X. *On the Anatomy of the Roots of Palms.* By ERIC DRABBLE, D.Sc., F.L.S.,
Lecturer on Botany, St. Thomas's Hospital, London.

(Plates 48-51 and 22 text-figures.)

Read 3rd December, 1903.

INTRODUCTION.

H. VON MOHL, in 1845, published an admirable account of the roots of Palms in his work 'De Structura Palmarum' (1). He described the typical arrangement of the tissues and observed that the central cylinder of the adventitious roots can be traced internally as a series of strands of xylem and phloem which penetrate deeply into the central cylinder of the stem. He also described and figured the cylinder of a large root of *Iriartia*, of which the outline is not circular, but deeply lobed in a stellate manner, the ends of the rays being usually bilobed. At the same time he gave an account of the medullary strands of fibrous or sclerenchymatous tissue, containing vessels and in some cases phloem also. He further noted that the fibrous ring in which are embedded the xylem- and phloem-bundles is often divided up into wedge-shaped masses by radial extensions of the medullary parenchyma.

The convergence internally of the xylem-bundles in pairs forming V's, between the arms of which lie phloem-groups, was described in *Diplothemium maritimum* and *Chamædorea elegans*.

Karsten (2), in 1847, added to our knowledge of the anatomy of palms in a magnificently illustrated paper, in which a figure of the origin of adventitious roots is given showing some indication of the internally penetrating vascular strands in *Iriartia præmorsa*, Kl., and a figure of the lobed cylinder in the same species. A longitudinal figure of the apex seems to show that he found a single undifferentiated apical meristem.

Naegeli, 1858 (3), Russow, 1875 (4), and Falkenberg, 1876 (5), contributed incidentally to our knowledge of the histological structure of palm-roots, and De Bary, 1877 (6), summarized the work of all preceding investigators.

Van Tieghem, 1870 (7), in his first monograph on 'La symétrie de structure dans les Plantes vasculaires, (i.) La Racine,' describes the roots of *Phœnix dactylifera* and *Seaforthia elegans*.

Olivier, 1880 (8), cites Flahault's work on the primary root-apex in *Phœnix dactylifera*, describing it as possessing a well-defined plerome-initial group and a second group common to the other layers. Olivier also describes and figures a zone of sclerenchyma in the internal portion of the parenchymatous cortex, immediately external to the endodermis.

Mangin, 1882 (9), in a very important paper entitled "Origine et Insertion des Racines adventives . . . chez les Monocotyledones," gives an accurate account of the connection of the bundles of adventitious roots with those of the stem. He shows that the young root first appears as a papilla formed by local hypertrophy of the pericycle; in this young root the vascular elements arise and differentiate both internally, *i. e.*, in the ground-tissue of the central cylinder of the stem, acquiring connection with the scattered stem-bundles, often penetrating very deeply into the stem, and also externally into the developing root-apex, keeping pace with the growth in length of the young root, in which the bundles are arranged in a circle embedded in a fibrous or sclerenchymatous zone generally conforming to the typical root-structure of Monocotyledons.

Drude, 1887 (10), in his article on the Palmaceæ in Engler and Prantl's 'Natürlichen Pflanzenfamilien,' gives a short account of the buttress-roots and contractile roots of some palms.

Cormack, 1896 (11), made a great step in advance when he discovered what he termed a "polystelic" condition in the roots of *Areca*, and the common occurrence of a lobed and interrupted cylinder in many palm-roots. He grouped the arrangements met with under several headings, commencing with the normal type possessing a complete endodermis surrounding a central fibrous or sclerenchymatous ring in which lie the xylem and phloem elements. Passing through the condition in which the cylinder is still complete, but longitudinally lobed, the endodermis dipping into the depressions but being quite continuous, he came to those roots in which the central cylinder is composed of a series of independently running strands of fibrous tissue presenting the form of arcs of circles in transverse section; between these the endodermis dips in and becomes discontinuous; and finally he described the case of *Areca*, where one or more of these independent strands presents a complete radially symmetrical cylinder or "stele," as he terms it, round which the endodermis is complete. Cormack further shows that some roots exhibit the more complicated of these conditions in the proximal regions and the simpler types in the distal, and discusses the question as to whether this is due to secondary changes in the proximal regions brought about by dilatation-parenchyma, or other agency, acting subsequently to the apical development, or whether it is due to progressive simplification of the apical mersitem. He inclines to the latter view, supporting his contention by an ingenious deduction from the number of protoxylem-groups. He finds that the number of these is less in the distal and apical regions than in the proximal, and points out that production of a greater number of protoxylem-groups by secondary changes is extremely improbable if not impossible, and hence concludes that we are here dealing with a gradual reduction and simplification as apical development proceeds.

Cormack attempts an explanation of the peculiarities of structure met with in palm-roots based on physiological considerations of mechanical support, but does not attempt a morphological explanation.

Gillain, 1900 (12), describes the structure of the roots in a large number of Palms, but, curiously enough, he finds none with lobed or divided cylinders. He notices that

the lateral roots in certain cases run through the cortex of the parent root for some distance before emerging. He finds three meristematic layers in the root-apex of *Kentia Forsteriana*, viz.: one for the plerome, one common to periblem and "dermatogen," and one for the root-cap.

Outline of Results of the present Investigation.

Mangin's account of the presence of many deeply penetrating strands of xylem and phloem establishing connection with the bundles of the stem is confirmed. These are traced into the apex of the young root as *separate strands* with such protoxylem as they possess arranged in an exarch manner, roughly alternating with phloem-groups. It is shown that these procambial strands, consisting of fibrous tissue enclosing xylem and phloem elements, are developed in a common ground-tissue at the non-stratified apex of the root, and that as development proceeds the more peripheral of these strands become arranged in what is at first an incomplete ring, passing distally into first a lobed cylinder, and finally into the normal cylinder of the root. All these stages are due to progressive changes in the procambial tissue of the meristematic apex.

Some of the more internal procambial strands do not enter into the fibrous ring, but persist as the well-known medullary strands, each presenting proximally a radial structure, with xylem and phloem well developed, but reduced distally, so that we find (i.) strands containing a few vessels only, accompanied by one or more phloem-groups; (ii.) one or two large vessels and a few smaller ones, unaccompanied by phloem; and (iii.) a single large vessel without accompanying smaller vessels or phloem.

All cases examined show the presence of a central cylinder composed of separate strands, passing into the lobed cylinder (*i. e.*, Cormack's *Areca*-type) in that portion of the root which runs through the cortex of the stem.

Usually the apex undergoes complete simplification while passing through the cortex of the stem, resulting in the production of a normal root cylinder, and hence the external root is normal; but in certain cases (e. g., *Areca*, *Kentia*, &c.) the simplification is much more gradual, the external root exhibiting the completely separate strands, as in *Areca* sp., or the lobed cylinder, as in *Kentia* sp.

In consideration of the method of development, it is claimed that the idea of a pith as a separate morphological entity is entirely precluded, the central parenchyma being merely that portion of the common ground-tissue which becomes enclosed by the gradually approximating and finally uniting procambial strands of the apex; it is always in complete continuity with "cortical" parenchyma proximally.

Buscalioni's account of the centrifugal appearance of the xylem elements of the bundle in roots of Monocotyledons, followed by the centripetal lignification, is confirmed for the palms; and the large scattered internal vessels of the fibrous cylinder are shown to be the persisting metaxylem elements of strands whose protoxylem has aborted.

ANATOMY AND HISTOLOGY OF THE ROOTS OF PALMS.

Origin of Adventitious Roots in the Stem.

The adventitious roots of the Palms have their origin in the pericyclic tissue of the base of the stem, in accordance with the method described by Van Tieghem and Douliot (13) for flowering-plants in general. The base of the stem is clothed with a dense cortex, usually very fibrous in nature and of considerable thickness, varying in different plants, but frequently several inches thick. Hence the pericyclic root arises deeply in the tissues of the parent stem. The root originates as a small papilla produced by division of the pericyclic cells. This papilla is provided externally with an extra-calyptral mantle or *poche* of small parenchymatous thin-walled cells, which presents its maximum thickness immediately over the apex of the papilla, thinning out laterally and exposing the underlying cells of the root-papilla.

Below the *poche* the apex is occupied by a group of meristematic cells, which, followed laterally, is seen to be separated into a thin external layer and a central group in which arises the procambial tissue, a zone of dark-coloured cells which eventually gives rise to the tegumentary system intervening between the two (Pl. 48. fig. 1, *a*, and fig. 3, *a*), exactly as figured by Karsten (2). The procambial tissue is here found in the form of a series of separate strands, which can be followed inwards into the stem for a considerable distance, running roughly at right angles to the stem-bundles (fig. 1, *proc.st.*). Thus only the distal extremities of the procambial strands are laid down in the shallow root-papilla, the internal portions arising by secondary divisions in the ground-tissue of the stem, as described by Mangin (9). The elements in this region are well differentiated, while the root itself is a mere pericyclic papilla (Pl. 48. fig. 1).

A slightly older root (fig. 3) presents essentially the same features. The papilla is now, however, considerably elongated and flexed downwards. Over the apex is the *poche*, which is continued for only a short distance up the root, the tegumentary tissue being exposed above it. The procambial tissue is here also in the form of separate strands (fig. 3, *proc.st.*).

In the cortex occur cells containing raphides. A transverse section through the apex of a pericyclic root-papilla shows a series of procambial groups of varying tangential extent scattered throughout the ground-parenchyma (fig. 7). In many cases the scattered procambial groups are much smaller and more numerous than in the root of *Kentia* figured. The more peripherally placed strands are delineated very definitely from the ground-parenchyma externally, but internally are much less distinctly bounded.

Passage of the Root through the Cortex of the Stem.

The root from its very inception projects into a well-formed cavity lying between it and the surrounding cortical tissues (Pl. 48. figs. 1, 2, and 3, *c*). This cavity is bounded by ragged cells, which show very clear signs of solution and disintegration. The external cells of the *poche* also show a similar appearance, and in some cases immediately outside the *poche* quite a mass of disorganized tissue occurs. The fibres of the cortex resist the solvent action longer than does the parenchyma, but eventually they,

too, are destroyed, and the mineral matter, so often associated with the fibres, remains in the disorganized tissue in the form of scattered crystalline bodies.

Some of the parenchymatous cells of the cortical tissue in front of the advancing root-apex possess very dense granular protoplasm and large nuclei, thus presenting the normal appearance of secretory cells (Pl. 48. fig. 4). The elements which intervene between these and the cavity surrounding the young root are very clear and refractive, showing signs of approaching solution. It seems highly probable that a process of partial auto-digestion of the cortex, no doubt in response to a stimulus received from the young rootlet, precedes the final solution and absorption by the *poche*. Should this prove to be the case, it will afford an interesting parallel to Prof. Reynolds Green's observations on the digestion of the endosperm in certain seeds. He shows that solution is not entirely dependent on the direct action of the embryo, but sets in as the result of metabolic activity induced by the endosperm-cells themselves.

Root-apex.

Janczewski (14) described the root-apex of Monocotyledons as presenting a well-defined plerome-initial layer, a calyptrogen-layer, and an intermediate layer only one cell in thickness which splits behind the apex into dermatogen and periblem.

Treub (15) finds in palm-roots a well-defined pleromic group, covered by an initial layer common to calyptrogen, dermatogen, and periblem.

Cormack (11) describes the larger roots as possessing an "enchevêtrement des trois initiales."

Gillain (12) investigated the apex of *Kentia Forsteriana*, and says: "dass derselbe dem gewöhnlichen Typus der *Monocotyledonen* entspricht, also drei Schichten zeigt: eine für Plerom, eine gemeinsame für Periblem und Dermatogen und eine für die Würzelhaube," being thus in agreement with Janczewski.

In the present investigation the apices of large roots of *Areca* sp. and *Kentia* sp. were examined in serial microtome-sections, taken both longitudinally and transversely. The meristem was found to consist of a common initial group similar to that described by De Bary for *Vanda* (6) and by Janczewski (14) for the Cucurbitaceæ and Papilionaceæ (Pl. 48. figs. 5 & 6). The apical meristem is very bulky, and this renders it somewhat difficult to determine the median section. There is no doubt, however, that from this common apical group radiate lines of cells in all directions, the outer cells giving rise to the root-cap, the lateral ones to the "cortical" portion of the ground-parenchyma, and the axial cells to the "medulla."

In the ground-parenchyma certain strands of cells become slightly elongated and produce the procambial strands, which are thus merely local differentiations in the common ground-tissue (Pl. 48. fig. 5, *proc.tiss.*).

If the root be a short one (*i. e.*, if it has not progressed far beyond the pericyclic-papilla stage), the procambial tissue will be found to have the form of a series of independent strands (Pl. 48. figs. 7 & 8). More distally in a longer root it will present the form of a lobed cylinder (Pl. 48. fig. 9), and in a still longer root that of a complete circle (Pl. 48. fig. 10) as in the normal roots of Monocotyledons.

A transverse section through the apex in the region of the meristem-group shows radiating lines of cells extending from the centre to the periphery, the various layers of the root arising by subsequent differentiation in these cells.

Root-cap.

A longitudinal section of the apex shows the root-cap to be merely a local specialization of parenchyma formed from the extremities of the rows of cells radiating from the common meristematic group. As these cells approach the surface they become elongated (Pl. 48. fig. 13) and gradually exfoliate. The cells are dark-coloured; the middle lamella is destroyed by strong sulphuric acid, and the individual elements can be thus isolated. The internal walls are highly cuticularized and very resistant to the action of the acid.

In the outer cells the lumina may be entirely occluded by a dark-coloured substance giving cork-reactions.

Partial occlusion resulting in considerable reduction of the lumen may occur in more internal cells of the root-cap (Pl. 48. fig. 14).

The macroscopic appearance presented by the root-cap in *Kentia* and most other forms is that of a much-indurated dark-coloured smooth coating to the apex, extending for about an inch up the root (Pl. 48. fig. 11).

In *Areca* sp. (Pl. 48. fig. 12) and *Iriartia* sp. a different form of root-cap is shown. Instead of presenting a smooth surface, the outer layers of the cap are partially exfoliated and appear as an irregular covering of overlapping scales, closely resembling the same structure in *Philodendron* figured by Olivier (8) and in *Pandanus* figured by Van Tieghem (16).

The Limiting or Piliferous Layer.

An inch or so from the apex the root-cap is entirely exfoliated, or only represented by a few isolated broken-down elements adhering to the surface of the root. More proximally the surface is occupied by the so-called "limiting layer" ("epidermis" of authors). The term "piliferous layer" is not generally applicable in a strict sense in Palms, as in no case was any development of root-hairs observed. Gillain (12), however, appears to have found them in one instance, as he says: "nur bei *Trachycarpus excelsus*, finden wir Haargebilde." The cells of this layer frequently project as papilliform structures, as described and figured by Karsten (2) for *Iriartia*.

The walls of this layer are generally cuticularized and comparatively thin. This layer is shown for *Kentia* in Pl. 48. fig. 14; for *Caryota ochlandra* in Pl. 48. fig. 15; for *Phoenix sylvestris* in Pl. 48. fig. 16; and for *Dypsis madagascarensis* in Pl. 48. fig. 17.

The limiting layer does not represent any definite morphological stratum, but cuts through a series of lines of cells radiating from the meristem. It can be traced in an apical direction for a considerable distance underneath the root-cap, the cells becoming gradually smaller the nearer they approach to the apex. At the apex it is quite impossible to say which cells will form the limiting layer.

The cells of this layer do not necessarily form a perfectly regular sheath, irregularities such as that figured in fig. 14 being not uncommon.

Tegumentary System.

Beneath the limiting layer usually lie several layers of elongated, lignified, and more or less pitted cells, followed internally by lignified fibrous elements. These together form the outermost cortical zone and will be referred to as the Tegumentary System. In such a case lignification commences in the external layers of the outer zone of square-ended cells and proceeds centripetally. Whilst this is going on, lignification sets in in the more internal fibrous zone and proceeds centrifugally. In many of the roots examined a layer of cellulose-walled elements intervenes between the two zones of the tegumentary system, which has not yet been reached either by the centripetally or the centrifugally proceeding lignification. This is well shown in *Phoenix sylvestris* (Pl. 48. fig. 16). In other cases lignification may be extensive in the outer zone but absent in the internal fibrous zone, and here lignification proceeds centripetally only, as in *Caryota ochlandra* (Pl. 48. fig. 15) and *Livistona chinensis*. In *Dyopsis madagascarensis* (Pl. 48. fig. 17) the two outer layers only are lignified; these are followed by six or seven layers of square cells with dark contents, which resist the action of strong sulphuric acid and give all the reactions of cork.

In *Cocos nucifera* the tegumentary layers are much indurated.

In *Corypha australis* the outer elements are lignified, thick-walled, and pitted; the inner ones are square-ended and pass gradually into the internal parenchymatous cortex.

In *Sabal Palmetto* the outer elements alone are lignified and *all* are parenchymatous. In *Plectrocomia elongata* the inner elements are densely lignified and their lumina are almost occluded, while the outer layers are much less strongly lignified. The same holds good for many roots of *Kentia* sp. In *Ptychosperma perbrevis* the outer elements are fibrous and possess transverse walls, while the inner consist of extremely thick-walled deeply-pitted fibres. In *Phoenix dactylifera* the tegumentary layers are non-lignified, but cuticularized.

Many roots possess mucilage-cells in the tegumentary layers. These may be scattered through the outer zone, any cell being potentially a mucilage reservoir, as in *Dictyosperma album* and *Kentia Forsteriana*, or through the inner zone, as in *Cyrtostachys Renda*; or very definite mucilage-elements may be present, as in *Caryota* sp. (Pl. 49. fig. 42), where they take the form of elongated very thick-walled cells arranged in longitudinal series and containing raphides.

Both outer and inner zones originate as small-celled parenchymatous tissue in the apex (Pl. 48. figs. 13 & 14). The outer elements usually elongate and become pitted, but retain their square ends, while the inner elements generally become prosenchymatous.

The Inner Cortex.

The inner cortex, or cortex proper, viz., that region intervening between the tegumentary layers and the endodermis, is always composed of parenchymatous tissue, and is usually provided with lignified elements and large air-spaces.

The inner cortex may be divided into three zones: an external, which is usually without air-spaces; a broad middle zone, with large air-spaces; and an internal zone, in

which the cells are more regularly arranged, conforming to the description given by Olivier (8) for the internal cortical zones in Monocotyledons.

Air-spaces.

The development of the cortical air-spaces was followed in *Kentia* sp. and in *Areca* sp. The process was found to be exactly similar in each.

A short distance behind the apex certain cells, usually in small groups of two or three as seen in transverse section, lose their contents and present a very refractive appearance in their walls (Pl. 48. fig. 18). These walls sooner or later disintegrate, and in this way a lysigenous space is formed (Pl. 48. fig. 19). These spaces enlarge by the disintegration of more cells, and their boundaries nearly always present the remains of the partially dissolved cells (Pl. 48. fig. 20).

Various Forms of Air-spaces.

In *Phytelephas macrocarpa* (Pl. 48. fig. 21) the air-spaces are always small, even in the mature root, being formed merely by the disintegration of 3-10 cells as seen in transverse section. These spaces are irregularly scattered throughout the cortex.

In *Kentia* sp. (Pl. 48. fig. 20) the air-spaces are more extensive and are radially elongated; they are very numerous and irregularly scattered.

In *Metroxylon Sagu* (Pl. 48. fig. 22) they are more confined to the internal zone of the cortex, and in *Iriartia* sp. (Pl. 48. fig. 23) only a single ring of rounded cavities is present in the innermost cortical zone, immediately surrounding the endodermis.

In *Phoenix sylvestris* (Pl. 49. fig. 30) they are very numerous and occupy nearly the whole of the cortical region. They are more or less rounded, having individually very little radial extension, and are separated from one another only by a single or double layer of cells.

In *Caryota australis* (Pl. 49. fig. 29) the disposition is similar, but here the remains of the disintegrated cells may be clearly seen as diaphragms in the lumina of the air-spaces. The same is true to a less extent in *Phoenix sylvestris* (Pl. 49. fig. 30). In *Licuala spinosa* (Pl. 49. fig. 28) the spaces are radially greatly extended and occur in two rings, the spaces of the inner ring being much larger than those of the outer. In *Licuala gracilis* (Pl. 48. fig. 24) there is only a single ring of radially very extensive spaces, which extend almost from the endodermis to the tegumentary layers.

