The Structure of the Palaeozoic Seeds, *Trigonocarpus Parkinsoni*, *Brongniart*, and *Trigonocarpus Oliveri*, sp. nov.¹ Part I.

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With Plates XI-XIV.

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I. INTRODUCTION.

IN January last we published a preliminary note on the structure of *Trigonocarpon olivaeforme*², giving a short account of a reinvestigation of a large number of the seeds. The object of the present paper is to illus-

¹ [The investigation recorded in the present paper was carried out jointly by my colleague and myself at the Jodrell Laboratory. The part of the paper now published, giving the results of our joint observations, has been written entirely by Mr. Maslen. In the second part we hope to discuss the more general questions arising out of our work.

D. H. SCOTT.]

² Scott and Maslen, 1906.

trate and describe in detail the structures there referred to, to describe a new species of *Trigonocarpus*¹, to briefly describe the specimens which are preserved as structureless casts and impressions and compare them with those in which the internal structure is preserved, and to discuss the probable affinities of *Trigonocarpus* and the general bearing of our work.

Among the many forms of seeds which occur in the British Coal-Measures none are more familiar to geologists and palaeobotanists than the more or less triangular nut-like seeds referred to Brongniart's genus *Trigonocarpus*. This name (or *Trigonocarpum*) was originally applied by Brongniart, in his *Prodrome d'une Histoire des Végétaux fossiles*², to French specimens, on account of their characteristic three-ridged form as seen in the ordinary sandstone casts, and equally well in transverse sections of the petrified seeds preserved in the calcareous concretions of the Lower Coal-Measures.

In the most common mode of preservation, the familiar three-angled 'nuts' of the miners were long ago shown by Hooker and Binney³ and by Williamson⁴ to be nothing more than internal casts of the cavity of the seed, and to be often surrounded by a thin coaly layer which was correctly interpreted as the remains of the testa. These internal structureless casts are found in all parts of the Coal-Measures. Wild⁵ instances the Peel Delf rock, near Worsley, in the Upper Coal-Measures, and the Bardsley Delf rock, near Ashton-under-Lyne, in the Middle Coal-Measures, as localities which have yielded a great many examples of these triangular internal casts, while in the Lower Coal-Measures *Trigonocarpus* is not uncommon in a petrified form. Some of the specimens exhibited at the Natural History and other Museums show hundreds of examples of *Trigonocarpus* on one slab of rock, and thus serve to illustrate in a striking manner the abundance of these seeds and of the plants on which they were borne in later Palaeozoic times.

Trigonocarpus occurs also at corresponding horizons in many parts of Europe. The French Stephanian (corresponding to our Upper Coal-Measures), especially at Grand'Croix, near St. Étienne, has yielded numerous types of Gymnosperm seeds, many of which were originally described by Brongniart⁶. These silicified Carboniferous seeds from St. Étienne have also been studied by Renault, and quite recently by Prof.

¹ Some reason should be given for our use of the form *Trigonocarpus* in this paper instead of *Trigonocarpon*, which was the name used in our preliminary note. The name of this seed has, unfortunately, been spelt differently by different authors. Brongniart himself in his original 'Prodrome' uses *Trigonocarpum*, in his 'Tableau' *Trigonocarpon* is used, while in the memoir on the St. Étienne seeds the genus appears as *Trigonocarpus*. Lindley and Hutton used *Trigonocarpum*, while Williamson adopted *Trigonocarpon*. Prof. F. W. Oliver, F.R.S., in his recent papers on some of the French seeds uses *Trigonocarpus* and for the sake of uniformity among present-day observers we have adopted the same form.

² Brongniart ('28).

³ Hooker and Binney ('55).

⁴ Williamson ('77), p. 251.

⁵ Wild ('00), p. 435.

⁶ Brongniart ('74), ('81).

F. W. Oliver, who has commenced a re-examination of the seeds and from whom valuable papers have already appeared on *Stephanospermum*¹, *Trigonocarpus pusillus*², and other forms.

In Brongniart's memoir on these silicified seeds from Grand'Croix, published in 1874³, they are divided into two series, according to shape, as follows:—

- (A) *Graines à symétrie binaire, plus ou moins aplaties et bicarénées.*
- (B) *Graines à symétrie rayonnante autour de l'axe à trois, six, huit divisions ou à section circulaire.*

For these series Prof. Oliver has proposed the names *Platyspermeae* and *Radiospermeae* respectively⁴.

The *Radiospermeae* are further divided into several groups based on the form of the transverse section, circular, triangular, hexagonal, or octagonal; and the three-angled forms are referred to three genera, *Trigonocarpus*, *Tripterospermum*, and *Pachytista*. Of these genera, *Trigonocarpus* and *Tripterospermum* appear to be so nearly alike as to be difficult of separation. Indeed, the first British specimens of *Trigonocarpus* of which the internal structure was described—by Hooker and Binney in 1855⁵—were regarded by Brongniart himself as probably belonging to his genus *Tripterospermum*. The specimens afterwards described by Williamson under the name of *Trigonocarpon olivaeforme*⁶ undoubtedly represent the same form as the Hooker and Binney seed, and in fact nearly all the structural specimens which we have examined from the British Coal-Measures, and they are numerous, are so generally similar in size, form, and structure as to lead us to the conclusion that they probably belonged to the same species of plant.

It is important, therefore, at the outset of our investigations, to critically consider the two genera *Trigonocarpus* and *Tripterospermum*, and to decide to which form our common British specimens should be referred.

The characters used by Brongniart for the separation of these two genera are given in the following extract. *Tripterospermum* is described as of the same general form as *Trigonocarpus*: 'Mais ce testa, très-épais, se prolonge en trois ailes très-saillantes, et est composé de deux couches très-distinctes: l'interne est formée d'un tissu serré, très-coloré et très-opaque, composé de cellules diversement dirigées; l'extérieure, plus large, est constituée par un tissu plus lâche et plus transparent'⁷. One of the distinguishing characters here given, viz. the double-layered testa, is now known to be shared by Brongniart's *Trigonocarpus pusillus*, as shown by Prof. Oliver in his recent re-examination of this seed from Grand'-Croix⁸. Prof. Oliver shows that the compact layer of the testa is

¹ Oliver ('04) (1).

⁴ Oliver ('04) (1), p. 389.

⁷ Brongniart ('74).

² Oliver ('04) (2).

⁵ Hooker and Binney ('55).

⁸ Oliver ('04) (2), p. 98.

³ Brongniart ('74).

⁶ Williamson ('77).

overlaid by two or three layers of thin-walled cells, which in all probability represent but a small portion of a much more extensive tissue, so that, according to this character, *Trigonocarpus pusillus* (Brongn.) is a *Tripterosperrum*.

The other distinguishing feature of *Tripterosperrum*, i. e. the more wing-like form of the ridges of the hard testa, remains to be considered. The difference would be best seen by a comparison of transverse sections of the body of the seed in the two genera. Comparing our common British form, described in this paper as *Trigonocarpus Parkinsoni* (see Pl. XI, Fig. 5), with the figures given by Brongniart, it seems to agree (as was evidently thought by this author himself) rather more closely with *Tripterosperrum* than with *Trigonocarpus*.

Should we, then, describe our British forms as belonging to the genus *Tripterosperrum*? We have already seen that the degree of prominence of the three principal ridges of the testa is the only remaining character by which to distinguish the two genera. Among our British forms there is some variation in this respect, not only in the principal ridges, but also in the less prominent ribs which occur between them, as will be more fully discussed later. Prof. Oliver, in his memoir on *Stephanosperrum*, one of the radiospermic Gymnospermous seeds from St. Étienne, and in a comparison of this form with other related Palaeozoic seeds, after pointing out that the seed described by Williamson as *Trigonocarpus olivaeforme* unquestionably belongs to the same affinity as the Hooker and Binney specimens, says: 'Consequently, for the present discussion, both these *Trigonocarpons* may conveniently rest in the Brongniartian genus *Tripterosperrum*'¹. Somewhat later, in his *Notes on Trigonocarpus and Polylphosperrum*, discussing the same subject, Prof. Oliver says that 'In any case the structural feature used by Brongniart to separate *Trigonocarpus* and *Tripterosperrum* seems unimportant'².

We concur in this opinion, and shall therefore describe our forms as belonging to *Trigonocarpus*. We are the more disposed to do this as this name has been extensively used in this country by Williamson and others for petrified specimens and casts similar to those described in this paper, and so has become well known to every one interested in fossil plants. *Tripterosperrum* has never been used for British forms.

We may now consider the question of the specific name which should be given to the common form. This question is made the more difficult of solution owing to the difficulty of accurately comparing the structural specimens preserved completely embedded in a matrix with the much more common form of preservation as a structureless cast. The specific names have usually been first applied to the casts and afterwards to structural specimens which appeared to agree in shape and size.

¹ Oliver ('04) (1), p. 391.

² Oliver ('04) (2), p. 97 note.

According to Mr. Kidston¹ the earliest figured specimens of *Trigonocarpus* are those given in Parkinson's *Organic Remains*², published in 1811. These are the familiar internal nut-like casts to which Brongniart, in his *Prodrome*³, gave the name *Trigonocarpum Parkinsoni*. This name appears to be the earliest applied to British specimens.

The other familiar specific name, *olivaeforme*, seems to have been first used by Lindley and Hutton for casts⁴, and afterwards by Williamson⁵ for specimens showing internal structure.

Lindley and Hutton figure and describe several species of *Trigonocarpus* (their *Trigonocarpum*) from the casts. Some of these forms differ from our common form in size and shape to such an extent that we feel no doubt as to their being distinct species, but two somewhat similar forms are figured as *T. Noeggerathi* and *T. olivaeforme*. Internal casts of *T. Noeggerathi* are said to be provided with six longitudinal ridges instead of three as in *T. olivaeforme*. Internal casts of any of our specimens would certainly have only three ridges, so that *T. Noeggerathi* may be excluded. Moreover, according to Mr. Kidston, *T. Noeggerathi* is an uncommon seed in Britain⁶.

It rests, then, between *T. Parkinsoni* (Brongn.) and *T. olivaeforme* (L. and H.), which Mr. Kidson, after examination of the casts in the Natural History and other Museums has pronounced to be really indistinguishable from one another⁷. If this identification as one species is correct—and as far as our own observations go they are in support of it—*T. Parkinsoni* (Brongn.), as the earlier name, should be used. The common British specimens will therefore be described in this paper as *Trigonocarpus Parkinsoni*.

Lindley and Hutton also figure, under the name of *Carpolithes alata*⁸, specimens which show not only the internal cast of the cavity of the body of the seed, but also that of the elongated micropylar canal, and an impression of the testa of the seed, as shown in Pl. XII, Figs. 16 and 17, and Pl. XIII, Fig. 18, of this paper. These specimens Mr. Kidston also identifies with *Trigonocarpus Parkinsoni*⁹, and we think that there is no doubt that they do represent a more complete form of preservation of the same or a similar form to that represented by the ordinary internal casts and the petrified specimens.

Thus we now know the common *Trigonocarpus* in three conditions:—

(1) As the common internal casts of the central cavity of the seed, the actual tissues having disappeared completely, or being represented only by a layer of structureless coal.

¹ Kidston ('86), p. 216.

² Parkinson ('11).

³ Brongniart ('28).

⁴ Lindley and Hutton ('31-'37), vol. ii, Pl. 222, Figs. 1, 3.

⁵ Williamson ('77).

⁶ Kidston ('86), p. 219.

⁷ Kidston ('86), pp. 218, 219.

⁸ Lindley and Hutton ('31-'37), vol. ii, Pl. 87.

⁹ Kidston ('86).

(2) As structureless casts and impressions showing, in addition to the ordinary cast of the body of the seed, the long micropyle and testa.

(3) As completely petrified specimens in which the internal structure is more or less perfectly preserved.

II. PREVIOUS WORK ON THE BRITISH FORMS OF TRIGONOCARPUS.

We propose next to pass in review the work which has previously been done on the British forms of *Trigonocarpus*, especially on the petrified specimens showing internal structure. The earlier papers have been referred to in the preceding section, but a connected, somewhat fuller account may be useful before passing to our own work. Lindley and Hutton, in the *Fossil Flora*¹, deal only with the ordinary structureless internal casts, and with impressions showing the outer coats, but without internal structure, which they described as *Carpolithes alata*. The internal casts are referred to several different species by differences of shape, number of longitudinal ridges and size. Some of these casts, *T. olivaeforme* and *T. Noeggerathi*, are common forms and closely resemble in size and shape the most commonly found petrified specimens as described in the present paper. These 'species' have already been discussed in this paper (p. 93). Other forms such as *T. ovatum* and *T. Dawesii* are less common as internal casts, and from their greater size and difference in shape almost certainly represent distinct species.

An important paper, and the earliest one dealing with the internal structure of the common British form of *Trigonocarpus*, is that by Hooker and Binney published in 1885². The specimens came from calcareous nodules in the lower part of the Lancashire Coal-field, and the slides are now preserved in the Geological Department of the Natural History Museum and in the Binney Collection at Cambridge. The authors give a good general account of the organization of the seed, as well as a short account of the relation of the petrified specimens to the common casts. The latter are described as being merely casts of the cavity of the seed, i.e. of the cavity within the hard integument. The two layers forming the coat of the seed are distinguished, and the microscopic structure of each described in some detail.

The rounded (basal) end of the seed is described as being surrounded by an annular ridge, an outgrowth of the harder, inner, layer of the testa, whilst at the other end of the seed the integuments are prolonged as a conical cylindrical or trigonous beak traversed by a narrow canal. The base of this micropylar beak is said to be surrounded, in some cases, by an annular ridge, but from our own observations of the original slides and many others of the seed, we are led to think that this appearance may

¹ Lindley and Hutton ('31-'37).

² Hooker and Binney ('55).

be explained as a result of obliquity of the plane of section, which will produce a deceptive appearance of an annular ridge surrounding the upper part of the seed, as will be more fully explained in a later part of this paper.

Some of the Hooker and Binney slides show the tracheal elements of the nucellus in a well-preserved condition, and these are described and figured in their paper. All the Hooker and Binney slides are longitudinal sections.

The next description of the structure of *Trigonocarpus* was by Williamson in 1877¹, under the name of *Trigonocarpon olivaeforme*. He described and figured a considerable number of vertical and transverse sections of good specimens from the Oldham deposits, at about the same geological horizon as that from which Mr. Binney obtained his examples. The specimens were cut into series of many longitudinal and transverse slices which are figured in natural size. The most instructive of these is a series of transverse sections (see Williamson's paper, Figs. 100-8), which start from the lower portion of the micropylar tube, and traverse successively lower zones of the seed, and which were very useful for comparison with the longitudinal sections which had previously been figured by Hooker and Binney. With the aid of these transverse sections, Williamson gave the first clear explanation of the origin of the ordinary triangular internal casts. He also described in detail the microscopic structure of the inner hard layer of the seed-coat which he calls the endotesta (=our sclerotesta) and gives a good figure.

