Character and Description of KINGIA, a New Genus of Plants found on the South-west Coast of New Holland: with Observations on the structure of its Unimpregnated Ovulum; and on the Female Flower of Cycadeæ and Coniferæ.

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In Marino Lagance

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In the Botanical Appendix to the Voyage to Terra Australis, I have mentioned a plant of very remarkable appearance, observed in the year 1801, near the shores of King George the Third's Sound, in Mr. Westall's view of which, published in Captain Flinders' Narrative, it is introduced.

The plant in question was then found with only the imperfect remains of fructification: I judged of its affinities, therefore, merely from its habit, and as in this respect it entirely agrees with Xanthorrhœa, included the short notice given of it in my remarks on Asphodeleæ, to which that genus was referred*. Mr. Cunningham, the botanist attached to Captain King's voyages, who examined the plant in the same place of growth, in February, 1818, and in December, 1821, was not more fortunate than myself. Captain King, however, in his last visit to King George's Sound, in Novenber, 1822, observed it with ripe seeds: and at length Mr. William Baxter, whose attention I had particularly directed to this plant, found it, on the shores of the same port in 1823, both in flower and fruit. To this zealous collector, and to his liberal employer, Mr. Henchman, I am

* FLINGERS' Voy. vol. ii. p. 576.

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indebted for complete specimens of its fructification, which enable me to establish it as a genus distinct from any yet described.

To this new genus I have given the name of my friend Captain King, who, during his important surveys of the Coasts of New Holland, formed valuable collections in several departments of Natural History, and on all occasions gave every assistance in his power to Mr. Cunningham, the indefatigable botanist who accompanied him. The name is also intended as a mark of respect to the memory of the late Captain Philip Gidley King, who, as Governor of New South Wales, materially forwarded the objects of Captain Flinders' voyage; and to whose friendship Mr. Ferdinand Bauer and myself were indebted for important assistance in our pursuits while we remained in that colony.

KINGIA.

ORD. NAT. Junceæ prope Dasypogon, Calectasiam et Xerotem.

- CHAR. GEN. Perianthium sexpartitum, regulare, glumaceum, persistens. Stamina sex, fere hypogyna: Antheris basi affixis. Ovarium triloculare, loculis monospermis; ovulis adscendentibus. Stylus 1. Stigma tridentatum. Pericarpium exsuccum, indehiscens, monospermum, perianthio scarioso cinctum.
- Planta facie XanthorrhϾ elatioris. Caudex arborescens cicatricibus basibusve foliorum exasperatus? Folia caudicem terminantia confertissima longissima, figura et dispositione XanthorrhϾ. Pedunculi numerosi foliis breviores, bracteis vaginantibus imbricatis tecti, floriferi terminales erecti, mox, caudice parum elongato foliisque novellis productis, laterales, et divaricati vel deflexi, terminati capitulo denso globoso floribus tribracteatis.

KINGIA Australis. Tab. C.

DESC. Caudex arborescens erectus simplicissimus cylindraceus, 6-18-pedes altus, crassitie femoris. Folia caudicem terminantia

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numerosissima patula, apicibus arcuato-recurvis, lorea, solida, ancipitia apice teretiusculo, novella undique tecta pilis adpressis strictis acutis lævibus, angulis lateralibus et ventrali retrorsum scabris. Pedunculi numerosi teretes 8-12-pollicares crassitie digiti, vaginis integris brevibus imbricatis hinc in foliolum subulatum productis tecti. Capitulum globosum, floridum magnitudine pruni minoris, fructiferum pomum parvum æquans. Flores undique densè imbricati, tribracteati, sessiles. Bractea exterior lanceolata brevè acuminata planiuscula erecta, extus villosa intus glabra, post lapsum fructus persistens: duæ laterales angustonaviculares, acutissimæ, carina lateribusque villosis, longitudine fere exterioris, simul cum perianthio fructifero, separatim tamen, dilabentibus. Perianthium sexpartitum regulare subæquale glumaceum: foliola lanceolata acutissima disco nervoso nervis immersis simplicissimis, antica et postica plana, lateralia complicata lateribus inæqualibus, omnia basi subangustata, extus longitudinaliter sed extra medium præcipue villosa, intus glaberrima, æstivatione imbricata. Stamina sex subægualia, æstivatione stricta filamentis sensim elongantibus: Filamenta fere hypogyna ipsis basibus foliolorum perianthii quibus opposita leviter adhærentia, filiformia glabra teretia: Antheræ stantes, ante dehiscentiam lineares obtusæ filamento paulo latiores, defloratæ subulatæ vix crassitie filamenti, loculis parallelo-contiguis connectivo dorsali angusto adnatis, axi ventrali longitudinaliter dehiscentibus, lobulis baseos brevibus acutis subadnatis: Pollen simplex brevè ovale læve. Pistillum: Ovarium sessile disco nullo squamulisve cinctum, lanceolatum trigono-anceps villosum, triloculare, loculis monospermis. Ovula erecta fundo anguli interioris loculi paulo supra basin suam inserta, obovata lenticulari-compressa, aptera: Testa in ipsa basi acutiusculâ foramine minuto perforata: Membrana interna respectu testæ inversa, hujusce nempe apici lata basi inserta, ovata apice angustato aperto foramen testæ obturante: Nucleus cavitate membranæ conformis, ejusdem basi insertus, cæterum liber, pulposus solidus, apice acutiusculo lævi aperturam membranæ internæ attingente. Stylus trigonus strictus, infra villosus, dimidio superiore glabro, altitudine staminum, iisdem paulo præcocior, exsertus nempe dum illa adhuc inclusa. Stigmata tria

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brevissima acuta denticuliformia. Pericarpium exsuccum, indehiscens, villosum, basi styli aristatum, perianthio scarioso et filamentis emarcidis cinctum, abortione monospermum. Semen turgidum obovatum retusum, integumento (testâ) simplici membranaceo aqueo-pallido, hinc (intus) fere a basi acutiuscula, raphe fusca verticem retusum attingente ibique in chalazam parvam eoncolorem ampliata. Albumen semini conforme densè carnosum album. Embryo monocotyledoneus, aqueo-pallidus subglobosus, extremitate inferiore (radiculari) acuta, in ipsa basi seminis situs, semi-immersus, nec albumine omnino inclusus.