The air-spaces present no resistance to the growth of the surrounding parenchyma, and in some cases (e. g., *Areca Catechu*) advantage is taken of this; some of the surrounding cells project into the cavity and there swell and undergo division (Pl. 48. figs. 25 & 26), and in this way the air-spaces may become completely filled with a secondary tissue. This tissue becomes lignified and pitted and the peculiar condition figured in fig. 27 results.

Lignified Elements of the Cortex.

Nearly all palm-roots possess some lignified elements in the parenchymatous cortex. Only in *Phytelephas macrocarpa* (Pl. 48. fig. 21), *Thrinax parviflora*, and the contractile roots of *Corypha umbraculifera* was lignification found to be entirely wanting.

The simplest form in which lignification appears is that of lignified parenchyma. This occurs in *Latania borbonica*, *Cocos nucifera*, and *Acanthoriza australis*. The cell-walls are thin, and only differ from normal parenchyma in their reactions. In *Sabal Adansonii* the elements are distributed throughout the cortex, and in all specimens of *Licuala* (Pl. 48. fig. 24 & Pl. 49. fig. 28) and *Livistona* examined they occur in longitudinal strands. In these genera the walls are thicker and are pitted.

In *Cocos botryophora*, *Diplothemium maritimum*, *Bactris minor*, and *Sabal Palmetto* (Pl. 49. fig. 33) some of the elements become definite stone-cells in the innermost zone of the cortex; and in *Cocos plumosa* and *Caryota urens*, a definite zone of stone-cells surrounds the endodermis. These elements are first mentioned as occurring in palm-roots by Gillain (12). He, however, only gives a short description and does not figure them. They are usually thick-walled, deeply pitted, square elements, but they may be quite spherical or may be elongated. In *Caryota urens* the thickening of the walls is so extensive that the lumina are almost entirely occluded.

Quite a different type of element is represented in the fibres so plentifully developed in most palm-roots. These are of two distinct types:—

(a) The *Kentia*-type. These are long-pointed elements, with comparatively thin and more or less pitted walls and large lumina. In some cases transverse walls are present, as in *Euterpe* sp.

These fibres may occur singly, as in *Hyophorbe amaricaulis* (Pl. 49. fig. 35), *Latania Loddigesii*, and *Euterpe* sp., but are much more generally collected into bundles as in *Kentia* (Pl. 48. fig. 20 & Pl. 49. fig. 36), *Areca Catechu* (Pl. 48. fig. 25), and *Cyrtostachys Renda*. In this last species the fibres conform generally to the *Kentia*-type, but are shorter than usual.

(b) The *Raphia*-type. These fibres are longer, narrower, thicker-walled, and more densely provided with simple pits than are those of the *Kentia*-type. They may occur singly, as in *Pinanga Kuhlii* and *Pinanga* sp.; but are nearly always collected into very definite bundles traversing the cortex, as in *Raphia Hookeri* (Pl. 49. fig. 37), all species of *Phoenix* examined (Pl. 49. fig. 30), *Metroxylon Sagu*, *Dictyospermum album*, and *Seaforthia elegans*, the last species being particularly richly supplied.

Bundles of fibres of the *Raphia*-type are generally provided externally with the so-called *stegmata*, under which name Mettenius (17) described certain small cells of the nature of "covering-plates" occurring in *Trichomanes*. Rosanoff (18) showed that these occur commonly in Monocotyledons also. De Bary (6) says "they always appear on the outer surface of sclerenchymatous or sclerotic bands of fibres (either such as pursue a separate course or accompanying vascular bundles) and are applied to these in longitudinal rows. The single elements are small and have the form of flat or (in Monocotyledons) plano-convex, usually rectangular plates with the flat side contiguous with the fibrous band. As regards their structure, they are characterized by unequal thickening on different sides, usually also by partial silicification of their walls. . . . The fibrous bands in the stems, leaves, and roots of . . . Palms (*Chamærops*, *Phoenix*, *Caryota*, &c.) . . . have interrupted longitudinal rows of plano-convex stegmata on their surface. The convex outer wall of these is thin, the inner thickened to a half-

spherical rough body, which almost fills the cavity and consists mostly of compounds of silicon."

In the Palms examined these stegmata have only been found in connection with the *Raphia*-type of fibre (Pl. 49. figs. 37 & 32, *steg.*). In general they agree very well with De Bary's description, but the body of the roughened inner wall, though showing some silification, also appears to be rich in calcium oxalate, as might be expected, when it is remembered how constant is the association of this substance with any rapidly growing tissue (apices) or elongating elements (fibres). Percival (19) has recently called attention to crystals of calcium oxalate in the cells bordering the developing fibres in *Trifolium*, and it appears certain that this substance is in some way intimately associated with carbohydrate metabolism, probably being formed by the precipitation of oxalic acid or acid potassium oxalate in an insoluble form, as believed by Schimper.

In the above account of the stereome-tissues of the cortex, no mention has been made of the association of different types of element, although it is very unusual to find one type alone represented.

Lignified parenchyma occurs alone in *Latania borbonica*. It is associated with stone-cells in *Cocos botryophora*, *Diplothemium maritimum*, *Bactris minor*, *Sabal Palmetto* (Pl. 49. fig. 33), *Caryota Rumphiana*, and *Caryota urens*, and with fibres of the *Raphia*-type in *Martenezia Lindeniana*, *M. caryotifolia*, *Hyphaene thebaica*, and *Plectocomia elongata*.

Stone-cells have in no case been found to occur alone. They are associated with lignified parenchyma in the roots mentioned above, and with fibres of the *Kentia*-type in *Oncosperma fasciculatum*.

Fibres of the *Kentia*-type occur alone, both individually and in bundles, in *Ptychosperma perbrevis*, and in *Actinorhysis Calapparia*, where they are of the *Kentia*-type in the external zones, but more definite within.

Fibres of the *Raphia*-type occur alone in *Dictyosperma album*, where they are very abundantly developed, and in *Metroxylon Sagu*.

In *Arenga Wightii* lignified parenchyma, stone-cells, and fibres of the *Raphia*-type occur.

In the young root of *Dictyosperma album* a bundle of fibres with two small tracheidal elements was found, and in *Iriartia* sp. each bundle of fibres contains centrally a thin-walled element, presenting the appearance of a young sieve-tube, but it was impossible to obtain material of roots in which the development was sufficiently advanced to settle this point. De Bary (6) observed the same thing, and says, "in the outer parenchyma of the cortex numerous small bundles of sclerenchymatous fibres lie, each enclosing in its centre 1-2 thin-walled elongated elements (perhaps sieve-tubes?)."

Lignification in any bundle of fibres commences in the external elements and progresses towards the centre.

In some mature roots the external fibres of any bundle may be fully lignified, while the inner elements retain their cellulose walls.

These results may be summarized as follows:—

The simplest form of lignified element—namely, the thin-walled parenchymatous cells,

whose walls give lignin-reactions—may undergo specialization in one of two directions:— (1) The walls may become thickened and pitted, the extreme form being a densely sclerosed stone-cell, or (2) elongation of the cell may take place, leading to the appearance of individual, comparatively thin-walled fibres scattered irregularly throughout the parenchymatous cortex. Fibres of this type are often collected into bundles—the *Kentia*-type of the foregoing description. In other cases the fibres are greatly extended and their walls considerably thickened with consequent reduction of the lumina. This latter type of fibre—the so-called *Raphia*-type—usually occurs in bundles, accompanied externally by small crystal-containing sacs, or stegmata.

Mucilage-sacs and Raphides-containing Elements.

The cells of the tegumentary layers frequently contain dark-coloured mucilage. Occasionally definite thick-walled mucilage-reservoirs containing raphides are also present in this zone, as in *Caryota* sp. (Pl. 49. fig. 42).

Individual mucilage-cells may also be scattered throughout the cortex and pith.

Specially developed elements containing bundles of raphides composed of calcium oxalate embedded in mucilage are regularly formed at the apex. These first appear as elongated cells in the cortical or medullary parenchyma, in which bundles of raphides develop, occupying nearly the whole lumen of the cell, the protoplasm and nucleus being relegated to one, usually the upper, end (Pl. 49. fig. 38).

These cells are arranged in rows, and keep pace in growth with the longitudinal extension of the stem, but do not undergo any division. Hence very considerably elongated elements result. The contents of these cells become very mucilaginous (Pl. 49. figs. 38, 39, & 40), and the nucleus appears to fragment (Pl. 49. fig. 40) and finally disappears. These elements are usually very abundant and well developed in the younger portion of the root, but become more or less obliterated in the older portions.

Hanstein (20) discussed the question as to whether the mucilage-spaces in Monocotyledons are formed by the fusion of more than one element by the disappearance of transverse walls, and from his study of *Commelina* concluded that such is the case—raphide-containing vessels resulting.

De Bary (6) was unable to substantiate this. He found, however, that the transverse walls might become perforated by the absorption of water and consequent swelling of the mucilage during the preparation of sections, and suggested that this might also occur in nature. De Bary's conclusion that absorption of transverse walls does not take place is entirely borne out by an examination of the roots of Palms. Here the crystal-sacs just behind the apex are nearly filled with raphides (Pl. 49. fig. 38). About half an inch behind the apex the cells have grown considerably in length, as have also the crystals themselves, but the transverse walls are still as definitely present as in the first case, no signs of any disappearing walls being seen (Pl. 49. fig. 39). In the older regions of the root the crystal-sacs have increased still further in length, and the bundles of raphides are very short in proportion to the length of the containing element (Pl. 49. fig. 40). If the long crystal-sac had been formed by cell-fusions several bundles of raphides should occur. Such is, however, not the case, and it is concluded that longitudinal fusion of cells

does not take place. It is probable that the walls of the original sac become mucilaginous and disappear in the old root, and that the bundle of raphides, with its enclosing mucilage, does not occupy a cell at all, but rather an intercellular space which may become enlarged to any extent by growth of the surrounding elements.

Endodermis.

Round the normal cylinder the endodermis forms a complete circle. In the roots with a lobed cylinder the endodermis follows the contours of this, and in those cases in which the cylinder is made up of a series of separate strands the endodermis is well developed on the peripheral surfaces, but internally is lost, becoming merged into the general ground-parenchyma, except in a few cases, e. g., *Areca* sp., where a complete endodermal investment surrounds one or more of the strands.

The endodermis is composed of a single layer of cells, except in *Iriartia* and *Kentia* (Pl. 49. fig. 48), where local doubling was observed. The constituent cells are generally 3-6 times longer than broad (Pl. 49. fig. 46), but in contractile roots of *Corypha umbraculifera* they are short and square.

Occasionally, as in *Sabal Palmetto*, *Areca Catechu*, *Hyphæne thebaica*, and *Latania Loddigesii*, the cell-walls are composed of cellulose; in contractile roots of *Corypha umbraculifera* they are cuticularized, but much more commonly they are lignified.

In *Plectocomia elongata* the walls are very slightly lignified; in nearly all cases, however, all the walls except the external tangential are densely lignified and thickened in a manner recalling that of the cells composing the fibrous layer of an anther, as first pointed out by Von Mohl (1) (Pl. 49. fig. 46). The internal wall is uniformly thickened and deeply pitted. From this extend bands of thickening on the radial walls, while the external walls are usually not thickened or only very slightly so (Pl. 49. figs. 45 & 47). This condition obtains in *Phœnix sylvestris* (Pl. 49. fig. 30), *Licuala gracilis* (Pl. 48. fig. 24), *Licuala spinosa* (Pl. 49. fig. 28), *Livistona olivæformis* (Pl. 49. figs. 45 & 46), *Kentia* (Pl. 49. fig. 47), and in the majority of palm-roots.

In *Raphia Ruffia* the thickening is almost equally deposited all round, the external tangential walls being thickened, and in *Metroxylon Sagu* the lumina are almost obliterated.

Non-lignified passage-cells are generally wanting, but occasionally occur. In *Phœnix sylvestris* they may occur at any point. In *Kentia* (Pl. 49. fig. 47) two or three may occur together, generally opposite the protoxylem.

The process of lignification of the endodermis was followed in *Phœnix reclinata*. There is a tendency for it to commence opposite the phloem-groups, but this is by no means invariably the case. Usually several cells in contact, forming a tangential row, undergo lignification at the same time, their lateral neighbours being at this time quite unaltered, although they may later all undergo complete lignification, the mature root in this species showing no passage-cells.

A peculiar condition was observed in the endodermis of *Corypha australis* and the non-contractile roots of *Corypha umbraculifera*, some cells being cuticularized, while the rest were lignified.

Pericycle.

The pericycle is usually a very definite layer, but in the contractile root of *Corypha umbraculifera* it is ill-defined. Lignification generally obtains (Pl. 49. figs. 45 & 46), but in *Plectocomia elongata* and *Phoenix sylvestris* the walls are thin and consist of cellulose. In *Sabal glaucescens* the elements are non-lignified, but scalariformly marked. In *Hyphæne thebaica* lignification is partial and in *Sabal filamentosa* general, but cellulose walls occur, particularly opposite the protoxylem.

The individual elements are almost invariably several times longer than broad, as in *Livistona olivæformis* (Pl. 49. fig. 46).

In *Arenga Wightii*, however, they are short and square.

The pericycle may be one layer of cells in thickness throughout, as in *Livistona oliviformis* (Pl. 49. figs. 45 & 46), *Caryota urens*, and *Caryota* sp.; or may be irregularly doubled opposite the phloem in *Sabal Adansonii*.

In other roots the pericycle is two-layered throughout. This occurs in *Areca Catechu*, *Caryota Rumphiana*, *Phoenix reclinata*, where the lignification is greatest opposite the phloem-groups; *Metroxylon Sagu*, in which the cells of the inner layer are much reduced in size opposite the protoxylem; and in *Geonoma pumila*, where the pericycle is compressed opposite the protoxylem and expanded opposite the phloem.

In *Cocos nucifera*, *Kentia* sp. (Pl. 49. fig. 47), *Sabal filamentosa*, and *Hyphæne thebaica* the pericycle is typically two-layered, but is irregularly reduced to one layer at any point; while in *Cocos botryophora* and *Cocos plumosa* reduction to one layer occurs only opposite the protoxylem, and in *Latania Loddigesii* opposite both xylem and phloem.

In *Arenga Wightii* the two-layered pericycle becomes irregularly three-layered locally, and in *Sabal glaucescens* three layers occur opposite the phloem, the pericycle being elsewhere two-layered.

In *Sabal Palmetto* the pericycle is three-layered, and only reduced to two layers opposite the protoxylem.

In *Phoenix sylvestris* the pericycle is interrupted opposite the protoxylem and the external vessels abut directly on the endodermis, as De Bary (6) showed to be the case in grasses.

Fibrous Zone of Sclerenchyma.

Following the pericycle internally is a zone of fibrous tissue, generally of considerable radial thickness, in which lie the elements of the xylem and phloem. This normally presents the form of a regular circle in cross-section, e. g., *Sabal filamentosa* (Pl. 50. fig. 75), but may be lobed internally, as in *Phoenix dactylifera* (Pl. 50. fig. 68), externally (Pl. 50. fig. 88), or may be incomplete on one side, as in *Dypsis madagascarensis* (Pl. 50. fig. 63), or broken up into a number of separate strands, as in *Areca* sp. (Pl. 50. fig. 56).

The elements of this zone are usually elongated lignified fibres, generally thick-walled and pitted. In some cases they are very densely lignified and indurated, as, for instance, in *Martinezia caryotifolia*.

Sometimes the elements are square-ended and shorter, being of a more definitely sclerenchymatous nature.

The fibres arise in the procambial strands, or procambial cylinder, as the case may be, at the apex of the root, and form the ground-tissue of these structures. The elements are at first small, somewhat elongated and square-ended, subsequent growth resulting in the fibrous nature of this tissue.

Lignification sets in in a number of circles, each surrounding a large internal vessel of this zone, and proceeds towards the vessel from all sides; often even in a very large and mature root one or more layers of cells immediately surrounding the vessel may be non-lignified.

The protoxylem elements also are frequently embedded in a cellulose-walled group of cells.

The Vessels.

The vessels of the xylem occur in radial groups with exarch protoxylem, having the normal arrangement for monocotyledonous roots. These are very often accompanied internally by large vessels scattered throughout the fibrous zone.

The external elements of the protoxylem are thickened in an annular manner (Pl. 49. fig. 46) and are generally lignified early. The vessels of the metaxylem are scalariformly thickened, as are also the large internally scattered vessels. These latter are frequently quite without lignification, even in the mature root, the wall giving a very different cellulose reaction with iodine and sulphuric acid.

The arrangement of the scalariformly marked areas is of the nature commonly met with in large roots of Monocotyledons and in large tracheids of ferns, but is here more regular than usual (Pl. 49. fig. 49).

In the large vessels the transverse walls marking the originally distinct elements from which the vessel is built up often partially persist, and in any case the vessel is constricted at these points, the whole structure when separated out by Schultze's macerating-fluid presenting a moniliform appearance.

The internal vessels are often very large, particularly in *Corypha umbraculifera* (Pl. 50. fig. 70).

In some cases they are closely packed and lateral pressure has led them to adopt a radially elliptic form instead of the usual circular outline.

The elements immediately surrounding one of these large vessels are sometimes marked in a scalariform manner in the same way as the vessel itself; these elements are expanded at the points of constriction of the vessel and fill the depression (fig. 49). A mass of deeply staining mucilaginous substance is often found in the vessels in the region of the partially disintegrated transverse walls.

In certain cases the transverse walls may be thickened and lignified in bands stretching across the end-plate; the rest of the end-plate may then disappear, leaving trabeculae of lignified material extending across the cavity of the vessel.

Thylosis-formation is of very frequent occurrence in the larger vessels. This is particularly well shown in *Areca concinna* (Pl. 49. fig. 51) and *Cocos flexuosa* (Pl. 49.

fig. 50), where the development was traced and was found to follow the normal course, the surrounding parenchyma extending into the lumen of the vessel through the pits, and presenting the appearance of small rounded globules projecting freely; these are then cut off by a wall and undergo division, finally filling the vessel with a parenchymatous tissue, which may later become lignified and pitted.

The development of the vessels was traced in *Kentia* sp. and in *Areca* sp. They first appear as longitudinal rows of cells in the apex, a short distance behind the meristematic group. Each cell is of considerable diameter as compared with the surrounding elements, but is very shallow. Each is richly provided with protoplasm and has a large nucleus. Further back the individual elements of the strand are much elongated and the nucleus is beginning to disappear, while still further up the root the nucleus has quite gone, and the disintegrating protoplasmic contents have shrunk from the walls of the cells except the end walls. In a still older vessel the protoplasmic contents are greatly reduced and have passed into a dark-coloured mucilaginous mass at one or both ends of the cells near the transverse walls, whose dissolution takes place only very late in the development of the vessel, and may even be incomplete in the mature root.

In no case was there any trace of the origin of vessels by the breaking down of more than one cell in the lateral direction as described by T. G. Hill for *Dioscorea* (21).

The order of appearance of the vessels is centrifugal, the large scattered vessels when present being the first to appear in centrifugal order, followed in turn by the metaxylem and the protoxylem of the bundles, the last elements to develop being the external vessels of the protoxylem. Thus the Palms conform to the account given by Buscalioni (22) and Pirotta (24) for several Monocotyledons, and confirmed by T. G. Hill (21) in *Dioscorea*. Lignification of the xylem takes place in a centripetal direction.

Sieve-tubes.

The sieve-tubes are principally grouped together into phloem-bundles alternating radially with the protoxylem group. In *Latania Commersonii* (Pl. 50. fig. 72), however, they occur also in strands scattered throughout the fibrous zone among the large internal vessels. Phloem also occurs in a few roots in connection with the vessels in the medullary strands described below, and in *Iriartia*, as already mentioned, what appears to be an immature sieve-tube occupies the centre of each fibrous group in the cortex.

The sieve-tubes are generally rather large thin-walled elements with somewhat oblique sieve-plates. Very little callus was found in any of the tubes.

The companion-cells are thin-walled elements with tapering extremities.

Arrangement of Xylem and Phloem.

