

XXIII. *Description of the Female Flower and Fruit of RAFFLESIA ARNOLDI, with Remarks on its Affinities; and an Illustration of the Structure of HYDNORA AFRICANA.* By ROBERT BROWN, Esq., V.P.L.S.

Read June 17th, 1834.

THE principal object of the present communication is to complete, as far as my materials enable me, the history of *Rafflesia Arnoldi*, the male flower of which is described and figured in the 13th volume of the Society's Transactions.

The specimens from which this additional information has been obtained, as well as those formerly described, were received from the late Sir Stamford Raffles; and for the drawings so beautifully representing their structure, I am indebted to the same distinguished botanical painter and naturalist, who obligingly supplied those already published.

In my former essay some observations were made on the affinities of *Rafflesia*, a subject on which I could not then speak with much confidence. From such knowledge as I possessed, however, I ventured to state that this genus appeared to be most nearly allied to *Asarina*, and especially to *Cytinus*, on the one hand, and on the other to *Aphyteia* or *Hydnora*, an equally remarkable parasite of South Africa, but the structure of which was at that time very imperfectly understood.

An examination of complete specimens of *Hydnora africana* has confirmed this view; and as there are points in its structure which seem to throw some light on one of the most difficult questions respecting *Rafflesia*, I have included an account of this genus in the present paper.

The accompanying drawings of *Hydnora africana*, which so admirably display its structure, were kindly made from these specimens by my lamented friend and fellow-traveller Mr. Ferdinand Bauer, when he revisited England in 1824; they were probably the last drawings he ever made of an

equally interesting and difficult botanical subject, and I consider them his best*.

Since the publication of my former memoir, much light has been thrown on the structure and œconomy of *Rafflesia*, chiefly by Dr. Blume, who in his 'Flora Javæ' has given a very full history of a nearly related species, his *Rafflesia Patma*, as well as of *Brugmansia*, a parasite of similar œconomy, very distinct as a genus, but evidently belonging to the same natural family. Before, however, noticing more particularly what has been done by others, I shall resume the subject where I left it at the conclusion of my former memoir, in adverting to those points which I then regarded as the principal desiderata in the botanical history of this extraordinary plant.

The first of these related to the reticulate base, which I ventured to consider a production of an intermediate kind, or rather as one derived from the stock or root of the Vine, but excited and determined in its form and nature by the specific stimulus of the parasite. I expected, therefore, to find it existing in the form of a covering to the bracteæ in the early state, as in *Cytinus*. This point has been fully confirmed, and is well shown in Mr. Bauer's drawings of the very young buds†. From the same figures it appears that the parasite is occasionally found on the stems of the Vine, as Dr. Jack had stated, but which seemed to me to require confirmation.

* Since this paper was read, the Linnean Society have had to lament the loss of Francis Bauer, who died in 1841 at the advanced age of eighty-three. Like his brother Ferdinand, he continued, till within a short time of his death, to take the same interest in those scientific investigations which formed the constant occupation and the chief pleasure of a long life.

The figures of *Rafflesia* and *Hydnora*, which so admirably illustrate, and form the more valuable part of this communication, are among the best specimens of the unrivalled talent of the two brothers Francis and Ferdinand Bauer, who, as botanical painters, equally united the minute accuracy of the naturalist with the skill of the artist.

To this brief note I may be permitted to add how fortunate I consider myself in having so long enjoyed the friendship and so often been indebted for the important assistance of these two distinguished men, whose merits in the branch of art which they cultivated have never been equalled, and to both of whom the illustrations of the present paper, so happily connected, may form an appropriate monument, the work of their own hands.

† That the whole of this covering belongs to the stock, is proved by its containing those raphides or acicular crystals which are so abundant in the root of the *Vitis* or *Cissus*, and which are altogether wanting in the parasite.

Of the structure of the female flower of *Rafflesia* I judged entirely from Dr. Jack's account in his letter published in my former essay; and respecting this structure several important points, which even his subsequent description in the 'Malayan Miscellany' did not supply, were regarded as undetermined.

Whether the ovarium is wholly distinct from the calyx or cohering with it at the base, was the first of these points which required further examination. The specimens now prove it to be chiefly superior or free in the flowering state, and wholly so in the ripe fruit.

The internal structure of the ovarium, especially the origin and arrangement of the numerous ovuliferous surfaces or placentæ, I considered one of the principal desiderata. Dr. Jack's account of these placentæ, which, as far as it extends, is essentially correct, is confirmed by Dr. Blume's description and figures of *Rafflesia Patma*, as well as by the more complete drawings which accompany the present paper. The important question, however, namely the analogy of this apparently singular arrangement with ordinary structure, may be regarded as still in some degree obscure.

The transverse section of the ovarium presenting an indefinite number of cavities irregular in form, having no apparent order, and over the whole of whose surfaces the ovula are inserted, is hardly reconcileable to the generally received notions of the type of the female organ; and as these cavities exist to the same extent and with similar irregularity from centre to circumference, they may with equal probability be considered as originating from the axis or from the parietes of the ovarium. The vertical section too, if viewed without reference to the external development of the top of the column, exhibits a structure equally anomalous. If, however, the corniculate processes terminating the disc of the column be regarded as styles, which is surely the most obvious and not an improbable view, their arrangement would lead to the supposition that the ovarium is composed of several concentric, circular series of simple pistilla, each having its proper placenta, bearing ovula over its whole surface. But the structure is so much obscured by the complete confluence of the supposed component parts, that this view might not at once present itself. It is readily suggested, however, by the seemingly analogous structure of *Hydnora*, in which the cylindrical placentæ, whose number is considerable and apparently indefinite, are all pendulous from the top of the cavity, neither

cohering with its sides or base, wholly distinct from each other, and uniformly and densely covered with ovula.

But although this is the most obvious view suggested by *Hydnora*, a more careful examination, especially as to the relation of stigmata to placentæ, leads to a very different notion of the composition of the ovarium in that genus: for as the placentæ correspond with, and may be said to be continuations of the subdivisions of the stigmata, and as these stigmata appear to be three in number, each with numerous subdivisions diverging from the circumference towards the centre of the ovarium, and each of these subdivisions bearing one or more placentæ pendulous from its internal surface, the ovarium of *Hydnora* may be regarded as composed of three confluent pistilla, having placentæ really parietal, but only produced at the top of the cavity; the sides of which, however, exhibit no indication whatever of composition.

Between this most remarkable structure of *Hydnora* and that of *Cytinus* there is some, though not perhaps a very obvious analogy, each of the strictly parietal placentæ in the latter being subdivided into distinct lobes, as in many *Orchideæ*, a family which *Cytinus* also resembles in the structure of the seed, and probably in the mode of impregnation, though so widely different in almost every other respect.

It would certainly be difficult to reduce *Rafflesia* to the view here taken of the formation of the compound ovarium in these two genera; and it may therefore, perhaps, be said, that although the structure of *Hydnora*, in one important particular, suggests or confirms the more probable notion of the composition of ovarium in *Rafflesia*, as already stated*, it is in other respects very distinct.

* My confidence in this hypothesis respecting *Rafflesia* is greatly lessened on considering the structure of the female flower of a lately discovered species of the genus, namely, *Rafflesia Cumingii* or *Manillana*, in which the style-like processes terminating the column are much fewer in number, and so arranged as to form a single circular series of about ten, not very distant from the limb, with only from one to three processes within it, which are placed near the centre, while the irregular cavities in the ovarium are evidently much more numerous, and in arrangement have no apparent relation to that of the supposed styles, there being as great complexity in the centre as towards the circumference. These relations between styles and ovarial cavities seem, according to the figures of *Rafflesia Patma*, to be reversed in that species, its styles being apparently more numerous than the cavities of the ovarium; and as even in *Rafflesia Arnoldi* their correspondence is far from obvious, it would seem that the number and arrangement of these processes afford no satisfactory evidence of the composition of the ovarium in any

Another point, which in my former paper I considered doubtful, namely the seat or limit of the stigmata, is not even now satisfactorily established; for the slender processes forming the hispid tips of the supposed styles, which have so much the appearance of the ultimate divisions of stigma, are merely hairs of a very simple structure, and exactly resembling those found in other parts of the column; though in several of the specimens examined they were greatly altered in appearance, from a coating of mucous matter taken up and again deposited by the spirit in which the specimens were preserved*. A slight difference, indeed, seems to exist between the tissue of the apices of the styles and the other parts of their surface; hardly sufficient, however, to prove it to be stigma, though this is no doubt the probable seat of that organ.

The next point of importance in the female flower of *Rafflesia* is the structure and gradual development of the ovula. These, in the earliest state observed, consist of merely conical or subcylindrical papillæ, having a perfectly smooth surface as well as uniform internal substance.