Tab. C. fig. 1. KINGLÆ AUSTRALIS pedunculus capitulo florido terminatus; fig. 2. capitulum fructiferum; 3, sectio transversalis pedunculi: 4, folium: hæ magnitudine naturali, sequentes omnes plus minus auctæ sunt; 5, flos; 6, stamen; 7, anthera antice et, 8, eadem postice visa; 9, pistillum; 10, ovarii sectio transversalis; 11, ejusdem portio longitudinaliter secta exhibens ovulum adscendens cavitatem loculi replens; 12, ovulum ita longitudinaliter sectum ut membrana interna solummodo ejusque insertio in apice cavitatis testæ visa sit; 13, ovuli sectio longitudinalis profundius ducta exhibens membranam internam et nucleum ex ejusdem basi ortum; 14, bracteæ capituli fructiferi; 15, pericarpium perianthio filamentisque persistentibus cinctum; 16, pericarpium perianthio avulso filamentorum basibus relictis; 17, semen.

OBS. I.—It remains to be ascertained, whether in this genus a resin is secreted by the bases of the lower leaves, as in Xanthorrhœa; and whether, which is probable, it agrees also in the internal structure of its stem with that genus. In Xanthorrhœa the direction of fibres or vessels of the caudex seems at first sight to resemble in some degree the dicotyledonous arrangement, but in reality much more nearly approaches to that of Dracœna Draco, allowance being made for the greater number, and extreme nar-

rowness of leaves, to which all the radiating vessels belong *.

OBS. II.—I have placed Kingia in the natural order Junceæ along with Dasypogon, Calectasia and Xerotes, genera peculiar to New Holland, and of which the two former have hitherto been observed only, along with it, on the shores of King George's Sound.

The striking resemblance of Kingia, in caudex and leaves, to Xanthorrhœa, cannot fail to suggest its affinity to that genus also. Although this affinity is not confirmed by a minute comparison of the parts of fructification, a sufficient agreement is still manifest to strengthen the doubts formerly expressed of the importance of those characters, by which I attempted to define certain families of the great class Liliaceæ.

In addition, however, to the difference in texture of the outer coat of the seed, and in those other points, on which I then chiefly depended in distinguishing Junceæ from Asphodeleæ, a more important character in Junceæ exists in the position of the embryo, whose radicle points always to the base of the seed, the external umbilicus being placed in the axis of the inner or ventral surface, either immediately above the base as in Kingia, or towards the middle, as in Xerotes.

* My knowledge of this remarkable structure of Xanthorrhee is chiefly derived from specimens of the caudex of one of the larger species of the genus, brought from Port Jackson, and deposited in the collection at the Jardin du Roi of Paris by M. Gaudichaud, the very intelligent botanist who was attached to Captain De Freycinet's voyage.

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OBS. III.—On the Structure of the UNIMPREGNATED OVULUM in Phænogamous Plants.

The description which I have given of the Ovulum of Kingia, though essentially different from the accounts hitherto published of that organ before fecundation, in reality agrees with its ordinary structure in Phænogamous plants.

I shall endeavour to establish these two points; namely, the agreement of this description with the usual structure of the Ovulum, and its essential difference from the accounts of other observers, as briefly as possible at present; intending hereafter to treat the subject at greater length, and also with other views.

I have formerly more than once * adverted to the structure of the Ovulum, chiefly as to the indications it affords, even before fecundation, of the place and direction of the future Embryo. These remarks, however, which were certainly very brief, seem entirely to have escaped the notice of those authors who have since written on the same subject.

In the Botanical Appendix to the account of Captain Flinders' Voyage, published in 1814, the following description of the Ovulum of *Cephalotus follicularis* is given: "Ovulum erectum, intra testam membranaceam continens sacculum pendulum, magnitudine cavitatis testæ," and in reference to this description, I have in the same place remarked that, "from the structure of the Ovulum, even in the unimpregnated state, I entertain no doubt that the radicle of the Embryo points to the umbilicus +."

My attention had been first directed to this subject in 1809, in consequence of the opinion I had then formed of

* FLINDERS' Voy. ii. p. 601, and Linn. Soc. Transac. xii. p. 136. + FLINDERS' Voy. loc. cit.

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the function of the Chalaza in seeds *; and sometime before the publication of the observation now quoted, I had ascertained that in Phænogamous plants the unimpregnated Ovulum very generally consisted of two concentric membranes, or coats, enclosing a Nucleus of a pulpy cellular texture. I had observed also, that the inner coat had no connexion either with the outer or with the nucleus, except at its origin; and that with relation to the outer coat it was generally inverted, while it always agreed in direction with the nucleus. And, lastly, that at the apex of the nucleus the radicle of the future Embryo would constantly be found. . On these grounds my opinion respecting the Embryo of Cephalotus was formed. In describing the Ovulum in this genus, I employed, indeed, the less correct term " sacculus," which, however, sufficiently expressed the appearance of the included body in the specimens examined, and served to denote my uncertainty in this case as to the presence of

I was at that time also aware of the existence, in several plants, of a foramen in the coats of the Ovulum, always distinct from, and in some cases diametrically opposite to, the external umbilicus, and which I had in no instance found cohering either directly with the parietes of the Ovarium, or with any process derived from them. But, as I was then unable to detect this foramen in many of the plants which I had examined, I did not attach sufficient importance to it; and in judging of the direction of the Embryo, entirely depended on ascertaining the apex of the nucleus, either directly by dissection, or indirectly from the vascular cord of the outer membrane: the termination of this cord affording a sure indication of the origin of the inner membrane,

* Linn. Soc. Transact. x. p. 35.

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the inner membrane.

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and consequently of the base of the nucleus, the position of whose apex is therefore readily determined.

