

RAFFLESIA REALITIES AND FANTASIES

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The belief that *Rafflesia* is a repeat-flowering holoparasite with an invasive endophytic mycelium-like vegetative body is not supported by evidence. Instead, the evidence favors *Rafflesia* as a localized holoparasite that bears one flower only, dying after a single reproductive event. Also, whereas angiosperms and gymnosperms begin life as seedlings with apical meristems that drive open-ended acropetal growth, *Rafflesia* has no seedling stage and no apical meristems. Its development is close-ended, resulting in a plant of fixed size, shape, and life-span. The *Rafflesia* flower and fruit differ fundamentally from the flower and fruit of angiosperms. The structure and behavior of *Rafflesia* seeds is unlike the seeds of other plants.

Keywords: Angiosperm, endophyte, evolution, holoparasite, homology, phanerogam, taxonomy

INTRODUCTION

The discovery of *Rafflesia arnoldii* (Brown 1821) was sensational because of its enormous one-meter diameter flowers bearing five conspicuous petal-like floral lobes. Based on specimens sent from Sumatra by Stamford Raffles, Brown gave the plant its name and classified it as a dicot because of its five conspicuous floral lobes. Thirteen years later, Brown (1834) published another paper in which he said in a footnote “*In conclusion, therefore, it may perhaps be said that Rafflesia, in the structure both of ovarium and antherae, is not obviously reconcilable to any hypothesis hitherto proposed to account either for the origin or for the common type of the sexual organs of Phanerogamous plants.*” This meant that the *Rafflesia* could not be a phanerogam and its flower could not be an angiosperm flower. However, the reaction of other botanists has been to confirm *Rafflesia* as an angiosperm by rationalizing all its unique features as modifications of angiosperm features to fit a holoparasitic lifestyle. Now, molecular biologists have placed *Rafflesia* close to or within the dicot family Euphorbiaceae (Davis 2008, Wurdack & Davis 2009).

The classification system of living things is a grand theory supposed to mirror the course of evolution. Theories in biology gain credibility if they are supported by narratives that connect form with function, cause with

effect, and evolutionary change with natural selection. Theories gain credibility if they have predictive and explanatory power. The classification of *Rafflesia* within the ambit of Euphorbiaceae falls short in credibility. What we know of *Rafflesia* does not predict or explain anything in Euphorbiaceae, and what we know of Euphorbiaceae does not predict or explain anything in *Rafflesia*.

In his second paper, Brown (1834) gave prominence to the development of *Rafflesia* embryos. The first external sign of embryo development is a slight swelling in the bark of the host. The swelling increases in size until the embryo emerges as a cabbage-like bud with many layers of leafy bracts covering an inner bud which is the flower bud. Brown concluded that “... *it is probable that each developed parasite is produced from a distinct seed.*”

The problem for Brown was how to explain the presence of the *Rafflesia* embryo inside the *Tetrastigma* host plant that Brown had identified as a *Vitis*. Brown commented, “*I may here advert to one of the most difficult points in the economy of Rafflesiaceae, 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*

arnoldii represented in Table 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 instead of into the stock.”

Brown’s illustrations are reproduced here as fig 1. There are two important features in Brown’s observations that are relevant to the present discussion.

- Brown referred to the *Rafflesia* bud as an embryo, not as a flower bud.
- The embryos are clearly illustrated (Figure 1) and shown to be endophytes until they emerge through the bark of the host plant. Brown did not recognize any other kind of endophytic body.

Brown regarded *Rafflesia* as a plant developed from seed and the illustration shows that it bears one flower only. However, the idea that got entrenched is that *Rafflesia* has an invasive mycelium-like vegetative body living as a persistent endophyte inside the body of

its host and producing multiple flowers. This is described by Kuijt in his book on parasitic plants (1969, p104) as follows: “*Evolution had stripped this parasite of irrelevant organs, leaving only an almost mycelial haustoria system and reproductive organs.*” On page 185 he further describes the endophyte as follows: “*The nature of the endophyte of Rafflesiaceae, constituting the entire vegetative body, defies description. The uniseriate filaments which form the youngest portion leave scarcely a tissue or an organ of the host unexplored. The endophyte has frequently been compared to a fungus mycelium, ramifying and anastomosing throughout the host.*”

Coming after Kuijt, Meijer’s 1997 revision of Rafflesiaceae, says in the first paragraph of his description of *Rafflesia* that the endophyte is “*like a thallus inside the woody stems and root of the host plant*”.