The first perceptible change taking place in the papilla is a slight contraction at its summit, the upper minute contracted apex being the rudiment of the nucleus. Immediately below this contracted portion a dilatation is soon observable, which, gradually enlarging and becoming slightly hollowed, forms a cup in which the nucleus, also proportionally increased in size, is partly immersed. This cup, the rudiment of the future integument, continues gradually to enlarge, until it completely covers and extends considerably beyond the nucleus, but without cohering with it. If a transverse section is made near the slightly-depressed apex of this integument, an extremely minute perfora-

known species of the genus. But if the placentation of *Rafflesia Arnoldi* and *Cumingii*, notwithstanding the objections stated in the text (p. 223), be considered parietal, as Blume has described it in *R. Patma*, and as from his figures it seems actually to be in *Brugmansia*, there would still be no means of determining the exact degree of composition of ovarium in *Rafflesia*; for in no species of the genus is there the slightest indication afforded by the arrangement of cavities or ramification of the assumed placentæ, to mark any definite number of component parts. Similar objections apply with equal force to the adoption of that opinion which regards placentation as in all cases central or derived from the axis.

In conclusion, therefore, it may perhaps be said that *Rafflesia*, in the structure both of ovarium and antheræ, is not obviously reconcileable to any hypothesis hitherto proposed to account either for the origin or for a common type of the sexual organs of Phænogamous plants.

* See Mr. Bauer's representation of the hairs in this state, TAB. XXIII. figs. 3, 4, 5, 6 & 7.

tion or capillary channel, extending to the free apex of the included nucleus, may be observed.

This account of the gradual development of the ovulum of *Rafflesia*, I believe, is in every essential point applicable to Phænogamous plants generally, except that here one coat only is developed. It is, however, in some important points different from the description given by M. Mirbel, who considers the nucleus in its earliest state as included in the integuments, which in the next stage open and dilate so as to leave it entirely exposed; they then, as he supposes, remain quiescent until the nucleus has considerably enlarged, when they again become active and increase in size until they once more completely cover it.

While the development, as I have here described it, of the nucleus and its integument in *Rafflesia* is going on, another change is at the same time gradually taking place, namely, at first a slight bending, which at last ends in a complete inversion, in the direction of the nucleus and its integument in regard to the placenta, with which, in this advanced stage, the perforated apex of the latter is nearly or absolutely in contact.

In this change of direction, the ovulum of *Rafflesia* resembles that of the far greater part of Phænogamous plants: the change, however, is effected in a way which is much less common, the curvature in *Rafflesia* taking place solely in the upper part of the funiculus, the direction of the inverted ovulum being parallel with, but distinct from, the portion below the curvature; whereas in Phænogamous plants generally, the curvature is produced in that part of the funiculus which is connate with the testa or outer integument. For this difference a reason, perhaps, may be assigned; the integument which generally forms the testa or outer coat being in *Rafflesia* entirely wanting, or only indicated by the remarkable dilatation of the apex of the funiculus*.

In the more essential points of structure, the ovula of *Hydnora* and *Cytinus* agree with that of *Rafflesia*. They differ, however, in both these genera in retaining their original direction.

In *Hydnora* I have ascertained the perforation of the single integument and

* The earlier production of the inner of the two coats generally present in the ovula of Phænogamous plants, and the absence of the outer in this and several other cases, will probably be considered a valid objection to the terminology of M. Mirbel.

the position of the included nucleus, but the very earliest stages I have not yet distinctly seen; while in *Cytinus*, in addition to the coat analogous to that of *Rafflesia* and *Hydnora*, a two-lobed or bipartite membrane is observable.

Of these three genera, I have hitherto observed the pollen or mucous tubes only in *Cytinus*, in which they pass along the surfaces of a definite number of cylindrical cords existing in the style until they reach the cavity of the ovarium, when they follow the direction of the placentæ and become mixed with the ovula, to which I have not yet, however, found them actually attached*.

The structure of the pericarpium and the ripe seed of *Rafflesia* have been satisfactorily ascertained from the examination of a single fruit found among the numerous flower-buds in various states which were received from Sumatra by Sir Stamford Raffles long after his return to England. In this fruit, which is very accurately represented of the natural size in Mr. Bauer's figure, the column, deprived entirely of its style-like processes, had become a compact fleshy mass, having deep fissures on its surface dividing it into nearly square lobes, somewhat resembling the surface of the dilated base of *Testudinaria*, and within, like the ovarium, exhibiting irregular cavities, whose surfaces were thickly covered with minute seeds.

These seeds, which are also beautifully shown in Mr. Bauer's figures, differ but little in form from the ovula of the expanded but unimpregnated flower; they are considerably larger, however, and the apex of the funiculus is still more dilated. From their great hardness, as well as from their internal structure, they appear to be quite ripe; and it is worthy of remark, that of the many thousands contained in the fruit, the very considerable portion seen were of uniform size and appearance.

The testa or outer integument, which is evidently that existing in the unimpregnated ovarium, is of such hardness and thickness that it may be termed a nut; it is of a chestnut colour, its surface regularly reticulate and deeply pitted, a depression occupying the centre of each areola.

The inner integument is a thin light-coloured membrane, very slightly

* In a few cases where the supposed pollen tubes were present I found them applied to the apices of the enlarged ovula. In some instances I have met with only a very loose tissue, consisting of elongated cells mixed with mucus, forming cords descending from the stigmata, and reaching to, but not extending beyond, the origin of the placentæ.

areolated, and of uniform surface. Within this the nucleus, of similar form and dimensions, seems to be more firmly attached at its upper extremity to the coat by a short and very slender funiculus.

The nucleus separated from its coat has an areolated surface, and at first appears to be entirely composed of a loose and uniform cellular tissue. But on a more careful examination this substance is found to contain another cellular body, of nearly cylindrical form, adhering with some firmness to the upper extremity of the including cellular mass, whose vertical axis it occupies for nearly three-fourths of its length.

This inner body, which I regard as the *embryo*, consists of large cells, disposed nearly, but not with absolute regularity, in two longitudinal series, and so transparent, that it may be safely affirmed that there is no included body nor any perceptible difference in the contents of any of the component cells.

This account of the embryo differs in some respects from Mr. Bauer's representation of it, especially as to the point of attachment, and in the distinct appearance and transparency of cells*.

The seed of *Hydnora* in many essential points resembles that of *Rafflesia*. Its nucleus consists of a dense albumen, the cells of which are so disposed as to exhibit, when slightly magnified, a kind of radiation in whatever direction it is cut. This albumen is much denser than that of *Rafflesia*, the greater density arising, perhaps, from the unusual thickness of the walls of each cell, its cavity bearing so small a proportion to the supposed external dimensions of the cell as to give it the appearance of a nucleus or more opaque central body†.

Enclosed in the albumen a perfectly spherical embryo is found, consisting entirely of a more minute and much less dense cellular tissue. On the surface of this embryo I have observed no point marking original attachment, nor any

* I have therefore added to TAB. XXV. a circumscribed figure, marked R. Br., in which I have endeavoured to represent (but not very successfully) the structure as I have seen it.

† But these supposed cells with thickened walls, admitting them to have been originally distinct, are in the ripe seed nearly or entirely obliterated, so that the substance of the cartilaginous albumen consists of a uniform, semitransparent mass, in which the more opaque nuclei or cells, containing minute granular matter, are as it were immersed,

indication of a channel connecting it with the surface of the albumen, in the centre of which it is seated.

In *Cytinus*, in which I believe I have at length found ripe fruits, the seeds are extremely minute, and generally retain at their base the bipartite membrane more distinctly observable in the unimpregnated ovulum. To this membrane the name of arillus may be given; but it may also, and, perhaps, with greater probability, be considered the imperfect production of the testa or outer membrane.

The seed itself is elliptical, with a slight inequality at top indicating the depression or perforation observable in the ovulum. The single integument of the seed is easily separable from the nucleus, and by moderate pressure splits longitudinally and with great regularity into two equal portions; in texture it is a crustaceous membrane, indistinctly reticulate, the areolæ, when very highly magnified, appearing to be minutely dotted with a semi-opake centre.

The nucleus, corresponding exactly in size and form with the integument, has its surface also reticulate, but the areolæ are not dotted; and it appears, as far as I can ascertain in so minute a body, to consist of a uniform cellular tissue, very exactly resembling the nucleus of an Orchideous plant.

The result of the comparison now made, and which might be extended to other points of structure of *Rafflesia*, *Brugmansia*, *Hydnora* and *Cytinus*, seems to be, that these four genera, notwithstanding several important differences, form a natural family to which the name of RAFFLESIIACEÆ may be given; and that this family is again divisible into three tribes or sections:

The first, *Rafflesieæ*, consisting of *Rafflesia* and *Brugmansia*, is distinguishable by the ovarium being either in part or wholly superior to the origin of the calyx, in its composition or internal structure, in the placentation and direction of the ovula, in the structure of the seed and in that of the antheræ.

The second section, *Hydnoreæ*, formed of *Hydnora* alone, is characterized by its completely adherent ovarium, singularly divided stigmata, the peculiar origin and structure of its pendulous placentæ, its embryo inclosed and seated in the centre of a dense albumen, and by the arrangement and structure of its antheræ.