Some roots conform to the typical monocotyledonous type in having all the vessels arranged in definite bundles, with exarch xylem followed internally by a series of gradually increasing metaxylem elements. This is found in *Kentia Forsteriana* (Pl. 50. fig. 75) and *Sabal filamentosa* (Pl. 50. fig. 74).

More frequently, however, a series of internal vessels not referable to any particular xylem-groups is also present. In *Phoenix dactylifera* (Pl. 50. fig. 68) only a few of these

are present; in *Phoenix sylvestris* (Pl. 50. fig. 73) there is a single irregular ring of them; in *Latania Commersonii* (Pl. 50. fig. 72) the number of internal elements is greatly increased and they are arranged in two or three irregular rings; while in *Raphia Hookeri* (Pl. 50. fig. 71) and *Corypha umbraculifera* (Pl. 50. fig. 70) they are closely packed and scattered throughout the whole of the fibrous zone, which here extends to the centre of the root, no pith being present.

Mohl (1) observed in *Diplothemium maritimum* and *Chamædorea elegans* that two peripheral xylem-groups might converge internally and abut on a single large internal vessel, thus forming a V-shaped structure, between the two arms of which might lie a phloem-group.

De Bary (6) described this phenomenon as follows:—"In thick root-bundles, some or all of the above xylem-plates converge in pairs in the form of a V, the groups of phloem lying inside a V are often smaller than those lying in between two V's. The latter are frequently large radially placed plates, while the former are roundish groups. This occurs in an exquisite form in the aerial roots of an Aroid cultivated in Halle under the name of *Philodendron Imbe* and also in Palms. . . . In *Chamædorea elegans* the irregularity goes further. In the corner of the V lies a small roundish group of phloem. Between every two V's a similar group lies towards the outside, while further inside a second occurs which is elliptical in cross-section, and is separated from the outer group by interstitial sclerenchyma in which vessels frequently lie. Thus both an inner and an outer row of phloem-groups are present in the otherwise typical bundle."

Simple xylem V's, between the arms of each of which lies a small phloem-group, are found in *Kentia Forsteriana* (Pl. 50. fig. 75) and *Livistona australis* (Pl. 50. fig. 64).

In *Raphia Hookeri* (Pl. 50. fig. 71) a further complication is found, a xylem V often embracing between its arms not a small phloem-group but a phloem V, which again embraces a xylem-group. In this species what may be described as xylem Y's also occur, the external xylem-groups abutting in pairs internally on the outermost element of a radial series of two or more large vessels.

In *Heterospathe elata* (Pl. 50. fig. 73) this peculiarity is still more pronounced. Two xylem-groups approximate internally, forming a V just incomplete at its apex. Between the arms of this lies a phloem V, which in turn embraces a xylem V, and this again a small phloem-bundle. In this root the phloem V's are sometimes incomplete, one limb being continuous with the phloem-group at the apex of the V, while the other is separated from it by an intervention of fibrous ground-tissue.

In *Raphia Hookeri* (Pl. 50. fig. 71) the phloem-groups extend centrally to a greater distance than usual, and in *Latania Commersonii* (fig. 72), as already mentioned, phloem-strands are distributed throughout the fibrous zone.

In *Phoenix sylvestris* (Pl. 50. fig. 73) there is a greater development of xylem-vessels in the radial bundles than is usually found, the metaxylem consisting not of a single radial row of vessels, but of two or more rows.

In *Licuala gracilis* (Pl. 50. fig. 64) internally to, and in close connection with, the larger elements of the metaxylem occur several smaller elements, a point of considerable interest which will be dealt with below.

In *Ptychosperma filifera* (Pl. 50. fig. 65) the metaxylem forms tangentially extensive groups, from the peripheral surface of which extend as many as three protoxylem-groups. In this way a ring of xylem is formed in the periphery of the cylinder, with numerous but narrow interruptions.

In *Cyrtostachys Renda* (Pl. 50. fig. 62) a highly interesting condition is found in the presence of two or more xylem-groups, with inverted orientation, accompanied by phloem, the protoxylem being placed towards the centre of the root, lying in the internal portion of the fibrous ring. These xylem-groups are accompanied laterally by one or two phloem-groups.

A similar but less pronounced feature is seen in *Licuala gracilis* (Pl. 50. fig. 64). Here, however, the inverted xylem is not accompanied by phloem.

In *Latania Commersonii* (Pl. 50. fig. 72) the internal boundary of the fibrous zone abutting on the pith is irregularly lobed and in some of the lobes lies one of the large internal vessels.

In *Phoenix dactylifera* (Pl. 50. fig. 68) two lobes of the fibrous zone, each enclosing a vessel, project deeply into the pith.

In *Sabal glaucescens* (Pl. 50. fig. 67) a band of fibrous tissue extends completely across the pith and in this lie two vessels.

In *Livistona australis* (Pl. 50. fig. 66) a fibrous strand completely separated from the fibrous zone of the cylinder traverses the pith and contains a single vessel, while a similar strand in *Ptychospermum filifera* (Pl. 50. fig. 65) encloses two vessels.

In *Licuala gracilis* (Pl. 50. fig. 64) there are three medullary strands, two of which contain a number of vessels, the larger occupying the centre and the smaller ones radiating from these in a manner generally resembling the arrangement of vessels in a small pithless root—i. e., an exarch radial arrangement of xylem.

In *Areca* sp. (Pl. 50. figs. 55 & 76) the presence of phloem-groups in the medullary strands alternating with the radial xylem-groups heightens the resemblance to a root-cylinder.

As the medullary strands are followed down the roots the number of vessels contained may decrease, but the strands remain as separate structures for a very long distance. In *Livistona australis* one was followed for 12.1 cms. without showing any sign of fusion with the fibrous zone.

JUNCTION OF BUNDLES OF ROOT AND STEM AND ESTABLISHMENT OF NORMAL ROOT-CYLINDER.

Mangin (9), in 1882, found that two distinct methods of junction of the bundles of adventitious roots with those of the stem occur in Monocotyledons. In the majority of forms the bundles of the root join on to a few of the outer bundles of the stem, or, in the case of large roots, on to a considerable number of peripheral stem-bundles. In the Palmaceæ and Pandanaceæ, however, connection is established not only with the peripheral stem-bundles, but also with others more deeply placed, the connecting strands being differentiated *in situ* in the ground-parenchyma of the stem.

In the present investigation the method of junction has been worked out in *Kentia* sp., *Latania borbonica*, and *Dictyosperma album*. In all these the phenomena presented are similar.

A transverse section taken through the stem in the region of connection shows a series of stem-bundles with internal scattered protoxylem followed externally by more densely packed metaxylem, and this in turn by the thin-walled phloem (Pl. 51. fig. 89).

In the ground-tissue separating these bundles run strands of xylem and phloem pursuing a somewhat sinuous course and at their inner extremities establishing connection with the xylem and phloem of the stem-bundles, some of which are peripherally, some deeply placed (Pl. 51. fig. 90). The xylem-elements of these strands are continued into the xylem-portion of the stem-bundles laterally and follow the course of this bundle as constituent elements of it.

In the same way the sieve-tubes pass into the phloem-portion of the stem-bundles (Pl. 51. fig. 89).

These strands may be followed externally into the young root arising in the pericycle, as distinct procambial strands (Pl. 48. fig. 1).

In transverse sections of mature roots close to the base (*i. e.*, just external to the pericycle of the stem), the centre is occupied by a number of free strands of fibrous tissue surrounding in the form of sheaths the xylem- and phloem-elements.

The xylem- and phloem-groups in each strand are radially arranged, with exarch protoxylem. Thus in this region, traversing the ground-parenchyma of the root, occurs not one but a series of cylinders each with a root-like structure.

The endodermis is not well-marked in this region of the root, but may sometimes be seen as an incomplete ring round several of the more external strands.

Some of the strands are very small and contain only a single xylem- and a single phloem-group (Pl. 51. fig. 101). These are the individual bundles, each of which is proximally connected with a single bundle of the stem. Distally, by fusion with one another, they give rise to the radially symmetrical cylinders of this region of the root. The latter again in turn fuse with one another and give larger cylinders with irregular outline and irregularly arranged xylem and phloem. Usually the more peripheral cylinders are the first to fuse, the central ones often remaining as free strands even in the fully developed root. The peripheral cylinders by their fusion give rise to a series of incurved arcs as seen in transverse section, sometimes completed internally, when they enclose a central strand of ground-parenchyma continuous above with the common ground-tissue of the root (Pl. 51. figs. 91 & 92).

By progressive fusion, the number of free strands becomes successively reduced in the more distal region. The closed rings of fused strands with central ground-tissue again open out internally and the edges fuse with those of neighbouring cylinders, and in this way a complete but deeply lobed ring is formed (Pl. 51. figs. 94 & 98). This always remains longest incomplete on the adaxial side. The lobes become gradually more shallow in the distal region, until eventually a simple non-lobed central cylinder of normal root nature is established.

In most roots these changes in the vascular anatomy are completed in that portion of

the root which is enclosed within the cortex of the stem ; but in some cases, particularly in *Kentia* sp., *Areca* sp., *Areca Catechu*, *Areca concinna*, *Dypsis madagascarensis*, and *Iriartia* sp., the separate strands forming an incomplete central cylinder are continued often for a foot or more in the apical direction into the extracauline free portion of the root.

The endodermis is first clearly recognizable in a root showing the condition figured in Pl. 51. fig. 91. Here the external surface of each of the arcs is provided with a lignified endodermal coating, which may be followed round towards the interior for a varying distance, but is eventually lost in the ground-tissue of the root. In a completely fused ring-like arrangement, such as that shown in Pl. 51. fig. 90, the endodermis often nearly encircles it, but on the inner face of the ring it becomes indistinguishable from the cells of the ground-tissue.

In the cylinder referred to, and other similar strands, the arrangement of the xylem and phloem, though distinctly radial, is not quite regular, the protoxylem-groups of the internally orientated bundles being either absent or abnormally orientated, and the phloem-groups are often tangentially extended. In some cases, however, as in *Areca Catechu*, the endodermis forms a complete investment around one or more of the closed rings, and here the arrangement of xylem and phloem is radial and perfectly regular, as it is also in the case of *Areca* sp. (Pl. 50. fig. 76).

The progressive union of the separate arcs distally is well shown in the figures of *Kentia* (Pl. 51. figs. 95, 96, 97, & 98).

In Pl. 51. fig. 95 the upper strand, *a*, is formed by the union of three originally distinct strands, the two lateral ones still possessing some of their internally orientated bundles, particularly the phloem-bundles; the central one has lost all trace of its internal bundles, except the large vessel which represents the internal metaxylem element of a bundle. This strand is reduced to a wedge of fibrous tissue with only the external bundles of the originally radial series remaining. Such wedge-formation is very common and will be referred to below. In the strand *b* (Pl. 51. fig. 95) fusion of the arc by its internal edges has occurred and a strand of ground-parenchyma is enclosed. A small internally placed strand in which the xylem is reduced to a single central vessel surrounded by five small phloem-groups is seen in Pl. 51. fig. 96 to join the strand *b*, which is becoming incomplete internally, and in Pl. 51. fig. 97 has opened internally, the enclosed strand of parenchyma being thus again in communication internally with the ground-parenchyma.

In fig. 98 the ring of fibrous tissue formed by fusion of the strands is seen, but is still deeply lobed and is incomplete on the adaxial side. In such a stage as this the endodermis at the bottom of a depression in the fibrous ring may extend internally as a single plate of cells, or may be doubled (Pl. 49. fig. 48).

The complete continuity of a "cortical" and "medullary" parenchyma through the gaps in the incomplete cylinder is shown in Pl. 51. fig. 100, where it obviously is quite impossible to distinguish between them.

An unusual occurrence is illustrated in the annexed diagram. The closed cylinder of text-fig. 2 is not formed by the usual method of incurving and final coalescence of an

apical meristematic procambial strand, but by the approximation of a central free strand which finally closes the gap in the arc, so completing the circle. The xylem-bundles of

Fig. 1.

Fig. 2.

the strand are three in number and radiate from a common centre alternating with three phloem-groups. When fusion with the incurved arc takes place one of these phloem-groups (*a*) disappears, while the two xylem-bundles, originally orientated towards the exterior of the root, rotate internally as seen in text-fig. 2.

Another interesting case is shown in text-figs. 3, 4, 5, and 6. In fig. 3 a complete cylinder has been established somewhat externally to the general ring of arcs of fibrous tissue. Followed distally this ring opens out internally, and at the same time one of the fibrous wedges bounding the gap between the two arcs just internal to the ring under consideration breaks free and passes internally as a medullary strand, its vascular elements being reduced to a single central vessel (text-figs. 4 & 5). At the same time

Fig. 3.

Fig. 4.

Fig. 5.

Fig. 6.

one edge of the internally opening ring establishes connection with the edge of the arc from which the medullary strand has become separated (text-fig. 6). This method of formation of a medullary strand is widely different from the usual method and has not been observed in any other case, the medullary strands being normally the reduced distal prolongations of the internal cylinders of the base of the root.

It has already been mentioned that generally the whole series of changes culminating in the formation of a normal complete central cylinder takes place in the intracauline portion of the root. This occurs, for instance, in *Latania borbonica*, and Pl. 51. fig. 102 shows the vascular cylinder of this species dissected out. The upper portion, which is enclosed in the cortex of the stem, is lobed, while the lower portion belonging to the external root is reduced to the normal condition.

Pl. 51. figs. 103 & 104 are from external portions of roots of *Kentia*. In fig. 104 the upper end shows a series of free strands which fuse below, resulting in a lobed cylinder.

A very curious appearance is presented in Pl. 51. fig. 105. The root appeared to dichotomize, and on dissection of the vascular cylinder this idea was strengthened as the partially separated strands are continuous, some into one section of the dichotomy, the rest into the other. Were there any trace of a blind ending of a principal root, the

bifurcation would be explicable as resulting from two large lateral roots arising close to the end of the principal one of the nature of those in *Areca Catechu* (Pl. 51. fig. 116); but such an explanation is here quite without support, and dichotomy seems to afford the only satisfactory explanation of this peculiarity.

The structure of the series of sections represented by Pl. 50. figs. 55 & 76 may now be explained in the light of the facts established by the examination of *Kentia*, *Latania borbonica*, and *Dictyospermum album*. Each section represents the most complex condition met with in the *extracauline portion* of the root under consideration.

The section of *Areca* sp. (Pl. 50. fig. 76) illustrates the most complicated root-structure met with in the Palms. The original cylinders of the base of the root become united to form not a single ring, but three complete cylinders each enclosing a "pith" composed of ground-parenchyma, and a large incomplete cylinder whose internal portion is made up of three of the original strands each preserving its radial structure. The complete cylinders show the internal lobing of the fibrous ring in the form of wedges, each representing an originally separate strand from which the internal phloem has disappeared and also internal protoxylem, leaving only a large vessel, sometimes accompanied by one or more smaller elements, to represent the metaxylem of originally centrally orientated xylem-bundles.

In the incomplete cylinder in one case an internally directed protoxylem-group persists, and in several cases two or three of the metaxylem-elements of these bundles remain.

The radial symmetry of the fibrous groups forming the edges of the incomplete cylinder exhibit a nearly complete radial structure, which is also exhibited by the three strands forming the internal portion of this cylinder.

In the parenchymatous tissue lying within this cylinder the medullary groups show a mass of xylem with two or three radiating protoxylem-groups and the same number of phloem-groups, the original radial strands not having lost their primitive structure, as is usually the case with medullary strands.

In *Iriartia* (Pl. 50. fig. 55) the peripheral strands have united into a series of arcs, the internal lobing of which indicates the boundary of the originally free strands. The internal protoxylem-groups have aborted and generally also the phloem-groups, but in the segments forming the free edges of the arcs an internal phloem-group often persists. The medullary strands preserve their original radial symmetry, usually possessing two or three xylem-groups alternating with as many phloem-groups. The endodermis bounds each arc externally and is continued inwards round the edges for a short distance, but is soon lost as a definitely marked layer in the common ground-parenchyma.

Areca sp. (Pl. 50. fig. 56) is essentially similar to *Iriartia*, but the medullary strands have lost their phloem-groups. The wedge-shaped internal lobes of the fibrous tissue of the arcs are well-preserved and an internal phloem-group is commonly present in the lateral lobes of any arc.

In *Kentia* sp. (Pl. 50. fig. 57) the fusion of the arcs is somewhat further advanced. The wedges are still well-marked, but medullary strands are absent, all the original strands

having apparently entered into the peripheral ring—a very uncommon occurrence. One of the strands composing the ring of arcs persists as a radially symmetrical cylinder. A similar thing occurs in another section of *Kentia* sp. (Pl. 50. fig. 59).

Dypsis madagascarensis (Pl. 50. fig. 58) shows much the same structure, but here medullary strands occur and the lateral fusion of the arcs is more extensive. An interesting peculiarity is evident in the small medullary strand *a*. It approximates very closely to the periphery of the ring, abutting on a gap between two arcs. This small strand is on its outer face provided with endodermal cells exactly like those outside the arcs. In this root also one peripheral strand retains its radial symmetry.

In *Areca* sp. (Pl. 50. fig. 60) the fusion of the arcs is much more extensive on one side of the root than on the other. The elements of the xylem-groups are more abundant than usual, and in some cases the larger internal vessels of the metaxylem are accompanied internally by smaller vessels which represent persistent traces of the internally directed xylem-groups of the radially symmetrical strands, the protoxylem of which has disappeared. A strand possessing two protoxylem-groups, one directed externally and one internally, is united with the inner extremity of a fibrous wedge of the peripheral system. A similar strand is found in *Cocos plumosa* (Pl. 50. fig. 61), but here the vascular elements are reduced to a single vessel as they are in most of the medullary strands. In one, however, the radial arrangement of four xylem-groups and four phloem-groups persists. The peripheral system forms a ring only incomplete on the adaxial side, and in the gap occurs a small strand like the one just described, but possessing five xylem- and phloem-groups.

Cyrtostachys Renda (Pl. 50. fig. 62) is of particular interest in retaining two of the internally directed xylem-groups of the original strands, accompanied by phloem laterally, and a third group of two vessels in another wedge representing the metaxylem-vessels of such a group whose protoxylem-elements have disappeared.

In the section of *Dypsis madagascarensis* (Pl. 50. fig. 63) the ring is only incomplete on the adaxial side. The wedges bounding the gap alone show internal phloem, and in one case internally directed protoxylem also.

In *Licuala gracilis* (Pl. 50. fig. 64) the ring is complete. In several cases the large metaxylem-elements are accompanied centrally by remains of the internally directed xylem, and in other cases a well-developed internal xylem-group persists. The three medullary strands show three stages in the normal reduction of these structures. One possesses a central vessel and two radiating protoxylem-groups. The second has lost its protoxylem, and the third only retains a single central vessel. Thus the fact that these medullary strands, which possess, as is usually the case, only a single central vessel, really represent reduced structures which had originally a radial arrangement of xylem, is here well illustrated, as is also the further fact that some of the large internally placed vessels of the fibrous zone are the metaxylem-elements of internally orientated xylem-bundles whose protoxylem has disappeared.

The rich development of metaxylem and its tangential extension in *Ptychosperma filifera* (Pl. 50. fig. 65) have been already described, as has also the abundant V-formation in *Livistona australis* (Pl. 50. fig. 66). It may here be noted that

V-formation is now explicable as due to the persistence of two of the radiating xylem-groups of the original strand instead of the one which usually alone persists.

Double V-formation, such as obtains in *Heterospathe elata* (Pl. 50. fig. 69), is entirely explicable in the same way. Thus in the group on the left of the figure we are probably dealing with four xylem-groups, two of which had originally had an internal orientation, but which became outwardly directed when fusion of the strand into the peripheral ring occurred. That such an alteration in orientation may occur has been already observed for *Kentia*, where the outward orientation of two xylem-groups becomes reversed on fusion of the strand with the peripheral arc (p. 446, figs. 1 & 2).

The interest of the sections of *Sabal glaucescens* (Pl. 50. fig. 67) and *Phoenix dactylifera* (Pl. 50. fig. 68) attaches chiefly to the medullary strands, which have already received attention.

In *Corypha umbraculifera* (Pl. 50. fig. 70) the internal vessels are extremely large and occupy almost the whole of the centre of the root, no pith being present.