We do not know where the idea of a fungus-like endophyte came from. No source was cited by Kuijt nor by Meijer. Nevertheless, belief in the existence of a persistent invasive endophyte has been so universal that there is a long history

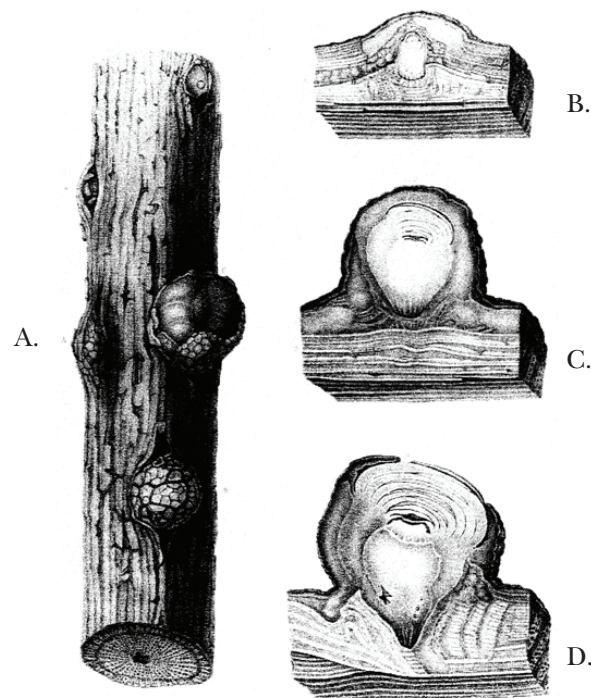


Figure 1 Copy of Table XXVI from Brown 1834. His captions are:

- A branch of the *Vitis*, on which are four very young buds of *Rafflesia arnoldii* (not separately figured) is merely a very slightly swelling, caused by the nascent parasite, but before the parts are distinguishable.
- (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.
- (in like manner separately figured, divided and magnified), in which the parasite is entirely enclosed in its reticulate covering.
- In which the reticular covering has burst, vertically divided and magnified.

of attempts to multiply *Rafflesia* by vegetative propagation of infected *Tetrastigma* plants. Vegetative propagation has been done by rooting stem cuttings of infected plants and by grafting infected stems on to uninfected plants. There is great euphoria when a flower appears, after an inexplicably long period of 2 to 8 years, but after that there is no further news. These failures suggest an alternative explanation: that the flowers are developed from *Rafflesia* entities already embedded in the infected stems and after these have flowered, no more flowers would appear unless the host plants are reinfected. *Rafflesia* has also been known to disappear from their host plants in the wild for no apparent reason (Ng 2023).

Barkman et al. (2017) analysed materials from 340 buds and flowers of *Rafflesia cantleyi*, *R. tuan-mudae* and the related *Sapria himalayana*, and found that the buds and flowers on a host plant could be of different or same genotypes. A *Rafflesia* fruit produces a vast number of seeds. One fruit of *Rafflesia keithii* has been found by Nais (2001) to contain 270,000 seeds. Recently, KKS Ng and Iylia Yusliza of FRIM examined one fruit of *Rafflesia cantleyi* and determined the number of seeds to be 316,000. We do not know whether all the seeds are products of independent pollination events or whether some may be produced by an asexual multiplication process.

Seed germination to floral anthesis

Contrary to the statement that *Rafflesia* lacks nearly all recognizable plant structures (e.g. Nikolov & Davis 2017), the plant structures of *Rafflesia* are clearly recognizable.

Tetrastigma plants produce two forms of stems: erect or semi-erect ones that climb by tendrils and horizontal ones that run along the ground for 10 m or more. *Rafflesia* buds are found on both but usually more on the runners. The runners have often been mistaken for roots but the roots are rarely thicker than 3mm and too thin to support *Rafflesia*.

In cross-section (Figure 2), the internal structure of a *Tetrastigma* stem has a core of xylem surrounded by a band of phloem. The cambium forms a boundary between xylem and phloem cells. When a cambial cell divides into two, one daughter cell become a phloem or xylem cell and the other remains cambial. The xylem and phloem cells appear as radial plates of cells separated by parenchyma. The parenchyma enables the *Tetrastigma* stem to be easily split into strips. Figure 2 shows the transverse section of a one-quarter strip of a stem, on which three seeds of *Rafflesia* (indicated by arrowheads) have been placed to show the size of the seeds relative to the cells and tissues of the host. Old stems may have repeated areas of xylem alternating with phloem.