In the third section, or *Cytineæ*, the placentæ are parietal, the ovarium is

connate with the calyx, and the cellular undivided embryo forms the whole mass of the seed, or is apparently destitute of albumen*.

That this third section is nearly related to *Asarinae* seems to me unquestionable: if, therefore, its affinity to *Hydnora* and *Rafflesia* be admitted, the place of this singular family would be nearly established.

That *Rafflesia*, *Hydnora* and *Cytinus* do not essentially differ from many of the more perfectly developed Phænogamous plants in their vascular structure, I have satisfactorily ascertained, and there is no sufficient reason to doubt that the same observation may be extended to *Brugmansia*.

In my former paper, in treating of the composition of the vascular bundles existing in various parts of *Rafflesia*, I too hastily assumed the absence of spiral vessels, the expression used evidently implying that I had satisfied myself of their non-existence in the fasciculi or bundles examined; instead of which I should only have stated that I had not been able to find them.

The absence of spiral vessels has since been affirmed by Dr. Blume with respect to his *Rhizanthææ*, consisting of *Rafflesia* and *Brugmansia*; and still more recently by Messrs. Endlicher and Lindley, who, overlooking probably the very positive statement of Dr. von Martius respecting *Langsdorfia*, have equally denied the existence of spiral vessels in *Balanophoreæ*; and partly, perhaps chiefly, determined by this supposed conformity and peculiarity of structure, have referred *Rafflesiaceæ* and *Balanophoreæ* to the same natural class.

* To the third section of *Rafflesiaceæ*, *Apodanthes* and *Pilostyles* may perhaps be referred. These genera indeed agree with *Cytinus* in their unilocular ovary with parietal placentation, in their cellular undivided embryo forming the whole mass of the seed, and in their adherent or semi-adherent ovary, whose cavity in *Pilostyles* extends even below the insertion of the bractæ. The existence of petals, however, in both, and especially in *Apodanthes*, will probably be considered as an objection of some weight to their absolute union with *Cytineæ*; and there is even an important difference in their placentation, the ovula being produced equally over the whole surface of the ovarial cavity, while in *Cytinus* the placentæ are distinct, definite in number, and subdivided into numerous lobes, nearly as in *Orchideæ*.

Whether *Apodanthes* and *Pilostyles* are to be included in the same genus, as Professor Endlicher (in Gen. p. 76) first conjectured, and as Mr. Gardner has more recently (in Hooker Ic., new ser., vol. iii. tab. 644) endeavoured to prove, though not improbable, must, I think, remain somewhat doubtful so long as we are unacquainted with the male flower of *Apodanthes*. In the mean time this genus may be distinguished from *Pilostyles* by the singular insertion of its petals, which also differ remarkably in texture from the quadrid persistent calyx, and by the two bractæ of the flower being seated below the origin of an angular ovarial cavity, and which, after the falling off of the parasite, remain attached to the stock.

I have in the first place to correct my own error respecting *Rafflesia*, in various parts of the female flower of which I have found spiral vessels of the ordinary structure, consisting of a single, easily unrolled fibre; and on re-examining the same specimen of the male flower respecting which my former assertion was made, I found these vessels equally distinct. Professor Meyer has already stated their existence in the procumbent stems or rhizomata of *Hydnora triceps*; in which I have also found them in *Hydnora africana*, as well as in other parts of the same species; and in *Cytinus* they are still more obvious.

I may also add, that wherever I have had specimens of *Balanophoreæ* in a fit state for minute examination, I have never failed to find spiral vessels in various parts of their tissue, particularly in *Cynomorium coccineum* and *Helosis guianensis**.

* Although in *Rafflesiaceæ* and in the genera at present referred to *Balanophoreæ*, spiral vessels undoubtedly exist, in the greater number, indeed, sparingly, but in some cases in hardly reduced proportion, it may still perhaps be alleged, by those botanists who have proposed to unite both families into one natural class, that the vascular system of all these parasites is uniform and more simple than that of the far greater part of Phænogamous plants; that the spiral or slight modifications of it is the only form of vessel hitherto observed in any of them; and that the large tubes or vessels, with frequent contractions, corresponding imperfect diaphragms, and variously marked surface, which have received several names, as vasa porosa, punctata, vasiform cellular tissue, dotted ducts, &c., and which are so conspicuous in the majority of arborescent Phænogamous plants, have never been observed in any part strictly belonging to these parasites. But even admitting the non-existence of the large vessels here referred to, their absence will hardly be regarded as a sufficient reason for the union into one class of the two families in question, especially when it is considered,

First, That conformity in vascular structure, even when accompanied by peculiarity of tissue, does not always indicate, much less determine, botanical affinity. This is strikingly exemplified in *Coniferae* and *Winteranae*, two families which, though so nearly agreeing in the uniformity and peculiarity of their vessels, and in both of which the large tubes referred to are wanting, yet differ so widely from each other in their organs of reproduction and in their leaves, that they may be regarded as placed at opposite extremities of the scale of *Dicotyledones*.

Secondly, That uniformity of vascular structure is not always found in strictly natural families. Thus many *tropical woody climbers* exhibit remarkable peculiarities of vascular arrangement not existing in the greater part of the families to which they respectively belong, but which peculiarities appear to have no influence whatever in modifying their reproductive organs.

Thus also in *Myzodendron*¹ the whole woody tissue consists of vasa scalariformia, a peculiar struc-

¹ *Myzodendron* of Banks and Solander, from μυζέω or μύζω *sugo*, and δένδρον, has been changed to *Misodendron* by DeCandolle and all following systematic writers; no doubt merely from a mistake as to the intended derivation. *Myzodendron*, hitherto referred to *Loranthaceæ*, to which it is certainly

I may hereafter have an opportunity of entering fully into the question whether *Rafflesiaceæ* and *Balanophoreæ* form merely different orders of the

ture, and very different from that of all the other genera belonging to *Loranthaceæ*, to which this genus has been referred, and to which, though it does not absolutely belong, it is nearly related. Even this peculiar structure of the stems of *Myzodendron* admits of considerable modifications in the different species of the genus, which is strikingly exemplified in comparing the loose vascular tissue with large and singularly-constructed medullary rays of *M. brachystachyum* and *quadriflorum* with the more minute vessels and extremely narrow rays of *M. punctulatum*.

I may also notice that in *Tillandsia usneoides*, as well as in the nearly-related species of that genus, the capillary stems are destitute even of spiral vessels, though in *Bromeliaceæ* generally the ordinary vascular system is found.

Whatever may be the state of vessels in the fully-developed parasites belonging to *Rafflesiaceæ*, it appears to me that at least *Rafflesia* in its very early stages is entirely cellular, and that this continues to be the case not only until that mutual adaptation of parasite and stock which enables the former to complete its development has taken place, but until the first indications of its future structure have become perceptible. It may also be remarked, that even after the formation of vessels in the parasite is obvious, the direct union between *Rafflesia* and the *Vitis* continues to be chiefly if not entirely cellular, the connexion consisting in a slight mutual penetration or indentation of the two substances, whose cells are easily distinguishable.

I may here advert to one of the most difficult points in the œconomy of *Rafflesiaceæ*, namely, by what means their minute embryos, which are at the same time of an extremely loose texture, are enabled to penetrate through the bark of the plants on which they vegetate, so as to account for such appearances as those exhibited in the nascent *Rafflesia Arnoldi* represented in TAB. XXVI. A., in which I have been unable to trace any perceptible communication with the surface, and where the parasite seems rather to grow out of than into the stock.

Connected with this point a question may also arise, whether the earliest effort of the seed after its deposition in the proper nidus, by whatever means this is effected, may not consist in the formation of a cellular tissue extending laterally under the bark of the stock and capable of producing the fully-developed parasite.

This question might not occur in regard to *Rafflesia* and *Brugmansia*, in both of which the individual plants are in general sufficiently distant on the root of the *Vitis* to make it probable that each developed parasite is produced from a distinct seed. But in *Pilosyles*, and even *Cytinus*, where they are closely

closely allied, especially through *Antidaphne* of Poeppig, appears to me to have characters sufficient to distinguish it as, at least, a subordo or tribe (*Myzodendree*), namely, the structure of its ovarium, in which it approaches to *Santalaceæ*, having three ovula suspended from the apex of a central placenta, only one of which ripens; the entire absence of floral envelope in the male; the singular feathery appendages of the female flower and fruit compensating in the dispersion and subsequent adhesion of its seeds, which are destitute of that viscidty existing in those of the parasitic *Loranthaceæ*; and lastly, the embryo being undivided, with its dilated and exerted radicle inclosed in a semitransparent covering, a continuation of the membrane lining the cavity of the albumen in which the embryo is lodged.

same natural class, in giving an account of a new and remarkable genus of the latter family*.