In 1900 Mr. George Wild published a paper: 'On New and Interesting Features in *Trigonocarpon olivaeforme*²' from observations based on a number of new slides which have since come into Dr. Scott's possession, and some of which have been made use of in the preparation of our paper. From a study of thirteen consecutive transverse sections, Wild was able to show (1) that the micropylar beak was very much longer than had previously been suspected, being nearly or quite equal in length to the body of the 'fruit' itself; (2) that the micropylar beak retains its characteristic triangular cavity nearly up to the apex, and (3) that the long micropyle was apparently winged, the soft (outer) layer of the testa being developed in a flattened form on both sides of the central harder tissue. This interesting feature will be discussed later on in this paper.

Wild also emphasized the fact of the frequent association of *Trigonocarpus* with *Myeloxylon*, which is now known to be the petiole of *Medullosa*. The block from which Wild's slides were cut abounds in petioles, roots and other parts belonging to *Medullosa*, and most of the other preparations which we have seen agree in this respect. In Wild's slides the limiting layers of the soft testa of the seed are often well preserved, and Wild pointed out the close similarity in structure between these and the outer

¹ Williamson ('77).

² Wild ('00).

tissues of the petiole of *Medullosa anglica*¹ as further evidence of the probable relationship of *Medullosa* and *Trigonocarpus*. As we shall show later on in this paper, the similarity is possibly not quite as close as Wild supposed.

The principal object of the present paper is to present the results of a detailed examination of a large number of sections of the common form of *Trigonocarpus* (*T. Parkinsoni*). Many of the sections and specimens are in Dr. Scott's collection, and others have been borrowed from various sources including the British Museum (Natural History), the Manchester Museum, the Newcastle Museum, the Cambridge University Collection, and that at University College, London. For facilities to examine these and other specimens we are indebted to Mr. E. A. Newell Arber, F.G.S., Mr. W. E. Hoyle, D.Sc., Prof. F. W. Oliver, F.R.S., Prof. M. C. Potter, F.L.S., Prof. A. C. Seward, F.R.S., and Dr. A. S. Woodward, F.R.S.

After describing the common form we shall briefly describe a new species obtained from a roof-nodule at Shore-Littleborough, Lancashire. The slides have been submitted to us for examination by Prof. F. W. Oliver, F.R.S., after whom we have named it *Trigonocarpus Oliveri*. A short account will then be given of some features of interest in connexion with the casts and impressions, and finally a second part of the paper will be devoted to a discussion of the general bearing of our work and the probable affinities of the seed.

III. TRIGONOCARPUS PARKINSONI, BRONGN.

General characters of the seed.

The seed as ordinarily preserved in the petrified condition is large, and of an oval form which is well shown in the longitudinal sections figured by Hooker and Binney² and by Williamson³. The general oval shape of the body of this seed as seen in the longitudinal sections is very characteristic, and different from that of the new species *Trigonocarpus Oliveri* (Pl. XIII, Fig. 19). The greatest width is about half-way up the body of the seed, i. e. of the rounded part excluding the micropylar beak. The transverse sections across the body of the seed show the three prominent ridges on which the generic name is based (see Pl. XI, Fig. 5). There is but little variation in size among the seeds which we have examined, and all appear to be in about the same stage of development. Some of the largest specimens which we have examined have a maximum diameter across the body of the seed (measuring to the outer margin of the hard testa only) of about 1.6 cm. The usual transverse diameter is less than this, about 1.3–1.4 cm. The length of the body of the seed, without the micropylar beak, is usually 2–2.5 cm.

¹ Scott ('99).

² Hooker and Binney ('55).

³ Williamson ('77).

In many Palaeozoic seeds with somewhat Cycadean organization, the micropylar region is elongated into a beak-like structure. Ordinary longitudinal sections of *Trigonocarpus Parkinsoni* commonly exhibit some trace of the micropylar beak, but it is rarely, if ever, preserved throughout its length. In many of the impressions, such as those from Newcastle figured in this paper (Pl. XII, Figs. 16, 17, and Pl. XIII, Fig. 18), the beak is about equal in length to the body of the seed, but as the sections show that the beak at the top was very slender and devoid of hard tissue, it is probable that part of it has been lost. In an impression of *Trigonocarpus Parkinsoni* figured in a paper by one of us¹ the long micropylar tube is quite double the length of the body of the seed, but this may possibly represent a distinct species from those described in this paper. In longitudinal sections of the petrified seeds, the micropylar beak is generally quite short, probably owing in some cases to the slightly oblique character of the section. In many cases it seems probable that the greater part of this elongated structure was broken off or had decayed prior to fossilization, when the seeds formed part of the medley of vegetable débris of which the coal-balls are composed.

Taking the micropylar beak into account, the total length of a full-sized seed must have been at least 4–5 cm., and may have been greater than this.

There is some evidence that the seed was attached to its parent axis by means of a stalk (see Pl. XII, Fig. 12).

A common feature of many of these old seeds is the possession of a thick two-layered testa, of which the outer thinner-walled zone or *sarcotesta* is always partly or entirely destroyed. The inner layer, which we shall describe as the *sclerotesta* (=Williamson's endotesta), consists of thick-walled elements, many cells in thickness, and all filled with dark contents. The sclerotesta bears three prominent ridges on its outer surface (Pl. XI, Fig. 5, *s'. t'.*), with corresponding furrows on the inner side marking the position of the three sutures, along which the testa may have split open when the seed was ripe. In each space between two main or principal ridges, are two, or more commonly three, less prominent elevations which we shall describe as secondary ridges (Pl. XI, Fig. 5, *s. t.*), so that the whole number of longitudinal ridges down the body of the seed is usually twelve. The ridges along the body of the seed undergo changes in number, and in the relative prominence of the principal and secondary ridges when traced upwards into the micropylar region, as will be described in detail later on in this paper. The degree of prominence of the various ridges is subject to considerable variation, even in the body of the seed; in some specimens the secondary ridges are scarcely visible, and the sclerotesta consequently becomes only three-ridged.

¹ Scott ('05), (1) Fig. 33, p. 146.

The sclerotesta is in many cases the outermost tissue preserved, but in good specimens this is succeeded on the outside by a delicate, thinner-walled tissue, the sarcotesta (Pl. XI, Fig. 5, *sa*). This layer is never preserved in its entirety, owing to its weak construction and to its position on the outside of the seed, though parts of it may be perfect. Owing to the more or less collapsed condition of the sarcotesta, it is impossible to make an accurate estimate of its total thickness in the natural state, but it must certainly have exceeded 2 mm., and was probably considerably thicker than this. The sarcotesta is bounded on the exterior by the well-differentiated limiting layers to which Mr. Wild first directed attention¹, and traces of which are found in most of the best slides (see Pl. XI, Figs. 1, 3, 5, 6, 7, 8, *l*, Pl. XII, Fig. 11, *h*. and *e*., and Pl. XIV, Fig. 23).

The two layers of the testa, when traced upwards, are continued into, and form the walls of, the long micropylar beak to which we have already drawn attention.

The sclerotesta of the micropylar beak is, in its lower part, more or less triangular in transverse section (Pl. XI, Fig. 7, *s. t.*), and throughout the greater part of its length the beak possesses a triangular central tube or micropylar canal. Outside the sclerotesta of the beak is a great development of the sarcotesta, appearing, as seen in the transverse sections, as a wide flat wing on either side of the micropyle (see Pl. XI, Figs. 7, 8, and Pl. XII, Figs. 9, 10). The 'wing' is bounded externally by the usual limiting layers. The question as to how far the flattened, wing-like form is natural, and how far it is caused by loss of the internal tissue of the sarcotesta and flattening by pressure is difficult to answer, but will be discussed later in this paper. Within the testa of the body of the seed, and usually separated from it by a space, is the nucellus (Pl. XI, Fig. 5, *n*.). Longitudinal sections show the chalazal attachment of the nucellus at the base of the seed (Pl. XII, Fig. 12, *p*.). Above the chalazal attachment the nucellus appears to have been free from the integument, agreeing in this respect with *Stephanospermum*² and some other Palaeozoic seeds, and differing from the modern Cycads, in which only a comparatively small upper portion of the nucellus is free. This view of the relation of nucellus and integument has already been suggested by Professor F. W. Oliver for a French form, *Trigonocarpus pusillus*³. At the micropylar end of the nucellus is the pollen-chamber, long ago indicated in some of Hooker and Binney's figures, and described and more fully illustrated by Williamson. The pollen-chamber (Pl. XII, Fig. 13, *p. c.*) forms a wide dome 2.5–3 mm. in diameter at the base, and was provided at the top with a narrow beak or canal, *be.* not more than 300 μ in diameter (see also Pl. XII, Fig. 14). In the section figured the pollen-chamber beak is barely half a millimetre in length, but presumably it extended much farther in the natural condition.

¹ Wild ('00).

² Oliver ('04) (1), p. 368.

³ Oliver ('04) (2), p. 99.

No pollen-grains are present in the pollen-chamber of any of the specimens which we have examined.

Within the nucellus, and separated from it by a space, is the megaspore membrane (Pl. XI, Fig. 5, *m.*), which in all our slides is preserved merely as a line without visible structure. No prothallium or archegonia are preserved.

The vascular supply to the seed consists of two sets of bundles, which are given off at different levels from the main bundle. The supply strand which enters the base of the seed, while still at a considerable distance below the base of the nucellus, gives off a number of bundles (probably six) which traverse the sarcotesta of the seed, lying opposite to some of the smaller (secondary) ridges of the sclerotesta. These sarcotestal bundles are embedded in the inner denser tissue of the sarcotesta, and were evidently complete bundles with phloem as well as xylem, although the former has not been preserved. From the best preserved examples it appears probable that the xylem was of mesarch structure, the smaller, protoxylem elements occupying an internal position.

The second vascular system of the seed runs in the nucellus and is rather complex in its arrangement. It springs from the upper end of the main bundle which spreads out in the lower part of the seed, and forms what appears to be a practically continuous sheath of tracheides, comparable with the tracheal mantle of a *Stephanospermum*¹. Transverse sections across the central part of the body of the seed show that the tracheides range themselves in more or less definite and crowded longitudinal strands, which are connected by transverse anastomoses running in a tangential direction. The nucellar vascular system has been traced through the whole length of the nucellus almost to the base of the pollen-chamber, and indications of possible tracheides have been detected even in the beak of the pollen-chamber itself.

The Testa.

The Outer Coat or Sarcotesta. The outer thin-walled layer of the seed-coat is usually either destroyed altogether, or is represented by only a few layers of cells, immediately external to the dark-coloured inner layer or sclerotesta. Externally the cells representing the sarcotesta usually have no definite limiting layer, while internally the junction with the sclerotesta is a sharp one, especially in transverse sections across the body of the seed. In good specimens, however, the sarcotesta is better preserved, and is then found to be a tissue of considerable extent, limited externally by well-differentiated epidermal and hypodermal layers (Pl. XI, Figs. 5, 6). The sarcotesta is never completely preserved, but is always more or less collapsed and disorganized, so that it is not possible to estimate its original

¹ Oliver ('04) (1), p. 363.

thickness with certainty. In the transverse section of the central part of the body of the seed shown in Pl. XI, Fig. 5, the sarcotesta *sa* at its thickest part measures about 2 mm., and there is clear evidence that the outer portion, with the exception of the limiting layers *l*, has been destroyed, so that the total thickness would have been considerably more than this, at least in the spaces between the ridges of the sclerotesta where it was probably thickest.

In some cases, as in the transverse section figured (Pl. XI, Fig. 5), the external boundary-line of the sarcotesta follows fairly closely the contour of the sclerotesta within, but we are inclined to think that this correspondence is not natural, but is merely a result of more or less desiccation and compression prior to fossilization, and that the transverse section of the whole seed may have been circular. The correspondence in outline between the sarcotesta and sclerotesta is seen in several of Williamson's original slides figured in his paper, and his remark that: 'though the external outline of the sarcotesta is less sharply defined than that of the endotesta [=our sclerotesta], we yet see that to a considerable extent the former follows the latter, the differences seen in the sections being due to shrinkage from some collapse in the soft parenchymatous cells of the outermost layer,'¹ seems to imply that Williamson thought the correspondence was a natural one.

The sarcotesta appears to have been thinnest around the body of the seed, and to have increased in thickness above and below. This is shown in some of the sections figured in this paper. Pl. XI, Fig. 3, is a transverse section across the base of the same seed as that shown in Pl. XI, Fig. 5. The central mass of dark sclerotic tissue, *s. t.*, continuous with the sclerotesta of the body of the seed, is surrounded by a well-developed sarcotestal tissue, which in places is quite 3 mm. thick, and in its natural condition must have been much thicker than this, as a considerable loss of tissue is indicated by the remains of disorganized cells, as well as by the doubling in of the limiting layers of the sarcotesta, *l*. Pl. XI, Fig. 1, is another transverse section of the same seed, but taken still lower: the inner part of the sarcotesta is preserved, but great loss of tissue is shown by the limiting layers which are in places doubled in and repeated four or five times.

Passing to the upper end of the seed, a transverse section across the lower part of the micropylar beak is shown in Pl. XI, Fig. 7, and it will be seen that the sarcotesta *sa* is here quite well-developed, as indeed it continues to be right up to the end of this organ.

The sarcotesta consists typically of thin-walled parenchyma without special peculiarities. The inner portion is compact and consists of cells without visible inter-cellular spaces. In the body of the seed, these thin-

¹ Williamson ('77), p. 250.

walled cells abut quite suddenly on the dark-coloured thicker-walled elements of the sclerotesta (Pl. XI, Fig. 5). The outer portion of the sarcotesta appears to have been lacunar, which fact helps to account for the almost complete destruction of this tissue. The lacunar zone is occasionally preserved to a slight extent in the bays between the longitudinal ridges of the sclerotesta. Pl. XIV, Fig. 24, shows the lacunar sarcotesta in one of Williamson's original slides, and a similar tissue can be made out in several sections belonging to the same series.

It has been stated above that the sarcotesta is sharply delimited from the sclerotesta; the sudden transition is well seen in sections passing across the central part of the body of the seed, such as that shown in Pl. XI, Fig. 5. A section showing the details of the structure of the inner sarcotesta and outer sclerotesta, such as that figured in Williamson's paper¹, shows that the sharp demarcation is not simply the result of thickening of the walls of the elements of the sclerotesta, for the radially elongated cells of the outer part of the sclerotesta abut suddenly on the rounded cells of the sarcotesta, so that there is seen to be a difference in the form of the elements as well as in the thickening of the walls.