In this state of my knowledge the subject was taken up in 1818, by my lamented friend the late Mr. Thomas Smith, who, eminently qualified for an investigation where minute accuracy and great experience in microscopical observation were necessary, succeeded in ascertaining the very general existence of the foramen in the membranes of the Ovulum. But as the foramina in these membranes invariably correspond both with each other and with the apex of the nucleus, a test of the direction of the future Embryo was consequently found nearly as universal, and more obvious than that which I had previously employed.

To determine in what degree this account of the vegetable Ovulum differs from those hitherto given, and in some measure, that its correctness may be judged of, I shall proceed to state the various observations that have been actually made, and the opinions that have been formed on the subject, as briefly as I am able, taking them in chronological order.

In 1672, Grew * describes in the outer coat of the seeds of many Leguminous plants a small foramen, placed opposite to the radicle of the Embryo, which, he adds, is "not a hole casually made, or by the breaking off of the stalk," but formed for purposes afterwards stated to be the aëration of the Embryo, and facilitating the passage of its radicle in germination. It appears that he did not consider this foramen in the testa as always present, the functions which he ascribes to it being performed in cases where it is not found, either, according to him, by the hilum itself, or in hard fruits, by an aperture in the stone or shell.

* Anatomy of Veget. begun p. 3. Anat. of Plants, p. 2.

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In another part of his work * he describes and figures, in the early state of the Ovulum, two coats, of which the outer is the testa; the other, his " middle membrane," is evidently what I have termed nucleus, whose origin in the Ovulum of the Apricot he has distinctly represented and described.

Malpighi, in 1675⁺, gives the same account of the early state of the Ovulum; his "secundinæ externæ" being the testa, and his chorion the nucleus. He has not, however, distinguished, though he appears to have seen, the foramen of Grew, from the fenestra and fenestella, and these, to which he assigns the same functions, are merely his terms for the hilum.

In 1694, Camerarius, in his admirable essay on the sexes of plants ‡, proposes, as queries merely, various modes in which either the entire grains of pollen, or their particles after bursting, may be supposed to reach and act upon the unimpregnated Ovula, which he had himself carefully observed. With his usual candour, however, he acknowledges his obligation on this subject to Malpighi, to whose more detailed account of them he refers.

Mr. Samuel Morland, in 1703 §, in extending Leeuwenhoek's hypothesis of generation to plants, assumes the existence of an aperture in the Ovulum, through which it is impregnated. It appears, indeed, that he had not actually observed this aperture before fecundation, but inferred its existence generally and at that period, from having, as he says, " discovered in the seeds of beans, peas, and Phaseoli, just under one end of what we call the eye, a

* Anat. of Plants, p. 210. tab. 80.

* Anatome Plant. p. 75. et 80.

‡ Rudolphi Jacobi Camerarii de sexu plantarum epistola, p. 8. 46. et seq.

§ Philosoph. Transact. vol. xxiii. n. 287. p. 1474.

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manifest perforation, which leads directly to the seminal plant," and by which he supposes the Embryo to have entered. This perforation is evidently the foramen discovered in the seeds of Leguminous plants by Grew, of whose observations respecting it he takes no notice, though he quotes him in another part of his subject.

In 1704, Etienne François Geoffroy*, and in 1711, his brother Claude Joseph Geoffroy †, in support of the same hypothesis, state the general existence of an aperture in the unimpregnated vegetable Ovulum. It is not, however, probable that these authors had really seen this aperture in the early state of the Ovulum in any case, but rather that they had merely advanced from the observation of Grew, and the conjecture founded on it by Morland, whose hypothesis they adopt without acknowledgment, to the unqualified assertion of its existence, in all cases. For it is to be remarked, that they take no notice of what had previously been observed or asserted on the more important parts of their subject, while several passages are evidently copied, and the whole account of the original state and developement of the Ovulum is literally translated from Camerarius's Essay. Nor does the younger Geoffroy mention the earlier publication of his brother, from which his own memoir is in great part manifestly derived.

In 1718, Vaillant ‡, who rejects the vermicular hypothesis of generation, supposes the influence of the Pollen to consist in an aura, conveyed by the tracheæ of the style to the ovula, which it enters, if I rightly understand him, by the

* Quastio Medica an Hominis primordia Vermis? in auctoris Tractatu de Materia Medica, tom. i. p. 123.

- † Mem. de l'Acad. des Sc. de Paris, 1711, p. 210.
- # Discours sur la Structure des Fleurs, p. 20.

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funiculus umbilicalis: at the same time he seems to admit the existence of the aperture in the coat.

In 1745, Needham *, and in 1770, Gleichen +, adopt the hypothesis of Morland, somewhat modified, however, as they consider the particles in the grains of Pollen, not the grains themselves, to be the embryos, and that they enter the ovula by the umbilical cord.

Adanson, in 1763[‡], states the Embryo to exist before fecundation, and that it receives its first excitement from a vapour or aura proceeding from the Pollen, conveyed to it through the tracheæ of the style, and entering the Ovulum by the umbilical cord.

Spallanzani §, who appears to have carefully examined the unimpregnated Ovula of a considerable variety of plants, found it in general to be a homogeneous, spongy, or gelatinous body; but in two Cucurbitaceæ to consist of a nucleus surrounded by three coats. Of these coats he rightly supposes the outermost to be merely the epidermis of the middle membrane or testa. Of the relative direction of the testa and inner coat in the two plants in question he takes no notice, nor does he in any case mention an aperture in the Ovulum.

Gærtner, who, in the preface to his celebrated work, displays great erudition in every branch of his subject, can hardly, however, be considered an original observer in this part. He describes the unimpregnated Ovulum as a pulpy homogeneous globule, whose epidermis, then scarcely distinguishable, separates in a more advanced stage, and becomes the testa of the seed, the inner membrane of which is

- * New Microscopical Discoveries, p. 60.
- * Observ. Microscop. p. 45. et 61. § cxviii.
- 1 Fam. des Plant. tom. i. p. 121.
- § Fisica Anim. e Veget. tom. iii. p. 309-332.