At present I shall only remark, that the sole remaining character employed to unite these two families and supposed to distinguish them from all others, namely the simple or acotyledonous embryo, exists equally in *Orchideæ*. And if it be employed along with those characters connected with their peculiar œconomy, namely the imperfect development of leaves, the want of stomata and absence of green colour, the class cannot be limited to *Rafflesiaceæ* and *Balanophoreæ*, for an embryo of exactly the same kind exists in *Orobanche*, and other, perhaps all other, genera parasitic on roots, a remark which I made, though not with sufficient precision, in my former essay. But such a classification, though founded on seemingly very important technical characters, would hardly be received in a strictly natural arrangement, and it seems to me quite as paradoxical to approximate two such genera as *Rafflesia* and *Balanophora*.

RAFFLESIA ARNOLDI.

Rafflesia Arnoldi, *R. B. in Linn. Soc. Transact.* vol. xiii. p. 201. tabs. 15–22.
Mas.

Rafflesia Titan, *Jack in Malayan Miscell., Append. to vol. i.*

approximated, their possible origin from one common basis or thallus is more readily suggested, especially on considering that in the former genus, which is diœcious, each group of parasites is generally, perhaps always, exclusively of one sex; and that these groups, often of great density, not unfrequently surround completely the branch of the stock. But although this view did occur to me as not very improbable, and as tending to remove some of the apparent difficulties, I have never been able to trace any substance decidedly distinct from the proper tissue of the stock: there are, however, some appearances favouring the hypothesis in both genera, especially in *Pilostyles*, but which require careful examination in the living plants.

* This genus, which was first found by Francis Masson, is the *Mystropetalon* of Mr. Harvey (in *South Afr. Gen.* p. 418), who has described two species, from both of which Masson's plant is perhaps distinct.

I may here advert to a note at p. 225 of my former memoir (in *Linn. Soc. Trans.* vol. xiii.), in which I thought it not improbable that a parasite briefly noticed by Isert (in *Reise nach Guinea*, p. 283) might be related to *Rafflesia*. I have now, however, reason to believe that Isert's plant is the *Thoningia sanguinea* of Vahl (in *Act. Soc. Hist. Nat. Hafn.* t. vi. p. 124, t. 6, and *Schumacher, Guineische Plant.* p. 431), a genus nearly related to, if really distinct from *Balanophora*.

DESC.—PLANTA FEMINEA masculæ omninò similis insertione, bracteis et perianthio.

Columna quæ figura, stylis disci et limbo elevato indiviso apicis, necnon annulo duplici baseos cum mascula per singula puncta convenit; ab eadem differt *externè* rudimentis solum minutis papillæformibus polline destitutis antherarum, et loco cavitatum antheris maris respondentium sulci tantum lineares angusti nec profundi: *internè* ovario processibus indefinitè numerosis irregulariter confluentibus in cavitatibus labyrinthi speciem formantibus divisa.

Ovula numerosissima parietibus cavitatum ovarii sine ordine sparsa, primò nucleo papilliformi sessili nudo, mox basi attenuato in funiculum rectum, apice incrassatum primordium annulare integumentum simplicis quod sensim auctum demum nucleum omninò includit apice perforato, funiculoque simul elongato extra medium arcuè recurvato et incrassato.

Pericarpium, bracteis, calyce, apiceque patelliformi styligero columnæ delapsis, denudatum, omninò superum vel liberum, subovatum carnosum crassum altè rimosum indehiscens, cavitatibus sicut in ovario indefinitè numerosis inordinatis amorphis polyspermis.

Semina pedicellata, funiculi dimidio *inferiore* cylindræo cellulari molli pallido: *superiore* maximè incrassato arcuè recurvato subovato castaneo lacunoso solido duro. *Semen ipsum* ovatum vix diametro apicis dilatati funiculi, castaneum altè lacunosum.

Integumentum exterius crasso-crustaceum subnucamentaceum; *interius* membranaceum pallidum lacunis exterioris leviter impressum.

Albumen magnitudine integumenti interioris laxè cellulosum aqueo pallidum.

Embryo e cellulis subduplici serie ordinatis iis albuminis majoribus constans, ex apice albuminis ortus, ejusque dimidio longior.

HYDNORA AFRICANA.

Hydnora africana, *Thunb. in Act. Holm.* (1775), vol. xxxvi. p. 69. tab. 2.

E. Meyer in Nov. Act. Acad. Cæsar. Nat. Curios. vol. xvi. par. 2. p. 775. tab. 58.

Planta Aphyteja, *Resp. Achar. cum tab.* (1776). *Amæn. Acad.* vol. viii. p. 310.

Aphyteia Hydnora, *Harv. Gen. South Afr.* p. 299.

Loc. Nat. Africa Australis parasitica in radicibus Euphorbiæ succulentæ cujusdam secundum Thunberg et Drege; et quandoque Cotyledonis orbiculatæ auct. D. Mundt in *Harvey, South Afr. Gen.* p. 299. Nuperrimè etiam in Africa boreali detecta, fid. sp. asserv. in Museo Parisiensi.

DESC. Primordia sunt Caules e dilatata radice plantæ sustentis orti, humifusi v. sæpius semisepulti, angulati (4-5-6-goni) digitum crassi simplices v. sæpius ramosi, solidi angulis tuberculatis, tuberculis approximatis obtusis, apice sæpe rimoso, quasi dehiscenti

sed nunquam fibras exserenti; intra corticem strato paulo laxiore magisque colorato, centro densiore e cellulis præsertim conflato et fasciculis tenuibus parcis vasorum instructo.

E tuberculo plurimum aucto exsertus est *Flos* erectus basi in pedunculum abbreviatum, intus vasculosum sensim paulo angustatus, penitus ebracteatus.

Perianthium monophyllum, tubulosum subinfundibuliforme, carnosum extus (uti pedunculus) rimis plurimis superficialibus in areolis subrotundis, plus minus angulatis squamas primò intuitu quodammodo referentibus divisum et quasi leprosum. *Tubus* intus glaberrimus sed sæpe transversim subrugosus. *Limbus* tubum subæquans tripartitus (rariissimè 4-partitus) æqualis, æstivatione induplicato-valvata; laciniis primum latere hiantibus, apicibus diutius cohærentibus demum distinctis, modicè patentibus ovalibus oblongisve obtusiusculis, marginibus veris latè et obliquè induplicatis majorem partem disci apicemque omninò occultantibus extus ramentis numerosis subulatis conspersis marginalibusque elongatis ciliatis; singulis disco lævi e majore parte tecto *pulvinulo* adnato oblongo carnosio, sæpè longitudinaliter striato, apice marginibus laciniarum ibi coalitis occultato acutiusculo, basi obtusa subcordata.

Columna staminea infra medium tubi orta, brevissima annulum efformans altè trilobum, lobis laciniis limbi oppositis rotundatis obtusis. *Antheris* indefinitè numerosis, connectivo communi crasso carnosio penitus adnatis, parallelo-approximatis, elongato-linearibus, bicurvis, crure altero plurimarum postico altero antico, nonnullis quasi pressione reliquarum et præcipuè iis ad ortum lorum columnæ sitis abbreviatis sæpiùs in dorso, rariùs in ventre lobi obviis; omnibus primum bilocularibus sed sulco unico longitudinali dehiscentibus.

Pollen simplex sphæroideum læve.

Ovarium totum adherens, parietibus cavitatis lævibus.

Stigma discum apicis ovarii occupans, sessile depressum trilobum; lobis iis annuli staminei et laciniis limbi perianthii oppositis; singulis striis linearibus numerosis, e peripheria cordata lobi centrum versus plus minus divergentibus, respondentibus totidem lamellis planis arctè approximatis sed ad cavitatem ovarii usque distinctis, ibique manifestiùs separatis et placentiferis.

Placentæ indefinitè numerosæ, una pluresve e superficie interiore lamellæ singulæ stigmatis ortæ, ideoque omnes ex apice ovarii pendulæ, cylindraceæ, dimidium cavitatis, cujus parietes læves omninò steriles, superantes, undique ovulis densè tectæ.

Ovula primum sessilia papillæformia uniformia, dein subcylindracea, brevè pedicellata, apice obtuso depresso, v. perforato v. membrana semitransparente tecto, nucleo incluso manifesto.

Pericarpium perianthio toto supero et annulo stamineo delapsis denudatum, stigmate persistenti apice clausum, sphæroideum magnitudine pomi minoris, areolis squamas æmu-

lantibus inæquale quasi leprosum, carnosum crassum indehiscens, cavitate placentis undique seminiferis densè repleta.

Semina subglobosa, pedicello brevi quandoque subnullo insidentia.

Integumentum exterius crasso-membranaceum subpulposum areolatum cellulis minutè granulatis: *interius* albumine arcètè adherens.

Albumen densum, subcartilagineum, aqueo-pallidum, per lentem modicè augmentem structura quasi radiata, sed magis auctum constare videtur substantia denso semitransparenti alba nec in cellulas manifestè divisa, sed undique farcta corpusculis celluliformibus figura variis, in serie extima majoribus oblongo-obovatis, reliquis minoribus vix symmetricè positis, omnibus semiopacis e membrana materia minutè granulosa repleta formatis.