In transverse sections passing across the lower part of the seed, such as are shown in Pl. XI, Figs. 1 and 3, the transition from sclerotesta to sarcotesta is much more gradual. In Fig. 1 the sclerotic tissue is seen surrounding a triangular space *b* enclosing the incoming vascular bundle: this dense tissue passes over quite gradually into the surrounding thin-walled sarcotesta. In Fig. 3, which is cut at a somewhat higher level across the same seed, the outermost sarcotestal cells are seen to be quite thin-walled, but nearer to the central sclerotesta *s. t.* the walls become thicker and the transition is more or less gradual.

Sections across the upper part of the seed also show a more or less gradual passage between the two layers, as will be seen by examining Pl. XI, Figs. 7 and 8, and Pl. XII, Fig. 9, which are transverse sections cut at successively higher levels across the micropyle.

The absence in certain regions of sharp demarcation between the two layers of the testa is of interest in the comparison of *Trigonocarpus* with the seeds of *Cycas* and other recent forms of similar organization. Miss Stopes has shown that it is usually difficult to draw a boundary line between the outer flesh and the stone layers in a modern Cycadean seed, and she insists that the stone layers, or at least the outer part of them, belong morphologically to the outer flesh and so form one layer, not two². We shall leave the further discussion of the bearing of this question of the single or double nature of the Cycadean integument, and the attempt to explain the complicated integument of a Cycad ovule as the morphological equivalent of a *Lagenostoma* with the cupule and integument fused together,

¹ Williamson ('77), Pl. 14, Fig. 112.

² Stopes ('05), p. 562.

to the concluding part of this paper. The relation of the sarcotesta and sclerotesta in *Trigonocarpus* is such as to indicate that they are morphologically one integument, just as is the case in the structurally very similar layers of a modern Cycad seed.

Other Palaeozoic seeds also agree in this respect. *Polylophospermum stephanense* (Brongn.), a radiospermic seed from Grand' Croix which agrees with *Trigonocarpus* in important characters, has been shown by Professor Oliver to exhibit gradual transition from the hard sclerotesta to the softer enveloping sarcotesta¹.

The sarcotesta is bounded externally by the definite limiting layers to which Wild first directed attention (p. 95). The figure given by Wild² shows an apparent epidermis consisting of closely set radially elongated dark-coloured cells forming a kind of palisade tissue, usually only one, but sometimes two, cells in thickness. These palisade cells are covered by what is described as a thin cuticle. From the resemblance of this tissue in *Trigonocarpus* to the limiting layer of the petioles of *Medullosa anglica*, in which the epidermis has a well-marked palisade form³, as well as from the constant association of these two forms, Wild was led to believe that *Trigonocarpus* is probably the seed of *Medullosa*. Re-examination of some of Wild's slides shows that some of them exhibit traces of a layer of small cells outside the palisade cells, and forming a true epidermis to them. The epidermal cells are better seen in some other slides, especially in some of those obtained from the Manchester Museum. The limiting layers of the sarcotesta is shown in Pl. XIV, Fig. 23, drawn from one of the Manchester slides, and magnified about 40 times. The epidermis is shown at *e*, and the hypodermis of palisade-like cells at *h*. The epidermal cells are quite small and apparently empty; their outer walls are thickened to form a continuous cuticle which is frequently preserved as a detached line, when the radial walls of the epidermal cells are wholly destroyed. The detached cuticle of the epidermis is visible in parts of Pl. XI, Fig. 1, as well as in some of the other photographs in Plates XI and XII. Occasionally the epidermal cells are visible in surface view as a simple layer of small isodiametric cells. The hypodermis consists of much larger cells usually more or less radially elongated and sometimes very irregular in shape (Pl. XIV, Fig. 23); sometimes only one elongated cell appears, elsewhere the place of a single elongated cell is taken by a row of two or three short cells. All the cells of the hypodermis agree in being filled with dark-coloured contents which give to the layer as a whole a very characteristic appearance much resembling that of the outer tissues of a *Medullosa* petiole. Re-examination of the *Medullosa anglica* slides has failed to detect any trace of an epidermis outside the rarely preserved palisade tissue which apparently includes the real epidermis of this form. At the same time, in

¹ Oliver ('04) (1), p. 101.

² Wild ('00), Fig. 14.

³ Scott ('99), Pl. II, Fig. 13.

view of the strong probability, on other grounds, of a relationship between *Medullosa* and *Trigonocarpus*, it is not impossible that a small-celled epidermis may be subsequently discovered in the former genus. In the meantime, the apparent absence of this layer in *Medullosa* renders Wild's comparison less close than he thought.

As already briefly described, the outer series of vascular bundles of the seed traverse the sarcotesta and they are occasionally seen in transverse sections of the seed, although, owing to the usual non-preservation of anything more than a few layers of the inner sarcotesta, such sections are quite rare. The bundles spring from the main supply-strand at a considerable distance below the chalaza, and bending outwards traverse the sarcotesta of the body of the seed, running opposite to the secondary ridges of the sclerotesta. The position of one of the sarcotestal bundles is indicated at *s. b.* in Pl. XI, Fig. 5. The bundle itself cannot be distinguished in this photograph, but is shown more highly magnified in Pl. XIV, Fig. 28. Traces of sarcotestal bundles can be seen in other slides, and in all cases they appear opposite to the secondary, never to the principal, ridges of the sclerotesta. The total number of sarcotestal bundles would thus have been nine, or perhaps only six, in ordinary specimens, such as that shown in Pl. XI, Fig. 5. It seems probable that the number was really six. In no single section are sarcotestal bundles seen opposite to all the secondary ridges of the sclerotesta, and in all the sections in which the bundles are visible, they appear invariably opposite to the two outer of each set of three secondary ridges, never to the central one. The central secondary ridge frequently differs from the lateral ones in being more rounded, and, moreover, as we shall see later, it is the first ridge to disappear when traced up to the upper end of the seed. It seems probable that it also differs in having no sarcotestal bundle opposite to it. That there are six, not nine, sarcotestal bundles is also favoured by examination of the section across the base of the seed shown in Pl. XI, Fig. 3. This is an approximately transverse section cut some distance below the chalaza; careful examination of the original section shows six bundles, *s. b.*, embedded in the compact sarcotesta, and doubtless these are the same bundles that afterwards appear opposite to some of the secondary ridges of the sclerotesta in the body of the seed. The central mass of sclerotic tissue which is seen in this section (Pl. XI, Fig. 3, *s. t.*) is produced on one side into a projection, which in all probability represents the lower end of one of the principal longitudinal ridges of the sclerotesta, cut through owing to slight obliquity of the plane of section. No sarcotestal bundle can be seen opposite to this ridge, although two occur symmetrically disposed on either side of it, so that this section helps to confirm the conclusion as to the number and position of the bundles arrived at above.

An individual sarcotestal bundle is shown, magnified about 200 times, in Pl. XIV, Fig. 28. The position of this bundle is shown at *s. b.* in Pl. XI, Fig. 5. These bundles are quite small; the total radial diameter of the one figured cannot have been greater than .15 mm., and the diameter of the largest tracheide about .025 mm. The bundle is only imperfectly preserved, and no trace of phloem elements are visible. The tracheides *t* are nearly in contact with the ordinary parenchyma of the sarcotesta *sa* on the inner side of the bundle, while on the outer side there is a space which is partly occupied by decomposed tissue *d. t.*, which probably represents the original phloem elements. The bundle was therefore probably a collateral one with external phloem. There is some evidence that the xylem was mesarch in structure, as the smaller elements, presumably protoxylem tracheides, occupy a more or less central position. This conclusion is also favoured by the examination of longitudinal sections, as will be explained later (p. 115). This bundle is separated from the sclerotesta of the secondary ridge, to which it runs parallel, by sarcotestal tissue about .3 mm. in thickness. The longitudinal sections are not sufficiently good to enable us to trace the sarcotestal bundles upwards to their termination. The transverse section shown in Pl. XI, Fig. 5, cannot be far removed from the middle of the body of the seed, and Pl. XI, Figs. 6–8, and Pl. XII, Figs. 9, 10, are cut at successively higher levels. In all these sections the inner sarcotesta is fairly well preserved, and it seems likely that if vascular bundles were present they would have been preserved also. No trace of such bundles is visible, so that it seems probable that they did not extend farther up than the body of the seed.

As *Trigonocarpus Parkinsoni* is the first of the Cycad-like seeds of the Carboniferous Period, the *Stephanospermeae* of Professor Oliver, in which it has been possible to give a fairly complete account of the sarcotesta, it will be useful to compare this layer with what is known of the corresponding tissue of other related fossil seeds, and with the 'outer flesh' of recent Cycadean seeds.

The possession of an outer soft layer to the seed is believed to be a common character of all the seeds which constitute Professor Oliver's *Stephanospermum*-Group of *Radiosperms*, although in the type genus, *Stephanospermum*, evidence for its existence, other than from analogy, is absent¹. In most of the genera included in this group, *Aetheotesta*, *Trigonocarpus*, *Tripterospermum*, *Polylophospermum*, *Codonospermum*, &c., an outer fleshy, or sometimes fibrous, sarcotesta has been proved to exist, although it is usually very badly preserved.

Trigonocarpus pusillus, Brongn., a small representative of the genus from the French deposits, recently re-described by Professor Oliver, possesses a sarcotesta of two or three layers of thin-walled, iso-diametric,

¹ Oliver ('04) (1).

parenchymatous cells which probably represent but a portion of a more extensive tissue¹.

The detailed structure of the seeds of the Cycads has been recently described by Miss Stopes². The 'outer flesh' or sarcotesta, which is universally present, is composed of parenchyma with numerous gum canals and tannin sacs and is bounded externally by an epidermis of radially elongated cells. The sarcotesta is traversed by a series of vascular bundles which spring from the central supply bundle entering at the base of the seed. In position these bundles lie opposite to the longitudinal ridges of the underlying 'stone' or sclerotesta as has been described above in *Trigonocarpus*. In the Cycads the number of sarcotestal bundles always corresponds exactly with the number of ridges, so that in *Macrozamia spiralis* where the stone is provided with twelve well-marked ribs there are also twelve bundles, while the bilateral seed of a *Cycas* which possesses only two ridges has only two bundles, although each bundle contains two vascular strands in some species. As described above, in *Trigonocarpus* it is probable that the sarcotestal bundles occur opposite to certain of the longitudinal ridges only, not to all.

Returning to the Cycads the individual sarcotestal bundles are described as collateral with mesarch xylem. In some forms, such as *Cycas circinalis*, the bundles are of a simple type with external phloem and internal xylem provided with a considerable development of transfusion-tracheides, the whole bundle being surrounded by a sheath composed of peculiar cells provided with reticulated lignified thickenings³.

In some other forms the sarcotestal strands are more complex in structure although their position remains the same. In *Cycas media* each strand consists of two collateral bundles with their phloems directed towards one another, so that the outer bundle of the two has, of course, reversed orientation. The xylem of each bundle is mesarch, and the inner one of the two possesses a considerable development of transfusion elements⁴. In *Cycas revoluta* the bundles run in pairs through the outer flesh.

In yet other species the structure becomes still more complex, for in *Cycas Beddomii* the whole strand, consisting of two bundles embedded in fine conjunctive tissue containing many transfusion elements, is surrounded by a well-differentiated sheath composed of the peculiar cells mentioned above in *Cycas circinalis*⁵.

As far as can be judged from the transverse sections of imperfectly preserved sarcotestal bundles around the body of the seed such as that shown in Pl. XIV, Fig. 28, *Trigonocarpus Parkinsoni* conforms to the simplest of these types, that of *Cycas circinalis*, but owing to the imperfect

¹ Oliver ('04) (2), p. 98.

² Stopes ('04).

³ Stopes ('04), p. 440.

⁴ Stopes ('04), p. 442.

⁵ Stopes ('04), p. 445, Fig. 8.

preservation the evidence is not conclusive. More perfectly preserved sarcotestal bundles at the base of the seed afford evidence of a more complex structure which may be compared with that of *Cycas Beddomii*, as will be explained in detail in our description of the lower end of the seed (p. 115).

The Sclerotesta. We may now consider some of the details of the hard layer of the testa, the sclerotesta, which lies within the sclerotesta. The structure of the sclerotesta has been previously described in some detail by Hooker and Binney¹, and later by Williamson², and as far as internal structure is concerned we have but little to add to their descriptions. This hard layer forms a complete investment to the seed excepting only at the upper end of the long micropylar beak, where it is, of course, perforated by the opening of the micropylar canal. Its thickness, when measured between the ridges of the body of the seed, in such a section as that shown in Pl. XI, Fig. 5, *s. t.*, is 1-1.5 mm. Most longitudinal sections show a thickening of the sclerotesta as it is traced from the chalaza upwards to the base of the micropylar beak. This may also be seen in some of the transverse sections, as by comparing Pl. XI, Fig. 5, and Pl. XI, Fig. 7, the former cut across the central part of the body of the seed, and the latter across the lower part of the micropylar beak, although as the two sections are not cut from the same seed the comparison as to thickness must not be carried too far. Comparison may also be made of Pl. XII, Fig. 12 and Fig. 13, which are longitudinal sections of the lower part, and of the upper part respectively, of two seeds; in Fig. 12 the thickness of the sclerotesta is at its thinnest part about .8 mm., while in Fig. 13 the maximum thickness is 2 mm. The sclerotesta of the lower part of the same seed as that figured in Pl. XII, Fig. 13, has a thickness of only 1 mm.

As already briefly described the sclerotesta has a very characteristic form when seen in transverse sections. The normal number of ribs projecting on the outer side is probably always twelve in sections cut across the body of the seed, such as Pl. XI, Fig. 5. The twelve ribs are usually easily distinguishable into two sets, the principal ribs (Pl. XI, Fig. 5, *s'. t'.*) always three in number, and the smaller or secondary ridges (Pl. XI, Fig. 5, *s. t.*) usually nine in number. The degree of prominence of the principal ridges is subject to considerable variation in different seeds as well as at different levels of the same seed. In most specimens the principal ridges are readily distinguished from the secondary ones by their greater prominence as shown in Pl. XI, Figs. 5, 6. In some other seeds the principal ridges are broader and less pointed, and in yet other cases there is only a slight difference in size and shape between these and the secondary ridges.

¹ Hooker and Binney ('55).

² Williamson ('77), p. 252.

In many transverse sections one or more of the principal ridges shows a central crack as though the seed naturally split open along these sutures (see Pl. XI, Figs. 5, 6). This splitting is never seen in relation to the secondary ribs.