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entirely the product of fecundation*. He asserts also that the Embryo constantly appears at that point of the ovulum where the ultimate branches of the umbilical vessels perforate the inner membrane; and therefore mistakes the apex for the base of the nucleus.

In 1806 Mons. Turpin[†] published a memoir on the organ, by which the fecundating fluid is introduced into the vegetable ovulum. The substance of this memoir is, that in all Phænogamous plants fecundation takes place through a cord or fasciculus of vessels entering the outer coat of the ovulum, at a point distinct from, but at the period of impregnation closely approximated to the umbilicus, and to the cicatrix of this cord, which itself is soon obliterated, he gives the name of Micropyle: that the ovulum has two coats, each having its proper umbilicus, or, as he terms it, omphalode; that these coats in general correspond in direction; that more rarely the inner membrane is, with relation to the outer, inverted; and that towards the origin of the inner membrane the radicle of the embryo uniformly points.

It is singular that a botanist, so ingenious and experienced as M. Turpin, should, on this subject, instead of appealing in every case to the unimpregnated ovulum, have apparently contented himself with an examination of the ripe seed. Hence, however, he has formed an erroneous opinion of the nature and origin, and in some plants of the situation, of the micropyle itself, and hence also he has in all cases mistaken the apex for the base of the nucleus.

A minute examination of the early state of the ovulum does not seem to have entered into the plan of the late celebrated M. Richard, when in 1808 he published his

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* Gært. de Fruct. et Sem. i. p. 57. 59. et 61. † Annal. du Mus. d'Hist. Nat. vii. p. 199. 13/

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valuable and original Analyse du Fruit. The ovulum has, according to him, but one covering, which in the ripe seed he calls episperm. He considers the centre of the hilum as the base, and the chalaza, where it exists, as the natural apex of the seed.

M. Mirbel, in 1815, though admitting the existence of the foramen or micropyle of the testa *, describes the ovulum as receiving by the hilum both nourishing and fecundating vessels +, and as consisting of a uniform parenchyma, in which the embryo appears at first a minute point, gradually converting more or less of the surrounding tissue into its own substance; the coats and albumen of the seed being formed of that portion which remains ‡.

In the same year, M. Auguste de Saint Hilaire § shews that the micropyle is not always approximated to the umbilicus; that in some plants it is situated at the opposite extremity of the ovulum, and that in all cases it corresponds with the radicle of the embryo. This excellent botanist, at the same time, adopts M. Turpin's opinion, that the micropyle is the cicatrix of a vascular cord, and even gives instances of its connexion with the parietes of the ovarium; mistaking, as I believe, contact, which in some plants unquestionably takes place, and in one family, namely, Plumbagineæ, in a very remarkable manner, but only after a certain period, for original cohesion, or organic connexion, which I have not met with in any case.

In 1815 also appeared the masterly dissertation of Professor Ludolf Christian Treviranus, on the development of

§ Mém. du Mus. d'Hist. Nat. ii. p. 270, et seq.

^{*} Elém. de Physiol. Vég. et de Bot. tom. i. p. 49.

⁺ Id. tom. i. p. 314.

¹ Id. loc. cit.

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the vegetable Embryo^{*}, in which he describes the ovulum before fecundation as having two coats; but of these, his inner coat is evidently the middle membrane of Grew, the chorion of Malpighi, or what I have termed nucleus.

In 1822, Mons. Dutrochet, unacquainted, as it would seem, with the dissertation of Professor Treviranus, published his observations on the same subject +. In what regards the structure of the ovulum, he essentially agrees with that author, and has equally overlooked the inner membrane.

It is remarkable that neither of these observers should have noticed the foramen in the testa. And as they do not even mention the well-known essays of MM. Turpin and Auguste de St. Hilaire on the micropyle, it may be presumed that they were not disposed to adopt the statements of these authors respecting it.

Professor Link, in his *Philosophia Botanica*, published in 1824, adopts the account given by Treviranus, of the coats of the ovulum before impregnation \ddagger ; and of M. Turpin, as to the situation of the micropyle, and its being the cicatrix of a vascular cord. Yet he seems not to admit the function ascribed to it, and asserts that it is in many cases wanting §.

The account which I have given of the structure of the vegetable ovulum, differs essentially from all those now quoted, and I am not acquainted with any other observations of importance respecting it.

Of the authors referred to, it may be remarked, that those who have most particularly attended to the ovulum ex-

- * Entwick. des Embryo im Pflanzen-Ey.
- + Mém. du Mus. d'Hist. Nat. tom. viii. p. 241, et seq.
- 1 Elém. Philos. Bot. p. 338.
- § Id. p. 340.

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ternally, have not always examined it at a sufficiently early period, and have confined themselves to its surface: that those who have most minutely examined its internal structure, have trusted too much to sections merely, and have neglected its appearance externally: and that those who have not at all examined it in the early stage, have given the most correct account of its surface. This account was founded on a very limited observation of ripe seeds, generalized and extended to the unimpregnated ovulum, in connexion with an hypothesis then very commonly received: but this hypothesis being soon after abandoned, their statement respecting the ovulum was rejected along with it.

In the ovulum of Kingia, the inner membrane, with relation to the external umbilicus, is inverted; and this, as I have already observed, though in direct opposition to M. Turpin's account, is the usual structure of the organ. There are, however, several families in each of the two primary divisions of phænogamous plants, in which the inner membrane, and consequently the nucleus, agrees in direction with the testa. In such cases the external umbilicus alone affords a certain indication of the position of the future embryo.

It is an obvious consequence of what has been already stated, that the radicle of the embryo can never point directly to the external umbilicus or hilum, though this is said to be generally the case by the most celebrated carpologists.

Another observation may be made, less obviously a consequence of the structure described, but equally at variance with many of the published accounts and figures of seeds, namely, that the radicle is never absolutely enclosed in the albumen; but, in the recent state, is either immediately in contact with the inner membrane of the seed, or this contact is established by means of a process generally very

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short, but sometimes of great length, and which indeed in all cases may be regarded as an elongation of its own substance. From this rule I have found one apparent deviation, but in a case altogether so peculiar, that it can hardly be considered as setting it aside.