Substantia densa Albuminis uniformis forsàn e cellulis parietibus incrassatis et oblitteratis singulis, nucleo (corpusculo) semiopaco fœtis.

Embryo in centro albuminis parvus subglobosus aqueo-pallidus e cellulis numerosis parvis mollibus, materia minutè granuloso repletis, ab albumine facilè separabilis, et absque ulla manifesta communicatione cum ejusdem peripheria vel ope suspensorii, v. canalis intermedio.

EXPLANATION OF THE PLATES.

RAFFLESIA ARNOLDI.

TAB. XXII.

Fig. 1. A female flower-bud, with the roots of the *Vitis* (or *Cissus*) vertically divided, which shows the numerous irregular cavities of the ovarium chiefly if not entirely above the insertion of bracteæ and calyx, and the vascular lines continued from the walls of the cavities through the upper solid part of the column into the axes of the style-like processes:—natural size.

Fig. 2. A female flower-bud in the same stage of development, the bracteæ and calyx entirely removed, to show its outward resemblance to the male flower-bud (figured in Linn. Trans. vol. xiii. TAB. XXI.):—natural size.

TAB. XXIII.

Fig. 1. A small segment of the column, of which part of the elevated undivided limb is removed, to show the narrow furrows of the sides of the column corresponding in number with the rudiments of antheræ, seen in

- Fig. 2, which is the portion of the limb removed from fig. 1 :—natural size.
- Fig. 3. The upper half of one of the styles of the disc, with its terminating hairs :—magnified 10 diameters.
- Fig. 4. A portion of fig. 3, somewhat more highly magnified (20 diameters), vertically divided.
- Figs. 5, 6 & 7. Some of the hairs still more highly magnified, which, according to Mr. Bauer, have a secreting surface seen in fig. 7, and which in figs. 5 and 6 is covered with the secretion, consisting of spherical particles enveloped in mucus at fig. 8 :—magnified 100 diameters (but see observations respecting them in page 225).
- Figs. 9 & 10. Longitudinal and transverse sections of a style :—magnified 50 diameters.
- Fig. 11. A transverse section of half the ovarium, to show the numerous irregularly ramified cavities, and the arrangement of vascular cords belonging to the bracteæ and calyx :—natural size.
- Fig. 12. A small portion of the ovarium, with the ovula covering the surface of the cavities, and the vascular lines passing through the axes of the parietes :—magnified 20 diameters.
- Figs. 13—18. Ovula in various stages (the earliest observed are not represented) :—magnified 100 diameters.

TAB. XXIV.

- Fig. 1. A ripe pericarpium, of the natural size, the calyx, bracteæ and apex of the column being deciduous.
- Fig. 2. The same divided vertically, and showing the thickness of the densely-fleshy and deeply-furrowed covering, and also that the whole of the ovarial cavity is above the insertion of bracteæ and calyx.

TAB. XXV.

- Fig. 1. A small portion of the wall of two adjoining cavities, the surfaces covered with numerous seeds, all of equal size :—magnified 20 diameters.
- Fig. 2. A seed with its funiculus, of which the lower erect portion is filiform, the recurved upper half being of the same texture, colour and surface with the seed, which it somewhat exceeds in thickness :—magnified 100 diameters.
- Fig. 3. The same divided longitudinally, to show the structure of the seed (according to Mr. Bauer), and that the enlarged apex of the funiculus is solid :—magnified 100 diameters.
- Fig. 4. The nucleus of the seed taken out of its thick nut-like outer covering :—magnified 100 diameters.

Fig. 5. The same nucleus, whose membranous coat is separated by pressure, to show the albumen:—magnified 100 diameters.

Fig. 6. The denuded loosely-cellular albumen.

Fig. 7. A portion of the albumen, exhibiting the embryo, its surface and lateral origin, according to Mr. Bauer:—magnified 100 diameters.

Fig. R. Br. is a longitudinal section of the albumen, exhibiting R. Brown's view of the origin, form and surface of the embryo.

TAB. XXVI.

Fig. 1. A branch of the *Vitis*, on which are four very young buds of *Rafflesia Arnoldi*:—natural size. Of these,

a. (not separately figured) is merely a very slight swelling, caused by the nascent parasite, but before its parts are distinguishable.

A. (also separately figured, vertically divided and moderately magnified), the youngest parasite whose parts are distinguishable, deeply seated, entirely enclosed, and before its cortical covering corresponds with it in form.

B. (in like manner separately figured, divided and magnified), in which the parasite is entirely enclosed in its reticular covering.

C. In which the reticular covering has burst, vertically divided and magnified.

HYDNORA AFRICANA.

TAB. XXVII.

Fig. 1. A flower of *Hydnora africana*, with its very short base.

Fig. 2. The same longitudinally divided:—both of the natural size.

TAB. XXVIII.

Fig. 1. Transverse section of a part of the tube of the perianthium, to show the three-lobed columna staminea:—moderately magnified.

Fig. 2. The inner surface of one of the three lobes of the column or antheral annulus.

Fig. 3. Outer surface of the same:—both magnified in the same degree with fig. 1.

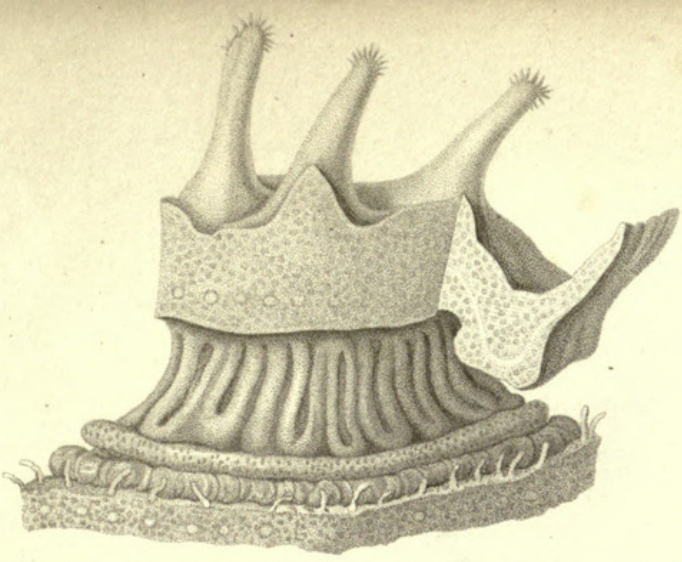
Fig. 4. Vertical section of a portion of one of the lobes of the columna staminea, to show the thickness and texture of the common connective.

Fig. 5. Transverse section of the same, which shows the original bilocularity of each anthera:—both more highly magnified.

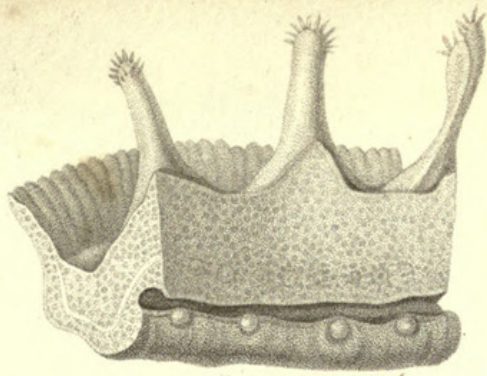
Fig. 6. Grains of pollen, still more highly magnified.



