsporophyll whorl. In this view I agree with Seward,¹ as opposed to Nathorst² and Lignier.³ Williamson himself regarded the specimen mentioned above as simply the other surface of the organ which he illustrated on Fig. 1 of the same plate. If any such organ did exist it is unknown to me, and it could only have been attached at the corona at the apex of the female flower, at which point indeed it has been restored by Lignier.⁴

CONCLUSIONS.

While in the absence of continuity between the male organs of the cone of *Williamsonia gigas* (L. and H.) and its axis it is impossible to prove the exact morphology of the fructifications of this plant, I conclude that the balance of probability points as follows in regard to the chief uncertainties which exist as to the organization of the fructifications of this fossil.

- (1) The cones were probably monosporangiate.
- (2) The female cone possessed a conical axis, sheathed in perianth segments below, and bearing seeds and interseminal scales above. The tip of the axis projected for about 2 cm. beyond the highest interseminal scales, as is also the case, but to a less extent, in *Williamsoniella coronata*. In all probability no other organ was borne on this axis, either at the tip or elsewhere.
- (3) The male cone possessed an urn-shaped axis sheathed in perianth segments below. This axis was of the nature of a gonophore. On it was seated apically the whorl of partly united male sporophylls. It did not bear interseminal scales.
- (4) There is no evidence of any sterile infundibular organ attached to or terminating either cone. All the organs of these cones have been known since 1870 in continuity, except the male sporophyll whorl and its gonophore.

¹ Seward (1917), vol. iii, p. 428.

² Nathorst (1909), pp. 12-13.

³ Lignier (1907).

⁴ Lignier (1903), Text-fig. 8, p. 35; see also Seward (1917), vol. iii, Fig. 548 on p. 432.

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