

ON LAGENOSTOMA LOMAXI, THE SEED OF LYGINODENDRON¹.—The existence in Palaeozoic times of a group of plants (the Cycadofilices of Potonié) combining certain characters of Ferns and Gymnosperms, has been recognized for some years past by various palaeo-botanists². The group in question embraces a number of genera, among which *Medullosa*, *Heterangium*, *Calamopitys*, and *Lyginodendron* may be mentioned; the fern-like foliage of these plants is placed according to its external characters in the form-genera *Alethopteris*, *Neuropteris*, *Sphenopteris*, and others.

The evidence for the intermediate position of the Cycadofilices is extremely strong, but at present it is drawn entirely from a detailed comparison of their vegetative organs, especially as regards their anatomical characters. In no case, as yet, is the fructification of any member of the group known with certainty; such indications as have hitherto been detected are still in need of corroboration. Thus, the suggestion has been made that the large seed, *Trigonocarpon olivaeforme*, may have belonged to some member of the genus *Medullosa*³; and in the case of *Lyginodendron* itself there is fairly strong reason to believe that one form of fructification (in the light of the observations to be described below, presumably the male), may have been of the *Calymmatotheca* type⁴, a type, however, of which the organization is not yet fully understood. In the absence of satisfactory data as to the fructification, so high an authority as M. Zeiller has expressed a doubt whether the Cycadofilices were, after all, anything more than a specialized group of Ferns⁵.

A re-examination of the seeds, placed by Williamson in his genus *Lagenostoma*, has revealed unexpected points of agreement between the structure of the envelopes of certain of these seeds on the one hand, and that of the vegetative organs of *Lyginodendron* on the other.

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² Williamson, Organization of the Fossil Plants of the Coal-measures, Pt. XIII, Phil. Trans., B, vol. clxxviii, p. 299, 1887; Solms-Laubach, Fossil Botany, 1887, Engl. ed., pp. 141, 163; Williamson and Scott, Further Observations on the Organization of the Fossil Plants of the Coal-measures, Pt. III, Phil. Trans., B, vol. clxxxvi, p. 769, 1895; Potonié, Lehrbuch der Pflanzenpalaeontologie, p. 160, 1899; Scott, Studies in Fossil Botany, pp. 307, 514, 1900.

³ G. Wild, On *Trigonocarpon olivaeforme*, Trans. Manchester Geol. Soc., vol. xxvi, 1900.

⁴ Scott, Studies, p. 334; Miss Benson, The Fructification of *Lyginodendron Oldhamium*, Ann. of Bot., vol. xvi, p. 575, 1902.

⁵ Zeiller, Éléments de Paléobotanique, 1900, p. 370.

Two species of *Lagenostoma* (*L. ovoides* and *L. physoides*) were described by Williamson¹; a third species, the subject of the present note, was left undescribed by him, though in his MS. catalogue he named it, after its discoverer, *Lagenostoma Lomaxi*, a name which we here provisionally adopt. This seed occurs in calcareous nodules of the lower Coal-measures, and chiefly at Dulesgate, in Lancashire.

In general structure the seed *L. Lomaxi* agrees with *L. ovoides*.

It is an orthotropous seed, circular in transverse section, and broadest midway between base and apex. The height of the seed slightly exceeds the diameter, and in general form it may be compared with a Jaffa orange. Its height in full-sized specimens is about $5\frac{1}{2}$ mm., the diameter at the equator $4\frac{1}{4}$ mm. Many of the specimens that have passed through our hands show signs of having become detached through the agency of a layer of separation and bear a low conical papilla centrally placed at the chalazal end, beneath which the actual layer of abscission was situated.

In the most general relations of its organization the seed approaches the Gymnosperm type in that the integument and nucellus are distinct from one another in the apical region only, whilst the body of the seed, which contains the large single macrospore with traces of prothallial tissue, shows complete fusion of the integumental and nucellar tissues. But in other respects the seed is remarkable. The free portion of the nucellus which stands above the macrospore is conical in form, its base is about 0.75 mm. across, and its height somewhat greater. The tapering apex reaches to the exterior, plugging the micropylar aperture like a cork. The whole of this structure, the 'lagenostome' of Williamson, constitutes a pollen-chamber, owing to the separation of the nucellar epidermis from the underlying parenchymatous body of the free part of the nucellus. The pollen-chamber thus has the form of a bell-shaped cleft situated between the persistent epidermis and the central cone of nucellar tissue. Access to the chamber is gained at the apex, which is open, and pollen-grains are found in its lower part. The integument, which is a simple shell where fused with the nucellus, becomes massive and complicated in its free part which corresponds to the upper fifth of the seed. In this region it is usually composed of nine chambers radially disposed around

¹ Organization, Pt. VIII, Phil. Trans., vol. clxvii, p. 233, Figs. 53-75, and 77-79, 1877; Pt. X, Phil. Trans., Pt. II, 1880, p. 517, Figs. 61-63. See Oliver, New Phytologist, vol. i, no. 7, 1902.

the micropyle. The existence of these chambers is indicated on the outside surface of the seed by the presence of nine little ridges disposed like the rays of a star around the micropyle, but dying out almost at once. These ridges over-lie the partitions of the chambered portion of the integument just as do the stigmatic bands the septa of a poppy capsule. The whole structure from within is like a fluted dome or canopy, the convexities of which correspond to the chambers, and actually engage with broad low grooves on the surface of the wall of the pollen-chamber.