The same condition is found in *Raphia Hookeri* (Pl. 50. fig. 71), but to a less extent. These large internal vessels almost certainly represent the metaxylem-elements of the central strands whose protoxylem has disappeared and are thus comparable with the large vessels of the medullary strands of most roots.

In *Latania Commersonii* (Pl. 50. fig. 72) a similar abundant development of large vessels occurs, but a central pith is here present. A further point of great interest lies in the fact that phloem-groups of the internal strands have here persisted, and appear as phloem-bundles scattered throughout the fibrous zone amongst the large internal vessels.

In *Phoenix sylvestris* (Pl. 50. fig. 73) the internal vessels are reduced to a single ring, while in *Sabal filamentosa* (Pl. 50. fig. 74) no vessels occur which cannot with considerable certainty be allotted to the same original strands as those to which the protoxylem-groups belong, while this is still further evident in the perfectly normal root of *Kentia Forsteriana* (fig. 75).

In Pl. 50. figs. 77 to 88 a diagrammatic *résumé* of the changes which take place in the root is presented.

In Pl. 50. fig. 77 the series of cylinders each with a number of exarch xylem-groups is seen scattered throughout the ground-parenchyma of the base of the root. Each cylinder shows a root-like structure with alternating xylem- and phloem-groups.

In Pl. 50. fig. 78 fusion of the peripheral cylinders has commenced, and in Pl. 50. fig. 79 reduction of the internally directed xylem-groups has set in, with disappearance of internal phloem.

The protoxylem-elements of the bundles in the medullary strands which are formed by those cylinders which do not enter into the peripheral system have aborted, but the phloem still persists.

In Pl. 50. fig. 80 the fusion is incomplete only at one point, and the internal xylem is represented only by the large metaxylem-elements. Reduction of the xylem and phloem of the medullary strands has progressed still further than in Pl. 50. fig. 79.

In Pl. 50. fig. 81 the peripheral ring is complete, and shows only a depression on one

side where the last fusion has occurred. The wedge-shaped internal projections of the fibrous ring still mark the limits of the originally free cylinders.

In Pl. 50. fig. 82 the root-cylinder is normal and the internal boundary of the fibrous ring, though sinuous, has lost its wedge-shaped projections. The medullary strands now each contain only a single vessel. The scattered internal vessels of the fibrous zone represent the metaxylem-elements of the internally orientated xylem-groups.

Sometimes the fusion of the cylinders of Pl. 50. fig. 77 takes place in a different manner. Instead of peripheral cylinders only fusing, fusion may involve some of the more internal cylinders also, as in Pl. 50. fig. 83. In this way the inrolled arcs of so many palm-roots are produced. Internal fusion of the edges of these arcs leads to the formation of cylinders enclosing parenchymatous ground-tissue, one of which is shown in Pl. 50. fig. 84 and a second in Pl. 50. fig. 85. Thus Cormack's "polystelic" structure is realized. While this has been progressing the internal protoxylem-groups have been disappearing, leaving only the large metaxylem-elements.

Distally these closed rings open out internally and the enclosed parenchyma is again in direct continuity with the common ground-parenchyma. Fusion of the edges of adjacent arcs now occurs, leading to the formation of a lobed ring, at first incomplete on the adaxial side, but later fusing here also.

Complete rounding of the external surface of the root-cylinder now occurs accompanied by loss of the internal wedge-formations, and thus normal root-structure is attained (Pl. 50. fig. 82).

The accompanying text-figure (7) illustrates the method of union of root and stem.

Fig. 7.

Lateral Rootlets.

The small lateral rootlets of the Palms, such as those shown in Pl. 48. fig. 11, *a*, have a perfectly normal origin in the pericycle of the relatively main root. The endodermis is ruptured and the cortex of the lateral root attains considerable thickness during its passage outwards. The endodermis is connected at its origin with that of the cylinder

of the relatively main root (Pl. 51. fig. 106). The xylem- and phloem-bundles establish connection with several bundles of the parent root. In many cases it was found that an incomplete (Pl. 51. fig. 106) or complete cylinder of the peripheral system of strands in the central cylinder of the root might function as a normal root-cylinder in giving rise to lateral roots.

In *Areca Catechu* two forms of lateral roots were found (Pl. 51. fig. 111)—the normal small roots passing directly outwards, and also roots with much more extensive origin, which run obliquely outwards and downwards through the cortex of the parent root, but, curiously enough, very seldom reach the periphery, undergoing degeneration during their passage outwards; even when they do reach the periphery they usually cease to grow and soon abort. The connection of such rootlet with the cylinder of the parent root is seen in Pl. 51. fig. 107, where the ruptured endodermis of the main root is shown and its connection with that of the lateral root.

A section taken a short distance above this shows the upward extension of the xylem- and phloem-bundles of the lateral root inside the endodermis of the parent root. Here and there the phloem-groups of the two are still separate, and in the xylem-groups the protoxylem occupies a position between the metaxylem of the main root and the upwardly extended xylem of the lateral root.

The deep penetration of the xylem-elements of the lateral root amongst those of the parent root first mentioned by Hugo von Mohl (1) is shown in Pl. 51. fig. 118. The protoxylem of the lateral root (*ptxy.* 2) occupies the periphery of the cylinder lying just beneath the pericycle, that of the parent root (*ptxy.* 1) lying much more internally. Elements from the lateral root are seen penetrating centrally as far as, and even beyond, the innermost metaxylem-element. The phloem-group shows the small-celled protophloem (*ptph.*) surrounded by the metaphloem, that lying internally belonging to the main root, that externally to the lateral root. Lower down a section shows the cylinders of lateral and parent roots quite separate from each other, that of the former being lobed and internally composed of separate strands (Pl. 51. fig. 108). More distally the cortex of the lateral root is well differentiated, showing the dense outer layers and the parenchymatous inner zone with its large air-spaces, the whole being still embedded in the cortex of the parent root (Pl. 51. fig. 109). Further down, the cylinder of the lateral root attains a normal structure (Pl. 51. fig. 110).

In *Areca concinna* these larger internal roots may project for some distance beyond the parent root (Pl. 51. fig. 111), but this is apparently an unusual feature.

Fig. 8.

Fig. 9.

In *Areca concinna* a striking peculiarity is shown in the accompanying diagrams (text-figs. 8 & 9), where the cylinder of the lateral root in leaving that of the parent

forms a root-gap which persists for some time, being still open when the cylinder of the lateral root has become complete.

Through the cortex of the extremities of some roots of *Areca Catechu* break many large lateral roots, giving to this region a swollen and irregular appearance (Pl. 51. fig. 114).

In some cases the growing-point of the parent root aborts, and one or more of the large lateral roots grow downwards and continue growth in the direction of the parent. Two lateral roots are seen doing this in *Areca Catechu* (Pl. 51. fig. 116).

A better example of the same thing is illustrated for *Actinorhysis Calapparia* in Pl. 51. fig. 117, where the downwardly growing portion *a* is a large lateral root proceeding from the main root *b*, the other large lateral roots at *c* ceasing to elongate.

Iriartia presents one of the few known examples of spiny roots, and is referred to by Goebel in his 'Organographie.' Pl. 51. fig. 112 illustrates a large aerial root arising from the slender stem. The lateral rootlets are all reduced to short spines, which present a curious internal structure. The outer layers of the cortex are parenchymatous, as are also the inner, but between these two zones occurs a lignified sclerenchymatous ring (Pl. 51. fig. 113). The parenchymatous elements just inside this ring show clear evidence of secondary division, having quite a cambiform appearance (fig. 115).

The central cylinder of the spiny rootlet is bilobed, but otherwise it is normal in structure.

The well-known contractile nature of the roots of Palms is splendidly shown in certain roots of *Corypha umbraculifera*; a small portion of one of these is figured in Pl. 51. fig. 120.

THEORETICAL CONCLUSIONS.

One result of the examination of the roots of Palms has been to show that the central cylinder in these organs is not the simple structure which Van Tieghem considered the root-cylinder to be, and upon which he based his conception of monostely.

The base of the root is occupied by a number of separate cylinders, each essentially "stele"-like in structure, as evidenced by the presence of regularly-arranged strands of xylem and phloem embedded in the fibrous ground-tissue of the cylinder, although no definitely marked endodermis is present.

Any objection to the term "stele" as applied to these cylinders, based upon the apparent absence of an endodermis, loses much of its force in view of Strasburger's demonstration that the histologically differentiated endodermis, even when present, does not always represent the innermost cortical layer, but may occur in any zone, while the first "extra-stelar" layer may differ in no respect from the ordinary ground-parenchyma.

The base of the root would therefore be termed, in the language of the stelar theory, "polystelic," and the normal root-cylinder, formed as it is by the fusion distally of the proximally free "steles," would be "gamostelic"—truly a curious result.

Cormack's "polystely," likewise produced by fusion distally of the free "steles," would be termed "gamostely"—a number of "gamosteles" traversing the ground-parenchyma.

If, however, it be still urged that a histologically differentiated endodermis is necessary

for the constitution of a "stele," then if the cylinders of the base of the root, which, it must be remembered, extend in all cases into the apices of the young roots and often into the apices of older roots also as separate procambial strands, be not "steles," may they be termed "bundles"?

De Bary regarded the central cylinder of the normal root as a single bundle, and stated further: "In the thick roots of Pandanaceæ and the genus of palms, *Iriartia*, there are found a number of parallel bundles which converge at the growing point." His further remark, "it may be doubted whether these should be called parts of one very large divided bundle or so many individual bundles," does not concern us here.

If, then, these strands at the base of the root are bundles, the root is "polydesmic" in this region, an interpretation leading to the result that the normal cylinder produced distally is "gamodesmic," unless here again an endodermis surrounding each bundle be considered necessary for true "polydesmic" nature.

If such an investment be considered necessary, then the only conclusion to be drawn would appear to be that the root in its basal portion is purely "astelic," a "meristelic" interpretation being out of court, since at no previous stage has any stelar structure been present, "meristeles" being the result of the splitting of a "stele."

Fusion of the separate strands distally, giving rise to series of arcs of fibro-vascular tissue, provided on their peripheral surfaces with an endodermal layer, leaves the root still in an astelic condition, often retained even in very long roots of certain palms, but usually giving place distally, by further fusion of the arcs, to a typical root-cylinder surrounded by a complete endodermal investment. In this state the root might be described as locally monostelic for purely descriptive purposes, without any reference to the real mode of origin and relationship of its constituent parts. It is at least doubtful, however, whether Van Tieghem's conception of "monostely" is here attained, the "monostele" in the present case being the result of a gradual change from an "astelic" condition.

The stelar theory thus failing to explain satisfactorily the conditions met with in palm-roots, it becomes of interest to see how far Hanstein's idea of the root as composed of several independent zones arising from as many individual initial layers at the apex will here hold good.

It has been already mentioned that in the apices examined (namely, those of *Kentia* sp. and *Areca* sp.) stratification is entirely absent, the apex in each case possessing a common group of initial cells, by division of which the ground-parenchyma of the root is formed. A short distance behind the apex the procambial tissue, from which the fibro-vascular elements are developed, appears in the ground-parenchyma, and any distinction of Hanstein's initial layer is quite wanting.

It is possible to extend this conception to include the structure in many other cases, among which may be mentioned the non-stratified root-apices of the Papilionaceæ, described by Janczewski; stem-apices of the Pteridophyta, occupied by a single initial cell or group of cells, which by division gives rise to a common ground-parenchyma, wherein arises the procambial tissue, in the so-called "polystelic" forms, each procambial strand being the precursor of a "stele."

The work of Tansley and Boodle shows that great irregularity exists in the development of these so-called "steles," a single cell sometimes giving rise on division to both "extra-stelar" and "intra-stelar" tissue.

Important evidence has recently come to hand in a memoir by Schoute, entitled 'Die Stelär-Theorie,' where he shows that even in the stratified apices of Phanerogams no hard-and-fast line can be drawn between the products of the various layers.

It thus becomes more and more evident that both in stem and root we have to deal with a common parenchymatous ground-tissue, through which run strands of xylem and phloem, usually accompanied by fibrous tissue, often in the form of sheaths—xylem, phloem, and fibres being all developed from the procambial tissue. This last sometimes arises in the form of separate strands in the stems of so-called "polystelic" Pteridophyta and in stems of Dicotyledons and Monocotyledons, each strand giving rise in the former case to a "stele" and in the latter case to a "bundle." Thus it appears that the "bundle" in a dicotyledonous stem and the "stele" in a "polystelic" fern arise in a precisely similar manner, whereas the "stele" of a dicotyledonous plant and the "stele" of a "polystelic" fern are, from the developmental standpoint, very different structures.

In other cases the procambial tissue takes the form of a single central strand, as in "pithless" roots and "protostelic" ferns, or of a hollow cylinder in roots with pith, while in yet other cases—for example, the roots of Palms—it may at first appear as separate strands, giving place later to a hollow cylinder.

It remains to be seen how far the results of future investigation will support the views expressed above, but at the present time there is great weight of evidence tending to show that all ideas of "monostely" and "polystely," and of "medulla" and "cortex" as separate morphological entities, are founded upon an artificial conception of the nature of the structures involved.

My thanks are due to the Director of the Royal Gardens, Kew; to the Director of the Royal Botanic Gardens, Ceylon; to Mr. Herbert Wright; to Professor Bower; and to Professor F. W. Oliver for the material on which the present investigation has been carried out; and particularly to Professor Farmer for his kind and unfailing interest and valuable criticism during the progress of the work.

BIBLIOGRAPHY.

- (1) MOHL, H. VON.—Vermische Schriften. Tübingen, 1845.
- (2) KARSTEN, H.—Die Vegetationsorgane der Palmen. Abh. Berl. Akad. Wiss. (Phys.) 1847, pp. 73-236.
- (3) NÄGELI, C. VON.—Beiträge zur wissenschaftliche Botanik, Heft i. Leipzig, 1858.
- (4) RUSSOW, E. A. F.—Betrachtungen über das Leitbündel- und Grundgewebe, u. s. w. Dorpat, 1875.
- (5) FALKENBERG, P.—Vergleichende Untersuchungen über den Bau der Vegetationsorgane der Monocotyledonen. Stuttgart, 1876.
- (6) DE BARY, H. A.—Vergleichende Anatomie der Vegetationsorgane der Phanerogame und Farne. Leipzig, 1877.
- (7) VAN TIEGHEM, P. E. L.—Recherches sur la symétrie de structure des plantes vasculaires. Ann. Sci. Nat. sér. 5, xiii. (1870-71) pp. 5-314, pls. 3-8.
- (8) OLIVIER, L.—Recherches sur l'appareil tégumentaire des racines. Ann. Sci. Nat. sér. 6, xi. (1880-81) pp. 5-133, pls. 1-8.

- (9) MANGIN, L.—Origine et insertion des racines adventives et modifications, etc. Ann. Sci. Nat. sér. 6, xiv. (1882) pp. 216–363, pls. 9–16.
- (10) DRUDE, O.—Palmaceæ; in Engler & Prantl, 'Die natürlichen Pflanzenfamilien,' ii. 3, pp. 1–93. [1887.]
- (11) CORMACK, B. G.—On Polystelic Roots of certain Palms. Trans. Linn. Soc., ser. 2, Bot. v. (1896) pp. 275–286, pls. 19, 20.
- (12) GILLAIN, G.—Beiträge zur Anatomie der Palmen- und Pandanaceen-Wurzel. Bot. Centralbl. lxxxiii. (1900) pp. 337–345, 369–380, 401–412, t. 3.
- (13) VAN TIEGHEM, P. E. L., & H. DOULIOT.—Recherches comparatives sur l'origine des membres endogènes. Ann. Sci. Nat. sér. 7, viii. (1888) pp. 1–60, pls. 1–40.
- (14) JANCZEWSKI, E. DE.—Recherches sur l'accroissement terminal des racines dans les Phanérogames. Ann. Sci. Nat. sér. 5, xx. (1874) pp. 162–201, pls. 13–16.
- (15) TREUB, M.—Le Méristème primitif de la racine dans les Monocotyledones. Leiden, 1876.
- (16) VAN TIEGHEM, P. E. L.—Traité de Botanique. Paris, 1884.—Ed. 2, ib., 1891.
- (17) METTENIUS, G.—Filices Horti botanici Lipsiensis. Lipsiæ, 1856.
- (18) ROSANOFF, S.—Ueber Kieselsäureablagerungen in einigen Pflanzen. Bot. Zeit. xxix. (1871) 749–753, 765–770.
- (19) PERCIVAL, J.—The Occurrence of Calcium-Oxalate Crystals in Seedlings of Alsike (*Trifolium hybridum*, Linn.). Journ. Linn. Soc., Bot. xxxv. (1902) pp. 396–402.
- (20) HANSTEIN, J.—Ueber ein noch nicht bekanntes System schlauchformiger Gefässe, u. s. w. Monatsb. Berl. 1859, pp. 705–713.
- (21) HILL, T. G., & Mrs. W. G. FREEMAN.—The Root-Structure of *Dioscorea prehensis*. Ann. Bot. xvii. (1903) pp. 413–424, pl. 19.
- (22) BUSCALIONI, L.—Sull' anatomia del cilindro centrale nelle radici delle Monocotiledoni. Malpighia, xv. (1902) pp. 277–296.
- (23) SCHOUTE, J. C.—Die Stelär-Theorie. Groningen, 1902.
- (24) PIROTTA, R.—Origine e differenziazione degli elementi vascolari primari nella radice delle Monocotyledoni. Rendic. Accad. Lincei, ser. 5, xi. (1902), pp. 49–52, 158–162.

DESCRIPTION OF INDIVIDUAL SPECIES.

In the order of the following descriptions, Drude's arrangement, as given in Engler and Prantl's 'Pflanzenfamilien,' has been adopted.

I. CORYPHINÆ.

(1) PHŒNIX RECLINATA, Jacq.

The limiting-layer is composed of slightly lignified cells, almost isodiametric as seen in transverse section, but about twice as long in longitudinal section. The walls, except the inner tangential, are considerably thickened, and the outer extremities project slightly as small papillæ. Succeeding these is a layer, some fourteen elements in depth, made up of elongated cells more or less fibrous in appearance, but generally with squared ends. These cells are slightly lignified, while here and there occurs an element much more strongly so. Then follows a zone, six elements in depth, of elongate lignified fibres with simple pits.

The internal cortex is composed of parenchymatous cells with large radially extending

air-spaces. The cells of the innermost portion of the cortex immediately surrounding the endodermis are more closely packed and tangentially compressed. Embedded in the inner cortex are bundles of strongly lignified fibres, with small lumina and simple small pits. The endodermis is generally well lignified and thickened on all its walls, except the outer tangential. The inner tangential walls may be so greatly thickened as to bring about almost total occlusion of the lumina. In the fully mature root not a single passage-cell was observed. The pericycle, usually two cells in thickness, is, in the mature root, lignified and pitted, the lignification being most strongly developed opposite the protophloem.

A thick zone of sclerenchyma, in which lie the xylem- and phloem-groups, surrounds a central irregular medulla. The vessels of the protoxylem are lignified and surrounded by a mass of small-celled parenchyma. The lignification decreases as we follow the metaxylem centripetally, and in the large inner vessels it may be wanting altogether, the original cellulose walls remaining unaltered. The layer of cells abutting directly on these large vessels is frequently parenchymatous, the elements having cellulose walls. Often two protoxylem-groups are found in connection with one large inner vessel, resulting in the V arrangement, the arms embracing a phloem-group.

The medulla is parenchymatous. Into it may project one or more masses of the lignified sclerenchyma which encloses it, each mass containing a large vessel, but no separate sclerenchyma-strands were observed in the medulla.

(2) PHŒNIX ZEYLANICA, Trimen.

This root is very similar to the last in all essential characters; the medulla is, however, much smaller, the sclerenchymatous zone of the central cylinder extending almost to the centre of the root. The vessels are confined to the periphery of this zone.

(3) PHŒNIX SYLVESTRIS, Roxb.

The limiting-layer is cuticularized and lignified. Then comes a cuticularized and slightly lignified zone of about four cells in depth. These elements are parenchymatous and about twice as long as broad. Then follow two or three layers of thin-walled cellulose parenchyma, followed internally by lignified fibres. The outer portion of the inner cortex is composed of parenchymatous cells only. This is succeeded by a broad zone, with large air-spaces and bundles of fibres enclosed in a sheath of stegmata as in *Ph. reclinata*, Jacq. The groups of fibres are here seen to become lignified from the exterior towards the interior. The innermost layers of cortex are as in *Ph. reclinata*.