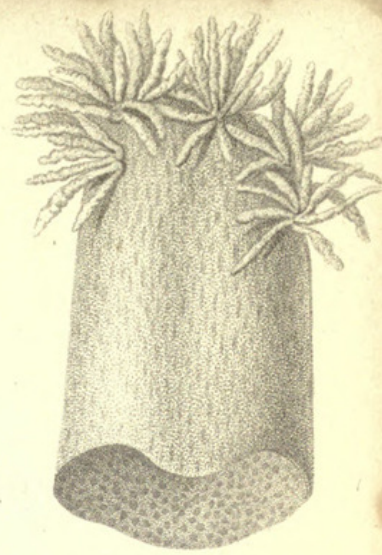




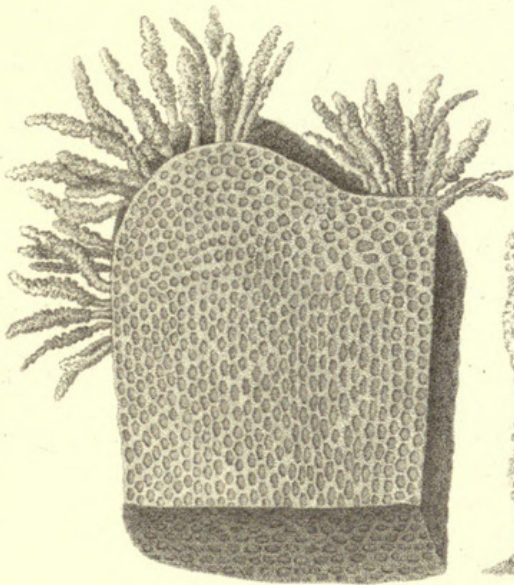
1



2



3



4



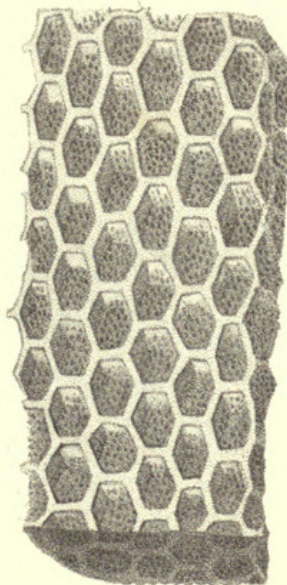
5



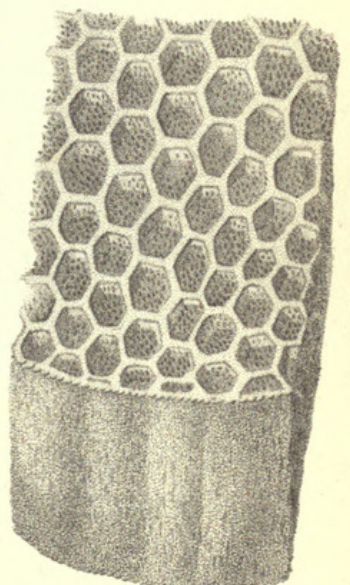
6



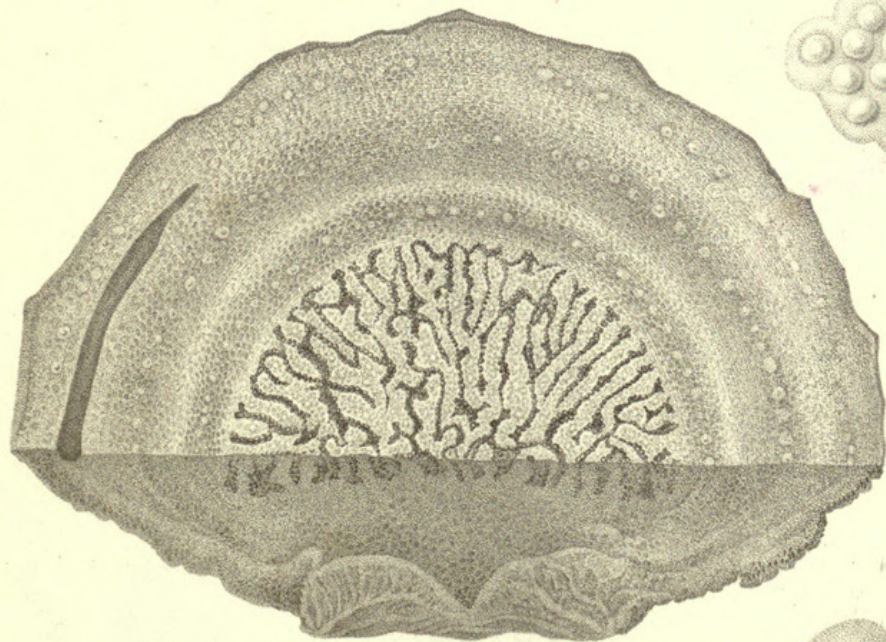
7



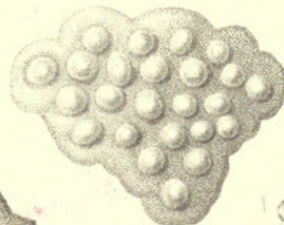
9



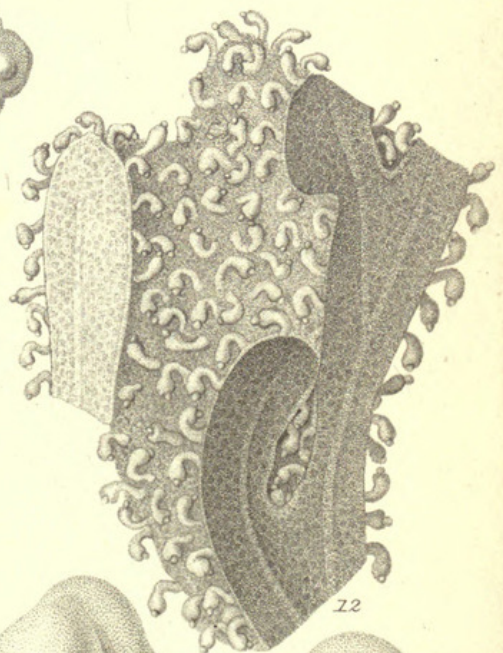
10



11



8



12



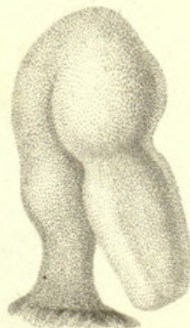
13



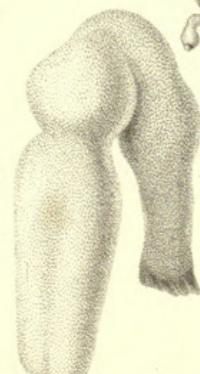
14