The principal ridges when traced from the centre of the body of the seed upwards to and along the micropylar beak gradually become less prominent and ultimately disappear. This change will be seen by examining the series of transverse sections represented in Pl. XI, Figs. 5-8. Fig. 5 is cut near the centre of the body of the seed and exhibits what may be called the normal arrangement, the principal ridges being easily distinguished by their size. In Fig. 6, which is cut at a somewhat higher level than Fig. 5, these ridges are still sufficiently large to be readily identified even without the characteristic splitting which is well shown in this slide. In Fig. 7, which is cut across the lower part of the micropylar beak the principal ridges of the body of the seed appear opposite to the angles of the triangular micropylar tube and although still large, some of the secondary ridges have become equal to them. Lastly, in Fig. 8, which is cut higher up the micropylar beak, the principal ridges lying opposite to the points of the micropylar canal have practically disappeared altogether.

Passing to the secondary ridges, these are also found to vary considerably in different specimens and at different levels. In a typical example, a section across the central part of the body of the seed, such as Pl. XI, Fig. 5, shows the three secondary ridges, *s. t.*, lying between two principal ribs and about equally developed. In some cases, however, the median ridge of each set of three is so slightly developed as to be practically absent, so reducing the total number of ridges (principal and secondary) to nine, while in yet other examples all the secondary ridges are ill-developed so that only the three principal ridges are at all conspicuous. Changes also take place in the secondary ridges when they are traced upwards as will be seen by again examining the series of transverse sections at various levels (Pl. XI, Figs. 5-8). In Fig. 5 all the secondary ridges are about equally developed; in Fig. 6 which is cut at a higher level the central ridge of each set of three has 'flattened out' so that it has nearly disappeared while the two lateral secondary ridges are equally prominent; in the still higher sections while the lateral secondary ridges still remain conspicuous the central one is unrepresented. Hence the most persistent longitudinal ridges appear to be the lateral secondary ribs, or those to which the sarcotestal bundles are probably opposite, as we have previously shown.

A knowledge of these regional variations in the ridges of the sclerotesta is of some importance in the attempt to interpret the structures seen in casts, as will be explained later.

On the inner side of the sclerotesta there are three furrows corresponding in position with the three principal external ridges. These furrows vary in depth in different parts of the seed, as is well seen in transverse sections. In sections cut across the lower part of the body of the seed, the grooves are very slightly developed, and are sometimes absent altogether, while in sections taken at successively higher levels, the furrows become more and more pronounced. Comparison of Pl. XI, Figs. 5–8, will serve to demonstrate this fact, as also that the points of the triangular micropylar tube are the upward prolongations of the three shallow grooves seen in sections across the body of the seed such as shown in Fig. 5. The three grooves on the inner side of the sclerotesta, of course account for the three ridges which are shown on the surface of the common internal casts of the cavity of the seed.

With regard to the minute structure of the sclerotesta, we have little to add to former descriptions. In good thin sections the sclerotesta is readily distinguishable into two regions, an inner zone (Pl. XI, Fig. 6, *s. t.*), which is very dark in colour, and consists mainly of elements which are elongated in the vertical direction, and an outer zone (Fig. 6, *s'. t'.*) in which, especially in sections cut across the body of the seed, many of the cells are seen to be elongated in a horizontal radial direction, and so form a kind of outer palisade layer to the sclerotesta. This is best shown, in Fig. 6, in the sclerotesta of the secondary ridges. If the section is a thicker one, the distinction of the sclerotesta into two zones is not so clearly seen. In more detail the structure of the sclerotesta of the central part of the body of the seed is as follows. Starting from within, and considering the region between the longitudinal ridges, we have first about four to six rows of small elongated elements running in the longitudinal direction, and filled with the dark-coloured material which is characteristic of all the elements of the sclerotesta. These cells are thick-walled and fairly uniform in size, many times longer than broad, and of prosenchymatous form. Hooker and Binney describe these cells as forming a lining of long slender tubes to the whole body of the fruit (i. e. seed), and assert that among these cells some may be found marked with annular or spiral bands¹. Williamson states that traces of the same structure appear in his sections². We have examined a considerable number of longitudinal sections of *Trigonocarpus*, including the original Williamson and Hooker and Binney slides, but we have been unable to confirm this observation.

Outside these longitudinally running cells are seen some rows of elongated elements which run in a horizontal direction around the body of the seed, and outside these is a zone in which the cells appear to meander irregularly, the elements passing across one another in all directions. In a tangential section of this part of the testa³, the elongated cells are seen

¹ Hooker and Binney ('55).

² Williamson ('77), p. 252.

³ Slide 944 S.

running in bundles which interweave with one another almost like basket-work. These cells are followed by the layer of radially elongated elements or palisade layer which usually constitutes the greater part of the thickness of the sclerotesta, and forms its outermost part. The actual proportion in thickness of the palisade layer to the rest of the sclerotesta is subject to considerable variation in different seeds. Many of the details of the structure of the sclerotesta are shown in Williamson's figures (Williamson, 1877, Pl. 14, Figs. 112, &c.). At the principal ridges the structure is somewhat different from that described above, as the majority of the cells follow a mainly longitudinal course, so that they are cut across in transverse sections of the seed. Many slides show dark-coloured elongated cells, passing radially through the centre of each principal ridge, and it is along these elements that the splitting which is so frequently seen takes place.

The general plan of structure as given above, appears to have been the usual one in the sclerotesta of the Palaeozoic Cycad-like seeds, and a similar structure has been described in detail by Prof. Oliver in *Stephanospermum akenioides*, Brongn., and *S. caryoides*, Oliver¹. It also appears to agree in a general way with the structure of the stony layers of the seed of a modern Cycad. Miss Stopes states that: 'It is very clearly marked in many Cycads that the stone has at least two layers, an inner one of mainly vertically running stone cells, as in the integument of *Lagenostoma ovoides*, and an outer one of mainly horizontally running stone cells.'² This layer is surrounded by the usually undifferentiated cells of the outer flesh. In some Cycads the structure of the outer layers of the testa is much more complex, as in *Cycas Beddomii*, described by Miss Stopes³. In this form the stony layer (sclerotesta) and outer flesh exhibit the following details of structure. The innermost part of the stone is formed of layers of vertically elongated sclerotic cells comparable with the inner zone of *Trigonocarpus Parkinsoni* as described above. These are succeeded on the outer side by a number of layers of elongated sclerotic cells which follow a horizontal direction and run circularly round the seed. A similar zone is found in *Trigonocarpus*. Next follows a thick layer of radially elongated horizontal cells, which are described as belonging to the outer fleshy layer. These cells have somewhat thickened slightly lignified walls, and may be compared in a general way with the outer layer or palisade-layer of the sclerotesta of *Trigonocarpus*. The radially elongated cells pass externally into others with reticulately thickened walls, and these again into the ordinary tissue of the outer flesh, consisting of large parenchymatous cells with pitted cellulose walls similar to the ordinary sarcotestal cells of *Trigonocarpus*. The reticulately thickened tracheide-like cells, which occur between the radially elongated inner cells and the ordinary parenchymatous

¹ Oliver ('04) (1), p. 364 and p. 373.

² Stopes ('05), p. 562.

³ Stopes ('04), p. 444 and Fig. 7.

outer cells of the sarcotesta in *Cycas Beddomii* are described as having a water-storing function, and their presence is perhaps to be correlated with the dry habitat of this species¹. No similar cells are found in *Trigonocarpus*. Apart from this difference it will be seen that in the details of structure of the testa, *Trigonocarpus Parkinsoni* exhibits somewhat close similarity with that of one of the most complicated of modern Cycads.

The Inner Flesh. The next question which may be considered is that of the possible existence of a thin-walled tissue within the sclerotesta, and corresponding in position with the 'inner flesh' of the seed of a Cycad. Such a layer may be called an 'endotesta,' but in view of the use of this term by Williamson and others for the stony layer or sclerotesta of *Trigonocarpus*, we have thought it better to avoid confusion by using the term 'inner flesh.'

In none of our specimens is such a layer preserved in a recognizable condition, excepting just at the base of the body of the seed. In one of our slides², a longitudinal section passing in a slightly tangential direction through the base of the seed, a tissue consisting of parenchymatous cells, is seen lying between the nucellus and the sclerotesta. The only evidence for the existence of an inner flesh higher up in the body of the seed is found in the commonly somewhat irregular and 'unfinished' appearance of the inner boundary of the sclerotesta. This 'unfinished' appearance is particularly noticeable at the upper part of the body of the seed, and the lower part of the micropylar tube. On the whole we think the evidence is sufficient to make it probable that *Trigonocarpus* possessed a continuous inner fleshy layer within the sclerotesta. The reason why the cells of this layer are not more generally preserved, is probably that the cells themselves were of a delicate nature, and also that the hard impermeable coat of the seed prevented the infiltration of the petrifying material before the tissue had undergone disorganization.

An inner fleshy layer probably existed in most of the Palaeozoic seeds of similar organization to *Trigonocarpus*, although it is never found even in a fair state of preservation. Prof. Oliver has described traces of such a tissue in *Stephanospermum caryoides*³, while in *Stephanospermum akenioides* a delicate network of thin-walled cells is sometimes seen lying in the angle between the base of the nucellus and the lining of the sclerotesta⁴, just as in some of our slides of *Trigonocarpus Parkinsoni*.

The very imperfect preservation of this tissue is unfortunate, in view of the great importance of determining its relation to the nucellus within, whether the nucellus stood up freely, separated from the testa throughout the greater part of its length, i. e. from the pollen-chamber to the chalazal

¹ Stopes ('05), p. 445.

³ Oliver ('04) (1), p. 374.

² Slide 941 S.

⁴ Oliver ('04) (1), p. 367.

attachment, as in *Lepidocarpon*, and, according to Prof. Oliver, probably in *Stephanospermum*¹, or whether the relations were as in the modern Cycads, and in *Lagenostoma*, in which the testa and nucellus are adherent excepting right at the top of the seed. A discussion of this question will best be deferred until after the structure of the nucellus has been described, but here we may say that in *Trigonocarpus* as in *Stephanospermum*, the evidence supports the view that the nucellus was free.

The Chalazal End of the Seed.

An account may now be given of some of the details of the structure of the lower part of the seed. Some of the longitudinal sections afford evidence that the seed was attached to the parent plant by means of a stalk. The stalk is shown in Pl. XII, Fig. 12. As shown in the figure, the sarcotesta of the stalk of this specimen has undergone considerable displacement and compression as is made evident by the crushed tissue on the right-hand side of the stalk and the repetition of the limiting tissues of the sarcotesta on the other. The form of the stalk shown in this section is therefore not the natural one, nor is the unsymmetrical position of the stalk with reference to the chalazal attachment above. Other sections show the stalk symmetrically placed. As shown in Pl. XII, Fig. 12, as well as in some other slides, the stalk appears to consist almost entirely of parenchymatous tissue continuous with the inner, denser, zone of the sarcotesta, but this appearance is really due to the fact that the section passes somewhat tangentially, not medianly, through the base of the seed, although, as it passes through the chalazal attachment of the nucellus it cannot be very far from the median plane. Apparently the median plane of the stalk is more closely approached right at the bottom of this section, as here it passes into sclerotic tissue, *s. t.*, which is probably part of the central core of the stalk continuous with the sclerotesta of the body of the seed.

Many of the more nearly median longitudinal sections show the central core of sclerotic tissue of the stalk in the form of a downwardly directed pointed prolongation of the sclerotesta, the shortness of which, in most of the slides, is doubtless due to the slight obliquity of the sections. In one section the sclerotic stalk has a length of about 1.5 mm., and in another slide it is traversed longitudinally by the main supply bundle of the seed. The sclerotic tissue of the stalk probably gradually died out below, the hard core becoming smaller as its tissue was replaced by the thinner-walled cells of the sarcotesta. We have already seen that in this part of the seed the passage from sclerotesta to sarcotesta is a gradual one. Judging from the longitudinal section shown in Pl. XII, Fig. 12, the sclerotic axis of the stalk must have had a length of more than 4 mm., as the sclerotic tissue, *s. t.*,

¹ Oliver ('04) (1), p. 368.

is at about that distance from the base of the sclerotesta of the body of the seed.

Passing to the transverse sections of the base of the seed we have in Pl. XI, Fig. 1, a section which is doubtless cut across the lower part of the stalk, probably about on a level with its lower end, as shown in the longitudinal section, Pl. XII, Fig. 12. In the section shown in Pl. XI, Fig. 1, the whole of the outer portion of the sarcotesta has been destroyed with the exception of the characteristic outer limiting layers, *l.*, which have evidently suffered much displacement by compression from without, as they are, in places, repeated as many as four times. The tissue preserved is mainly composed of thin-walled cells which pass gradually into the sclerotic tissue which surrounds the triangular space, *b.*, containing the entering vascular bundle. No trace of bundles or tracheides can be seen in the sarcotesta of this slide, probably because the section is just below the level at which the sarcotestal bundles are given off from the main bundle. The triangular form of the space in which the main bundle is contained is probably of some significance, especially as this form is much less marked in sections across the upper part of the stalk, such as the one shown in Pl. XI, Figs. 3 and 4. There is evidence from the longitudinal sections that the sarcotestal bundles were given off from the main bundle at a considerable distance below the base of the body of the seed, although, unfortunately, no section shows the actual branching. In the section figured in Pl. XII, Fig. 12, sarcotestal bundles can be seen in the slide at the points marked *s. b.*, *s. b.*, and one of these is figured in detail in Pl. XIV, Fig. 25, which will be described later. From the position of these bundles in the stalk it is clear that they must have arisen some distance below the level at which they are seen in Pl. XII, Fig. 12, so that the junction with the main bundle must have been at least 4 mm. below the base of the nucellus.

It is probable that the section which is shown in Pl. XI, Fig. 1, is cut quite near to the level at which the sarcotestal bundles are given off, and that the triangular form of the space is to be correlated with this fact. The six sarcotestal bundles may have been given off in pairs corresponding in position with the angles of the space, or they may have been only three in number, each afterwards dividing into two. That the section is below rather than above the plane of branching seems evident from the entire absence of sarcotestal bundles, since the preservation of the inner tissues of the testa is so good that they would almost certainly be seen if they had been present.

Pl. XI, Fig. 2, shows the central part of Fig. 1, magnified about 100 times. The xylem of the main supply bundle is preserved (*b.*), and has a width in the longest direction of .28 mm. The surrounding thinner-walled tissue has been entirely destroyed, but presumably it was a similar

parenchyma to that seen surrounding the bundle in the higher section shown in Pl. XI, Fig. 4, *a*.