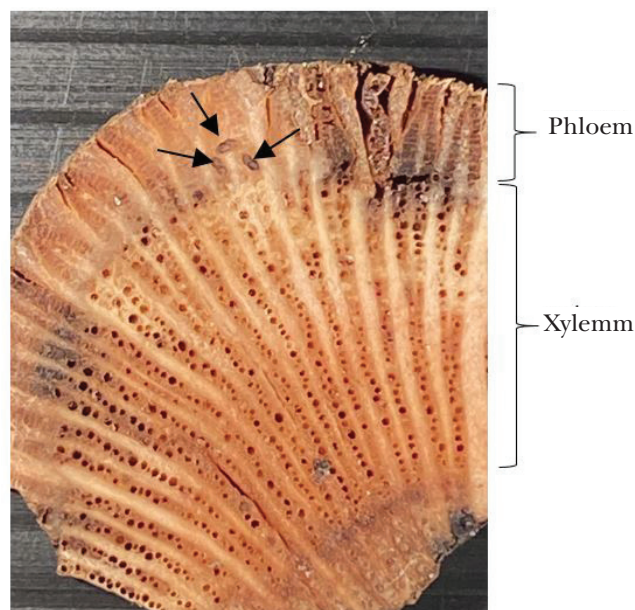


Figure 2 *Tetrastigma rafflesiae* cross-section of a stem with three seeds of *Rafflesia* (indicated by arrowheads) placed on the phloem for comparison of sizes.

The seed of *Rafflesia* (Figure 3) is bilobed, maturing 0.9 mm long in *R. arnoldii* (Brown 1834) *R. patma* (Meijer 1997) and *R. cantleyi* (Ng 2019), and ‘about 1mm long’ in *R. speciosa* (Molina et al. 2017). The seed coat is a single layer of large cells with rigid cell walls. Of the two lobes, the proximal one is the chalazal lobe (Ng 2019) because it is the swollen end of the funicle that connects the seed to the placenta. The distal lobe is what Brown called the nuclear lobe. The nuclear lobe contains the ‘nucleus’ of the seed, which I have named the Brownian nucleus. The Brownian nucleus is an ellipsoid body of about 40 turgid translucent cells enclosed within a thin tight-fitting transparent membrane. The Brownian nucleus remains translucent and turgid even after two months of seed storage at room temperature.

Experiments to germinate *Rafflesia* seeds have always failed (Nais 2001, Molina et al. 2017). I have placed seeds of *Rafflesia cantleyi* within incisions in the stems of *Tetrastigma rafflesiae* and after intervals of 4 to 14 days, I would dissect the stems to see what had happened to the seeds. Some seeds would have disappeared but most would still be intact. The Brownian nucleus is inert and appears to have no ability to emerge from the seed by itself. The first stage in the germination of a *Rafflesia* seed appears to be the disintegration of its seed coat by the host to release the Brownian nucleus. Next, the

membrane of the Brownian nucleus has to be disintegrated to release the cells that it contains. In microscope examinations of sections of the host plants, *Rafflesia* entities have been seen as short uniseriate strands or small clusters of cells with large nuclei, embedded among host tissues and cells, (Nikolov et al. 2014; Nikolov & Davis 2017). These would be cells of the Brownian nucleus released by dissolution of its nuclear membrane.

Mr. Abidin of Adenna Rafflesia Garden in Ranau, Sabah (*pers. comm.*, November 2023) says that he introduced a *Tetrastigma* plant that had been infected by *R. pricei* into his garden in the district of Poring where *R. pricei* does not occur. The transplanted *Tetrastigma* produced a new runner in his garden, and it was on the new runner that a *R. pricei* flower appeared. Hence Abidin thinks *Rafflesia* entities can move from one place to another in the stem of the host vine. Abidin’s opinion is supported by Wicasono et al (2017) who grafted a scion of *Tetrastigma* that had hosted *Rafflesia patma* onto an uninfected plant and found that new *Rafflesia* buds could emerge as far as 2 m from the point of grafting. Mursidawati et al. (2019), sectioned a piece of stem of a *Tetrastigma leucostaphylum* (*T. rafflesiae*) vine, located clusters of *Rafflesia* cells and hypothesized that these clusters can move through the vine by the activity of the cambial cells of the vine.



Figure 3 Seeds of *R. cantleyi* with three in longitudinal section showing their Brownian nuclei.