The endodermis consists principally of thin-walled cells slightly lignified, but non-lignified cells may occur at any point, as frequently opposite the protophloem as opposite the protoxylem. In longitudinal section the endodermic cells are seen to be from two to three times as long as broad. The pericycle is entirely non-lignified, consisting of ordinary cellulose parenchyma. Opposite the protoxylem it may be wanting entirely, so that the external protoxylem-elements abut directly on the endodermis. Opposite the protophloem the pericycle expands and is here two or three elements in depth.

The protoxylem and protophloem are enclosed in parenchymatous tissue. The

remaining ground-tissue of the central cylinder, excepting a small central pith whose limits are not well defined, consists of sclerenchyma, in which are embedded the phloem- and xylem-vessels. The vessel-walls are generally well lignified, but in some of the innermost vessels they may still retain their cellulose nature.

The small irregular central medulla is parenchymatous and surrounds a central air-space.

(4) *PHŒNIX DACTYLIFERA*, Linn.

The limiting and next three layers are more or less cuticularized and non-lignified. Then follows a lignified zone of elements, some six or seven elements in depth and of the usual elongated type. The inner cortex is composed of parenchyma, with large air-spaces of no great radial extent, arranged in many irregular zones, and of bundles of fibres with their accompanying stegmata.

The endodermic cells are lignified and very greatly thickened, except on the outer tangential walls, the lumina being nearly occluded.

The endodermic cells are four or five times longer than broad, and the thickening is of that nature described by Mohl as "fibrous."

No passage-cells were observed. The pericycle consists of elongated, square-ended, lignified cells. A small group of cellulose-walled parenchyma surrounds each protoxylem-group.

A broad zone of sclerenchyma encloses the pith, and in this are embedded the xylem-vessels and the phloem. The protoxylem is lignified, but the inner vessels usually retain their cellulose walls. Two or more protoxylem-groups often abut on one large vessel, and internally are irregularly arranged large vessels which do not appear to belong to any xylem-group. These latter are embedded in masses of lignified ground-tissue, on the peripheral side continuous with the sclerenchymatous zone, but internally projecting into the medulla.

The medulla is parenchymatous, with a few air-spaces. Between the internally projecting sclerenchymatous masses the cells of the medulla are considerably crushed, showing that a differential rate of growth has taken place between the medullary cells and the sclerenchymatous masses in these regions.

(5) *ACANTHORHIZA ACULEATA*, H. Wendl.

The limiting-layer is of the usual type. The underlying zone of lignified elongated elements shows clearly that lignification commences in the external layer, and shortly afterwards appears also in the internal layer. It then proceeds centripetally and centrifugally, and in the mature root leaves only one or two layers of cells non-lignified in the middle of the sclerenchymatous zone. Interior to this zone comes the inner cortex, the outer part of which is composed of closely packed and slightly lignified cells. This portion of the cortex is relatively much wider than usual. The internal zone of the inner cortex with its air-spaces follows. The air-spaces are irregular and comparatively small, and usually separated only by a single layer of cells. In this region the only strengthening elements are short, square-ended, not greatly thickened, parenchymatous cells.

The endodermis is of the usual lignified type.

The pericycle is two cell-layers in thickness.

The sclerenchymatous zone is well developed and composed of densely lignified and thickened elements. In the centre is a parenchymatous pith.

The sclerenchymatous ring is lobed internally, rays of the pith extending in an outward direction between the wedge-shaped lobes of sclerenchyma. There is only one irregular ring of large vessels, and these are placed very peripherally. They are fewer in number than the protoxylem-groups, and hence **V**-formation is general.

(6) *THRINAX PARVIFLORA*, Sw.

In the young root the limiting-layer is lignified, as are also the subperipheral layers of elongated cells, these latter being also slightly cuticularized. The greater part of the cortex consists of ordinary parenchyma with no fibres. There are very large, radially extended air-spaces, with occasionally a thin tangential diaphragm of cells. These cavities extend to within one or two cells of the endodermis. The endodermal cells are lignified and "fibrously thickened" on all but the outer tangential walls. The pericycle is generally only one cell in thickness, and is followed by the broad sclerenchymatous zone in which the xylem-vessels and the phloem are embedded.

The vessels of the protoxylem are lignified, but the larger internal vessels are not. These latter vessels do not extend far centrally. **V**'s are formed embracing the phloem. In the centre is a small parenchymatous pith.

The older roots are extremely hard, lignification being very extensive and the elements very small and closely packed. The outer portion of the cortex is made up of elongated elements with almost totally occluded lumina, with irregular radial rows of thinner-walled elements, along which the sections invariably split in cutting. This zone is succeeded by a parenchymatous cortex with very irregular air-spaces and a large proportion of lignified, thick-walled, pitted parenchyma. The endodermic cells are greatly thickened and lignified on all the walls. The pericycle is lignified and is two cells in thickness.

The sclerenchyma enclosing the xylem- and phloem-elements is greatly sclerozed and pitted. There is no pith, but in many cases the centre of the root is occupied by a cavity, the walls of which are blackened as though diseased. The xylem-plates extend a considerable distance centrally, and occasionally a **V** is formed. All the vessels are lignified.

The phloem-bundles show considerable radial extension.

(7) *THRINAX EXCELSA*, Lodd.

A distal portion of the root shows a limiting-layer of thin-walled lignified cells, nearly exfoliated. Underneath this are many layers of somewhat lignified, elongated cells. The parenchymatous inner cortex has irregular air-spaces and lignified, fibrous, pitted cells. The innermost portion of the cortex is made up of smaller, more tightly packed cells, without air-spaces, but with many lignified fibres. The endodermis is lignified, and

the cells much thickened on all except the outer tangential walls. They are considerably elongated and the thickening is of a "fibrous" nature.

The pericycle comprises one or two layers of lignified pitted cells. The xylem-plates and the phloem are embedded in a sclerenchymatous zone. The xylem forms very wide V's, and internally are vessels that appear to have no relation to the xylem-plates. There is a small pith, chiefly occupied by two strands of sclerenchyma, connected externally with the sclerenchyma-zone. In the centre of each is a single vessel.

In a more proximal portion of the root the outer subperipheral elements are separated from those more internally placed by several layers of unaltered parenchymatous cells. This means that the centripetally proceeding lignification has not yet met that proceeding centrifugally.

The internal cortex, as in the more distal region, contains very irregular air-spaces and many fibres scattered singly.

On one side of the central cylinder the sclerenchymatous zone is interrupted, and at the same point the endodermis, instead of completing the circle, dips in very deeply, forming a groove occupied by cortical ground-tissue. Down the sides of this groove the endodermis is continuous, but towards the base it becomes broken up, and at the very bottom is wanting as a specially differentiated layer, so that the ground-tissue internal to ("medulla") and external to ("cortex") the sclerenchymatous zone is continuous.

The general structure of the central cylinder is the same as that in the more distal portion described above, but there are many more medullary sclerenchymatous strands, some of which are completely separated from the sclerenchymatous zone enclosing the medulla. In the centre of each medullary strand is a single vessel.

(8) *CORYPHA AUSTRALIS*, R. Br.

The limiting-layer consists of almost isodiametrical thin-walled lignified cells, most of which are exfoliated—exposing the underlying layers of thick-walled, elongated, pitted cells, which are only slightly lignified. Following this zone is one of some six or seven cells in depth, composed of parenchyma. Then comes a zone of elongated, square-ended cells, comparatively slightly lignified, and passing gradually into a large-celled parenchymatous inner cortex, with very irregular air-spaces and many scattered lignified parenchyma-cells with thick pitted walls. No fibres are present in the cortex. In the innermost zone the air-spaces are absent, but there is much lignified parenchyma.

The endodermal cells are about four times as long as broad. Some of these are thickened and lignified on all but the outer tangential walls; others are thin-walled and slightly cuticularized.

The pericycle, usually two cells in depth, is parenchymatous.

The ground-tissue of the central cylinder is composed chiefly of cellulose-walled parenchyma, but intermingled with it are many lignified sclerenchymatous elements.

The protoxylem-vessels are lignified, but the larger internal vessels retain their cellulose walls.

Occasionally a V is formed enclosing a phloem-group.

In the centre of the root is a thin-walled, parenchymatous pith, in which are air-

spaces formed in the usual manner. In the centre of the pith runs a vessel surrounded by a sheath of prosenchymatous elements, some of which are lignified.

(9) *CORYPHA UMBRACULIFERA*, Linn.

Some of these roots show the contractile nature very clearly. The surface is transversely wrinkled and the whole root is very parenchymatous.

(a) *Large contractile Root*.—The limiting-layer is much disorganized and is followed by a parenchymatous cortex with extremely irregular air-spaces, the cells bounding which often show signs of extensive mucilagization of their walls. No fibres or lignified cells are present. The endodermis is cuticularized and consists of square cells with no trace of lignification. The pericycle is ill-defined, but appears to consist of one layer of parenchyma with rather dense contents.

The whole of the ground-tissue of the central cylinder is parenchymatous, the xylem-plates and the phloem-groups being widely spaced in its periphery. There is no medulla, the whole central portion being occupied by polygonal strands of small thin-walled parenchyma, each enclosing a single lignified vessel. These strands are separated from one another by compressed and disorganized bands of cells. These strands correspond to the sclerenchymatous medullary strands which occur in so many palm-roots.

(b) *Non-contractile Roots*.—The cortex is composed of parenchyma, some of the cells of which contain starch-grains staining bright red with saffranin.

The grains show the leucoplasts very admirably, they are of the normal small conical form. Through the cortex run bundles of fibres, bounded by cells containing crystals of calcium oxalate. Very irregular air-spaces are present.

The endodermis is composed of cells about three times as long as broad, many of which are lignified, the rest being cuticularized. The pericycle is made up of two layers of lignified cells with large pits in their walls.

The ground-tissue of the cylinder is very greatly reduced.

The protoxylem- and phloem-groups occupy the periphery of the cylinder, while the whole interior is occupied by enormous vessels embedded in sclerenchymatous sheaths, partially separated from one another by the ground-parenchyma.

(10) *LICUALA GRACILIS*, Blume.

Limiting-layer of thin-walled lignified non-cuticularized cells.

The outer cortex is composed of small-celled slightly lignified parenchyma. In some roots the lignification proceeding both centripetally and centrifugally has not met, so leaving a narrow zone of non-lignified elements. This is best seen in young roots and appears to have undergone lignification in older roots. This is followed by a parenchymatous inner cortex with large radially extensive air-spaces and provided with elongated, square-ended, deeply pitted, lignified cells. There are no fibres. The innermost layers of the cortex are without air-spaces. The endodermic cells are much thickened and lignified in the "fibrous" manner.

The pericycle consists of two layers of lignified pitted cells. Internally to this comes a zone of sclerenchyma in which are embedded the protoxylem- and phloem-groups. This

surrounds a central parenchymatous pith, which may be more or less lignified. In the smallest roots available for examination there were no fibrous strands in the medulla, but older portions showed all stages from a single fibrous bundle with its central vessel to sections in which nearly the whole pith is occupied by these strands, and instead of a single vessel, two to six may be present in each strand, generally one large vessel accompanied by from one to five smaller ones. In some cases two groups of vessels may be found in one fibrous strand.

(11) *LICUALA SPINOSA*, Thunb.

Similar in all essential respects to *L. gracilis*. The central pith is occupied by fibrous strands enclosing several vascular elements and in some cases two groups of vessels are present in each strand.

(12) *LIVISTONA INERMIS*, R. Br.

The limiting-layer is more or less lignified and consists of small regularly arranged cells. The outer cortex is made up of elongated lignified cells. The inner cortex is parenchymatous, with very irregular air-spaces and elongated, lignified, pitted cells.

The cells of the innermost portion of the cortex are tangentially compressed, and among these are many densely lignified and extremely thick-walled stone-cells, some of which are quite spherical. The endermic cells are lignified and much thickened, except on the outer tangential walls. The pericycle consists of one layer of lignified elements. A broad sclerenchymatous zone contains the xylem and phloem, and very definitely delimits the central pith, through which run fibrous elements, but no sclerenchymatous strands with vessels.

(13) *LIVISTONA ROTUNDIFOLIA*, Mart.

The cortex is parenchymatous with admixture of single lignified and pitted elements, but without fibrous strands. The air-spaces are irregular and comparatively small. The endodermis is of the usual lignified type. The pericycle is two cells in thickness, lignified and pitted. The sclerenchymatous zone is very densely lignified and thickened, giving to the central cylinder an extremely hard and solid character. No V's are formed, and there are no vessels which cannot be definitely allotted to their respective protoxylem-group.

There is a parenchymatous pith in which are present some lignified elements.

(14) *LIVISTONA AUSTRALIS*, Mart.

Externally occur three or four layers of oblong, strongly lignified, much thickened and pitted cells, the lumina of which are almost obliterated. Then follows a broad zone of prosenchymatous elements, generally lignified, and then the parenchymatous inner cortex with small irregular air-spaces and lignified elongated cells scattered singly or in small groups; no fibrous strands occur.

The endodermis and pericycle are as in *L. rotundifolia*. There is a sclerenchymatous zone in which the xylem and phloem are embedded. The xylem frequently shows

V-formation. In the centre is a parenchymatous pith, through which runs a single sclerenchymatous strand, enclosing a central vessel. This strand was followed for more than 12 cms. as a freely running strand without exhibiting any tendency to fusion with the sclerenchymatous zone. The central element in this strand was clearly shown to be a normal vessel, similar to the larger vessels occurring in the sclerenchymatous zone.

(15) *LIVISTONA OLIVÆFORMIS*, Mart.

The limiting-layer is almost entirely exfoliated and is succeeded by a few layers of square-ended, oblong cells, more or less lignified. These pass gradually into fibrous elements internally, which become lignified centrifugally. Then follows the parenchymatous cortex with comparatively small and very irregular air-spaces and some lignified elongated individual elements. The endodermis is like that in *Livistona rotundifolia*. The pericycle is two cells in thickness and encloses the sclerenchymatous zone in which the xylem and phloem lie. Irregular V's are formed, and the large vessels extend some distance internally. The central pith is not very clearly delimited from the sclerenchymatous zone; it consists of parenchyma with many irregular air-spaces.

(16) *LIVISTONA CHINENSIS*, Hort.

The limiting-layer is entirely exfoliated. The periphery is occupied by a zone four elements in thickness, much lignified and thickened, and is followed by thin-walled prosenchymatous cells which more internally exhibit lignification. The inner parenchymatous cortex has small air-spaces and some square-ended, pitted, lignified cells. The endodermis and pericycle resemble those of the other species of *Livistona* examined. The protoxylem-groups and the phloem occupy the periphery of the central cylinder and are embedded in a sclerenchymatous zone. The larger vessels extend some distance internally. In roots of small diameter the medulla is entirely parenchymatous, but in larger roots several sclerenchymatous strands in which are embedded one or two vessels traverse the medulla. Generally these strands are quite free from the sclerenchymatous zone, but occasionally one is seen in lateral continuity with it.

The central cylinder shows in the larger roots a slight lateral invagination, into which the endodermis extends.

This is the only irregularity in these roots.

(17) *SABAL GLAUCESCENS*, Lodd.

The limiting-layer is composed of isodiametric, thin-walled, lignified cells. Under this layer are several layers of lignified fibrous cells, a single layer in the middle being non-lignified. This zone passes gradually into a large-celled parenchymatous cortex with large irregular air-spaces. There are no fibrous elements and comparatively little thin-walled lignified parenchyma. In some cases the remains of the elements whose disorganization has given rise to the air-spaces are very well shown. The innermost layers of the cortex are more compact and without air-spaces. The endodermic cells are about six times as long as broad and of the usual lignified type. The pericycle is

generally two-layered, but opposite the phloem it becomes three-layered. The cells are non-lignified, but the cellulose walls are thickened in a scalariform manner. The sclerenchyma in which the xylem and phloem lie extends to the centre of the root. The protoxylem- and the phloem-groups run in the periphery. More internally there is a single ring of large vessels. In some cases one of these forms the apex of a V, the arms of which are formed by two protoxylem-groups.

Towards the centre of the root are two bands of parenchyma separated by a broad sclerenchymatous mass enclosing two large vessels. This band represents the medullary sclerenchymatous strands of many other palm-roots.

In another root a definite parenchymatous pith without sclerenchymatous strands but with air-spaces and some lignified cells occurs.

(18) *SABAL ADANSONI*, Guerns.

The limiting-layer is composed of thin-walled isodiametric cells with dark contents and slight lignification of the walls. Then follows a zone of parenchymatous elements, the outer members and a few of the innermost of which are lignified, lignification proceeding centripetally and centrifugally. The inner cortex is parenchymatous, the middle region being composed of longitudinal diaphragms of cells separating large radially arranged air-spaces. In this region also occur elongated, lignified, and pitted elements, but no fibres. The innermost zone consists of smaller cells and some lignified elements, but no air-spaces. The endodermis is similar to that in *S. glaucescens*. The pericycle is only one cell in thickness, except opposite the phloem, where it becomes two cells in thickness. It is lignified and pitted. The sclerenchymatous zone extends nearly to the centre of the root and carries peripherally the protoxylem and the phloem. There is a single ring of large internal vessels; occasionally this ring is doubled locally. Centrally a parenchymatous pith occurs, having in its midst a large air-space formed by disintegration of parenchymatous elements.

(19) *SABAL PALMETTO*, Lodd.

The slightly lignified limiting-layer is succeeded by a prosenchymatous zone, of which the outermost elements alone are lignified. This zone passes gradually into a large-celled parenchymatous cortex with large radially extending air-spaces and without fibrous bundles or individual lignified elements. The innermost layers of the cortex are composed of smaller-celled parenchyma without air-spaces. This layer is incompletely separated from the main body of the cortex by an irregular zone of lignified pitted elements similar to those scattered irregularly throughout the cortex of many other species. The endodermic cells are thin-walled, non-lignified, and non-cuticularized. The pericycle is generally three cell-layers in thickness, except opposite the protoxylem, where only two layers may be present. The pericyclic cells have thin cellulose walls.

The xylem and phloem are embedded in non-lignified prosenchyma and parenchyma. The innermost prosenchyma of this zone alone is lignified. The outermost protoxylem-

elements alone are lignified, the inner vessels being quite thin-walled and retaining their cellulose nature. There is a central non-lignified parenchymatous pith with irregular air-spaces formed by disintegration of cell-walls.

In other cases the xylem and phloem are embedded in lignified sclerenchyma, the vessels are all lignified, and there is a very small pith in the centre.

(20) *SABAL FILAMENTOSA*, H. Wendl.

The limiting-layer is of the usual type and is succeeded by a zone of elongated lignified elements, generally square-ended. These are followed by the parenchymatous inner cortex with air-spaces in three or four irregular circles and separated from one another by diaphragms only one cell in thickness. In this region occur lignified cells which may be isodiametric or elongated. No fibres are present. The cells of the endodermis are so strongly thickened and lignified on all but the external tangential walls that the lumina are almost occluded.

The pericycle varies from one to two cells in thickness; it is generally lignified, but some of the cells retain their cellulose nature, the cellulose regions generally occurring opposite to a phloem-group.

The central cylinder is almost entirely occupied by sclerenchymatous tissue in which lie the xylem and phloem. The phloem-groups extend centrally to a somewhat greater extent than usual. There is a double ring of large internal vessels without apparent relation to the protoxylem-groups. Centrally there is a very small parenchymatous pith consisting in transverse section of four or five elements only.

II. BORASSINÆ.

(21) *HYPHÆNE THEBAICA*, Mart.