Pl. XI, Fig. 3, is a transverse section probably cut quite close to the base of the body of the seed, or across the upper part of the stalk, of the same specimen as that illustrated in Figs. 1 and 2. The central core of sclerotic tissue, *s.t.*, continuous with the hard coat of the body of the seed, is well seen, as also the gradual transition of this tissue into the surrounding sarcotesta with the characteristic bounding layers, *l*. The main vascular bundle, *b.*, is just discernible occupying a sub-central position in the sclerotesta, while in the surrounding sarcotesta six bundles, *s.b.*, can be seen. The outer part of the sarcotesta has been destroyed, with the exception of the external layers, *l*, which are pressed in on the more durable tissues.

The central sclerotic tissue is produced on one side, probably owing to the section being somewhat oblique, so that it passes across the lower portion of one of the principal longitudinal ridges of the body of the seed. As before mentioned no sarcotestal bundle is seen opposite to the point of this projection, although two are seen occupying a fairly symmetrical position opposite to its sides. The bundle and surrounding tissues of Pl. XI, Fig. 3, are represented magnified about 100 times in Pl. XI, Fig. 4. The magnification of Figs. 2 and 4 is equal, so that the bundle at the two levels may be directly compared. In Fig. 4 the main supply bundle, *b.*, is shown, and appears to have a diameter of about .14 mm., or is about half the size of the bundle of Fig. 2 cut at the lower level. The larger size of the bundle in Fig. 2 favours the view which has been already expressed, that in this section the sarcotestal bundles had not yet been given off, as the section is below the level of branching.

Returning to the section shown in Fig. 4, no clear evidence of a differentiated phloem surrounding the xylem can be made out, but the bundle is embedded in a comparatively large-celled, apparently parenchymatous tissue, which occupies the space within the core of hard tissue. It will be noticed that the triangular form is still preserved to a certain extent, though it is not as sharply marked as in the lower section (Pl. XI, Fig. 2).

In all probability the main supply bundle was concentric in structure. A definite protoxylem cannot be made out in this transverse section, and, unfortunately, the longitudinal sections which show the main bundle are not sufficiently good to help us in this matter. Miss Stopes has shown that in Cycads: 'The main supply bundle is usually either completely concentric or has a strong tendency in that direction; the bundles given off to the outer flesh are collateral and orientated with the phloem outwards, and with a considerable development of centripetal xylem; the strand continuing to supply the inner system has a strong concentric tendency¹.' In

¹ Stopes ('05), p. 560.

all probability *Trigonocarpus Parkinsoni* agreed with the modern Cycads in all these respects.

After giving off the sarcotestal strands, the main bundle, accompanied by its parenchyma, continues unbranched through the stalk of the seed, until it passes into the nucellus and gives rise to the inner vascular system to be described later. At the bottom of the body of the seed a pad of parenchymatous tissue is frequently seen between the nucellus and the sclerotesta; this tissue is doubtless continuous with the tissue which surrounds the vascular bundle of the stalk. Laterally this tissue may have been continuous with the presumed 'inner flesh,' or it may have narrowed down beyond the limits of the tracheal disk and become continuous with the hypoderm of the nucellus. On analogy with *Stephanospermum*¹ the latter view would appear to be probably the correct one.

In Pl. XII, Fig. 12, the position of some sarcotestal bundles is indicated at *s.b.*, *s.b.*, and in Pl. XIV, Fig. 25, this portion of the seed is shown magnified about eighty times. The tissues are very much disturbed, although the preservation of some of the elements is excellent. Parts of at least two and probably three sarcotestal bundles appear to be represented at *b.*, *b.*, *b.* In places the dark-coloured hypodermal cells of the sarcotesta, *h.*, have been pushed inwards until they are quite close to the bundles. Immediately surrounding the bundle on the right are the remains of a delicate cell-reticulum representing the tissue in which the bundles were embedded. Bounding the space in which the bundles are contained are some of the ordinary cells of the sarcotesta, *sa.*

Scattered about in the fine tissue which separates the bundles are numerous short tracheides or transfusion elements, *s.t.*, which remind one forcibly of the very similar elements contained in the fine conjunctive tissue surrounding the pairs of sarcotestal bundles in *Cycas Beddomii*. In this Cycad the two bundles of the outer flesh are complex in structure. Each is really double, and consists of two complete collateral mesarch bundles orientated with their phloems towards one another. The bundles are surrounded by a considerable development of very fine conjunctive tissue containing numerous transfusion tracheides with thickened walls and fine reticulate or spiral markings, and the whole is enclosed in a common sheath of relatively large cells with reticulately thickened lignified walls (see Miss Stopes' paper, 1904, Fig. 8, p. 445).

In *Trigonocarpus Parkinsoni* the sarcotestal bundles of the body of the seed are always very imperfectly preserved, but as far as the evidence goes a simpler type of bundle, such as is found in *Cycas circinalis*², is indicated, rather than the complex one of *Cycas Beddomii*. In the longitudinal section shown in Pl. XII, Fig. 12, and Pl. XIV, Fig. 25, however, a more complex type of bundle may be represented. Comparing our Pl. XIV, Fig. 25, with

¹ Oliver ('04) (1), p. 367 and Pl. 43, Fig. 21.

² Stopes ('04), p. 439.

Miss Stopes' figure, we see in *Trigonocarpus* two, or possibly three, bundles, *b.*, *b.*, *b.*, enclosed in a space bounded by cells of the sarcotesta, some of which, *a.*, show fine spiral markings, and perhaps indicate a sheath somewhat similar to that of *Cycas Beddomii*. In the fine tissue around and between the bundles are seen abundant fine transfusion elements or short tracheides, *s.t.*, very similar to those of this species of *Cycas*. It would thus appear that the sarcotestal bundles of *Trigonocarpus Parkinsoni*, at least in the lower part of the seed, were of a complex type.

Leaving the general structure of the bundle we may next consider some points of detail. In Pl. XIV, Fig. 25, one of the bundles (the upper one) is traversed for a distance in a longitudinal direction, while the other (below) is cut more obliquely. The upper bundle affords evidence of being mesarch in structure, as the elements with more diffuse thickening bands occupy a more or less central position. It thus confirms the conclusion arrived at from the transverse sections (p. 104). The commonest type of tracheide in the bundle is apparently thickened in a very fine spiral, whilst others show loose or compact reticulate markings. Some of the tracheides are shown more highly magnified in Pl. XIV, Fig. 26. The commonest type is that shown at A with exceedingly fine spiral or scalariform markings. A distinctly scalariform tracheide is shown at D with the same exceedingly delicate thickenings. As supporting the probable connexion of *Trigonocarpus* with *Medullosa* it is interesting to note the similarity of these tracheides of *Trigonocarpus* with the fine scalariform elements characteristic of the primary tracheides of *Medullosa anglica*¹. Pl. XIV, Fig. 26, B, shows one of the tracheides from the central part of a bundle, perhaps one of the elements of the protoxylem, while C shows a common type in which two crossing series of spiral bands are present. Similar tracheides to the latter are common in *Medullosa anglica*, and, as the two series of thickenings are not quite equally in focus at the same time, they probably represent the markings of two adjacent tracheides on the common wall between.

Pl. XIV, Fig. 27, shows two of the short tracheides or transfusion elements of Pl. XIV, Fig. 25, *s.t.* Like the most typical tracheides of the bundles their markings are of a particularly fine character.

The Micropylar End of the Seed. The Question of a Wing.

A remarkable feature of this seed is the great prolongation of the micropylar tube, which in some specimens considerably exceeds the body of the seed in length. In the specimens figured in this paper, Pl. XII, Figs. 16 and 17, and Pl. XIII, Fig. 18, the micropyle is only slightly longer than the body of the seed, but it is possible, and indeed probable, that the full length of the beak is not preserved, although Fig. 17 has the appearance of being complete. A specimen of *Trigonocarpus Parkinsoni* in Mr. Kidston's

¹ Scott ('99), pp. 89, 95; Pl. 10, Fig. 5; Pl. 12, Fig. 15.

collection¹ has a micropylar beak almost 3 cm. in length, or quite double that of the body of the seed. As will be pointed out later in this paper it is quite possible that more than one species of *Trigonocarpus* is represented among these casts, and some forms may have had a longer micropylar beak than others.

The series of transverse sections cut at successively higher levels, shown in Pl. XI, Figs. 6–8, and Pl. XII, Figs. 9–11, will serve to illustrate the changes which take place in the micropylar region of this seed. Figs. 6, 8–10 are magnified about six times, Fig. 7 about six and a half, and Fig. 11 about thirty-two times. The sections from which Figs. 9–11 were made are among those which were described by Mr. Wild in the paper previously referred to². The changes which take place in the degree of prominence of the principal and secondary longitudinal ridges of the sclerotesta as they are traced from the body of the seed into the micropylar beak have already been described (p. 107), and are illustrated in Figs. 6–8.

Pl. XI, Fig. 6, is a transverse section across the upper part of the body of the seed, and probably passes through the walls of the pollen-chamber seen at *p*. The central cavity of the seed is beginning to assume a triangular outline, showing that the section is cut quite close to the base of the micropyle. The sclerotesta, *s.t.*, *s'.t'*, and sarcotesta, *sa.*, are fairly well preserved, and the former shows the usual splitting along the principal ridges. The outer, lacunar part of the sarcotesta is destroyed, with the exception of the limiting layers, *l.*, which can be traced round the greater part of the seed. In some places the limiting layers of the sarcotesta have been so pressed in as to be in contact with the sclerotestal ridges, so that the rest of the sarcotesta in these places has been totally destroyed. There seems no reason to suppose that the transverse section of the complete seed at this level was other than circular.

Pl. XI, Fig. 7, shows a transverse section cut at a somewhat higher level. It evidently traverses the lower thicker part of the micropylar beak. The micropylar canal, *t.m.*, has now acquired its characteristic triangular form, and in one place the sclerotesta, *s.t.*, shows splitting in a position corresponding to one of the principal ridges of the body of the seed. The limiting layers, *l.*, of the sarcotesta can be traced the whole distance round the seed, although in places they have evidently been much disturbed, as is shown by the overlap on the right side. The sarcotesta has the form of two wings, one on either side of the boss formed of the central sclerotic tissue. The total spread of the 'wings' in this slide is about 19 mm., or, allowing for the overlap of about 3.5 mm. on the shorter (right) side, this would make the two sides roughly equal and the total spread of the 'wings' about 21 mm. The width of one side of the triangular micropyle is nearly 2 mm.

¹ Figured in Scott ('05) (1), Fig. 33, p. 146.

² Wild ('00).

Pl. XI, Fig. 8, is another transverse section from the same specimen as that shown in Fig. 7, but it is cut at a considerably higher level across the micropylar beak. The sclerotesta, *s.t.*, has become thinner and the ridges are less developed. The triangular form of the micropyle, *t.m.*, is still preserved, although it is no longer equilateral, one side being somewhat shorter than the others. The wing-like form of the sarcotesta is clear, but there has been much loss of tissue and consequent deformation. Allowing, as before, for the overlap on the shorter side, the total spread of the wings would be the same as before, about 21 mm. In some places the sarcotestal tissue, with the exception of the limiting layers, *l.*, has entirely disappeared, and the two surfaces of the wing are pressed together.

Pl. XII, Fig. 9, is another transverse section from the same specimen as Figs. 7 and 8, but is cut at a still higher level. The sclerotesta, *s.t.*, is here very much reduced in quantity, and evidently at a slightly higher level it would disappear altogether. The micropyle, *t.m.*, is still triangular, and the departure from the equilateral form is still more marked than in Fig. 8. The total spread of the 'wings' is almost exactly equal to that of Figs. 7 and 8.

Pl. XII, Fig. 10, is from another slide cut from the same specimen as the others. Sclerotic tissue, *s.t.*, around the micropyle can still be seen, although it is quite small in amount. There is now no sign of a triangular micropyle, but its place is taken by a slit; however, it is quite evident that in this part of the seed, owing to the small amount of sclerotic tissue, a triangular micropyle might readily have been converted into a crevice by crushing from without. Compared with the lower sections, the micropylar boss in this slide is not well defined, while the whole structure varies irregularly in thickness, owing partly to collapse consequent on disappearance of tissue, and partly to the intrusion of Stigmarian rootlets. The best-preserved part of the wing, however, does not look as if much loss of tissue has taken place.

The section shown in Pl. XII, Fig. 11, from another seed, is the highest of our transverse series, and is cut, apparently, near to the extreme tip of the micropyle. This figure is magnified about thirty-two times, or about five times the scale of the other figures in this transverse series. The limiting layers, epidermis, *e.*, and hypodermis, *h.*, are quite well preserved, and the inner tissues are fairly well so. The micropyle appears to be nearly or quite closed, and is surrounded by a little group of brown cells, *b.*, not more than 300 μ in diameter, and that by a light zone, *l.*, the maximum diameter of which is not more than 400 μ , so that the whole is on an extremely small scale. This section apparently shows more than half the circumference of the micropylar tube, and as the maximum distance from the centre of the micropyle to the outside of the testa is only 1.2 mm. there is no question of a wing, unless one supposes that the micropyle is entirely

displaced, which can scarcely be the case as the tissues are fairly well preserved.

It is from the examination of sections such as those shown in Figs. 7-10 (and there are others which exhibit the same features), that the opinion has grown that the long micropylar region of *Trigonocarpus Parkinsoni* was provided with a broad wing continuous with the outer layer of the testa.

We have found it impossible to satisfy ourselves on the question whether the wing is a natural structure or is merely a result of the flattening of the soft tissues of an originally cylindrical sarcotestal investment of the micropyle. In all the sections which we have examined there has certainly been much loss of tissue; sometimes, as in parts of Pl. XI, Fig. 8, where the limiting layers of the sarcotesta are pressed into contact, the whole of the tissue between has disappeared. In the section represented in Pl. XI, Fig. 8, the total spread of the wings, allowing for the overlap, is about 21 mm. Supposing the epidermis filled out to form a circle (i. e. with no wings) the circumference would be about 45-50 mm., which would correspond to a diameter of about 14-16 mm. The seed represented in Pl. XI, Fig. 5, has an average diameter of about 17 mm., but as the outer part of the sarcotesta has been destroyed the diameter in the original condition would doubtless have been somewhat greater than this. Anyhow, the measurements show that if the seed remained circular at the micropylar region there was only slight diminution in size up to the levels represented by Pl. XI, Fig. 8, and Pl. XII, Figs. 9 and 10. On the other hand, if the wing is natural, its spread would have been greater than the diameter of the seed below, which seems very unlikely to have been the case. Taking an intermediate view, that the wings had been somewhat reduced in thickness and exaggerated in spread, we might suppose that the maximum diameter of the seed remained almost constant up to the level of these sections, the micropylar region being flattened instead of cylindrical.