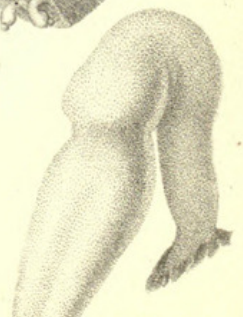
15



16

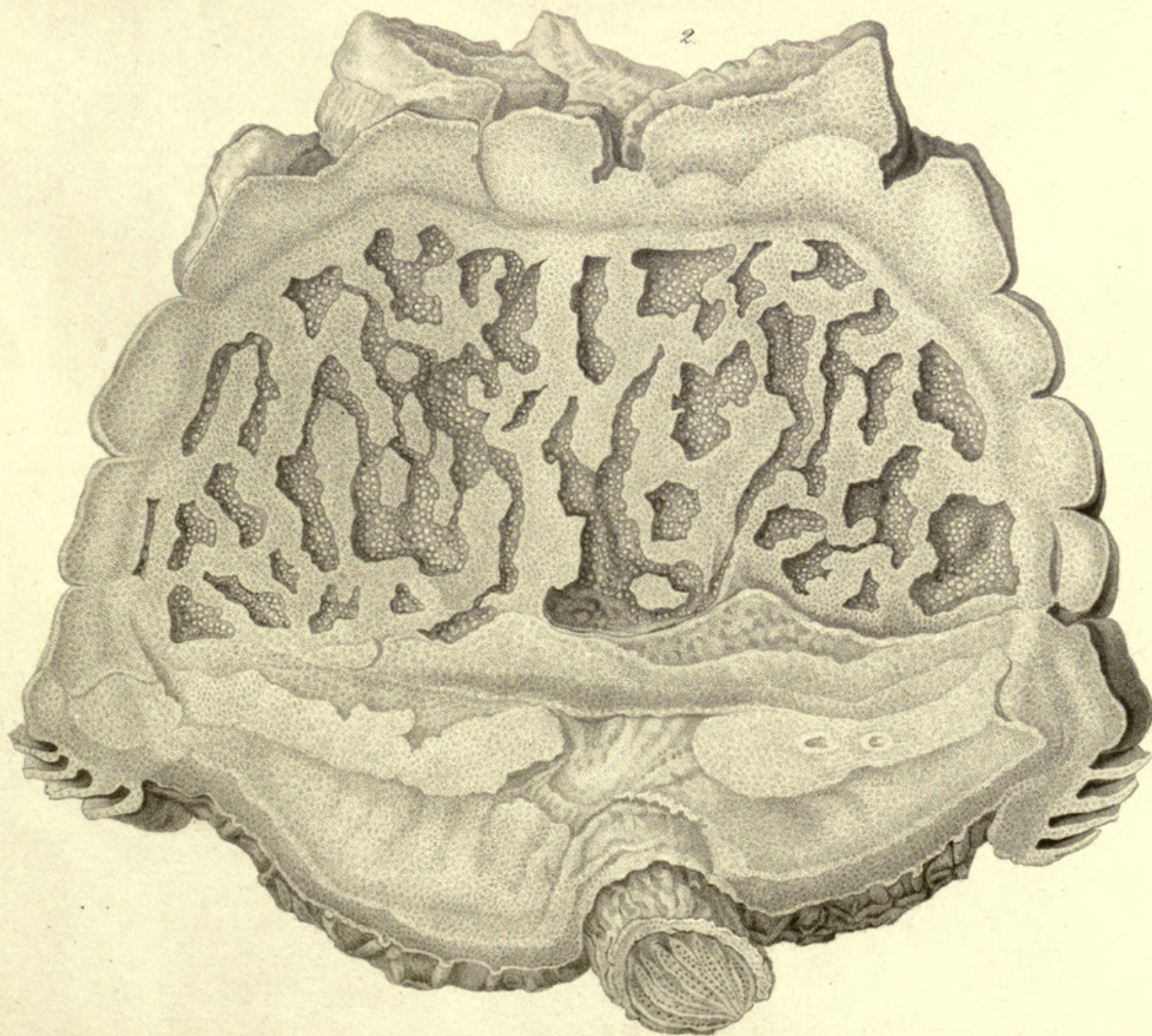
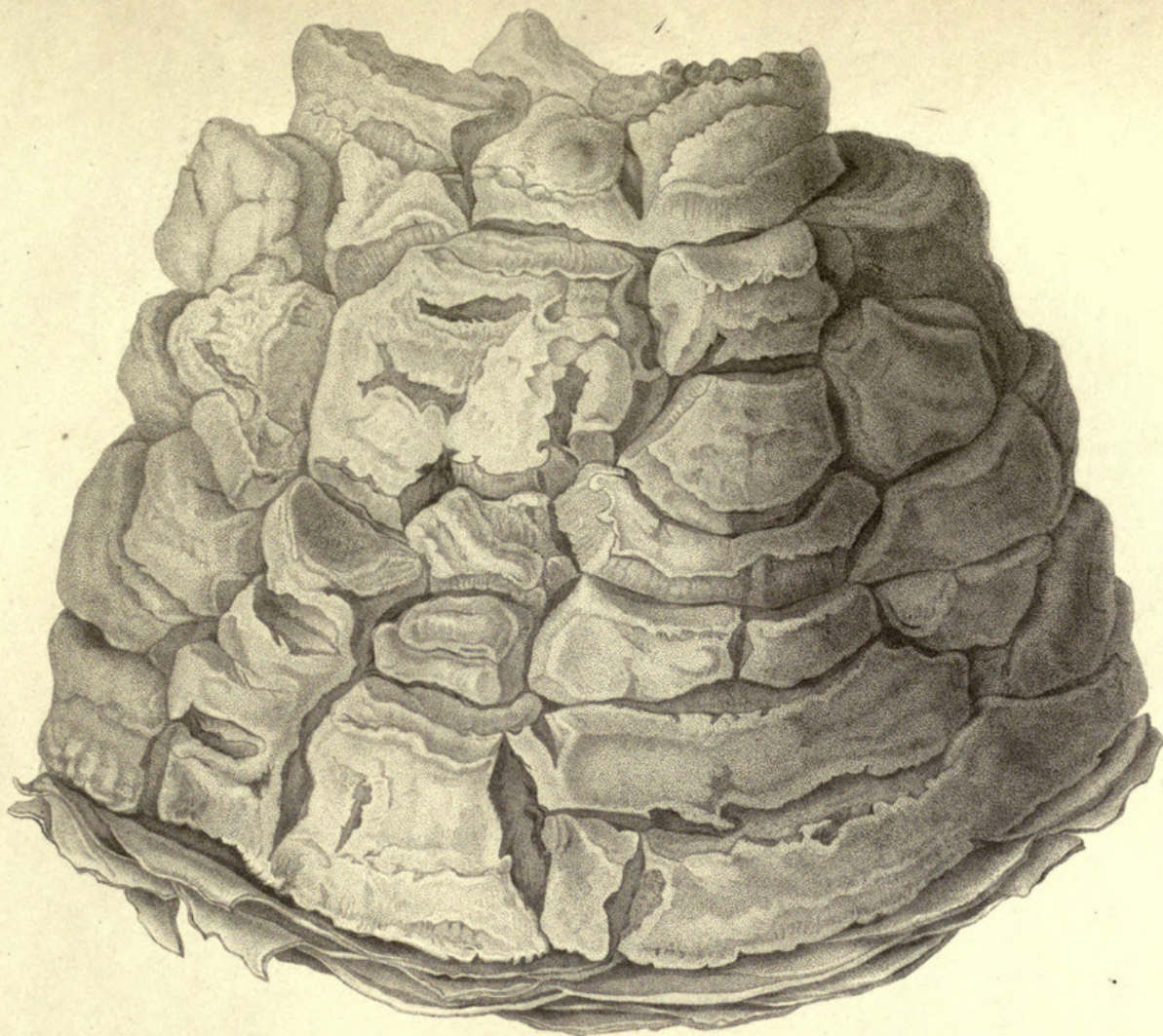


17

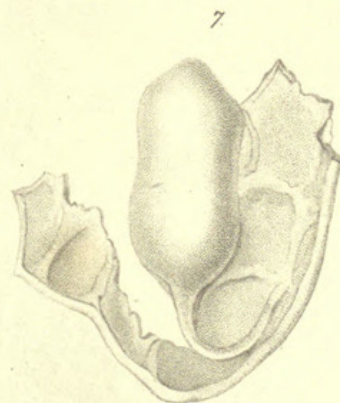
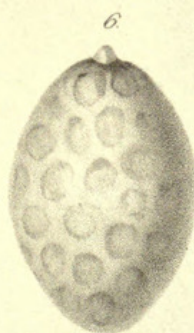
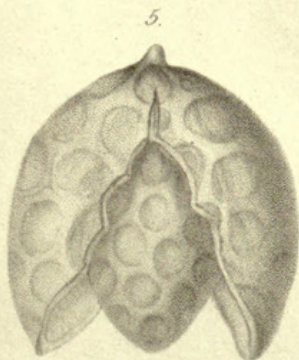
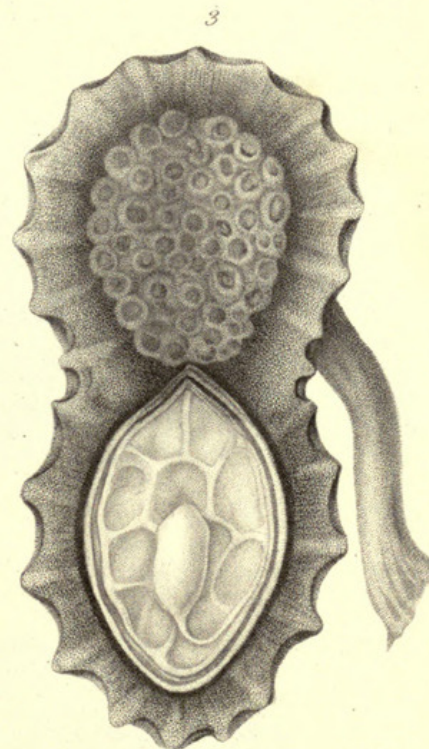
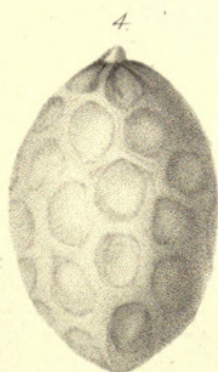
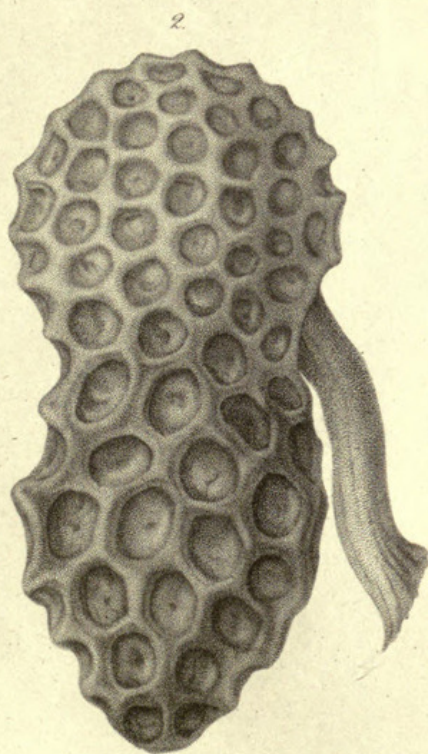
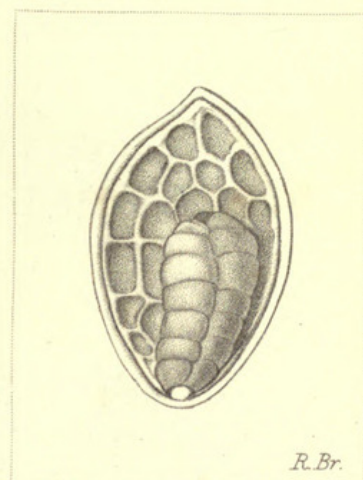
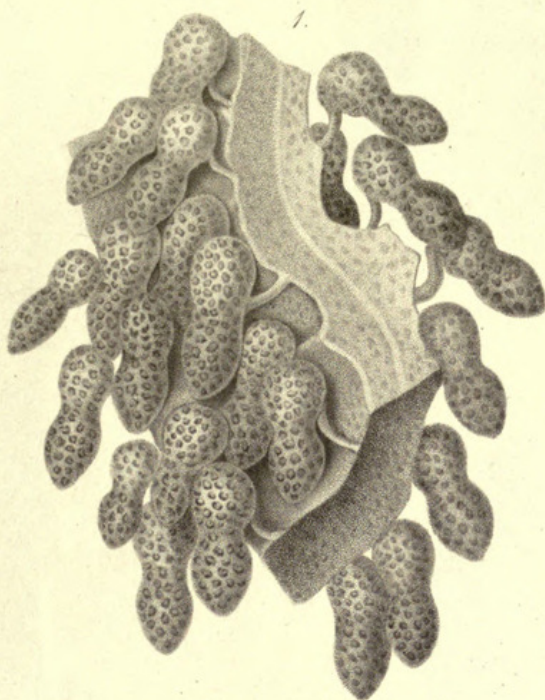