It is necessary to observe, that I am acquainted with exceptions to the structure of the ovulum as I have here described it. In Compositæ its coats seem to be imperforated, and hardly separable, either from each other or from the nucleus. In this family, therefore, the direction of the embryo can only be judged of from the vessels of the testa*. And in Lemna I have found an apparent inversion of the embryo with relation to the apex of the nucleus. In this genus, however, such other peculiarities of structure and economy exist, that, paradoxical as the assertion may seem, I consider the exception rather as confirming than lessening the importance of the character.

It may perhaps be unnecessary to remark, that the raphe, or vascular cord of the outer coat, almost universally belongs to that side of the ovulum which is next the placenta. But it is at least deserving of notice, that the very few apparent exceptions to this rule evidently tend to confirm it. The most remarkable of these exceptions occur in those species of Euonymus, which, contrary to the usual structure of the genus and family they belong to, have pendulous ovula; and, as I have long since noticed, in the perfect ovula only of Abelia[†]. In these, and in the other cases in which the raphe is on the outer side, or that most remote from the placenta, the ovula are in reality resupinate; an economy apparently essential to their developement.

The distinct origins and different directions of the nou

* Linn. Soc. Transact. xii. p. 136. + ABEL's China, p. 377

rishing vessels and channel through which fecundation took place in the ovulum, may still be seen in many of those ripe seeds that are winged, and either present their margins to the placenta, as in Proteaceæ, or have the plane of the wing at right angles to it, as in several Liliaceæ. These organs are visible also in some of those seeds that have their testa produced at both ends beyond the inner membrane, as Nepenthes; a structure which proves the outer coat of scobiform seeds, as they are called, to be really testa, and not arillus, as it has often been termed.

The importance of distinguishing between the membranes of the unimpregnated ovulum and those of the ripe seed, must be sufficiently evident from what has been already stated. But this distinction has been necessarily neglected by two classes of observers. The first consisting of those, among whom are several of the most eminent carpologists, who have regarded the coats of the seed as products of fecundation. The second of those authors who, professing to give an account of the ovulum itself, have made their observations chiefly, or entirely, on the ripe seed, the coats of which they must consequently have supposed to be formed before impregnation.

The consideration of the *arillus*, which is of rare occurrence, is never complete, and whose developement takes place chiefly after fecundation, might here, perhaps, be entirely omitted. It is, however, worthy of remark, that in the early stage of the ovulum, this envelope is in general hardly visible even in those cases where, as in Hibbertia volubilis, it attains the greatest size in the ripe seed; nor does it in any case, with which I am acquainted, cover the foramen of the testa until after fecundation.

The *testa*, or outer coat of the seed, is very generally formed by the outer membrane of the ovulum; and in most

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cases where the nucleus is inverted, which is the more usual structure, its origin may be satisfactorily determined; either by the hilum being more or less lateral, while the foramen is terminal; or more obviously, and with greater certainty where the raphe is visible, this vascular cord uniformly belonging to the outer membrane of the ovulum. The chalaza, properly so called, though merely the termination of the raphe, affords a less certain character, for in many plants it is hardly visible on the inner surface of the testa, but is intimately united with the areola of insertion of the inner membrane or of the nucleus, to one or other of which it then seems entirely to belong. In those cases where the testa agrees in direction with the nucleus, I am not acquainted with any character by which it can be absolutely distinguished from the inner membrane in the ripe seed; but as a few plants are already known, in which the outer membrane is originally incomplete, its entire absence, even before fecundation, is conceivable; and some possible cases of such a structure will be mentioned hereafter.

There are several cases known, some of which I have formerly noticed *, of the complete obliteration of the testa in the ripe seed; and on the other hand it appears to constitute the greater part of the substance of the bulb-like seeds of many Liliaceæ, where it no doubt performs also the function of albumen, from which, however, it is readily distinguished by its vascularity†. But the most remarkable deviation from the usual structure and economy of the outer membrane of the ovulum, both in its earliest stage and in the ripe fruit, that I have yet met with, occurs in Banksia and Dryandra. In these two genera I have ascertained that the inner membrane of the ovulum, before fecundation, is

* Linn, Soc. Transact. xii. p. 149. + Ibid.

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entirely exposed, the outer membrane being even then open its whole length; and that the outer membranes of the two collateral ovula, which are originally distinct, cohere in a more advanced stage by their corresponding surfaces, and together constitute the anomalous dissepiment of the capsule; the inner membrane of the ovulum consequently forming the outer coat of the seed.

The *inner membrane* of the ovulum, however, in general appears to be of greater importance as connected with fecundation, than as affording protection to the nucleus at a more advanced period. For in many cases, before impregnation, its perforated apex projects beyond the aperture of the testa, and in some plants puts on the appearance of an obtuse, or even dilated stigma; while in the ripe seed it is often either entirely obliterated, or exists only as a thin film, which might readily be mistaken for the epidermis of a third membrane then frequently observable.

This third coat is formed by the proper membrane or cuticle of the Nucleus, from whose substance in the unimpregnated ovulum it is never, I believe, separable, and at that period is very rarely visible. In the ripe seed it is distinguishable from the inner membrane only by its apex, which is never perforated, is generally acute and more deeply coloured, or even sphacelated.

The membrane of the nucleus usually constitutes the innermost coat of the seed. But in a few plants an additional coat, apparently originating in the inner membrane of Grew, the vesicula colliquamenti or amnios of Malpighi also exists.

In general the Amnios, after fecundation, gradually enlarges, till at length it displaces or absorbs the whole substance of the nucleus, containing in the ripe seed both the embryo and albumen, where the latter continues to exist.

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In such cases, however, its proper membrane is commonly obliterated, and its place supplied either by that of the nucleus, by the inner membrane of the ovulum, or, where both these are evanescent, by the testa itself.