On the circular hypothesis the epidermis, in such a section as Pl. XI, Fig. 8, must have been squashed in upon the micropylar boss, for the diameter here would have been more than double what it is now. Unfortunately, a critical section is not available, as in no slide is the preservation of the tissues sufficiently good to enable us to trace continuity of structure between the sclerotic tissue of the boss and the dark hypodermal layer of the sarcotesta. That there has been loss of tissue is certain, but the structure does not suggest so great a displacement as is necessitated on the circular hypothesis. In other sections, also, the limiting layers of the sarcotesta round the micropylar boss seem to be in nearly their natural position.

On the other hand, the fact that somewhat wing-like appendages may be produced by mere pressure is demonstrated in sections taken across the stalk, or even the body of the seed. Pl. XI, Fig. 5, shows a small 'wing' on one side, while Pl. XI, Fig. 3, from the stalk of the seed, exhibits

a 'wing' comparable in length and form with one from the micropylar region. At the same time the 'wings' in the micropylar region are much more symmetrically developed than elsewhere. We think that, on the whole, the evidence favours the existence of real wings, but the examination of specimens with still better preservation of the outer part of the testa will be necessary before the presence of wings can be positively affirmed.

The Nucellus and Pollen-Chamber.

In all our longitudinal sections of *Trigonocarpus Parkinsoni* the nucellus stands up freely from the base of the seed, with a space between it and the sclerotesta (see Pl. XII, Figs. 12 and 13). The width of this space varies considerably in different specimens, and in some cases it is quite narrow. In a fairly median longitudinal section (941 S.) in which the nucellus does not appear to have suffered much displacement or contraction, the average width of the space is only .25 mm. In most slides contraction has taken place, and the space is consequently much greater.

On the assumption of an 'inner flesh' (p. 110) this space would have been partly occupied, so that if, as seems probable, the nucellus was free from the integument, the space between must have been a very narrow one.

The nucellus itself is also quite narrow, and in good sections preserves a fairly constant width throughout its extent, from the chalazal attachment below to the base of the pollen-chamber above. The nucellus shown in Pl. XII, Fig. 15, has an average thickness of .1 mm. In other sections, in which the nucellus is less perfectly preserved, the thickness is commonly not more than .05 mm., probably owing to the fact that the nucellar epidermis is usually destroyed.

Within the nucellus is a dark-coloured structureless line (Pl. XI, Fig. 5, *m.*), which doubtless represents the membrane of a large, solitary megaspore. The megaspore membrane is always found contracted away from the nucellus, with which it was doubtless originally always in contact. Unfortunately, the prothallus and archegonia are never preserved.

Transverse sections of the body of the seed made at different levels exhibit some characteristic differences in the appearance of the nucellus. In sections across the lower part of the seed the nucellus frequently possesses numerous blunt or pointed outgrowths projecting into the space between it and the testa. These processes are often rather irregular in their distribution and size, and are well shown in some of the original Williamson slides¹. In sections above the middle of the seed these outgrowths are usually less conspicuous, so that this feature is of some value in determining whether a single transverse section is cut above or below the middle of the seed. With regard to the origin of these processes, we believe that they are caused by the contraction of the tissue of the nucellus which lies between

¹ e.g. No. 1460 W.

them, and that they generally correspond in position with the longitudinal vascular strands to be described later.

The structure of the nucellus, as seen in the best-preserved sections, is shown in Pl. XII, Fig. 15, and Pl. XIV, Figs. 29-31. Externally, there is a single layer of cells forming an epidermal layer, *n.e.*, readily distinguishable from the underlying tissue. These cells are usually filled with dark contents similar in appearance to those of the hypodermal cells of the sarcotesta. In longitudinal sections (Pl. XII, Fig. 15) these cells, *n.e.*, are usually somewhat elongated in the longitudinal direction, and have an average length of about .08 mm., but vary considerably among themselves in this respect. Fig. 15 is magnified about forty times, and is taken from a portion of the nucellus which is quite low down in the seed, but similar cells can be seen around the nucellus in most parts of this longitudinal section, so that it is clear that they extend from the chalazal attachment upwards. The nucellar epidermis closely resembles that of *Stephanospermum*, described and figured by Prof. Oliver¹.

Pl. XIV, Fig. 29, represents a portion of the nucellus from a section of *Trigonocarpus Parkinsoni* lent by Prof. Oliver, and is magnified about 560 times. The nucellar epidermis is shown at *n.e.*, and, as is commonly the case, the cuticle of the cells, *c.e.*, is separated. In this section the epidermal cells are empty, but usually they are filled with the characteristic dark contents.

Pl. XIV, Figs. 30 and 31, are made from the same section, a good transverse one lent by the Manchester Museum. The magnification is about 160 times. In Fig. 30 the nucellar epidermis, *n.e.*, is poorly preserved, and only the cuticle is clearly seen. In Fig. 31 the cuticle of the nucellar epidermis is shown at *e.*, and the contracted contents of the cells at *c.e.* In many sections the nucellar epidermis is represented only by its cuticle, which persists as a fine line separated by a space from the rest of the nucellus.

Within the epidermis good sections show a tissue consisting of thin-walled flattened cells (Pl. XIV, Fig. 31, *i.*). As shown in Fig. 31, the cells of this intermediate layer are flattened in the radial direction, and as far as can be made out from the longitudinal sections they are elongated vertically. The corresponding cells shown in Pl. XIV, Fig. 30, *i.*, are less flattened, possibly because they are opposite to one of the outwardly directed processes already mentioned.

The innermost layer of the nucellus may be distinguished as the tracheal zone, consisting as it does mainly of delicate tracheides with spiral or scalariform thickenings (Pl. XIV, Fig. 31, *t.*). The vascular bundle which comes in at the chalaza spreads out into what is apparently a continuous mantle of tracheides in the lower part of the seed. In some of the transverse sections across the lower part of the body of the seed the

¹ Oliver ('04) (1), Pl. 43, Fig. 21.

tracheides can be traced continuously for about a quarter of the circumference of the nucellus, so that there is no doubt as to their forming a continuous investment to the megaspore in this part of the seed. Higher up in the body of the seed the tracheides appear to range themselves in more or less definite longitudinal bundles, which are connected by transverse anastomoses running in a tangential direction. The structures observed are shown in Pl. XIV, Figs. 30 and 31. Fig. 30 shows a portion of a transverse section of the nucellus, including one of the outwardly directed processes already mentioned. On the inner side of the nucellus a flattened longitudinal nucellar bundle is shown, *n.b.* The tracheides of which the strand is composed are usually much flattened radially, as shown in the figure. In its central part the bundle shown is about three elements thick, but laterally it becomes reduced to but one layer of longitudinally running tracheides.

Pl. XIV, Fig. 31, is drawn from the same transverse section as Fig. 30, and shows at the lower end part of one of the flattened longitudinal bundles, *n.b.*, consisting of fairly thick-walled elements which can be seen to be tracheides in other parts of the section where the nucellus is cut somewhat obliquely. Outside the longitudinally running tracheides—cut transversely in the section—other tracheides, *t.*, are shown running in a horizontal or oblique direction. Laterally, as shown in the upper part of Fig. 31, the longitudinal tracheides disappear, and are replaced by others which run in an approximately horizontal direction, and so form transverse anastomoses between the longitudinal bundles. Similar longitudinal strands are seen in this section opposite to other projections on the outer side of the nucellus.

The nucellar tracheal system has been traced through the whole length of the nucellus, almost to the base of the pollen-chamber. There is no evidence of phloem in connexion with the nucellar tracheides.

A tracheal investment of this kind to the megaspore appears to have been a common feature of many of the old Cycadean seeds of the Palaeozoic era. Prof. Oliver has described a somewhat similar tracheal investment in *Stephanospermum*. In *Stephanospermum akenioides* the structure of the nucellus as a whole is almost identical with that of *Trigonocarpus Parkinsoni*, excepting that, whereas in *Stephanospermum* the tracheal mantle forms a thin but continuous sheath without trace of local segregation into bundles¹, in *Trigonocarpus* there are definite longitudinal bundles.

The question of the relation of the nucellus to the integument, whether coherent with it throughout the greater part of its extent as in the modern Cycadeae, or free from it as in *Stephanospermum* or *Lagenostoma*, is one of importance. From the fact that the nucellar epidermis in *Trigonocarpus* can be traced throughout the whole length of the nucellus from the chalaza upwards, as in *Stephanospermum*, and is not confined to the upper part, as

¹ Oliver ('04) (1), pp. 367, 368.

it probably would be if the nucellus were free only at the tip as in the Cycads, we believe that in *Trigonocarpus* the nucellus was free from the integument throughout its whole length.

The Pollen-Chamber.—Above the prothallial region of the nucellus is seen a relatively small pollen-chamber (Pl. XII, Fig. 13, *p.c.*), a very characteristic feature in these old seeds. This structure in *Trigonocarpus* was indicated in some of the figures of Hooker and Binney¹, and afterwards described and more fully illustrated by Williamson². Curiously enough, the best preservation of the pollen-chamber which we have yet seen is in one of the original Hooker and Binney slides, now preserved in the Binney Collection at Cambridge, and figured in our Pl. XII, Figs. 13 and 14, and Pl. XIV, Fig. 32.

As shown in Pl. XII, Fig. 13, the pollen-chamber forms a wide dome, 2.5–3 mm. in diameter at the base. We have to add the new fact that the pollen-chamber was provided at the top with a narrow channel or beak, *be*, not more than 300 μ in diameter. The presence of a beak is also obscurely indicated in the Williamson section (1478 w.), which is shown in Fig. 114 of his Memoir before referred to. The beak, as shown in the Binney slide, is barely half a millimetre in length, but presumably it extended much farther in the natural condition, and connected the pollen-chamber with the micropyle, or even extended for some distance along the latter.

The pollen-chamber as a whole is smaller than in *Stephanospermum*. In *S. caryoides* the pollen-chamber forms about one-seventh of the height of the whole nucellus, and in *S. akenioides* about one-fourth or one-fifth³, while in *Trigonocarpus Parkinsoni* the proportion, judging from the Binney section represented in Pl. XII, Fig. 13, and excluding the beak, is about one-tenth. In general structure the pollen-chamber of *Trigonocarpus* appears to have been very similar to that of *Stephanospermum*, but on account of the small number of sections in which the pollen-chamber is shown and the imperfect preservation, it is impossible to describe its structure in much detail. The megaspore wall was doubtless separated from the cavity of the pollen-chamber by a transverse septum continuous with the nucellus. In Pl. XII, Fig. 13, the septum is wholly destroyed, unless the pad of tissue shown at *p.* has been displaced from the floor of the pollen-chamber, as is probably the case. In other sections⁴ (not figured) part of the septum remains at the sides.

In *Stephanospermum akenioides* the septum between the megaspore and the pollen-chamber is a vascular sheath consisting largely of tracheides continuous with those of the wall of the nucellus below and around, thus completing the vascular investment of the nucellus⁵. Tracheides are never

¹ Hooker and Binney ('55), Pl. IV, Figs. 7, 8, 12.

² Williamson ('77), Pl. XIII and XIV, Figs. 113–15.

³ Oliver ('04) (1), pp. 363, 374.

⁴ e. g. 940 (S); Wild 1939 (S).

⁵ Oliver ('04) (1), p. 369.

found beyond the septum, i. e. they never penetrate to the walls or roof of the pollen-chamber itself. In our specimens of *Trigonocarpus* no trace can be seen of tracheal elements either in the septum or in the walls of the pollen-chamber, excepting, perhaps, in the beak to be described later. In the case of the septum this negative evidence does not necessarily imply that tracheides were absent, as the septum in our specimens of *Trigonocarpus* is only poorly preserved, but the absence of tracheides in the pollen-chamber wall in such a slide as that shown in Pl. XII, Fig. 13, when quite well-preserved tracheides are seen lower down in the nucellus in the same section, appears to indicate that such elements were probably really absent. In this respect, then, *Trigonocarpus* probably agrees with *Stephanospermum*.

In all the slides the megaspore membrane (Pl. XI, Fig. 5, *m.*) is contracted away from the nucellus and from the septum above, but doubtless in the natural condition the two tissues were in close contact all round. At the apex, as suggested by Professor Oliver for *Stephanospermum*¹, the megaspore membrane probably bulged the septum upwards, so that the septum and the top of the megaspore encroached somewhat on the pollen-chamber, and may have reduced its size considerably from that which is shown in Pl. XII, Fig. 13, *p.c.* As in *Stephanospermum*, the pollen-chamber was provided laterally with cushions or shoulders of nucellar tissue of considerable thickness, composed of thin-walled elongated cells, the elongation being parallel to the slope of the wall. One of these cushions is shown in Pl. XII, Fig. 13, *c.*, and the other on the opposite side of the pollen-chamber is quite visible in the slide, although not in the photograph. The patch of tissue shown at *p.* in this figure is probably not a portion of one of the cushions, but, as shown by comparison with other slides, part of the floor of the pollen-chamber displaced from its natural position. The tissue of the cushion dies out on the roof of the pollen-chamber.

The wall of the pollen-chamber is covered externally by a layer of epidermal cells apparently similar to, and doubtless continuous with, those of the nucellus below. When traced to the base of the nucellar beak the epidermal cells become radially elongated and palisade-like in form (Pl. XII, Fig. 14, *w.*). A somewhat similar change in the epidermal cells of the pollen-chamber wall has been described by Professor Oliver in *Stephanospermum caryoides*. In this form the flanks of the pollen-chamber are included in a well-marked epidermis of cubical cells which become columnar as the insertion of the beak is approached².

In *Trigonocarpus Parkinsoni*, within the epidermal cells of the pollen-chamber beak, there is an inner layer of small prosenchymatous elements, shown in Pl. XII, Fig. 14, *t.*, and Pl. XIV, Fig. 32, *t.* These fibrous elements are not more than about .01 mm. in width, and when examined under a high power and with good illumination exhibit a very faint 'barring'

¹ Oliver ('04) (1), p. 364.

² Oliver ('04) (1), p. 374 and Pl. 44, Fig. 38.

which somewhat resembles tracheal thickenings. The question as to whether these elements are really tracheides or not must be left open for the present, but in view of the absence of tracheides from the wall of the pollen-chamber in both *Trigonocarpus* and *Stephanospermum* we are inclined to think that the elements in question are non-tracheal.

On the whole the pollen-chamber with its beak in *Trigonocarpus Parkinsoni* resembles in a somewhat striking manner the Cordaitean pollen-chamber as shown in Renault's well-known figure¹, while there is also fair agreement with the corresponding structures in a recent Cycadean ovule as in *Stangeria*².