The limiting-layer is exfoliated. Peripherally there is a dense zone of lignified elements. This is followed by the parenchymatous inner cortex with small irregular air-spaces and individual lignified parenchymatous elements and bundles of very thick-walled and pitted fibres. The endodermic cells are thin-walled, non-lignified, and non-cuticularized. The partially lignified pericycle is one or two cells in thickness. There is a ground-mass of sclerenchyma in which lie the xylem and phloem. A single ring of large vessels lies internally to the protoxylem-groups, and these form the apices of irregular V's. Two adjacent phloem-groups also frequently converge centrally and may form a phloem V, the arms of which enclose a small xylem-group. In other cases an isolated phloem-group occupies the apex of the phloem V, and the arms instead of being continuous with this are separated from it by portions of the sclerenchymatous tissue. In the centre of the root is a parenchymatous pith, largely occupied by sclerenchymatous strands each enclosing a vessel; usually the vessel is placed quite laterally in the strand instead of in the centre as in most roots. Some of the strands are connected laterally with the sclerenchyma-zone.

(22) *LATANIA LODDIGESII*, Mart.

The limiting-layer is exfoliated and a zone of elongated more or less lignified elements occupies the periphery; a parenchymatous cortex follows, in which occur comparatively small and irregular air-spaces and a few lignified and pitted elements. The innermost cortical zone consists of much more regularly arranged cells, without air-spaces, but with a considerable proportion of fibrous elements with thick lignified walls scattered irregularly and not grouped into bundles.

The endodermic cells are thin-walled, non-cuticularized, and non-lignified.

The pericycle is one cell in thickness opposite the xylem- and phloem-groups, two cells in thickness between these groups.

The xylem and phloem are embedded in non-lignified prosenchyma, the inner portion of this zone alone being lignified, the process commencing internally and proceeding centrifugally.

The large vessels of the interior are arranged roughly in one ring, but deep bays of prosenchyma projecting into the pith also enclose vessels occasionally. Small-celled groups occur amongst the large internal xylem-vessels. These appear to be of the nature of phloem, but differentiation has not gone far enough to state with certainty.

A parenchymatous pith occupies the centre of the root in which runs a single prosenchymatous strand, the outer elements of which are lignified, lignification proceeding centripetally.

This strand encloses a single large vessel.

(23) *LATANIA COMMERSONI*, Mart.

The outer cortex forms a narrow zone. The inner parenchymatous cortex possesses small irregular air-spaces and bundles of well-developed strongly lignified fibres with stegmata. The endodermis is thin-walled and non-lignified. The pericycle is one-layered.

There is a broad zone of sclerenchyma enclosing centrally a very irregular pith. The xylem and phloem lie in the sclerenchymatous zone.

The protoxylem-groups, as usual, are arranged peripherally, while the large internal vessels are scattered throughout the sclerenchyma, without relation to the protoxylem-groups. The phloem-groups alternating with the protoxylem-groups are practically undeveloped, but scattered patches of phloem lie amongst the large internal vessels of the xylem, being distributed centrally nearly as far as are these vessels.

III. *LEPIDOCARYINÆ*.(24) *RAPHIA RUFFIA*, Mart.

The limiting-layer cells are somewhat elongated; these together with the three or four underlying layers, which are composed of cells of similar form, are slightly cuticularized. They are succeeded by a zone of lignified elongated cells, more or less square-ended. The parenchymatous inner cortex has large and irregular air-spaces, often

separated from one another by only a single layer of cells. Through this portion of the cortex run lignified fibres, usually singly, sometimes in pairs, but never in bundles. The innermost zone of the cortex is composed of smaller, more tightly packed cells, without fibres or air-spaces.

The endodermic cells are lignified and thickened almost equally on all the walls. The cells are about four times as long as broad. The pericycle varies from one to two cells in thickness; the cells are about three times as long as broad, somewhat lignified and pitted. Inside the pericycle comes a broad zone of sclerenchyma enclosing a central parenchymatous pith. In this zone the xylem and phloem are embedded.

The majority of the xylem-groups consist of a few protoxylem-vessels followed internally by a single large vessel, but sometimes the large vessel is wanting, or represented by only a comparatively small structure.

(25) *RAPHIA HOOKERI*, C. Mann & H. Wendl.

The limiting-layer consists of thin-walled isodiametric cells which are cuticularized and slightly lignified. This is followed by about six layers of slightly lignified small fibrous cells, succeeding which internally is the parenchymatous inner cortex, the external layers of which are composed of small tightly packed cells. The middle layers consist of larger cells with large air-spaces arranged in many series, and bundles of fibres provided with well-developed stegmata. Immediately outside the endodermis are two or three layers of cells without air-spaces, but with bundles of fibres, which here approach much more closely to the central cylinder than is usually the case.

The endodermic cells are elongated and fibrously thickened and lignified as usual, and the lumina are largely occluded.

The pericycle is one or two cells in thickness, consisting of cells about twice as long as broad, slightly lignified and minutely pitted. The ground-tissue of the central cylinder is sclerenchymatous, and generally extends to the centre, no pith being developed. In other cases there is a lignified central tissue distinct from the sclerenchymatous zone, and containing a few non-lignified elements. It is seen as a distinct tissue when the section is treated with sulphuric acid.

The protoxylem-vessels are succeeded internally by a series of vessels gradually increasing in size, the innermost nearly reaching the centre of the root. The peripheral xylem-groups form V's and enclose the phloem-groups. Occasionally a xylem V encloses a phloem V, and this, again, a small xylem-group.

(26) *METROXYLON SAGU*, Roxb.

The limiting-layer is exceptionally well preserved and consists of thin-walled isodiametric lignified elements. This is succeeded by a zone of more or less square-ended, elongated, lignified, pitted cells, and this again by the parenchymatous inner cortex with an irregular development of air-spaces, and strands of fibres bounded by stegmata. The cells of the endodermis are very greatly thickened and the lumina almost occluded. The lignified pericycle is two elements in thickness; the inner cells are, however, much reduced opposite the protoxylem. The whole of the ground-tissue of the central

cylinder is sclerenchymatous, no pith being present. Two rings of large vessels succeed the protoxylem-groups internally, and V's are formed. Not infrequently the phloem-groups also form V's, and thus we find a xylem V enclosing a phloem V and this again enclosing a small xylem-group.

(27) *METROXYLON RUMPHII*, Mart.

This root resembles that of *M. Sagu* in all respects, except that no complete phloem V's were found. One incomplete phloem V occurred, one limb being separated from the rest of the structure by a portion of sclerenchyma, the apical group being continuous with the other limb.

(28) *PLECTOCOMIA ELONGATA*, Blume et Mart.

The limiting-layer is exfoliated, the periphery being occupied by fibrous lignified elements. More internally these elements become extremely densely lignified and sclerozed, the lumina being almost occluded. The inner cortex is mainly parenchymatous with small air-spaces, and through this portion run strands of long narrow fibres surrounded by stegmata. Of the parenchymatous elements many individual cells are lignified and deeply pitted. These may occur in long strings, cell after cell being lignified in the same manner, and some of the elements are usually much elongated. In some cases large elongated elements are also present with very thick walls, and containing mucilage and raphides. The endodermis is thin-walled and only slightly lignified. The pericycle is also thin-walled. The sclerenchymatous zone is composed of elements extremely densely lignified, thickened and sclerozed, very dark-coloured, and with their lumina nearly occluded.

The vascular elements are normal in structure and arrangement. There is a central parenchymatous pith, in which are a few lignified elements.

IV. CEROXYLINÆ.

(29) *CARYOTA OCHLANDRA*, Hance.

The limiting-layer is well marked and of the usual type. It is succeeded by a narrow zone of small elongated lignified elements with reduced lumina.

These are followed by the parenchymatous inner cortex, the outer layers of which are dense, while the broad inner zone is provided with large air-spaces very irregularly developed. Amongst these are scattered bundles of fibres. The endodermis is of the usual lignified type; the pericycle is two cells in thickness; the sclerenchymatous zone extends to the centre of the root (*i. e.*, there is no pith), and in this are arranged peripherally the protoxylem- and phloem-groups. The large internal vessels are exceptionally well developed and extend to the centre of the root, the structure recalling that of the non-contractile root of *Corypha umbraculifera*, Linn., but here on a much smaller scale V-formation occurs with the outer members of these internal vessels.

(30) *CARYOTA RUMPHIANA*, Mart.

The cortical tissues are generally similar to those in *C. ochlandra*, but not so much broken down by air-space formation. The lignified tissue of the outer cortex is more strongly developed. The bundles of fibres of the inner cortex are present as in the last species, and in addition to these is a zone of stone-cells just external to the endodermis. There is a very dense sclerenchymatous zone in the central cylinder, but here there is usually a small irregular pith in the centre, which may contain an air-space and some mucilaginous elements. The phloem-bundles are considerably prolonged centrally, and the large internal vessels of the xylem are developed to within a short distance of the central pith. Xylem and phloem V's are very frequent, and we may even get a phloem-group embraced by a xylem V, this again by a phloem V, the whole complex being embraced by a xylem V just incomplete at the apex, as shown in the accompanying diagram (text-fig. 10).

Fig. 10.

(31) *CARYOTA URENS*, Linn.

The cortex is here much less richly supplied with air-spaces than in the last two species. The fibrous bundles are well developed, as are also the stone-cells surrounding the endodermis. These elements have extremely thick walls, almost occluding the lumina. The endodermis is of the usual lignified type and the pericycle is one-layered. The sclerenchymatous zone is broad and encloses a central pith. The phloem-groups do not extend nearly so far centrally as in *C. Rumphiana*, Mart., and the large internal vessels are much more peripherally placed, and they can with greater certainty be relegated to their own one or two protoxylem-groups. In the central pith run three strands of sclerenchyma, each with its central vessel. One of these strands is laterally connected with the sclerenchymatous zone.

In a smaller root the structure is much the same, but only one medullary sclerenchyma-strand is present.

(32) *CARYOTA* sp. (Queensland).

The limiting and underlying layers are normal, but the latter contain large mucilage-cells with thick walls. The inner cortex has small and very irregular air-spaces. It has some thick-walled parenchyma and a few stone-cells. There are relatively few fibrous bundles in the cortex. The most striking feature of the inner cortex in this species is the extraordinarily rich development of mucilage-reservoirs, generally formed by the lengthening and thickening of the walls of a single cell. These cells may form rows, and are full of dense dark-coloured mucilage, in which lie raphides. The endodermis is typical and the pericycle is one-layered. Inside this is a comparatively narrow

sclerenchymatous zone enclosing a parenchymatous pith. The xylem- and phloem-groups lie peripherally in this zone, and there is only one irregular ring of large internal vessels. V-formation occurs, as there are fewer of the large vessels than there are protoxylem-groups. In the central pith run three sclerenchymatous strands each enclosing a large vessel.

(33) *ARENGA WIGHTII*, Griff.

The limiting-layer is persistent, and consists of thin-walled slightly lignified isodiametric cells and is succeeded by a zone of small, square-ended, elongated, lignified, thick-walled elements. The inner cortex is parenchymatous with very irregular air-spaces and strands of fibres bounded by stigmata. In addition to the fibres, individual thick-walled, pitted, lignified, parenchymatous cells occur, particularly well developed immediately around the endodermis, in which region air-spaces and fibrous bundles are wanting. The endodermis is thick-walled and lignified; the pericycle is two or three cells in thickness, and the elements are short and isodiametric. The xylem and phloem are embedded in a sclerenchymatous zone in which the vascular elements do not extend far centripetally. There is one ring of larger internal vessels, and centrally there is a parenchymatous pith with some lignified elements.

(34) *IRIARTIA* sp.

The limiting-layer cells are slightly lignified and project as papillæ on the surface. A layer of thickened lignified elements with narrow lumina succeeds the limiting-layer, and is followed by a zone of prosenchyma, of which the outer layers are lignified. The parenchymatous inner cortex is traversed by bundles of fibrous elements, only the outer members of which are lignified. In the centre of each bundle runs a long element with transverse walls very like those of the sieve-tubes, but no definite pitting could be made out. Of these De Bary says, "perhaps sieve-tubes." Unfortunately older roots could not be obtained, and it was found impossible to settle the question from the available material. In the most internal part of the cortex run definite rounded air-spaces, and in this region also occur individual lightly lignified parenchymatous elements. In a root $\frac{1}{4}$ inch in diameter a complete endodermis of lignified cells exists. At one point it was doubled, two cells occurring on the same radius. The central cylinder in this root is elliptical in outline. The pericycle is two cells in thickness, except just opposite the protoxylem-groups, where it is reduced to one cell in thickness. The xylem and phloem are embedded in a prosenchymatous zone, only the periphery of which is lignified. The protoxylem-elements, which are only very slightly lignified, are embedded in patches of non-lignified tissue. V-formation is rare, but there is a tendency to xylem V's at the ends of the ellipse. Only one ring of internal vessels exists; these are non-lignified, but are embedded in lignified sheaths. Centrally there is a parenchymatous pith with very irregular air-spaces.

In the transverse section of a larger root the endodermis, instead of forming a complete ring, forms a series of arcs of small radius as compared with the radius of the whole central cylinder. This gives a lobed outline to the cylinder, and in the depressions between the lobes the endodermis cannot be recognized as a definite layer, the ground-

parenchyma of pith and cylinder being in all respects similar and quite continuous. Immediately internal to such a gap is often a large vessel, sometimes accompanied laterally by one or two phloem-groups, sunk in the ground-tissue of the cylinder. At other points two phloem-groups may be in close proximity at such a gap, no xylem-group intervening. The arrangement of the arcs conveys the impression, borne out by examination of the apices, that they have arisen as independent procambial strands in the meristem.

In the large parenchymatous pith are developing strands of fibres, each with a central element, of the same nature as those described as occurring in the cortical strands.

In some cases the aerial roots bear lateral rootlets, which are reduced to spines. The structure of these spines is as follows:—

The periphery is occupied by a more or less disorganized layer of thin-walled cells, beneath which is a zone of parenchyma, followed by three or four layers of lignified elements with pitted walls and square ends, and succeeded by about three layers of cells of a similar character, but non-lignified. The parenchymatous inner cortex then follows; many of the outer cells show clear evidence of secondary division, as do also some of the other cells irregularly scattered throughout this region. The endodermis is in the form of two arcs, incurved at either end, where they are not continuous with one another, but may project inwards as plates of cells for some distance. The endodermic cells are lignified and somewhat thickened. The central cylinder consists of parenchymatous ground-tissue in which are embedded some lignified elements. The phloem-groups consist of three to five elements and are arranged peripherally as usual. The xylem is very greatly reduced, but the protoxylem may be seen to be exarch and to consist of annular elements, those developed more internally being scalariform. The whole ground-plan is that of a root, but greatly reduced as to its xylem-constituents.

(35) *HYOPHORBE AMARICAULIS*, Mart.

The limiting-layer is thin-walled and lignified, and is followed by a zone of more or less elongated and pitted cells, succeeded in turn by the parenchymatous inner cortex, through which are scattered individual lignified fibres, not collected into bundles. Comparatively small and very irregular air-spaces are present. In the zone immediately surrounding the endodermis occurs a complete circle—two or three elements in thickness—of very strongly lignified stone-cells with deep simple pits. The endodermic cells are comparatively thin-walled and slightly lignified on all except the outer tangential walls. The two-layered pericycle is also thin-walled. The central cylinder is laterally depressed on one side, and here the endodermis dips in, but is quite continuous. The protoxylem-elements are embedded in non-lignified parenchyma, but the ground-mass of the cylinder is sclerenchymatous, forming a ring enclosing a central pith into which bays of the sclerenchyma project. The pith is parenchymatous, with a few elongated, generally square-ended elements. Through this pith run sclerenchyma-strands, most of which surround a central non-lignified vessel. Some of these strands unite externally with inwardly projecting bays of sclerenchyma of the ring. In larger roots the central cylinder is much lobed, and into each depression the endodermis dips, and at the bottom

of the larger depression it is discontinuous as a specially differentiated layer, the cortical and medullary parenchyma being quite continuous. At these points the sclerenchymatous ring is incomplete, and the adjacent ends are inflected, carrying inwards with them the last two or three xylem- and phloem-groups. The pith is parenchymatous, and there are many sclerenchymatous strands with central vessels.

(36) *GEONOMA SEEMANNI*, H. Wendl.

The limiting-layer is of the usual type, and is followed internally by a zone of elongated elements densely lignified in the external layers, but becoming less and less densely lignified centripetally, the innermost layer of the zone being entirely non-lignified. Passing further in a central direction lignification gradually increases, but not to the same extent as in the outer layers just mentioned. The parenchymatous inner cortex contains air-spaces and bundles of fibres. Immediately around the endodermis are several isolated lignified elements, somewhat elongated, thick-walled, and pitted. The endodermis is of the usual lignified type. The pericycle is two cells in thickness. In a sclerenchymatous zone lie the xylem and phloem. Only one ring of large internal vessels is present. In other roots the outer portion of the ground-tissue of the central cylinder is non-lignified, and the phloem- and protoxylem-groups are embedded in parenchyma.

(37) *GEONOMA PUMILA*, H. Wendl.

The limiting-layer is almost entirely exfoliated, the periphery being then occupied by an external cortex of the usual type of elongated cells, passing gradually into the parenchymatous inner cortex, which is provided with comparatively large and irregular air-spaces. In this region lie long, square-ended, lignified elements. The endodermis is of the usual lignified type. The pericycle is two layers in thickness; its elements are parenchymatous, much compressed opposite the protoxylem, but expanding opposite the phloem. The zone in which the phloem and protoxylem are embedded is parenchymatous and non-lignified, but internally there is a zone of lignified elements in which lies one ring of large internal vessels. There is centrally a loose parenchymatous cortex with irregular air-spaces.

(38) *CHRYSALIDOCARPUS LUTESCENS*, H. Wendl.

The limiting and tegumentary layers are developed as usual, and are followed by the outer dense zone of the parenchymatous inner cortex, in which are many elements containing dark-coloured mucilage. The inner zone shows small well-developed air-spaces arranged roughly in three circles. In this region are also bundles of fibres very richly developed, especially in the innermost layers. The endodermis is lignified and the pericycle is one-layered. The sclerenchymatous zone encloses a large central pith. In the sclerenchyma lie the xylem and phloem. There is only one ring of internal vessels, and these can usually be allotted to their particular protoxylem-groups, but occasionally V-formation obtains. The pith contains many small definite air-spaces.

In a section of a large root taken some distance from the stem-base, the central cylinder exhibits a depression on one side, and into this the endodermis dips. In this region the

sclerenchymatous zone shows wedge-formation and xylem V's occur. More proximally a complete gap in the sclerenchyma is found, and the endodermis dips in and becomes discontinuous. In addition to this several depressions occur in the cylinder, into which the endodermis sinks, but is quite continuous. At such a depression the arrangement of bundles is rather peculiar, the insinking of a phloem-group and convergence of two protoxylem-groups by their external ends being very well marked. (fig. 11.)

Fig. 11.

In the pith of such a root several free sclerenchymatous strands occur, each with one to three central vessels.

(39) *DYPsis MADAGASCARENSIS*, Hort.

The outer walls of the limiting-layer cells are often much thickened, all the other walls remaining of the usual thin type. Following this is a zone of small elements filled with dark brown contents. Internally this zone gives way to the inner parenchymatous cortex, through which run bundles of fibres. The internal layers are provided with many-ranked small air-spaces. The endodermis is lignified and much thickened in the usual manner. The pericycle consists of one or two layers of cells. The xylem and phloem are embedded in a more or less lignified fibrous zone. V's are of frequent occurrence in the xylem, the elements of which are confined to the periphery of the cylinder. In the centre is a large parenchymatous pith with very irregular air-spaces. One sclerenchymatous strand enclosing a single vessel runs laterally in the pith.

In larger roots the histological structure is similar, but the sclerenchymatous zone, instead of forming a complete circle, is composed of two entirely separate lobes, the free ends of which are inflected. Into the space between the two lobes the endodermis of each lobe dips and is lost in the general ground-tissue of the root. In these gaps are found bundles of fibres exactly like those of the cortex; these may penetrate the internal ground-tissue of the cylinder for a short distance. In the medulla are free sclerenchymatous strands with central vessels. One of these occurs just opposite one of the gaps in the cylinder, and externally to the central vessel in this strand runs a phloem-group. (Text-fig. 12.)

Fig. 12.

In still older portions the cylinder is split up into many separate arcs, the larger ones containing as many as forty xylem-groups. The ends of the arc are inflected as in the section just described. The smaller arcs may contain only one xylem-group, flanked

on either side by a phloem-group. Both large and small arcs are externally bounded by an endodermis which dips into the gaps between the arcs and is lost in the common ground-tissue.