In other cases the albumen is formed by a deposition of granular matter in the cells of the nucleus. In some of these cases the membrane of the amnios seems to be persistent, forming even in the ripe seed a proper coat for the embryo, the original attachment of whose radicle to the apex of this coat may also continue. This, at least, seems to me the most probable explanation of the structure of true Nymphæaceæ, namely, Nuphar, Nymphæa, Euryale, Hydropeltis, and Cabomba, notwithstanding their very remarkable germination, as observed and figured in Nymphæa and Nuphar by Tittmann *.

In support of this explanation, which differs from all those yet given, I may here advert to an observation published many years ago, though it seems to have escaped every author who has since written on the subject, namely, that before the maturity of the seed in Nymphæaceæ, the sacculus contains along with the embryo a (pulpy or semi-fluid) substance, which I then called Vitellus, applying at that time this name to every body interposed between the albumen and embryo †. The opinion receives some confirmation also from the existence of an extremely fine filament, hitherto overlooked, which, originating from the centre of the lower surface of the sacculus, and passing through the hollow axis of the Albumen, probably connects this coat of the Embryo in an early stage with the base of the nucleus.

* Keimung der Pflanzen, p. 19. et 27. tab. 3. et 4. + Prodr. Flor. Nov. Holl. i. p. 306.

The same explanation of structure applies to the seeds of Piperaceæ and Saururus; and other instances occur of the persistence either of the membrane or of the substance of the amnios in the ripe seed.

It may be concluded from the whole account which I have given of the structure of the ovulum, that the more important changes consequent to real, or even to spurious fecundation, must take place within the nucleus : and that the albumen, properly so called, may be formed either by a deposition or secretion of granular matter in the utriculi of the amnios, or in those of the nucleus itself, or lastly, that two substances having these distinct origins, and very different textures, may co-exist in the ripe seed, as is probably the case in Scitamineæ.

On the subject of the ovulum, as contained in an ovarium, I shall at present make but one other remark, which forms a necessary introduction to the observations that follow.

On the Structure of the female Flower in CYCADEE and CONIFERE.

That the apex of the nucleus is the point of the ovulum where impregnation takes place, is at least highly probable, both from the constancy in the appearance of the embryo at that point, and from the very general inversion of the nucleus; for by this inversion its apex is brought nearly, or absolutely, into contact with that part of the parietes of the ovarium, by which the influence of the pollen may be supposed to be communicated. In several of those families of plants, however, in which the nucleus is not inverted, and the placentæ are polyspermous, as Cistineæ *, it is difficult

* This structure of ovulum, indicated by that of the seed, as characterizing and defining the limits of Cistineæ, (namely, Cistus,

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to comprehend in what manner this influence can reach its apex externally, except on the supposition, not hastily to be admitted, of an impregnating aura filling the cavity of the ovarium; or by the complete separation of the fecundating tubes from the placentæ, which, however, in such cases I have never been able to detect.

It would entirely remove the doubts that may exist respecting the point of impregnation, if cases could be produced where the ovarium was either altogether wanting, or so imperfectly formed, that the ovulum itself became directly exposed to the action of the pollen, or its fovilla; its apex, as well as the orifice of its immediate covering, being modified and developed to adapt them to this economy.

But such, I believe, is the real explanation of the structure of Cycadeæ, of Coniferæ, of Ephedra, and even of Gnetum, of which Thoa of Aublet is a species.

To this view the most formidable objection would be removed, were it admitted, in conformity with the preceding observations, that the apex of the nucleus, or supposed point of impregnation, has no organic connexion with the parietes of the ovarium. In support of it, also, as far as regards the direct action of the pollen on the ovulum, numerous instances of analogous economy in the animal kingdom may be adduced.

The similarity of the female flower in Cycadeæ and Coniferæ to the ovulum of other phænogamous plants, as I have described it, is indeed sufficiently obvious to render the opinion here advanced not altogether improbable. But the

Helianthemum, Hudsonia and Lechea), I communicated to Dr. Hooker, by whom it is noticed in his *Flora Scotica*, (p. 284,) published in 1821; where, however, an observation is added respecting Gærtner's description of Cistus and Helianthemum, for which I am not accountable.

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proof of its correctness must chiefly rest on a resemblance, in every essential point, being established, between the inner body in the supposed female flower in these tribes, and the nucleus of the ovulum in ordinary structures; not only in the early stage, but also in the whole series of changes consequent to fecundation. Now as far as I have yet examined, there is nearly a complete agreement in all these respects. I am not entirely satisfied, however, with the observations I have hitherto been able to make on a subject naturally difficult, and to which I have not till lately attended with my present view.

The facts most likely to be produced as arguments against this view of the structure of Coniferæ, are the unequal and apparently secreting surface of the apex of the supposed nucleus in most cases; its occasional projection beyond the orifice of the outer coat; its cohesion with that coat by a considerable portion of its surface, and the not unfrequent division of the orifice of the coat. Yet most of these peculiarities of structure might perhaps be adduced in support of the opinion advanced, being apparent adaptations to the supposed economy.

There is one fact that will hardly be brought forward as an objection, and which yet seems to me to present a difficulty, to this opinion; namely, the greater simplicity in Cycadeæ, and in the principal part of Coniferæ, of the supposed ovulum which consists of a nucleus and one coat only, compared with the organ as generally existing when enclosed in an ovarium. The want of uniformity in this respect may even be stated as another difficulty, for in some genera of Coniferæ the ovulum appears to be complete.

In Ephedra, indeed, where the nucleus is provided with two envelopes, the outer may, perhaps, be supposed rather analogous to the calyx, or involucrum of the male flower,

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than as belonging to the ovulum; but in Gnetum, where three envelopes exist, two of these may, with great probability, be regarded as coats of the nucleus; while in Podocarpus and Dacrydium, the outer cupula, as I formerly termed it *, may also, perhaps, be viewed as the testa of the ovulum. To this view, as far as relates to Dacrydium, the longitudinal fissure of the outer coat in the early stage, and its state in the ripe fruit, in which it forms only a partial covering, may be objected †. But these objections are, in a great measure, removed by the analogous structure already described in Banksia and Dryandra.