Abidin has successfully inoculated *Tetrastigma* hosts with seeds of *Rafflesia keithii* by making slits in the stem and introducing seeds of *Rafflesia* into each slit. He says it takes four to five years for *Rafflesia keithii* buds to become visible externally after seed-inoculation. Abidin's account is essentially the same as what Molina et al. (2017) learnt by interviewing the owners of another *Rafflesia* garden in Ranau but the time from inoculation to appearance of visible buds was given as two to seven years. To discover how such a cell cluster can move within the host that is already packed full with its own cells would present a great challenge for research. The long period of two to seven years between inoculation and the first external indication of a *Rafflesia* bud indicates that the rate of movement could be very slow.

The next stage is the development of protocorms. On naturally infected stems, it is

possible to locate small swellings that contain *Rafflesia* protocorms. In a freshly dissected specimen there is no visible boundary between the protocorm and the host tissue (Figure 4). The protocorm stands out only after about 12 hours when the tissues of the host have darkened presumably by differential oxidation (Figure 5). There is nothing that can be interpreted as a haustorium. Nevertheless, the union is so strong that it is impossible to detach a *Rafflesia* protocorm without destroying it. However, most of the protocorms are abortive (Figure 6).

Next, the protocorm develops into an embryo (Figure 7) that consists of a fleshy flat-topped body or 'podium' bearing a prominent central floral disc surrounded by a multilayered dome made up a 5-lobed perianth and about 20 bracts arranged in concentric circles. The floral disc, perianth, and bracts appear at the same time but because of the concentric arrangement,



Figure 4 A freshly cut stem of *Tetrastigma rafflesiae* 13mm wide containing a protocorm of *R. cantleyi*

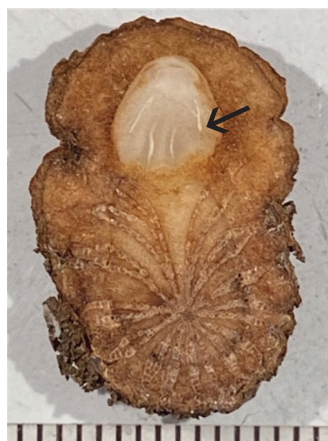


Figure 5 The same section as in Figure 6 after keeping overnight, with protocorm indicted by arrowhead



Figure 6 Protocorms of *Rafflesia* in various states of abortion except the intact one at the top left corner



Figure 7 Young bud with newly differentiated embryo. Left: external view of the bud with the bark surface forming polygonal patterns. Right: longitudinal section containing the *Rafflesia* embryo. Arrowhead shows the floral disc, overtopped by a dome made up of layers of perianth lobes and bracts

the central point would have been fixed first, followed by the other organs in centrifugal sequence. Up to this stage, *Rafflesia* is enclosed within its *Tetrastigma* host and is therefore completely endophytic. The surface of the bark (which is host tissue) is fractured into a pattern of polygons.

At the next stage, the top of the *Rafflesia* embryo emerges through the bark and the disc is seen to be the upper part of a short central reproductive column (Figure 8). In the male, the stamens form a circle of solid bodies under the rim of the disc. In the female (Figure 9) the stamens are replaced by a circular stigmatic surface.

The ovule-bearing structures are initiated as fissures in the upper half of the interior of the

podium (Figure 9 & 10). The walls of the fissures bear the ovules. It takes 10 – 17 months for an externally visible young bud to get to the stage of floral anthesis, with the exception *R. azlanii* that takes 40 – 50 days (see review in Ng 2023).

Figure 11 shows a 6 cm diam bud dissected to show the bracts ranging with the smallest (top left), to those that fit the current size of the bud, then the 5-lobed perianth (with corona) as a hemispherical dome, and the floral disc (bottom right).

The bracts and perianth mature in centripetal sequence, starting with outermost bracts and progressing inwards. The bracts act as fleshy cushions to provide protection. When the buds are small, the protective bracts are correspondingly small. As the bud enlarges,



Figure 8 Male bud 7 cm diam, with stamens indicated by arrowheads

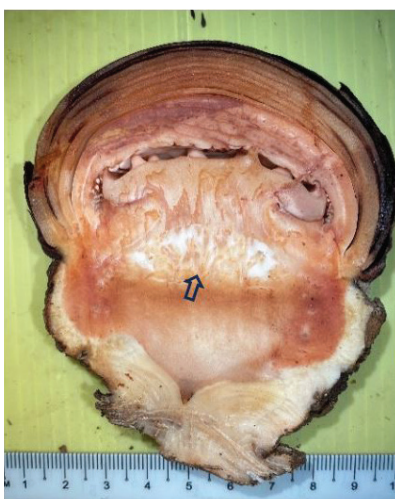


Figure 9 Female bud 7 cm diam with placental tissues (indicated by arrowhead) developing in the upper half of podium.