(40) *OREODOXA REGIA*, H. B. & K.

There is a thin-walled limiting-layer, followed by elongated lignified pitted elements. The cortex is largely parenchymatous, but widespread lignification obtains, and a special ring of lignified elements, two or three cells in thickness, surrounds the endodermis. The air-spaces are small and extremely irregular. The endodermis is of the ordinary lignified type; xylem V's are frequent and also more complicated arrangements, as shown in the accompanying woodcut (text-fig. 13). There is generally only one ring of large internal

Fig. 13.

vessels, which are peripherally placed. The xylem and phloem are embedded in a fibrous zone of very densely packed, thick-walled, and lignified elements. There is centrally a pith, through which run one or more sclerenchymatous strands with central vessels.

(41) *HOWEA FORSTERIANA*, Becc.

A. *Specimen from Glasgow*.—Limiting-layer and tegumentary layer normal, the latter containing much mucilage. The inner parenchymatous cortex contains irregularly arranged fibres, not usually united into bundles. In the internal portion of the cortex rather large air-spaces occur, together with bundles of fibres. The endodermis is lignified and the pericycle is generally one- (locally two-) layered. The sclerenchymatous zone contains the xylem and phloem as usual. The large vessels of the interior are so arranged that each protoxylem-group has its own large vessel (occasionally a V is formed). This leads to close packing of the large vessels, which are consequently radially compressed into an elliptical shape. The phloem extends centrally to a greater extent than in the majority of roots. In the centre there is a large parenchymatous pith.

B. *Specimen from Ceylon*.—The cortical air-spaces are here much smaller and the fibres more generally occur in bundles. The vascular elements are all peripherally placed in the sclerenchymatous zone. Where no large internal vessel abuts on the space between two xylem-groups, the intervening phloem-group may extend for a considerable distance centrally. (Text-fig. 14.) This is the only root in which this character has been seen so

Fig. 14.

well developed. The large pith contains small air-spaces, and in a large root one or more free sclerenchymatous strands may occur, each with its central vessel. In large roots

the sclerenchymatous zone is interrupted on one side, and into this gap the endodermis dips, being continuous round the inrolled margins of the sides of the gap, but lost internally, the cortical and medullary ground-tissue being quite continuous.

(42) *HETEROSPATHE ELATA*, Scheff.

The limiting and subjacent layers are of the usual type. The parenchymatous cortex has large air-spaces, and in the external layers of the inner cortex are lignified elements of two kinds—rows of lignified parenchyma and true fibres. In the internal layers the fibres occur in bundles. The endodermis is typically lignified. The non-lignified pericycle is one-layered. The xylem and phloem are embedded in a fibrous zone. The large vessels extend for a greater distance internally than usual, as do also the phloem-groups. Xylem and phloem V's of a type similar to those in *Caryota Rumphiana*, Mart., are formed. In somewhat larger roots the central cylinder is lobed. Opposite the depressions the arrangement of xylem- and phloem-groups is peculiar (see text-fig. 15).

Fig. 15.

There are no completely free medullary strands, but many strands attached laterally to the fibrous zone project into the medulla, each strand having its central vessel. Some fibres occur in the pith, with tendency to arrangement into bundles.

In still larger roots the cylinder is completely broken up into lobes. The endodermis dips into the spaces between the lobes and there loses its identity. Bundles of fibres are well developed in the medullary parenchyma of these roots.

(43) *ONCOSPHERMA FASCICULATUM*, Thw.

The parenchymatous cortex has small, very irregular air-spaces arranged in many zones, and bundles of fibres of the larger less densely lignified type, not arranged into definite strands bounded by stegmata such as we find in many roots, but agreeing closely with those found in *Kentia* sp. (*q. v.*). The endodermis is lignified; the pericycle one-layered. The xylem and phloem lie in a rather broad fibrous zone; V-formation occurs occasionally, but is not general. Many of the protoxylem-groups are without internal large vessels. In one V the xylem-groups instead of converging to the outer portion of the large vessel, as is usually the case, converge to the sides. (Text-fig. 16.)

Fig. 16.

The central medulla contains some irregular air-spaces.

(44) *EUTERPE* sp.

The limiting-layer is slightly lignified. It is succeeded by a narrow zone of small elongated lignified elements. Through the parenchymatous inner cortex run lignified fibres with transverse walls, and also other lignified elements arranged in strands, whose fibrous nature is not nearly so evident. The air-spaces are large and irregular. The innermost cortical zone is much denser than the rest and is without air-spaces. The endodermis is lignified, and the pericycle one or two cells in thickness. The fibrous zone is of comparatively small width, and contains the xylem- and phloem-groups. Xylem V's are of frequent occurrence. There is only one ring of large internal vessels, and these are very peripherally placed. The pith is large and parenchymatous and contains regular air-spaces.

(45) *KENTIA* sp.

The peripheral layer is composed of large isodiametric thin-walled lignified cells. These are followed by elongated lignified small elements, the outer of which are provided with dark contents. These pass internally into more densely lignified fibrous elements and these again are followed by the parenchymatous cortex with its large irregular air-spaces and bundles of fibres. These fibrous bundles, though fairly definite, are not by any means so well formed as those in *Raphia Hookeri* for example, and in other roots provided with stegmata. The fibres themselves are much broader, relatively thinner-walled, and with more considerable lumina, closely resembling those found in *Areca concinna*. The endodermis is much lignified and thickened on all but the outer tangential walls. The pericycle is generally two elements in thickness, but opposite to the protoxylem-groups it may be reduced to one. The xylem and phloem are embedded in a lignified zone of fibrous elements. Xylem V's are of frequent occurrence. There is only one irregular ring of large internal vessels. Centrally there is a parenchymatous pith in which lie some pitted fibres.

In large roots, passing from distal sections to proximal ones, the following stages are observed:—

(a) Outer cortex parenchymatous, with no air-spaces, but with sparsely scattered fibrous elements. Inner cortex of larger parenchymatous cells, among which run fibrous bundles and large air-spaces. The central cylinder presents a slightly lobed outline, the endodermis dipping into the lobes, but being quite continuous. The cylinder is incomplete on one side, and here the endodermis follows the incurved edges of the fibrous zone, and is lost internally in the parenchymatous ground-tissue. These free edges of the fibrous zone are very much inrolled, carrying in with them at least two phloem-groups. The gap between them is broad, and through it the ground-tissues of cortex and medulla are continuous. In both are embedded exactly similar fibrous bundles, except that those of the pith tend to be slightly less strongly lignified.

(b) In a section taken more proximally the cylinder is still more lobed, and several gaps, bounded by the inrolled edges of the fibrous zone, are present. Into these gaps the endodermis dips and is lost. Some of the arcs of fibrous tissue are so greatly

inrolled that a complete ring of tissue is formed in which the xylem- and phloem-groups are only wanting for a short space internally. Round these the endodermis is nearly continuous. Through each gap the parenchymatous tissue of cortex and medulla is continuous, and fibrous bundles are very abundantly developed in the medullary portion.

(c) In sections from a still more proximal portion of the same root the vascular cylinder consists of a greater number of separate arcs, many of which form nearly complete cylinders. The xylem-groups of the internal portion of these cylinders are approximated by their protoxylem-elements, the metaxylem portions divaricating widely. A phloem-group occupies the innermost point of such a cylinder (text-fig. 17). Such a

Fig. 17.

complete ring of fibrous tissue encloses a portion of the general parenchymatous ground-tissue, continuous below with the medulla, when the ring becomes incomplete internally. In this central parenchyma occur two or more strands of fibres similar to those of the pith and cortex.

The endodermis is in this region strongly lignified on all but the external tangential walls, and here and there occurs a non-lignified passage-cell. When present, such a cell usually occurs opposite to a protoxylem-group, but they are rarely developed, the endodermal cells opposite the protoxylem being generally quite as densely lignified and thickened as elsewhere. Not infrequently the endodermis is locally doubled; this occurs generally immediately distally to the closure of the gaps in the central cylinder.

Between two inrolled edges of the fibrous zone, just before fusion takes place, the parenchymatous cells of the ground-tissue are often greatly crushed, and their lumina may even be entirely obliterated, showing that a differential rate of expansion has taken place since the procambial tissue was laid down in the apex.

Similar crushing may also occur between the nearly fused internal edges of greatly inrolled arcs of the fibrous zone. Some of the segments of the central cylinder are very small and may contain as few as one xylem- and two phloem-groups, the endodermis only bounding the peripheral surface. Others contain three xylem- and five phloem-groups; others are more extensively provided with endodermis investment. In the medullary tissue run isolated strands of fibrous tissue, many of which possess a xylem-group consisting of one large vessel and two or three smaller ones. In other cases only the large vessel is present. In one case an interesting condition was observed in the presence of a phloem-group, quite unaccompanied by xylem, running just internally to a gap in the fibrous zone. Occasionally a medullary fibrous strand may enclose a central large vessel from which protoxylem-groups to the number of 3-5 radiate, alternating with which two or more phloem-groups occur.

At some gaps in the fibrous zone, even when the endodermis is complete across the

gap, a line of cells of endodermic nature extends inwards into the cylinder. (Text-fig. 18.)

Fig. 18.

One greatly incurved arc of the central cylinder was found to be completed in a curious fashion. A medullary strand possessing three symmetrical protoxylem-groups radiating from a central vessel, and alternating with the protoxylems, approaches distally to the interior of the incurved arc and closes the gap by fusion of the fibrous tissues, thus enclosing a central parenchyma continuous above and below with the medullary ground-tissue. Of the three protoxylem-groups, two become arranged tangentially in a straight line, the third, pointing inwards, is considerably reduced. The endodermis is only incomplete at the most internal point of the cylinder thus formed.

Another interesting condition was observed where a complete cylindrical portion of the central cylinder is approached distally from the interior by a medullary strand, with four xylem- and four phloem-groups, which eventually fuses with it, thus causing a very irregular arrangement of xylem and phloem on the interior of the composite cylinder so formed. On following this cylinder distally, the ordinary symmetrical alternation of xylem and phloem is gradually attained, and thus a cylinder is produced with four more xylem-groups than the original one.

Lower down in the root this opens internally and its central parenchyma becomes continuous with the medullary parenchyma, and finally, traced to the apex, the group is represented as a distinct, curved, procambial strand, consisting of xylem- and phloem-groups embedded in fibrous ground-tissue.

The internal fibrous strands which contain xylem and phloem tend to fuse with the peripheral system of the cylinder. In those strands possessing only a single central vessel no such tendency manifests itself, these being continued as separate procambial strands into the apex.

On following the separate arcs of the cylinder towards the apex, they are seen to open out internally and finally to unite, gradually losing the lobed outline, and eventually forming a complete uninterrupted meristematic cylinder. Sometimes where fusion of the arcs takes place the endodermis is doubled.

Only in a long root can all these changes be observed; in shorter roots the reduction to normal root-structure is incomplete. Only a very small proportion of the roots examined showed complete simplification. The union of the arc is always completed earlier (*i. e.* more proximally) on the abaxial than on the adaxial side, a single gap in the fibrous zone often persisting for a very considerable distance on the adaxial side after the cylinder is otherwise complete and regular. Occasionally small groups lying well to the interior of the cylinder are externally provided with endodermis.

(46) CYRTOSTACHYS RENDA, Blume.

The limiting and subjacent layers are of the usual type, and are followed by a closely packed parenchyma with mucilage-canals, and this again by the loose layers of the cortex, with their air-spaces and bundles of fibres, which are shorter than usual, and belong rather to the *Kentia*-type than to the more elongated, narrow type of *Oreodoxa* and *Raphia*. Individual elements of the same nature occur in the zone immediately surrounding the endodermis. The endodermis is lignified, and is followed by a one- or two-layered pericycle.

The fibrous zone of the central cylinder is broad, and generally each protoxylem-group has its own one, two, three, or more large internal vessels. Some of the protoxylem-groups are, however, without internal vessels. V-formation is not well shown. The central medulla possesses fibrous bundles and air-spaces like those of the cortex. Three or four bays of fibrous tissue project into the pith, and nearly form free medullary strands.

In large roots the fibrous zone is incomplete on one side, and the incurved edges are followed by the endodermis more deeply than usual; the endodermis is, however, finally lost in the common ground-tissue.

An interesting feature in this root is the occurrence of two strongly inwardly projecting bays of fibrous tissue in which the protoxylem is well developed internally and accompanied laterally on one side by a phloem-group (text-fig. 19).

Fig. 19.

In other cases this internal xylem is disappearing, the smaller elements having quite aborted, leaving only the small metaxylem-group abutting on the large internal vessel. In other cases, again, only the large internal vessel persists. Thus some of the large internal vessels of these roots undoubtedly represent the remains of what were originally inwardly directed xylem-groups.

(47) PTYCHOSPERMA PERBREVIS, H. Wendl.

Immediately beneath the normal limiting-layer is a zone of three or four fibrous elements lignified and thickened and with transverse walls. Then follows a zone of extremely densely thickened and pitted fibres. The inner cortex is parenchymatous, and is provided with definite bundles of fibres with small lumina and also with some less thickened fibres generally running singly. In the internal portion of this cortex are air-spaces. Through this region run ducts, containing much mucilage and some crystals of calcium oxalate. The endodermis is of the usual thickened and lignified type. The central cylinder is normal and uninterrupted; a broad zone of parenchyma contains the xylem and phloem peripherally. Only one ring of large internal vessels is present. Centrally there is a parenchymatous pith containing some lignified elements.

(48) PTYCHOSPERMA MACARTHURI, H. Wendl.

The cortical tissues are very similar to those in *P. perbrevis*. The central cylinder is very greatly broken up as in *Kentia*, but there is still more strongly marked inrolling of the separate arcs. Internal fibrous strands are present, but are few in number. Each contains a central vessel, in one case accompanied by a phloem-group. The medullary and cortical tissues are quite continuous, and similar bundles of fibres are present in each.

(49) PTYCHOSPERMA FILIFERA, H. Wendl.

The limiting-layer is, as usual, composed of isodiametric cells with thin lignified walls. This is followed by a narrow zone of elongated cells with slightly lignified walls and dark mucilaginous contents. In the parenchymatous cortex occur bundles of fibres and air-spaces. The endodermis is of the usual lignified type; the pericycle is one cell thick.

In a small root all the elements of the fibrous zone are not yet lignified. The pith is represented by a few parenchymatous cells. A very great tendency to V-formation obtains in this root. Out of fourteen protoxylem-groups twelve are arranged as V's with six internal larger vessels. The other two groups, which occur at either end of a diameter of the cylinder, are in conjunction each with its own large vessel. It is impossible to say whether this diametrical arrangement has any morphological significance, since the orientation with regard to the stem could not be determined.

In a larger root a considerable pith occupies the centre and is surrounded by a comparatively narrow fibrous zone. Here again V-formation is very strongly marked. This root differs from all other palm-roots examined in the fact that to each protoxylem-group there is a considerable number (often four or five) of larger vessels, two of which are often placed tangentially. In some cases three of these groups may join tangentially, producing a xylem-band connected externally with three protoxylem-groups. Such a formation is usually followed laterally by V's with extensive internal xylem-groups, and in this way a nearly complete xylem-ring may be formed with exarch protoxylem-groups between which lie the rounded phloem-masses.

The pith contains bundles of lignified elements, in transverse section looking very much like fibres, but seen in longitudinal section to be short and square-ended. Two groups of fibrous tissue, each enclosing one large and several smaller vessels, occur in the pith. In these large roots the contour of the cylinder is slightly lobed, but no complete gap was observed.

(50) PTYCHOSPERMA CUNNINGHAMIANA, H. Wendl.

The limiting-layer is as normal, and is followed by the usual small elongated elements, and these again by a parenchymatous cortex through which run lignified fibrous elements, but no definite fibrous bundles. The inner part of this cortex has fairly regularly developed air-spaces, and here there is a tendency to grouping of the fibres into bundles. The endodermis is of the usual lignified type. The pericycle is generally one cell thick, but occasionally it is doubled. There is a well-developed fibrous zone in which the xylem and phloem are embedded. V-formation is not infrequent. An interesting

feature is the presence of two or three small vessels interior to the large internal elements. The pith is large and parenchymatous, with small air-spaces and fibres like those of the cortex.

(51) *Dictyosperma album*, H. Wendl. et Drude.

The limiting-layer is normal, and is succeeded by a zone of lignified elongated cells with dark mucilaginous contents. This again is succeeded by a zone of fibrous elements among which are scattered some parenchymatous cells; more internally the parenchyma very greatly preponderates, and the fibres are here arranged in definite bundles, very abundantly developed. In this zone small irregular air-spaces occur. The endodermis is lignified.

The pericycle is one- or two-layered. Inside this lies a zone of lignified thick-walled fibres in which are embedded the xylem and phloem. The vascular elements occupy only the periphery of the central cylinder. V's are occasionally found in the xylem, but not in the phloem. A few medullary strands of fibrous tissue, containing one large vessel, sometimes accompanied by one or two smaller ones, generally occur. In the pith some individual fibres are present, but no fibrous bundles like those of the cortex.

Proximally a gap in the cylinder is present and the edges are rounded off and inturned; the endodermis follows these and is finally lost in the ground-tissue, being thus incomplete across the gap.

The latest gap to close up is on the adaxial side of the cylinder. In this region there is greater development of the medullary fibrous groups with central vessels, as well as greater central extension of the large vessels of the cylinder.

Still more proximally the cylinder is more strongly lobed.

(52) *Pinanga* sp.

The limiting and tegumentary layers are developed as usual. In the external layers of the inner parenchymatous cortex are individual fibres, resembling those generally occurring in very definite strands. More internally fibrous strands of the type found in *Kentia* occur. The endodermis is lignified and the pericycle one-layered. A comparatively narrow, but very definite fibrous zone contains the xylem and phloem. V-formation is not often found, but is very well shown when it does occur. In the pith occur strands of fibres like those of the cortex; air-spaces and mucilage elements with dark contents are also present.

(53) *Pinanga kuhlii*, Blume.

The external layers agree generally with those in the last species. The air-spaces of the inner cortex are, however, much larger and more definite. The endodermis and pericycle are similar, as is also the fibrous zone. Only one ring of internal vessels occurs, and they are comparatively small and peripherally situated, and the protoxylem-groups are widely separated. V-formation is unusual, but is found occasionally. Two groups of fibrous tissue were found in the pith, and a third not quite free from the fibrous zone, each with a single internal vessel.

In the pith are mucilage-spaces and bundles of fibres.

(54) ARECA CATECHU, Linn.

(i.) *Small root*.—The limiting-layer is, as usual, followed by elongated elements with dark contents, and these again by a parenchymatous cortex. The outer part of this is without air-spaces, but contains lignified elongated elements, with comparatively large lumina, and more internally bundles of fibres also occur. In the inner layers of the cortex are many large air-spaces in several irregular rings, and in the parenchyma enclosing these are large bundles of fibres. The endodermis is lignified and the pericycle is two layers in thickness. The fibrous zone in which the xylem and phloem are embedded forms a series of bays projecting into the pith. The xylem-elements extend some considerable distance centrally, and most of the large inner vessels can be definitely brought into line with the protoxylem-groups. V's are often formed, and two protoxylem-groups may form a V with the outer of three internal vessels, thus giving a well-marked Y. In the pith are some fibrous elements like those of the outer cortex.

(ii.) In larger roots the pith is much more extensive and the fibrous zone relatively narrower. The internal vessels are more scattered and generally lie in sets of two or three, or one or two large ones may be accompanied by two or three smaller ones. Into both large and small vessels well-developed thyloses project.

(iii.) In still larger roots, or in sections more proximally placed, the central cylinder has a slightly lobed outline. The xylem- and phloem-groups usually lie in threes, two xylem-groups or a xylem V and a phloem-group, or one xylem-group and two phloem-groups, being embedded in wedge-shaped masses of fibrous tissue, whose apices project centrally. The wedges are separated from one another by extensions of the medullary parenchyma extending as far as the pericycle (text-fig. 20). The medulla is parenchymatous, and in it are bundles of fibres similar to those of the inner cortex.

Fig. 20.

The cylinder is incomplete at one point, and here the endodermis dips in and is lost internally, the medullary and cortical parenchyma being continuous. Opposite to the gap is a group of fibrous ground-tissue enclosing two vessels.