18

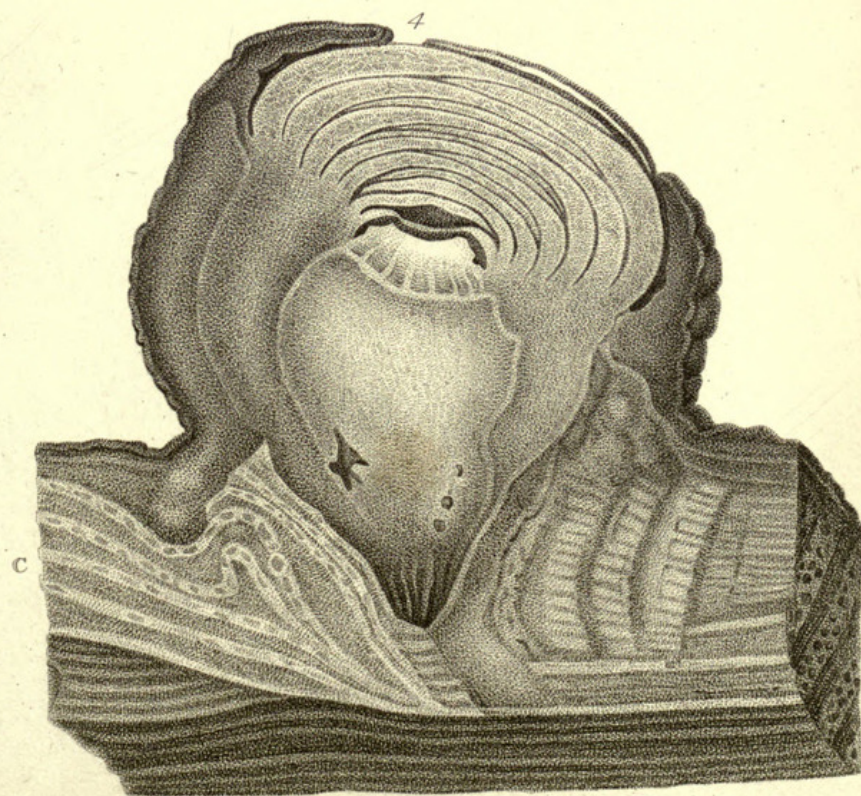
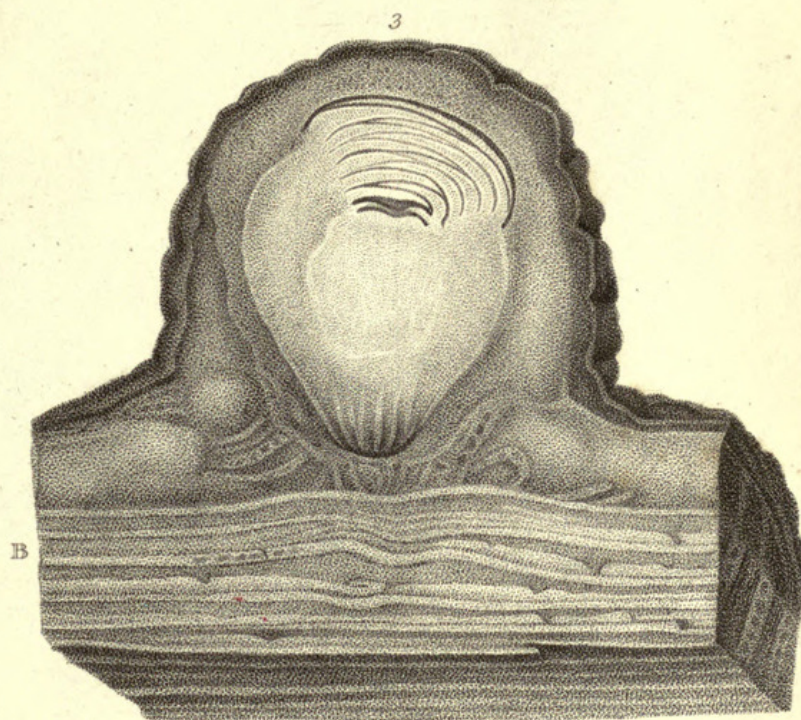
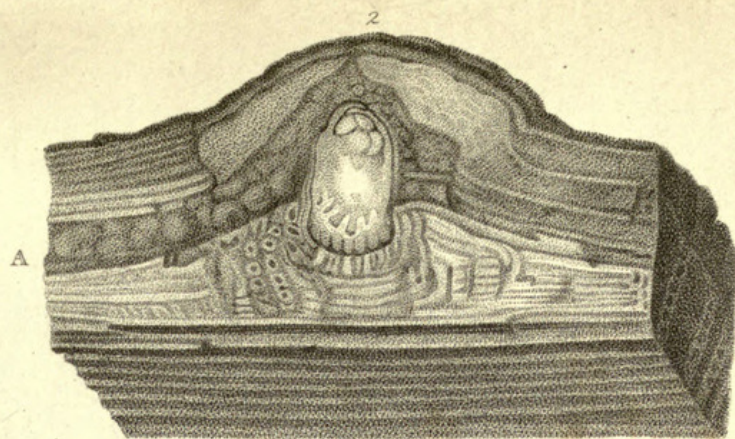
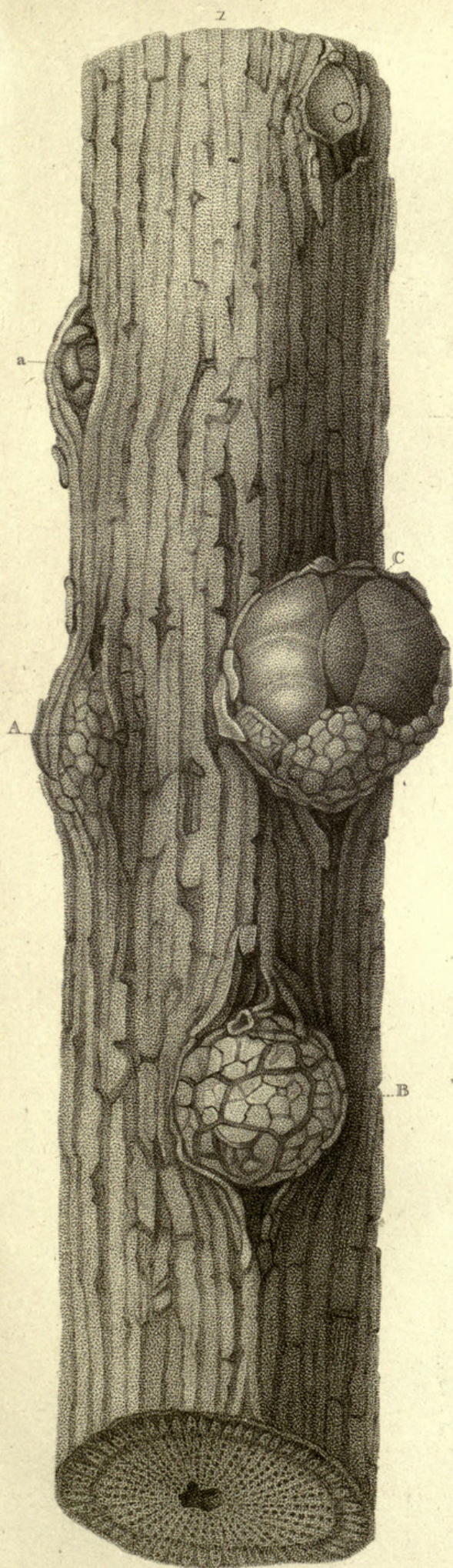














Brown, Robert. 1844. "XXIII. Description of the Female Flower and Fruit of *Rafflesia Arnoldi*, with Remarks on its Affinities; and an Illustration of the Structure of *Hydnora Africana*." *Transactions of the Linnean Society of London* 19, 221–247. <https://doi.org/10.1111/j.1096-3642.1842.tb00365.x>.

View This Item Online: <https://www.biodiversitylibrary.org/item/19473>

DOI: <https://doi.org/10.1111/j.1096-3642.1842.tb00365.x>

Permalink: <https://www.biodiversitylibrary.org/partpdf/16633>

Holding Institution

Natural History Museum Library, London

Sponsored by

Natural History Museum Library, London

Copyright & Reuse

Copyright Status: Public domain. The BHL considers that this work is no longer under copyright protection.

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.