Figure 10 Ovule-bearing fissures (indicated by arrowheads) within the podium.



Figure 11 A dissected 6 cm diam bud of *Rafflesia cantleyi* showing the bracts, a dome made up the five-lobed perianth and corona, and the floral disk with rudimentary processes



Figure 12 An 18cm diam bud with flower bud beginning to emerging through the bracts



Figure 13 Dissected 18 cm bud showing the succession of bracts and the flower bud

the inner bracts expand while the outer bracts dry up and become brittle (Figure 12 & 13). Finally, the perianth emerges as a large ball dwarfing the bracts before opening to display the magnificent flower. The way in which the bracts take turns to cover and protect the growing bud is reminiscent of the way crabs and snakes change their skins to fit their expanding bodies but in *Rafflesia* the obsolete parts do not get shed. Instead they dry up *in situ*.

The main features of *Rafflesia* are illustrated in Ng (2019), which is accessible via <https://doi.org/10.26525/jtfs2019.31.3.286>.

Brown offered three interpretations of the stamen (Brown 1821) but was not satisfied with them. He wrote of the stamen that “... *in form and structure, it presents the most singular modification of the stamen that has yet been observed.*” Later, he was baffled by the pistil, uncertain about the location and form of the stigma, and unable to explain the ovary’s internal structure (Brown 1834). Several decades later, the stigma was identified by Solms-Laubach (1898) as a circular band of pollen-receptive tissue on the underside of the disc. In 2014 Nikolov et al. discovered that there are no carpels involved

in the development of the ovary. Nikolov *et al.* stated, “... *the Rafflesiaceae have evolved an alternative form of gynoecium development that has no equivalent in other angiosperms.*”

In angiosperms, the anthers and ovaries are interpreted as containers for pollen and ovules that have developed through evolution by the folding of bifacial structures (leaf-homologs) and fusion at their margins. In contrast, the stamens and ovary of *Rafflesia* are solid structures that become internally fissured to form spaces for the development of pollen or ovules.

The fruit

William Jack sent specimens of *Rafflesia* to Robert Brown and in his letter to Brown, reproduced in Brown (1821), he wrote “*The flower rots away not long after expansion and the seeds are mixed with the pulpy mass.*” Jack did not see any structure that he could recognize as a fruit. However, Brown discovered one fruit among the materials that had been sent to him by Raffles and described it as “*a compact fleshy mass having deep fissures on its surface...*”

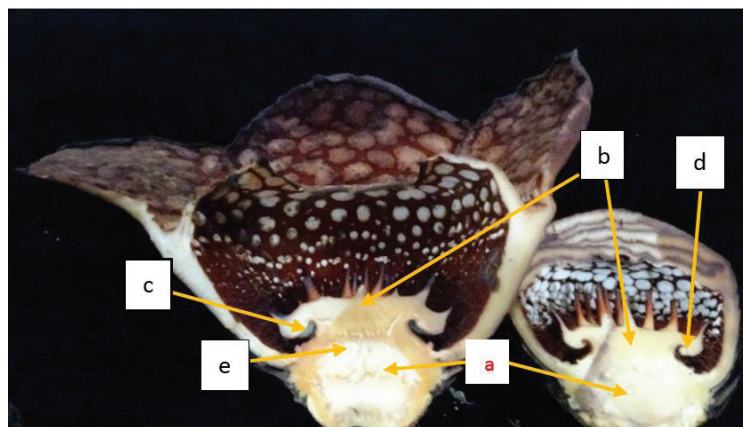


Figure 14 *Rafflesia cantleyi*. Left: section through female flower; Right: section of male bud. (a) podium (b) floral disc bearing processes, (c) stigmatic surface (d) stamen (e) interior of podium of female, filled with placentas and ovules



Figure 15 Decayed male flower of *R. keithii* with collapsed podium surrounded by decayed floral lobes

In *Rafflesia*, as the male flower decays after flowering, the podium collapses and leaves a hole (Figure 15). In the female, the podium becomes the fruit, which looks like a knob of decaying wood (Figure 16). The maturation of the seeds is supported by the internal tissues of the podium that remain alive while the external tissues of the podium die and decay. In contrast, an angiosperm fruit, developed from one or more carpels, has a living pericarp with a well-defined shape, able to resist decay, and to enlarge and develop color and scent but such features are lacking in the *Rafflesia* fruit. In Figure 17 the fruit is cut open to show the seed chamber occupying the top half of the podium, containing masses of tiny seeds attached to white placental tissues. For comparison, some seeds and capsular fruits of *Hevea brasiliensis*, a member of Euphorbiaceae, are included. The period from flower blooming to fruit ripening for *R. keithii* is about 6 months, according to Mr. Abidin of Adenna Rafflesia Garden.