IV. TRIGONOCARPUS OLIVERI, SPEC. NOV.

This is a new species of *Trigonocarpus* which has kindly been communicated to us for description by Professor F. W. Oliver, F.R.S., after whom it has been named. The locality from which it was obtained—Shore-Littleborough in Lancashire—is a comparatively new one for petrified fossil plants, the colliery having recently been reopened for scientific purposes by Mr. W. H. Sutcliffe, F.G.S. This rich locality has yielded many well-preserved and interesting fossils which are found in nodules from the roof of the workings, as well as in the ordinary nodules or coal-balls lying in the coal-seam immediately below.

Trigonocarpus Oliveri occurs in a roof-nodule, and is at present represented by one specimen only, which has been cut by Mr. Lomax into the four longitudinal sections shown in Pl. XIII, Figs. 19–22. As no transverse sections are available for examination we are unable to fully diagnose the new form, but, as far as can be judged from the longitudinal sections, it is similar in many respects to *Trigonocarpus Parkinsoni*, and we have provisionally placed it in the same genus. At the same time there are differences from the ordinary form which are quite sufficient for its separation as a distinct species.

Trigonocarpus Oliveri is a somewhat smaller seed than *T. Parkinsoni*. None of our sections pass radially through the seed from base to apex, so that the true length of the seed is not shown. The longest section, that shown in Pl. XIII, Fig. 19, has a length of about 1.8 cm., or slightly less than that of *T. Parkinsoni*, specimens of which, excluding the micropylar beak, vary between just over 2 cm. and 2.5 cm. in length. The maximum width of *T. Oliveri* across the body of the seed, measuring to the outside of the sclerotesta, is nearly .9 cm., or half the length. In *T. Parkinsoni* the corresponding maximum width varies between about 1.3 and 1.6 cm. The new seed is therefore somewhat shorter and narrower, and is also slightly narrower in proportion to its length, than most specimens of *T. Parkinsoni*. The sarcotesta is not preserved, excepting, perhaps, slight traces of it at the

¹ Renault ('81-'85), T. i, Pl. 14, Figs. 5 and 6.

² e.g. Lang ('00), Pl. XVII, Fig. 15.

base of the seed within the angles of the sclerotesta (Pl. XIII, Fig. 20, *sa.*). The sclerotesta is shown at *s.t.* in the figures and exhibits certain differences from that of the ordinary form. The section figured in Pl. XIII, Fig. 19, is, on the whole, the most median one we have, and shows the characteristic 'coffin-shape' of the sclerotesta and of the cavity within it, which is quite different from the oval form with a rounded base which is seen in all the longitudinal sections of *Trigonocarpus Parkinsoni* (cp. Pl. XII, Fig. 12). This section (Fig. 19) is evidently not quite radial at the base of the seed, as it misses the chalazal attachment of the nucellus *n.* The nucellus shows a ragged appearance due to a number of irregularly disposed processes similar to those described in dealing with the nucellus of *Trigonocarpus Parkinsoni* (p. 119). The base of the sclerotesta is characteristically flat or nearly so, and in this section it has a width, to the outside limit of the sclerotesta, of about .6 cm.

At the base of the seed the sclerotesta is produced at the angles into two downwardly pointing processes, *p.*, *p.*, which appear to be sections of a circular ridge surrounding the base of the seed. At the apex the section is clearly not radial, as it escapes the micropylar beak altogether. Three processes are seen rising from the top of this section, the interpretation of which is not without difficulty; they probably represent some of the longitudinal ridges of the sclerotesta as they converge to the base of the micropylar beak.

Pl. XIII, Fig. 20, is another obliquely longitudinal section of the same seed. The basal part of the seed is evidently cut nearly radially, as the chalazal attachment of the nucellus, *n.*, is shown. In the upper part of the seed the pollen-chamber, *p.c.*, is apparently cut through. The base of this section shows the downwardly directed processes of the sclerotesta, *p.p.*, better developed than in Fig. 19, and we think that these two sections make it practically certain that there was a circular ridge around the base of this seed, a feature which constitutes one of the most distinctive characters of the species. In Fig. 20 these processes (*p.p.*) evidently extended farther downward than is shown in the specimen; only the proximal part of the circular ridge is preserved.

The upper part of this section (Pl. XIII, Fig. 20) is not cut in the median plane. The three ridges shown, *r.*, *r.*, *r.*, give rise to an appearance as though the apex of the seed was provided with a circular ridge similar to the crown of a *Stephanospermum*. This appearance, however, is probably deceptive, and is due to the obliquity of the section, which thus passes through three of the ordinary longitudinal ridges of the sclerotesta. Three similarly placed ridges are sometimes shown in *Trigonocarpus Parkinsoni* when the seed has been cut obliquely, and the two outermost of these have frequently been described as caused by the presence of an annular ridge. Truly radial sections of *T. Parkinsoni* passing through the micropyle show

no trace of an annular ridge. That the three processes shown in Pl. XIII, Fig. 20, *r.*, *r.*, *r.*, are only longitudinal ridges is also made clear by their absence in the more radial section of the upper part of the same seed shown in Pl. XIII, Fig. 19.

Pl. XIII, Fig. 21, is a vertical tangential section, and shows the cavity of the seed, *c.*, and the surrounding sclerotesta, *s.t.* The sclerotesta is much thicker on one side than on the other, probably because the section passes through one of the longitudinal ridges on that side. On the thicker side a nearly detached portion of the sclerotesta is shown, probably corresponding to another longitudinal ridge.

Pl. XIII, Fig. 22, is still more tangential, as it shows little more than the sclerotesta, *s.t.*, with a trace of the cavity of the seed within. The sharply pointed upper and lower ends of this section probably indicate that the section passes through one of the longitudinal ridges, and that these had very acute edges. In *Trigonocarpus Parkinsoni* the ridges were more blunt or round, and none of the numerous sections which we have examined of this form are at all like the section shown in Pl. XIII, Fig. 22. We do not think that the form represented in this figure is a possible one for *Trigonocarpus Parkinsoni*.

The innermost cells of the sclerotesta, especially in the section shown in Fig. 22, have dark contents and are quite different from the rest of the cells of this layer. They are continued as fine lines from the centre of the section (Fig. 22) through the middle of the longitudinal ridge shown above and below. The splitting of the testa along the ridges, which can be seen in Figs. 20 and 22, appears to proceed along these cells, which seem to be in a state of disorganization. In this form the splitting of the testa along the ridges would thus appear to have been a natural process correlated with the presence of special cells occupying the central parts of the sclerotestal ridges.

The presence of a circular ridge surrounding the base of the seed, and enclosing, presumably, the stalk by which it was attached to the parent plant, is a character which *Trigonocarpus Oliveri* possesses in common with *Polylophospermum stephanense*, a French seed which has been recently re-described by Professor Oliver¹. Indeed longitudinal sections of the base of this seed compare closely with similar sections of *Trigonocarpus Oliveri*.

Polylophospermum stephanense is a long prismatic seed, hexagonal in transverse section and prominently ribbed along the salient angles, while both at the apex and base there are cup-shaped incurved outgrowths of the testa which produce two false chambers at the ends of the seed. One of these chambers encloses the micropylar beak, and the other the stalk of the seed. The length of this seed is about 1.5 cm., or somewhat less than that of *Trigonocarpus Oliveri*.

¹ Oliver ('04) (2).

Trigonocarpus Oliveri differs essentially from *Polylophospermum stephanense* in its general shape and in the absence of the cup-shaped outgrowth of the testa around the micropyle. Its general shape is much less narrow and cylindrical, the proportion of length to breadth being about 2 : 1, while in *Polylophospermum* it is about 3 : 1. The shape in transverse section cannot be determined from our sections.

On the whole, judging from the characters which are available in a series of longitudinal sections of a single seed, we think that this seed more closely resembles *Trigonocarpus*, and we have therefore provisionally placed it in this genus.

The following is a brief diagnosis of the distinctive characters of the new seed :—

Trigonocarpus Oliveri, sp. nova.

Horizon. Lower Coal Measures. Shore-Littleborough, Lancashire.

Size. Length nearly 2 cm. ; maximum transverse diameter about .9 cm.

Shape. Characteristically 'coffin-shaped' in vertical sections. Base flattened. Sclerotesta produced around the base of the seed in the form of a circular ridge enclosing the stalk of the seed. Longitudinal ridges of the sclerotesta acute-angled, not rounded as in *Trigonocarpus Parkinsoni*.

V. THE CASTS AND IMPRESSIONS.

It is not intended in this paper to enter into a full discussion of the specimens of *Trigonocarpus* which do not exhibit internal structure—the internal casts of the cavity of the seed and the more or less flattened specimens of the whole seed which have usually been described under the name of *Carpolithes alata* (Lindley and Hutton). At the same time, a correlation of the features shown in those specimens with those of the petrified seeds showing internal structure is of some interest and importance, and we propose to devote some attention to this matter in the present paper, especially with reference to the three good specimens of *Carpolithes alata* represented in Pl. XII, Figs. 16 and 17, and Pl. XIII, Fig. 18.

Taking first the ordinary internal casts, some account has already been given of these nut-like 'seeds' in the present paper (pp. 90, 94), and a few additional details may be given here. The common type of these internal casts—those described under the names of *Trigonocarpus Parkinsoni* and *T. olivaeformis*—although they vary somewhat among themselves in size and shape, still agree closely with the petrified specimens showing internal structure, so that it is highly probable that they represent the same form. The probable identity of the casts described as *T. Parkinsoni* and *T. olivaeformis* has already been pointed out (p. 93).

Many of the internal casts show a triangular fracture at the narrower (upper) end, which doubtless represents the place where the cast of the

triangular micropylar tube had broken off. Many of the specimens also show a circular or oval scar at the lower or more rounded end; this scar probably indicates the edge of the tracheal disk from which the free nucellus sprang (see Pl. XII, Fig. 12, *p.*). The internal casts show, as a rule, three well-marked longitudinal ridges, which doubtless represent the three longitudinal furrows on the inner side of the sclerotesta of *Trigonocarpus Parkinsoni*. We have described (*p.* 108) how these furrows become less deep or pronounced towards the base of the body of the seed in petrified specimens; it is interesting to find that the internal casts show the three ridges dying out towards the bottom, exactly as shown in the sections. None of the sections of *Trigonocarpus Parkinsoni* which we have examined would yield internal casts with more than three longitudinal ridges, so that the casts described as *Trigonocarpus Noeggerathi* (Stern.), which are in size and shape comparable with ours, but are provided with six longitudinal ridges instead of three, must have belonged to a different but probably closely related plant.

We pass now to the impressions shown in Pl. XII, Figs. 16 and 17, and Pl. XIII, Fig. 18, which are similar to those described by Lindley and Hutton as *Carpolithes alata*, and identified by Mr. Kidston with *Trigonocarpus Parkinsoni*¹. Whether the three specimens figured here and others figured elsewhere all belong to the same species may perhaps be left for the present an open question, but that they are specimens of *Trigonocarpus* seems certain, although the correlation of the features presented by these impressions with the parts of the structural specimens presents considerable difficulty.

The specimens shown in Pl. XII, Figs. 16 and 17, now belong to the Copenhagen Museum, but were originally contained in the Hutton Collection at Newcastle. The specimens were obtained for us through the good offices of Mr. E. A. Newell Arber, F.G.S. The photographs are about twice the natural size, so that the total length of the specimens as preserved is about 4.5–5 cm. Of the total length, the rounded body of the seed forms about four-ninths in the specimen shown in Fig. 16, and about half of that shown in Fig. 17. In a figured specimen of *Trigonocarpus Parkinsoni* belonging to Mr. Kidston² the body of the seed forms only one-third of the total length. The latter specimen may represent a different species from ours, unless in our specimens the micropylar beak is incompletely preserved. Of the three examples figured in this paper (Pl. XII, Figs. 16 and 17, and Pl. XIII, Fig. 18), one, Fig. 17, has every appearance of being complete at the upper end, but in the other specimens (Figs. 16 and 18) the micropylar beak quite probably extended farther than shown, especially so as we know that the upper portion of the beak consisted almost wholly of thin-walled, easily destroyed tissue.

The specimen shown in Pl. XII, Fig. 16, is probably to be interpreted

¹ Kidston ('86), pp. 218, 219.

² Figured in Scott ('05) (1), Fig. 33, p. 146.

in the following way. The outer surface of the sclerotesta surrounding the micropylar canal is shown at *s.t.b.*, the reference line passing to one of the longitudinal ridges of the micropylar beak (compare the transverse section across the lower part of the micropylar beak shown in Pl. XI, Fig. 7). The beak shown in Fig. 16 gradually tapers upwards, so that while the width at the base is about 6 mm., at the upper end it is less than 3 mm. These dimensions agree approximately with those of the sclerotesta shown in Pl. XI, Figs. 7 and 8, from which it appears that these two sections were cut at a considerable distance from one another, perhaps nearly equal to the length of the micropylar beak shown in Fig. 16. The upper end of the micropylar beak of Fig. 16 has an unfinished appearance, probably because the distal portion, consisting of thinner-walled tissue, is lost. That the outer surface of the sclerotesta of the beak, and not that of an internal cast of the micropylar canal, is shown in Fig. 16, is made probable, then, by its size agreeing with that of the petrified specimens. The width of the base of the beak compared with that of the body of the seed also confirms this explanation. A typical transverse section across the body of the seed, such as that shown in Pl. XI, Fig. 5, has a diameter (measuring to the outside of the sclerotesta) of about 1.3 cm., while the diameter at the base of the beak is almost exactly half this, and the same proportion holds good in the specimen represented in Pl. XII, Fig. 16. On one side of the micropylar beak is seen a flat area (Pl. XII, Fig. 16, *sa.*), which we interpret as the impression of the sarcotestal covering. The appearance presented might very well be due to a wing of soft tissue more or less 'doubled' under. This 'wing' cannot be traced with certainty below the beak portion of the seed.

The body of this seed (Fig. 16) has such a form and dimensions as to quite well agree with the petrified specimens of *Trigonocarpus Parkinsoni*. The body of the seed is split in such a way as to provide us with a tangential section showing the sclerotesta, *s.t.*, preserved in coaly material which is continuous with the similar substance forming the micropylar beak, *s.t.b.*, and the material, *c.*, filling up the central cavity of the seed.

Pl. XII, Fig. 17, shows another seed impression which has a remarkable appearance of being complete, especially at the upper end, so that the whole seed has a symmetrical, elongated, oval outline. The body of this seed is about equal in width to that of the specimen shown in Fig. 16, but its length is about .5 cm. greater. The micropylar beak, *m.b.*, can be seen extending from the top of the body of the seed for a distance of 2.25 cm., preserving an almost equal size the whole distance. The lower (darker) portion of the beak, 1 cm. in length, is preserved in relief, and has a triangular form, with an edge or longitudinal ridge to which the reference line, *m.b.*, passes, and possibly another on the left of this. The upper (lighter) part of

the beak is represented by a furrow with a median groove, because the actual micropylar beak has been broken off and only its impression remains.