The vascular system of the seed enters as a single supply-bundle at the chalazal papilla, and branches, a little below the base of the macrospore, into nine radially-running bundles. Each of these bundles passes, without further branching, to the apex of the seed, running outside the macrospore and a little distance below the surface. At the canopy the bundles enter the chambers and end at the tips.

Lagenostoma Lomaxi was thus a seed or seed-like structure detached as a whole and containing pollen-grains in the remarkable cleft-like pollen-chamber; the integument in its free part, when compared with that of Williamson's *Lagenostoma physoides*, suggests a number of originally free arms or processes that have become laterally fused into a complex chambered organ.

The seed, *L. Lomaxi*, is in some cases still attached to its pedicel¹; the great peculiarity of this seed, as compared with other members of the genus, is that when young, and sometimes even at maturity, it is found enclosed in an envelope or cupule, springing from the pedicel just below the base of the seed, and extending above the micropyle—at least in young specimens. The cupule appears to have been ribbed below, and deeply lobed in its upper part; in form it may be roughly compared to the husk of a hazel-nut—of course on a very small scale.

The pedicel and cupule bear numerous capitate glands, of which some are practically sessile, others shortly stalked, while in others again the stalk is of considerable length. The head, or secreting portion of the gland, which is spherical in form, is almost invariably empty, only the multicellular wall persisting. The tissue of the stalk of the gland, consisting of many layers of cells, is preserved, though in a somewhat disorganized state.

These cupular glands present the closest agreement in size, form,

¹ Cf. Williamson, loc. cit., Pt. VIII, Fig. 68 (*L. ovoides*).

and structure with the glands which occur on the vegetative organs of *Lyginodendron Oldhamium*¹, and which are especially abundant on the particular form of that plant found in association with *Lagenostoma Lomaxi*. Both on petiole and cupule the majority of the glands are short, those which are not sessile being commonly about 0.4 mm. in height. Long-stalked glands, exceeding a millimetre in height, sometimes occur both on the vegetative organs and on the cupule. The dimensions of the head of the gland agree exactly on cupule and petiole, the diameter averaging about 0.2 mm. in each case. In both, the stalk is usually somewhat narrower than the head, except at the base, where it is often considerably enlarged. On the stem, as might be expected, the glands are usually somewhat larger than on petiole or cupule.

As a rule, the structure of the glands on the vegetative organs is well preserved, the secretory tissue in the head being perfect. But occasionally the vegetative glands are found in the same state of preservation as those on the cupule, with the head hollow, owing to disappearance of the secretory mass. Where we thus have the two organs in a corresponding state of preservation, the agreement between the vegetative glands of *Lyginodendron* and those on the cupule of *Lagenostoma Lomaxi* is found to be exact.

There is no other known plant from the Coal-measures with glands at all similar to those described, nor is it likely that any unknown Gymnosperm should so exactly resemble *Lyginodendron* in these characters. On the ground, then, of the glandular structure we are led to the conclusion that the seed *Lagenostoma Lomaxi* can have belonged to no other plant than *Lyginodendron Oldhamium*, and more particularly to the glandular form of that type with which the seed is associated.

The state of preservation of the glands and of the cupule as a whole, indicates clearly that this organ, as we find it, was in an effete condition, having, no doubt, already discharged its functions while the seed which it protected was still quite young.

The vascular system of the cupule was well developed, and is very fairly preserved. A number of bundles branched off from the main strand of the pedicel, and traversed the cupule throughout its whole

¹ It has long been realized that the name *Lyginodendron Oldhamium* characterizes a type rather than a species. It is probable that the very glandular form occurring at Dulesgate may deserve specific rank.

extent. The structure of the large bundle, seen in the pedicel, agrees with that of a petiolar strand in *Lyginodendron*. The minute characters of the tracheides are also in close agreement with those observed in the xylem of the foliar organs of the same plant.

Hence, characters presented by the internal anatomical structure strengthen the conclusion drawn from a comparison of the glands, and thus further support the attribution of *Lagenostoma Lomaxi* to *Lyginodendron*.

The evidence thus indicates that in a transitional type, such as *Lyginodendron Oldhamium*, with leaves wholly fern-like in structure and form, but with decided Cycadean as well as Filicinean characters in the anatomy of stem and root, the seed habit had already been fully attained, as fully, at any rate, as in any known Palaeozoic Gymnosperm. *Lyginodendron* retains, so far at least as its vegetative structure is concerned, the intermediate position already assigned to it, but whereas the fern-like characters have hitherto seemed to preponderate, the discovery of the seed inclines the balance strongly on the Gymnospermous side. It is not likely that *Lyginodendron* stood alone in this; we must now be prepared to find, what has long been recognized as a possibility, that many of the plants grouped under Cycadofilices already possessed seeds, and thus that a considerable proportion of the so-called 'fern-fronds' of the Palaeobotanist really belonged to Spermatophyta. It is at present impossible to say at what stage in the evolution of the Fern-Cycad phylum the great change in reproductive methods came, whether it followed in the wake of general anatomical advance, or *vice versa*. The discovery of further evidence as to the reproductive processes of these ancient plants is likely to yield interesting results.

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Mr. J. Lomax deserves high praise for his good judgement and skill in collecting and preparing the material for the investigation.

A full account of the fossils dealt with in the present note is in preparation, and will shortly be submitted to the Royal Society.

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