When *Rafflesia* dies what remains is a soft lump of decayed tissue inside a strong and rigid cup-like receptacle. The receptacle is formed by the xylem and phloem of the host. In Figure 18 the upper piece shows how the xylem vessels are arranged to form the cup. The lower piece shows the corresponding layer of bark separated and flipped over. Arrow-head shows the remains of *Rafflesia*.

Rafflesia's closed plan of development

A phanerogam seedling characteristically has two apical meristems, one responsible for making a shoot system and the other for making a root system. When a seedling is activated, the apical meristems develop acropetally. This results in open-ended development. The shoot apical meristem produces a shoot to explore and occupy space for sunlight while the root apical meristem produces a root system (or haustorium in the case of parasitic plants but not *Rafflesia*) that serve to anchor the plant and explore for water and nutrients. From the large body of literature on phanerogam seeds and seedlings, including my own extensive studies on over 600 species in 86 families of angiosperms and gymnosperms (Ng 2014), phanerogams are characterized by seeds that produce seedlings

with apical meristems to drive open-ended development.

The alternative is a closed plan of development in which the size, shape and life-span of the organism is fixed and all the organs of the body are formed in an embryo. Animals characteristically have a closed plan of development. *Rafflesia* is unique among plants in having a closed plan of development in which all its organs are initiated in an embryo. The center is occupied by the flower while the bracts are in concentric circles around the flower. The various parts mature in centripetal sequence, starting with the outermost bracts and ending with the expansion of the perianth of the flower and the maturation of the pollen and ovules.

Why Rafflesia is not angiosperm nor phanerogam

The closed plan of development found in *Rafflesia* and other members of Rafflesiaceae makes *Rafflesia* and Rafflesiaceae different from phanerogams. Instead of a seedling equipped with apical meristems to grow, explore, and occupy space, the Brownian nucleus of the seed becomes a proembryonic entity consisting of a strand or cluster of cells that may be able move through the stem of its host before it gets fixed as a protocorm. Only after it is properly oriented and fixed can the protocorm develop into an embryo with its flower facing outwards. There are no cotyledons. In inoculation experiments, it takes at least two years for the *Rafflesia* bud to become visible externally. In form and behavior, the *Rafflesia* seed is totally different from a phanerogam seed.

The *Rafflesia* flower initiates the development of the plant because it occupies the central position of the embryo, but in angiosperms, the flower terminates the acropetal development of a shoot. The pollen and ovule-bearing cavities in *Rafflesia* arise as fissures within solid bodies, not by the folding of leaf-homologs to form chambers. The flower of *Rafflesia* is therefore analogous, not homologous with an angiosperm flower. The fruit lacks a pericarp and does not behave like an angiosperm fruit.

Contrary to the idea that *Rafflesia* lacks nearly all recognizable plant structures, *Rafflesia* has a full complement of recognisable plant



Figure 16 A fruit of *Rafflesia keithii* with rubber (*Hevea brasiliensis*) fruits and seeds (on a palm leaf) for comparison



Figure 17 The fruit of *R. keithii* cut in half, the upper half filled with tiny seeds attached to their placentas (indicated by arrowhead), compared with rubber (*Hevea*) fruits and seeds (placed on a palm leaf)



Figure 18 Cup-like receptacle formed by the *Tetrastigma* stem to accommodate a *Rafflesia* plant. Arrowhead shows remains of the *Rafflesia* plant

structures. It is the observer who chooses what to describe, what to ignore, and what to exaggerate. Among the exaggerated claims are the reported stench of rotting meat attracting carrion flies. We transported an open flower in a crowded car for a journey of many hours and detected no smell. We never found any fly maggots. Time lapse photography shows that the thick large perianth lobes display opening and closing movements (Fletcher & Bayliss, 2021). There are patches of luminous tissue on the inner walls of the corona surrounding processes of the disc that reflect white light against a background of dark tissues (Figure 14). We do not know their function nor the function of the processes that are illuminated by the white patches. As we discover more about *Rafflesia* it appears to represent a branch of evolution separate from angiosperms and phanerogams.

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