The body of the seed shown in Fig. 17 presents much the same appearance as that of Fig. 16; what appears to be the sclerotesta is shown at *s.t.*, while *c* is perhaps the surface of the coaly shale which forms a cast of the interior cavity. A fact which is difficult of explanation, on the supposition that *c* in Figs. 16 and 17 represents the surface of an internal cast of the cavity of the seed, is the complete absence of any sign of the longitudinal ridges which are so characteristic a feature of the ordinary sandstone internal casts of *Trigonocarpus*. Mr. E. A. Newell Arber informs us that he has seen hundreds of such smooth specimens. The absence of longitudinal ridges would be equally difficult to explain if we assume that the smooth surface *c* represents the surface of the whole seed squashed flat, for we should expect the sclerotestal ridges of the body of the seed to be shown.

The most interesting feature of the specimen shown in Pl. XII, Fig. 17, is the impression of the sarcotesta, *sa.*, which surrounds the whole seed and gives to it a regular, elongated, oval form. The whole seed may have been symmetrically flattened out into the form shown, or, if a real wing was present, it is probably seen in this specimen. On the whole, we think that the specimens shown in Figs. 16 and 17 favour the presence of a real wing, although the evidence from the impressions, as well as from the study of the petrified specimens, is not conclusive.

The third of our figured specimens of *Carpolithes alata* (*Trigonocarpus Parkinsoni*?) is shown in Pl. XIII, Fig. 18, the magnification being equal to that of the others. The specimen comes from Jarrow, and belongs to the Hutton Collection in the Newcastle Museum. The total length of the seed as shown is about 4 cm., the body of the seed being 1.8 cm. and the micropylar beak 2.2 cm. in length, while the maximum width of the body is 1.5 cm. The size is therefore approximately equal to that of the other two impressions and to the ordinary petrified specimens. The micropylar beak, *m.b.*, has a triangular form, and tapers rather rapidly above. The body of the seed and the micropylar beak are apparently represented as internal casts in the coaly shale. One of the internal grooves of the sclerotesta is represented by the conspicuous ridge, *r.*, which is seen passing across the body of the seed, and continuing as the prominent edge of the triangular micropyle and traceable almost to the summit of the latter. That the surface of the body of the seed shown is really that of an internal cast, and not the outer surface of the sclerotesta, is clear from the fact that but one longitudinal ridge can be seen either here or along the micropylar tube. Preservation of the outer surface of the sclerotesta sufficiently good to show one well-marked ridge would be practically certain to show others also. Moreover, the sclerotesta itself is seen in this specimen as a layer of coaly material, *s.t.*, which encloses the internal cast in places, although the greater part of it has been broken away.

One difficulty in the interpretation of the specimen shown in Pl. XIII, Fig. 18, is that the longitudinal ridge apparently extends to the bottom of the body of the seed, while, as we have before mentioned in this paper, the ordinary internal casts usually show the ridges disappearing towards the base of the seed. Examination of a number of specimens of *Carpolithes alata* and of the ordinary internal casts at the Natural History Museum makes it highly probable that in Fig. 18 the real base of the seed is not seen. The ridge shown is of exactly the same length as one of the ridges of many of the internal casts, and the real base of the seed was in all probability unribbed. We feel little doubt as to the specimen shown in Fig. 18 being really mainly preserved as an internal cast, with a thin coaly layer representing the sclerotesta preserved in places.

The true interpretation of impressions such as those shown in Figs. 16, 17, 18, presents considerable difficulty, and becomes possible only after the internal structure of the petrified specimens has been worked out in detail.

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EXPLANATION OF PLATES XI–XIV.

Illustrating Messrs. Scott and Maslen's paper on *Trigonocarpus*.

PLATE XI.

Fig. 1. First of a series of transverse sections across a seed of *Trigonocarpus Parkinsoni*. This section is the lowest of the series and is cut across the base of the seed some considerable distance below the chalaza. Slide 627 (S)¹. Magnification between 6 and 7 times.

b. triangular space containing main supply bundle of the seed and surrounded by a zone of dark-coloured sclerotic tissue continuous with the sclerotesta; *l.* limiting layers of sarcotesta.

Fig. 2. The central portion of the same slide as shown in Fig. 1 more highly magnified. Magnification 100.

s.t. sclerotic tissue continuous with sclerotesta; *b.* main supply bundle of seed; *s.* triangular space enclosing bundle.

Fig. 3. Transverse section of same specimen at a higher level across the base of the seed. Inner part of sarcotesta preserved with about six sarcotestal bundles. Slide 626 (S). Magnification 6.

b. main supply bundle of seed; *s.t.* sclerotestal core surrounding bundle; *s.b.* six sarcotestal bundles embedded in compact sarcotesta; *l.* limiting layers of the sarcotesta.

Fig. 4. Central part of same more highly magnified. *s.t.* part of core of sclerotesta; *b.* main supply bundle of seed; *a.* cells surrounding bundle.

Fig. 5. Transverse section across the central part of the body of the same seed as shown in Figs. 1–4, showing general form and three principal and nine secondary sclerotestal ridges. Slide 325 (S). Magnification 6.

m. megaspore membrane (contracted); *n.* nucellus; *s'.t'.* one of the principal ridges of the sclerotesta; *s.t.* one of the secondary ridges of the sclerotesta; *sa.* sarcotesta; *l.* limiting layers of sarcotesta; *s.b.* position of one of the sarcotestal bundles (shown more magnified in Pl. XIV, Fig. 28).

Fig. 6. Transverse section across the upper part of the body of the seed probably passing across the pollen-chamber. The central cavity is beginning to assume a triangular form and the sclerotesta shows the differentiation into two zones. Slide 1470 (W). Magnification 6.

p. wall of pollen-chamber; *s.t.* inner zone of sclerotesta; *s'.t'.* outer zone of sclerotesta; *sa.* sarcotesta; *l.* limiting layers.

Fig. 7. Transverse section near base of micropyle showing triangular form of micropyle and 'wing' of sarcotesta. Slide Q. 585 (M). Magnification 6½.

t.m. triangular micropyle; *s.t.* sclerotesta of micropylar beak; *sa.* sarcotesta; *l.* limiting layers of sarcotesta.

Fig. 8. Transverse section across micropylar beak at a higher level than Fig. 7. From same specimen as Fig. 7. Slide 487 (S). Magnification 6.

t.m. triangular micropyle; *s.t.* sclerotesta of micropylar beak; *sa.* sarcotesta; *l.* limiting layers of sarcotesta.

¹ [The reference letters after the number of the slide refer to the collections to which the slides belong. O=in the collection of Prof. Oliver, F.R.S. M=in the Manchester Museum. B=the Binney Collection at Cambridge University. S=Dr. Scott's Collection. W=Williamson Collection at the Natural History Museum.]

PLATE XII.

Fig. 9. Transverse section across micropylar beak at a still higher level. Slide 1943 Wild (S). Magnification 6.

t.m. triangular micropyle; *s.t.* sclerotestal tissue surrounding micropyle; *l.* limiting layers of sarcotesta.

Fig. 10. Transverse section across beak at a still higher level. Same specimen as Fig. 9 Slide 1942 Wild (S). Magnification 6.

s.t. small amount of sclerotic tissue surrounding micropyle which was apparently slit-like in form; *l.* limiting layers of sarcotesta.

Fig. 11. Transverse section of extreme tip of micropylar beak. Opening of micropyle apparently blocked. Slide 1952 Wild (S). Magnification 32.

b. dark cells surrounding micropyle; *l.* light-coloured zone surrounding micropyle; *h.* hypodermis of sarcotesta; *e.* epidermis of sarcotesta.

Fig. 12. Longitudinal section of the lower part of a seed of *Trigonocarpus Parkinsoni*. The section is not strictly radial and therefore does not pass through the chalazal bundle. The attachment of the apparently free nucellus is shown. Slide R. 763 (M). Magnification 7.

n. nucellus; *p.* chalazal attachment of nucellus; *s.b.*, *s.b.* position of sarcotestal bundles one of which is shown more highly magnified in Pl. XIV, Fig. 25; *s.t.* sclerotestal tissue at base of stalk of seed.

Fig. 13. Longitudinal section of upper part of seed showing pollen-chamber and beak. Slide 224 (B). Magnification 6.

p.c. pollen-chamber occupying apex of nucellus; *c.* lateral cushion at side of pollen-chamber; *p.* pad of tissue probably displaced from the floor of pollen-chamber; *be.* beak of pollen-chamber; *s.t.* sclerotesta at base of micropylar beak.

Fig. 14. The pollen-chamber beak of Fig. 13 more highly magnified. Magnification 107.

w. wall of beak consisting of palisade-like cells (see Pl. XIV, Fig. 32); *t.* possible tracheides forming inner portion of wall of beak.

Fig. 15. Portion of the nucellus showing the covering of epidermal cells. From the lower part of a seed. Slide 222 (B). Magnification 40.

n.e. nucellar epidermis; *i.n.* inner tissue of nucellus.

Fig. 16. *Carpolithes alata* (*Trigonocarpus Parkinsoni*?). From a specimen in the Copenhagen Museum originally contained in the Hutton Collection at Newcastle. Magnification 2.

s.t.b. outer surface of sclerotesta bounding the micropylar beak; *sa.* impression of sarcotesta; *s.t.* sclerotesta of body of seed; *c.* substance filling cavity of seed.

Fig. 17. Another specimen from the same collection. Magnification 2.

m.b. micropylar beak; *sa.* impression of sarcotesta; *s.t.* sclerotesta of body of seed; *c.* substance occupying cavity of seed.

PLATE XIII.

Fig. 18. *Carpolithes alata* (*Trigonocarpus Parkinsoni*?). Specimen from the Hutton Collection in the Newcastle Museum. Showing internal cast of body of seed with sclerotestal covering and internal cast of micropylar canal.

r. ridge of cast; *s.t.* sclerotestal covering; *m.b.* micropylar beak (internal cast).

Fig. 19. *Trigonocarpus Oliveri*. Longitudinal section of seed showing characteristic 'coffin shape' of the sclerotesta. Slide S. 28, *b.* (O). Magnification 6½. Loc. Shore-Littleborough (roof-nodule).

n. nucellus; *s.t.* sclerotesta; *p., p.* processes of sclerotesta representing annular ridge at base of seed.

Fig. 20. Another vertical section of the same specimen, more median below but less median above. Slide S. 28, *c.* (O). Magnification 6½.

n. nucellus; *p.c.* pollen-chamber; *s.t.* sclerotesta; *sa.* sarcotesta (?) preserved in the angles of the sclerotesta; *p., p.* processes due to annular ridge at base of seed; *r., r., r.* three of the longitudinal ridges of the seed which are cut through on account of the obliquity of the section.

Fig. 21. More tangential section of the same seed passing through a longitudinal ridge of the sclerotesta on one side. Slide S. 28, *d.* (O). Magnification $6\frac{1}{2}$.

s.t. sclerotesta; *c.* cavity of seed.

Fig. 22. Still more tangential section of the same seed showing the sharply angular form of the ridges. Slide S. 28 *a.* (O). Magnification $6\frac{1}{2}$.

s.t. sclerotesta; *c.* trace of cavity of seed.

PLATE XIV.

Trigonocarpus Parkinsoni.

Fig. 23. The limiting layers of the sarcotesta. Slide R. 763 (M). Magnification about 40.
e. epidermis of small cells; *h.* hypodermis of larger cells with dark contents; *sa.* ordinary cells of the sarcotesta.

Fig. 24. Lacunar tissue of the outer part of the sarcotesta. Slide 1459 (W). Magnification about 45.

Fig. 25. Sarcotestal bundles at base of seed. Same slide as Pl. XII, Fig. 12. Slide R. 763 (M). Magnification about 80.

sa. cells of sarcotesta; *b.*, *b.*, *b.* vascular bundles; *s.t.* short tracheides (transfusion elements) in delicate tissue between the bundles; *a.* other short tracheides among cells of sarcotesta; *h.* hypodermal cells of sarcotesta (displaced).

Fig. 26. Types of tracheides from the sarcotestal bundles shown in Fig. 25. Slide R. 763 (M).

A. Commonest type of tracheide with very fine spiral or scalariform markings. Magnification about 280.

B. One of the small elements (protoxylem) from the central part of a bundle. Magnification about 460.

C. Tracheide with two series of crossing spiral bands. Magnification about 280.

D. Oblique view of a scalariform tracheide.

Fig. 27. Two short tracheides (transfusion elements) from the same slide. Slide R. 763 (M). Magnification 560.

Fig. 28. A sarcotestal bundle. Apparently mesarch. The position of this bundle is shown in Pl. XI, Fig. 5, *s.b.* Slide 325 (S). Magnification 200.

sa. cells of sarcotesta; *d.t.* decomposed tissue. The arrow points towards the outside of the seed.

Fig. 29. Portion of the nucellus showing the nucellar epidermis. Slide 4 (O). Magnification 560.

n.e. nucellar epidermis; *c.e.* separated cuticle of epidermal cells; *i.e.* inner tissue of nucellus.

Fig. 30. Part of a transverse section of the nucellus showing a nucellar bundle. Slide R. 762 (M). Magnification 170.

n.b. flattened nucellar bundle; *i.* intermediate layers of nucellus; *n.e.* remains of nucellar epidermis.

Fig. 31. Another part of the same transverse section. Slide R. 762 (M). Magnification 160.

n.b. part of flattened nucellar bundle; *t.* tracheide in longitudinal section; *i.* intermediate layers of nucellus consisting of flattened cells; *c.e.* contracted contents of epidermal cells; *e.* cuticle of epidermal cells.

Fig. 32. A part of the pollen-chamber beak shown in Pl. XII, Fig. 14. Slide 224 (B). Magnification 400.

w. wall of beak consisting of a palisade-like tissue; *t.* possible tracheides.

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W. Tams, photo.

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W. Tams, photo.

Huth lith. London.

SCOTT & MASLEN — TRIGONOCARPUS.

L.A. Boodle and W. Tams photo.

L.A. Boodle and W. Tams photo.

Huth coll.

L.A. Boodle and W. Tams, photo.

Huth, lith. London.

SCOTT & MASLEN — TRIGONOCARPUS.

A. J. Maslen, del.

Scott, Dukinfield Henry and Maslen, Arthur J. 1907. "The structure of the palaeozoic seeds, *Trigonocarpus parkinsoni*, Brongniart, and *Trignoocarpus oliveri*, sp.nov. Part I." *Annals of botany* 21, 89–134.

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