(iv.) In still more proximally situated sections the lobing of the central cylinder is more extensive and several gaps are present. Opposite each gap is an internal fibrous strand with vessels and in some cases phloem also.

(v.) In other sections much greater splitting of the central cylinder is shown, the fibrous zone being composed of a number of separate arcs of varying size, the ends of which are incurved and accompanied by the endodermis, which is eventually lost in the ground-tissue. In the smaller segments the fibrous tissue is more and more infolded, until in some cases it fuses internally and a complete ring is produced, only lacking endodermis on its central surface. Finally a complete endodermis occurs round one such cylinder, which lies outside the general fibrous zone. Just internal to it is a gap in this zone, and it would appear that this portion of the central cylinder has failed to establish

complete continuity owing to a portion of the zone having extended too far peripherally, this latter having formed a cylinder on its own account, leaving a gap in the normal ring. The excentric cylinder has eleven xylem-groups with two V's and eleven phloem-groups. It gives off a lateral root, and behaves in all respects exactly like an ordinary root-cylinder. Below, this structure passes into the normal root-cylinder by a method illustrated in Pl. 51. figs. 99 to 102 and fully described above.

The medullary parenchyma in this region contains masses of fibrous tissue with central vessel or vessels and sometimes also phloem.

(55) *ARECA CONCINNA*, Thw.

The limiting and tegumentary layers are like those in *A. Catechu*, L.

The parenchymatous cortex is without air-spaces, or only with very small ones. In this zone occur mucilage containing parenchymatous elements. Small bundles of fibres are also present. The endodermis is lignified, and the pericycle one- or two-layered. The fibrous zone containing the xylem- and phloem-elements encloses a parenchymatous pith with mucilage elements. Xylem V's are occasionally formed.

In the smaller roots the large internal vessels can be allotted to a single protoxylem-group or to a pair of such groups.

In larger roots the general arrangement is similar, but the xylem-groups are much more numerous and the internal large vessels are more scattered. Thyloses are abundant in the vessels.

In still larger roots xylem V's and Y's are abundant, and the xylem arrangement is irregular. The large central pith contains five or six fibrous masses, each with one or more vessels.

(56) *ARECA* sp.

On the surface is a layer of thin-walled limiting cells, followed by small elongated elements. The well-developed parenchymatous cortex is provided with strands of fibres and small scantily developed air-spaces. The endodermis is non-lignified and the pericycle is one-layered. The fibrous zone consists of wedges of tissue completely or nearly completely separated from one another by radiating extensions of medullary parenchyma. These wedges contain the xylem, usually one xylem-group to each wedge. The phloem-bundles may lie laterally in the fibrous wedges or in the parenchymatous tissue between them.

On one side there is a more distinct break in the fibrous ring, and here the incurved edges carry phloem-bundles internally. The endodermis is slightly inflected, but is continuous over the gap. At such a point there is a tendency for the fibrous wedges to become free medullary strands. More proximally the central cylinder is broken up into arcs, and into the gap between each pair the endodermis dips in and is discontinuous. At these gaps some of the wedges are present as free medullary strands, and in the general medullary parenchyma are developing masses of fibres enclosing one or more vessels, and sometimes also a little phloem. Bundles of fibres similar to those of the cortex are also present.

Small and regular air-spaces occur in the cortex of these large roots.

57. ARECA sp. (from Glasgow).

These roots were only obtainable in small detached portions, and are described below under the headings *A*, *B*, and *C*, according to the type presented.

A. Limiting-layer and cortex are as in the last root. The endodermis is only partially lignified, lignification delaying longest opposite to the protoxylem-groups. The pericycle is one or two cells thick. The cylinder is quite complete for at least half its circumference, while the other half consists of a series of separate arcs, whose free edges are generally somewhat incurved, but in no case is the incurving very extensive. The fibrous zone consists of partially separated wedges in which lie the xylem, the phloem often lying in the parenchyma between two wedges. At the gaps there is often an insunk fibrous mass with a central vessel.

The xylem of the lateral wedges of the arcs shows a peculiar radial extension (text-fig. 21).

Fig. 21.

In some cases a fibrous strand may run in the interior with several vessels, quite independently of any gap in the cylinder. **V**'s are of frequent occurrence, and there is considerable metaxylem-formation which always favours such an arrangement. It is by the lateral approximation of these metaxylem-groups that the **V**'s are formed.

In the pith are bundles of fibres and some few air-spaces similar to those in the cortex.

B. The whole cylinder is composed of a number of small arcs, the ends of each being strongly incurved. The fibrous wedges which contain the xylem are almost entirely separated by parenchyma, and the xylem-groups of the ends of the arcs tend to point outwards as in the last case. Often between these arcs are found individual wedges which have not entered into arc-formation. Such wedges have externally developed endodermis, and may possess three or four xylem-groups accompanied by as many phloem-groups. Many internal fibrous strands are present with xylem and phloem, not in any way entering into the peripheral system of the cylinder. The most internally placed of such strands possess only a single vessel.

In this root the very great parenchymatous development is not accompanied by a corresponding development of the fibro-vascular tissue, and hence the separation of the fibrous arcs is much more marked than in any other root examined.

C. (Pl. 50. fig. 76.) In this root the arrangement of the fibro-vascular tissue is very peculiar. On one side there is a large cylinder with continuous endodermis on the whole

of that surface presented to the exterior of the root. The portion of this cylinder presented to the interior of the root is composed of a number of isolated small fibrous masses with endodermis on the surface nearest to the centre of the root. Each of these fibrous masses has a radially symmetrical development of xylem and phloem.

The fibrous tissue is throughout usually in the form of wedges.

In the parenchymatous tissue occupying the interior of this cylinder are many fibrous masses each with xylem and phloem generally radially arranged in several groups.

Accompanying this incomplete cylinder are three complete cylinders, round each of which the endoderm is continuous. The whole arrangement in this root is of great interest as bearing on the question of the morphological value of medulla and cortex in these organs. The general ground-tissue in which the cylinders are embedded is provided throughout with well-developed bundles of fibres and air-spaces.

(58) *Cocos plumosa*, Hook.

The tegumentary layers are normal. A thin-walled layer of isodiametric, slightly cuticularized cells is followed by a more than usually broad zone of small elongated elements, only slightly lignified, and this again by the parenchymatous inner cortex with small and very irregular air-spaces.

Immediately surrounding the endodermis is a narrow zone of thick-walled and pitted stone-cells. The endodermis is lignified, and the pericycle two cells in thickness except just opposite to the protoxylem, where it is reduced to one cell. Opposite the phloem the inner pericyclic cells are often considerably crushed, but seem to be always present. A broad zone of fibrous tissue carries the xylem and phloem and surrounds a central pith. There is a well-developed system of scattered internal vessels which do not extend to the inner margin of the fibrous zone. V-formation is very general by the approximation of two xylem-groups to the exterior of one large internal vessel. The phloem-groups vary greatly in outline, from small peripheral circular patches to radially elongated internally-stretching bands.

In larger roots the inner vessels are much more regularly arranged, usually in two rings. Others occur in fibrous masses distributed in the medulla. Some of these strands are connected externally with the fibro-vascular cylinder, but the majority are free.

In still larger roots the medullary fibrous groups are more abundant and more than one vessel may occur in each. Wedge-formation also obtains in the fibrous zone, which is interrupted by a wide gap on one side, the free edges being incurved. The asymmetry of the xylem-groups is here not so marked as usual, internally pointing protoxylem-groups being found.

The phloem, however, tends to retain its outward orientation. Just inside the gap are two little cylinders, with xylem and phloem radially arranged, one being almost completely surrounded by endodermis. The other little group, which lacks internally arranged protoxylem, lacks also internally developed endodermis.

(59) *Cocos Romanzoffiana*, Cham.

Essentially similar to *C. plumosa*, Hook.

(60) *Cocos flexuosa*, Mart.

The small roots are essentially similar to those of *C. plumosa*, Hook., and *C. Romanzoffiana*, Cham. In larger roots the cylinder is incomplete on one side, the free edges being incurved, and at this point there is no protoxylem, a single vessel representing the xylem-group. Into the medullary tissue opposite to a gap a fibrous mass, containing one large vessel and several phloem-groups, is sunk.

In the centre of the pith are several fibrous strands, each with one, two, or three large vessels. The fibrous zone is here much less regular than usual, consisting of partially separated wedges, united internally with other fibrous groups containing several vessels, but without protoxylem. (Text-fig. 22.) These enclose among themselves little groups

Fig. 22.

of parenchyma, shut off from the pith by the growth of fibrous tissue. Many of the larger vessels contain thyloses consisting of pitted parenchymatous cells. Similar to these are large cells, staining yellow with aniline chloride, occupying irregular spaces in the pith. They are almost certainly formed in the same manner as the "thyloses" described in the cortical air-spaces of *Areca concinna*, Thw.

(61) *Cocos botryophora*, Mart.

The outer part of the parenchymatous cortex is comparatively broad and is without air-spaces. Through the inner part run irregular small air-spaces. Scattered throughout the cortex are isolated, somewhat elongated and lignified parenchymatous elements, with square or rounded ends. Just external to the endodermis is a specially well-developed layer of these, some few of which are thinner-walled and isodiametric. The endodermis is lignified and followed by a two-layered pericycle, which becomes one-layered opposite to the protoxylem.

The fibrous zone consists of a series of wedges, continuous with one another at the periphery, but free internally. Xylem V's are frequently developed.

Many internal fibrous groups connected with the inner extremities of the fibrous wedges occur, each containing a single large vessel.

Some free medullary fibrous groups of the same nature also occur in the well-developed pith.

(62) *COCOS NUCIFERA*, Linn.

The tegumentary layers are of the usual type, but greatly indurated. In the outer zone of the parenchymatous cortex are abundant mucilage reservoirs, containing mucilage of a brown colour and raphides. More internally are regular small air-spaces.

The lignified elements of the cortex, consisting of small, square stone-cells, are almost confined to a zone immediately external to the endodermis.

The endodermis is lignified; the pericycle is two cells in thickness, but frequently interrupted. There is a broad, greatly indurated, fibrous zone in which the xylem and phloem are embedded peripherally.

There is only one ring of large internal vessels. A medullary strand of fibrous tissue, with a single internal vessel, is present in the small pith.

In a larger root air-spaces are well developed in the inner cortical layers, but are very irregular, and lignified elements are more generally distributed. Internally is an extensive pith, with large and very regular air-spaces.

(63) *DIPLOTHEMIUM MARITIMUM*, Mart.

The limiting-layer is normal, and is succeeded by elongated elements with pitted walls, which give place internally to longer and less lignified fibrous elements.

These become more parenchymatous internally, and finally pass into the parenchymatous inner cortex, with its small, irregular air-spaces. Throughout this region occur small lignified parenchymatous elements, particularly richly distributed just outside the endodermis, where they form a more or less definite zone. In this zone the elements are true stone-cells. The endodermis is lignified, and the pericycle consists of two layers of lignified and pitted cells. The fibrous zone is fairly broad, and contains the considerably extended xylem-groups and the large internal vessels arranged in one irregular ring, with a few vessels still more internally placed. The phloem-groups are also greatly extended radially, generally as far as the internal limits of the xylem-groups. The central medulla contains many fibrous strands, each with one central vessel. Sometimes two of these strands run in contact with one another, and occasionally they are connected externally with the fibrous zone.

(64) *MARTINEZIA CARYOTÆFOLIA*, H. B. & K.

The limiting-layer and tegumentary layers are normal. The parenchymatous cortex possesses a system of irregular air-spaces and bundles of fibres, each bundle being provided externally with longitudinal rows of stegmata. Individual lignified parenchymatous elements are also found in these regions and form a specially developed layer around the endodermis. The endodermis is lignified and the pericycle is one-layered. A broad zone of fibrous tissue contains the xylem and phloem. V-formation occurs occasionally, but usually there is a large internal vessel to each protoxylem-group.

In a larger root the arrangement of internal vessels is more irregular, and xylem V's and Y's are of frequent occurrence.

(65) MARTINEZIA LINDENIANA, H. Wendl.

The cortex is generally similar to that of *M. caryotæfolia*. The bundles of fibres with stegmata are present, but the individual lignified elements are wanting, though the whole cortex is more or less slightly lignified. The air-spaces are very definite and are arranged in several irregular circles. The endodermis is lignified. There is a broad fibrous zone composed of extremely densely lignified and indurated fibres, whose lumina are almost occluded. This zone encloses a central parenchymatous pith provided with some lignified elements. The xylem- and phloem-groups are quite normal, with occasional V-formation in the xylem.

In large roots bundles of fibres occur in the cortex, and a zone of lignified stone-cells immediately surrounds the endodermis. A number of fibrous groups, with one, two, or three vessels, traverses the pith.

(66) BACTRIS MINOR, Jacq.

The external layers are as usual. The inner cortex is provided with irregular air-spaces. Stone-cells occur in a zone surrounding the endodermis, and scattered lignified elements are found throughout the cortex. The endodermis is lignified and the pericycle is two-layered. The fibrous zone is nearly filled with vascular elements. The large internal vessels occur in two rings, and the individual elements are closely packed and laterally flattened. Xylem V's and Y's are abundant. Internally there is a pith with large air-spaces.

V. PHYTELEPHANTINÆ.

(67) PHYTELEPHAS MACROCARPA, Ruiz et Pavon.

The cortex is entirely parenchymatous, without any lignified elements or fibres. Somewhat irregular air-spaces are present. The endodermis is lignified and the pericycle one-layered.

A broad fibrous zone encloses a central pith.

The protoxylem-groups extend inwards for a long distance, and generally each is provided with two or more large inner vessels. Occasionally these are accompanied centrally by one or two smaller vessels. The vessels are closely packed laterally and are flattened. The phloem-groups extend inwards nearly as far as do the xylem-groups.

EXPLANATION OF THE PLATES.

PLATE 48.

- Fig. 1. Longitudinal section of stem of *Kentia* sp. showing origin of root.
 2. Diagram of do.
 3. More advanced apex of young root.
 4. Group of cells in cortex of stem, in front of advancing root-apex. (See text.)
 5. Longitudinal section through the common initial group in meristem of apex of *Areca*.
 6. Diagram of apex of root of *Areca*.
 Figs. 7-10. Transverse sections of apices of roots showing progressive changes in the procambial tissue.
 Fig. 11. Apex of root of *Kentia* sp. showing root-cap.
 12. „ „ *Iriartia* sp. „ „
 13. Longitudinal section taken a short distance above the apex of the root in *Kentia*, showing root-cap and "epidermis" or limiting-layer extending below root-cap.
 14. Longitudinal section of root of *Kentia* sp. showing the very thick-walled cells of the root-cap and an irregularity in the limiting-layer.
 15. Transverse section of outer layers of root in *Caryota ochlandra*.
 16. Transverse section of outer layers of root in *Phœnix sylvestris*, showing lignification proceeding both centripetally and centrifugally.
 17. Transverse section of outer layers of root in *Dypsis madagascarensis*.
 18. Development of air-space in *Kentia* sp.
 Figs. 19 & 20. Air-spaces in *Kentia* sp.
 Fig. 21. Air-spaces in *Phytelephas macrocarpa*.
 22. „ *Metroxylon Sagu*.
 23. „ *Iriartia* sp.
 24. „ *Licuala gracilis*.
 Figs. 25-27. Development of thyloses in air-spaces of *Areca Catechu*.

PLATE 49.

- Fig. 28. Air-spaces in *Licuala spinosa*.
 29. „ *Corypha australis*.
 30. „ *Phœnix sylvestris*.
 31. Tracheids in fibrous bundle of young root of *Dictyosperma album*.
 32. Stegmata in *Raphia Hookeri*.
 33. Stone-cells in cortex of *Sabal Palmetto* in longitudinal section.
 34. Lignified elements in cortex of *Livistona australis*.
 35. „ „ *Hyophorbe amaricaulis*.
 36. Fibres in cortex of *Kentia* sp.
 37. „ „ *Raphia Hookeri*, with stegmata.
 Figs. 38-40. Development of crystal-sacs in *Kentia* sp.
 Fig. 41. Crystal-sacs of *Kentia* sp. in transverse section.
 42. Mucilage-cells in *Caryota* sp.
 43. Endodermis and pericycle in contractile root of *Corypha umbraculifera* (transverse section).
 44. „ „ in longitudinal section.
 45. „ „ in *Livistona olivæformis* (transverse section).

Fig. 46. Endodermis in longitudinal section.

47. „ in *Kentia* sp. (transverse section).

48. „ showing local doubling (transverse section).

49. Longitudinal section of vessel in *Phœnix sylvestris*.

50. Thyloses in vessel of *Cocos flexuosa*.

51. „ „ *Areca concinna*.

Figs. 52 & 53. Development of vessels in *Kentia* sp. (transverse section).

Fig. 54. Xylem-bundle in *Kentia* sp.

PLATE 50.

Fig. 55. Transverse section of root of *Iriartia* sp.

56.	„	„	<i>Areca</i> sp.
57.	„	„	<i>Kentia</i> sp.
58.	„	„	<i>Dypsis madagascarensis</i> .
59.	„	„	<i>Kentia</i> sp.
60.	„	„	<i>Areca</i> sp.
61.	„	„	<i>Cocos plumosa</i> .
62.	„	„	<i>Cyrtostachys Renda</i> .
63.	„	„	<i>Dypsis madagascarensis</i> .
64.	„	„	<i>Licuala gracilis</i> .
65.	„	„	<i>Ptychosperma filifera</i> .
66.	„	„	<i>Livistona australis</i> .
67.	„	„	<i>Sabal glaucescens</i> .
68.	„	„	<i>Phœnix dactylifera</i> .
69.	„	„	<i>Heterospathe elata</i> .
70.	„	„	<i>Corypha umbraculifera</i> .
71.	„	„	<i>Raphia Hookeri</i> .
72.	„	„	<i>Latania Commersonii</i> .
73.	„	„	<i>Phœnix sylvestris</i> .
74.	„	„	<i>Sabal filamentosa</i> .
75.	„	„	<i>Howea (Kentia) Forsteriana</i> .
76.	„	„	<i>Areca</i> sp. (from Glasgow).

Figs. 77-88. Diagrammatic representation of the method of formation of the normal cylinder in the roots of Palms.

PLATE 51.

Fig. 89. Junction of bundle of root with bundle of stem in *Kentia* sp.

Figs. 90-94. Progressive distal changes in the arrangement of vascular tissue in the root of *Kentia* sp.

95-98. Progressive changes in arrangement of vascular tissue in root of *Kentia* sp.

Fig. 99. Section through base of stem of *Latania borbonica*, showing the lobed cylinders of the intracauline portions of the roots.

100. A gap between two portions of the central cylinder in *Kentia* sp., showing complete continuity of "cortical" and "medullary" parenchyma.

101. Transverse section of base of root of *Dictyosperma album*.

102. Dissections of central cylinder of *Latania borbonica*, showing lobed intracauline portion and normal extracauline portion.

Figs. 103 & 104. Dissections of lobed extracauline roots of *Kentia* sp.

- Fig. 105. Apparent dichotomy of root in *Kentia* sp.
106. Lateral rootlet coming from an arc of the central cylinder in *Kentia* sp.
Figs. 107-110. Structure of a large lateral rootlet in *Areca Catechu*, and connection of this with the parent root.
Fig. 111. Illustrating the two forms of rootlet in *Areca concinna*.
112. Spiny root of *Iriartia* sp.
113. Transverse section of a spine of *Iriartia* sp.
114. End of root in *Areca Catechu* bearing a number of large lateral roots.
115. Zone of dividing-cells in cortex of spine of *Iriartia* sp.
116. End of roots of *Areca Catechu* with two large lateral roots.
117. End of root of *Actinorhysis Calapparia* with one well-developed lateral root (*a*) and several arrested ones at *c*.
118. Penetration of the xylem-elements of the lateral root among those of the parent root in *Corypha australis*.
119. Root of *Areca concinna* with several large lateral roots.
120. Contractile root of *Corypha umbraculifera*.

ROOTS OF PALMS.

E Drabble, del

Huth.lith et imp

ROOTS OF PALMS.

E. Drabble, del.

Huth, lith et imp.

ROOTS OF PALMS.

E. Drabble, del.

Huth lith. et. imp.

ROOTS OF PALMS.