The plurality of embryos sometimes occurring in Coniferæ, and which, in Cycadeæ, seems even to be the natural structure, may also, perhaps, be supposed to form an objection to the present opinion, though to me it appears rather an argument in its favour.

Upon the whole, the objections to which the view here taken of the structure of these two families is still liable, seem to me, as far as I am aware of them, much less important than those that may be brought against the other opinions that have been advanced, and still divide botanists on this subject.

According to the earliest of these opinions, the female flower of Cycadeæ and Coniferæ is a monospermous pistillum, having no proper floral envelope.

To this structure, however, Pinus itself was long considered by many botanists as presenting an exception.

Linnœus has expressed himself so obscurely in the natural character which he has given of this genus, that I find it difficult to determine what his opinion of its structure really

* FLINDERS'S Voy. vol. ii. p. 573.

+ Id. loc. cit.

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was. I am inclined, however, to believe it to have been much nearer the truth than is generally supposed; judging of it from a comparison of his essential with his artificial generic character, and from an observation recorded in his *Prælectiones*, published by Giseke *.

But the first clear account that I have met with, of the real structure of Pinus, as far as regards the direction, or base and apex of the female flowers, is given, in 1767, by Trew, who describes them in the following manner: "Singula semina vel potius germina stigmati tanquam organo feminino gaudent †," and his figure of the female flower of the Larch, in which the stigmata project beyond the base of the scale, removes all doubt respecting his meaning.

In 1789, M. de Jussieu, in the character of his genus Abies ‡, gives a similar account of structure, though somewhat less clearly as well as less decidedly expressed. In the observations that follow, he suggests, as not improbable, a very different view, founded on the supposed analogy with Araucaria, whose structure was then misunderstood; namely, that the inner scale of the female amentum is a bilocular ovarium, of which the outer scale is the style. But this, according to Sir James Smith §, was also Linnæus's opinion; and it is the view adopted in Mr. Lambert's splendid monograph of the genus published in 1803.

In the same year in which Mr. Lambert's work appeared, Schkuhr || describes, and very distinctly figures, the female flower of Pinus, exactly as it was understood by Trew, whose opinion was probably unknown to him.

- * Prælect. in Ord. Nat. p. 589.
- * Nov. Act. Acad. Nat. Curios. iii. p. 453. tab. 13. fig. 23.
- : Gen. Pl. p. 414.
- § REES'S Cyclop. art. Pinus.
- || Botan. Handb. iii. p. 276. tab. 308.

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In 1807, a memoir on this subject, by Mr. Salisbury, was published *, in which an account of structure is given, in no important particular different from that of Trew and Schkuhr, with whose observations he appears to have been unacquainted.

M. Mirbel, in 1809⁺, held the same opinion, both with respect to Pinus and to the whole natural family. But in 1812, in conjunction with M. Schoubert[‡], he proposed a very different view of the structure of Cycadeæ and Coniferæ, stating, that in their female flowers there is not only a minute cohering perianthium present, but an external additional envelope, to which he has given the name of cupula.

In 1814 I adopted this view, as far, at least, as regards the manner of impregnation, and stated some facts in support of it §. But on re-considering the subject, in connexion with what I had ascertained respecting the vegetable ovulum, I soon after altogether abandoned this opinion, without, however, venturing explicitly to state that now advanced, and which had then suggested itself.

It is well known that the late M. Richard had prepared a very valuable memoir on these two families of plants; and he appears, from some observations lately published by his son, M. Achille Richard \P , to have formed an opinion respecting their structure somewhat different from that of M. Mirbel, whose cupula is, according to him, the perianthium, more or less cohering with the included pistillum. He was probably led to this view, on ascertaining, which I had

* Linn. Soc. Transact. viii. p. 308.

+ Ann. du Mus. d'Hist. Nat. tom. xv. p. 473.

* Nouv. Bulletin des Sc. tom. iii. pp. 73, 85, et 121.

§ FLINDERS'S Voy. ii. 572.

|| TUCKEY'S Congo, p. 454. et Linn. Soc. Transact. vol. xiii. p. 213.

I Dict. Class. d'Hist. Nat. tom. iv. p. 395. et tom. v. p. 216.

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also done, that the common account of the structure of Ephedra was incorrect *, its supposed style being in reality the elongated tubular apex of a membranous envelope, and the included body being evidently analogous to that in other genera of Conifere.

To the earliest of the opinions here quoted, that which considers the female flower of Coniferæ and Cycadeæ as a naked pistillum, there are two principal objections. The first of these arises from the perforation of the pistillum, and the exposure of that point of the ovulum where the embryo is formed to the direct action of the pollen; the second from the too great simplicity of structure of the supposed ovulum, which, I have shewn, accords better with that of the nucleus as existing in ordinary cases.

To the opinions of MM. Richard and Mirbel, the first objection does not apply, but the second acquires such additional weight, as to render those opinions much less probable, it seems to me, than that which I have endeavoured to support.

In supposing the correctness of this opinion to be admitted, a question connected with it, and of some importance, would still remain, namely, whether in Cycadeæ and Coniferæ the ovula are produced on an ovarium of reduced functions and altered appearance, or on a rachis or receptacle. In other words, in employing the language of an hypothesis, which, with some alterations, I have elsewhere attempted to explain and defend, respecting the formation of the sexual organs in Phænogamous plants +, whether the ovula in these two families originate in a modified leaf, or proceed directly from the stem.

* Dict. Class. d'Hist. Nat. tom. vi. p. 208.

+ Linn. Soc. Transact. vol. xiii. p. 211.

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Were I to adopt the former supposition, or that best agreeing with the hypothesis in question, I should certainly apply it, in the first place, to Cycas, in which the female spadix bears so striking a resemblance to a partially altered frond or leaf, producing marginal ovula in one part, and in another being divided into segments, in some cases nearly resembling those of the ordinary frond.

But the analogy of the female spadix of Cycas to that of Zamia is sufficiently obvious; and from the spadix of Zamia to the fruit-bearing squama of Coniferæ, strictly so called, namely, of Agathis or Dammara, Cunninghamia, Pinus, and even Araucaria, the transition is not difficult. This view is applicable, though less manifestly, also to Cupressinæ; and might even be extended to Podocarpus and Dacrydium. But the structure of these two genera admits likewise of another explanation, to which I have already adverted.

If, however, the ovula in Cycadeæ and Coniferæ be really produced on the surface of an ovarium, it might, perhaps, though not necessarily, be expected that their male flowers should differ from those of all other phænogamous plants, and in this difference exhibit some analogy to the structure of the female flower. But in Cycadeæ, at least, and especially in Zamia, the resemblance between the male and female spadices is so great, that if the female be analogous to an ovarium, the partial male spadix must be considered as a single anthera, producing on its surface either naked grains of pollen, or pollen subdivided into masses, each furnished with its proper membrane.

Both these views may at present, perhaps, appear equally paradoxical; yet the former was entertained by Linnæus, who expresses himself on the subject in the following terms, "Pulvis floridus in Cycade minime pro Antheris agnoscen-

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dus est sed pro nudo polline, quod unusquisque qui unquam pollen antherarum in plantis examinavit fatebitur *." That this opinion, so confidently held by Linnæus, was never adopted by any other botanist, seems in part to have arisen from his having extended it to dorsiferous Ferns. Limited to Cycadeæ, however, it does not appear to me so very improbable, as to deserve to be rejected without examination. It receives, at least, some support from the separation, in several cases, especially in the American Zamiæ, of the grains into two distinct, and sometimes nearly marginal, masses, representing, as it may be supposed, the lobes of an anthera; and also from their approximation in definite numbers, generally in fours, analogous to the quaternary union of the grains of pollen, not unfrequent in the antheræ of several other families of plants. The great size of the supposed grains of pollen, with the thickening and regular bursting of their membrane, may be said to be circumstances obviously connected with their production and persistence on the surface of an anthera, distant from the female flower; and with this economy, a corresponding enlargement of the contained particles or fovilla might also be expected. On examining these particles, however, I find them not only equal in size to the grains of pollen of many antheræ, but, being elliptical and marked on one side with a longitudinal furrow, they have that form which is one of the most common in the simple pollen of phænogamous plants. To suppose, therefore, merely on the grounds already stated, that these particles are analogous to the fovilla, and the containing organs to the grains of pollen in antheræ of the usual structure, would be entirely gratuitous. It is, at the same time, deserving of remark, that were this view adopted on

* Mém. de l'Acad. des Scien. de Paris, 1775, p. 518.

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more satisfactory grounds, a corresponding developement might then be said to exist in the essential parts of the male and female organs. The increased developement in the ovulum would not consist so much in the unusual form and thickening of the coat, a part of secondary importance, and whose nature is disputed, as in the state of the nucleus of the seed, respecting which there is no difference of opinion; and where the plurality of embryos, or at least the existence and regular arrangement of the cells in which they are formed, is the uniform structure in the family.

The second view suggested, in which the anthera in Cycadeæ is considered as producing on its surface an indefinite number of pollen masses, each enclosed in its proper membrane, would derive its only support from a few remote analogies : as from those antheræ, whose loculi are sub-divided into a definite, or more rarely an indefinite, number of cells, and especially from the structure of the stamina of Viscum album.

I may remark, that the opinion of M. Richard *, who considers these grains, or masses, as unilocular antheræ, each of which constitutes a male flower, seems to be attended with nearly equal difficulties.

The analogy between the male and female organs in Coniferæ, the existence of an open ovarium being assumed, is at first sight more apparent than in Cycadeæ. In Coniferæ, however, the pollen is certainly not naked, but is enclosed in a membrane similar to the lobe of an ordinary anthera. And in those genera in which each squama of the amentum produces two marginal lobes only, as Pinus, Podocarpus, Dacrydium, Salisburia, and Phyllocladus, it nearly resembles the more general form of the antheræ in other Phænogamous

* Dict. Class. d'Hist. Nat. tom. v. p. 216.

plants. But the difficulty occurs in those genera which have an increased number of lobes on each squama, as Agathis and Araucaria, where their number is considerable and apparently indefinite, and more particularly still in Cunninghamia, or Belis*, in which the lobes, though only three in number, agree in this respect, as well as in insertion and direction, with the ovula. The supposition, that in such cases all the lobes of each squama are cells of one and the same anthera, receives but little support either from the origin and arrangement of the lobes themselves, or from the structure of other phænogamous plants: the only cases of apparent, though doubtful, analogy that I can at present recollect occurring in Aphyteia, and perhaps in some Cucurbitaceæ.

That part of my subject, therefore, which relates to the analogy between the male and female flowers in Cycadeæ and Coniferæ, I consider the least satisfactory, both in regard to the immediate question of the existence of an anomalous ovarium in these families, and to the hypothesis repeatedly referred to, of the origin of the sexual organs of all phænogamous plants.

In concluding this digression, I have to express my

* In communicating specimens of this plant to the late M. Richard, for his intended monograph of Coniferæ, I added some remarks on its structure, agreeing with those here made. I at the same time requested that, if he objected to Mr. Salisbury's Belis as liable to be confounded with Bellis, the genus might be named Cunninghamia, to commemorate the merits of Mr. James Cunningham, an excellent observer in his time, by whom this plant was discovered; and in honour of Mr. Allan Cunningham, the very deserving botanist who accompanied Mr. Oxley in his first expedition into the interior of New South Wales, and Captain King in all his voyages of survey of the Coasts of New Holland.

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regret that it should have so far exceeded the limits proper for its introduction into the present work. In giving an account, however, of the genus of plants to which it is annexed, I had to describe a structure, of whose nature and importance it was necessary I should shew myself aware; and circumstances have occurred while I was engaged in preparing this account, which determined me to enter much more fully into the subject than I had originally intended.

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