On a New Saprophytic Monocotyledon.

BY

PERCY GROOM, M.A., F.L.S.

—♦—
With Plate III.
—♦—

IN 1871 Beccari¹ described a Bornean plant under the name of *Petrosavia stellaris*; he referred the plant to the Melanthaceae, and mentioned that it was parasitic on roots. Later Mr. H. N. Ridley² discovered on the Malay Peninsula a very similar plant, which, without a minute examination of the flowers, seemed to be identical with *Petrosavia*. From his material I gave an account of the seed and embryo³. Recently Mr. Ridley was good enough to send me some more material of this plant with flowers. On investigating the flowers by means of microtome-sections, I found that the floral structure was very different from that assigned to *Petrosavia*. As none of Beccari's plants were available for examination, it seemed improper to assume that his description was imperfect: so a new name has been given to the plant—*Protolirion paradoxum*. Still Beccari's figures of *Petrosavia* agree closely with Mr. Ridley's plant; and if

¹ O. Beccari, *Petrosavia*, Nuovo Genere di Piante Parassite della Famiglia delle Melanthaceae. Nuov. Giorn. Bot. Ital. T. 3, 1871.

² H. N. Ridley, reprint from Proceed. Asiat. Soc. Singapore, Vol. xxiv, p. 170.

³ Percy Groom, Botanical Notes, No. 3, p. 380; Annals of Botany, Vol. vi. 1892.

[Annals of Botany, Vol. IX. No. XXXIII. March, 1895.]

Beccari's description be incorrect, the plant is doubtless merely another species of *Petrosavia*, the characters of which would require emendation. Hence any observations on the morphology and nature of *Petrosavia* are of interest.

Beccari described the plant as parasitic on roots. Now there are many saprophytes, devoid of chlorophyll, amongst Monocotyledons, represented by all the Triuridaceae, nearly all the Burmanniaceae, and many Orchidaceae¹. Dismissing the Corsieae, which are doubtless saprophytes, the remarkable fact becomes apparent that there is but one stated monocotyledonous parasite—*Petrosavia*. However, when it is borne in mind that for a long time botanists had failed to recognize the existence of many holosaprophytes, having assumed that those known were parasites, it would not be surprising to find that the same mistake had been made with regard to *Petrosavia*, especially as Beccari assumed that saprophytic Burmanniaceae and Triuridaceae were parasitic. So I asked Mr. Ridley if he would specially note whether or not the roots of his plant were connected with the roots of any other plants. In response Mr. Ridley pointed out the extreme difficulty in proving a negative when dealing with such fine roots, but he stated that he failed to detect any parasitic connexion. It may be stated at once that the histological evidence afforded by *Protolirion* goes to show that its ally *Petrosavia* is a saprophyte.

Beccari gave a brief description of the histology of the stem of *Petrosavia*. He says, 'Una sezione trasversale del caule presenta esternamente una parte corticale formata da 4-5 strati di cellule assai grandi, poi viene un intiero e largo anello di fibre liberiane che in circa 9 punti, discosti fra di loro, si cambiano in fasci fibrovascolari; il centro è ripieno da tessuto midollare molto lasso.'

¹ Mr. J. G. Baker has kindly directed my attention to a probably saprophytic Iridaceous plant from Madagascar—*Genosiris aphylla*, Baillon. Bull. Linn. Soc. Paris, No. 145.

EXTERNAL MORPHOLOGY.

The plant has a slender subterranean rhizome, closely beset with very small sheathing leaves (Fig. 1). From this rises up the simple scape which bears a corymbose raceme of flowers at its apex. Attached to the rhizome are the lengthened stumps of one or two older scapes; probably, then, *Protolirion* is a perennial. The successive scapes appear to arise in the axils of the lowest scales on the preceding scapes.

As the plant is entirely devoid of chlorophyll, all the leaves are reduced to small scales. On the rhizome and bases of the scapes they are sheathing and completely conceal the axis. Ascending the scape, the scales gradually become separated by longer internodes, lose their sheathing bases, and assume a longer and more slender form (Figs. 1, 2).

Long, delicate roots, very feebly branched, spring from the rhizome, and particularly from the base of the scape. (In Fig. 1 all the roots except the lowest two arise from the flowering axis.)

HISTOLOGY.

1. *The Root.*

I had very few intact roots at my disposal, in fact only some of those shown in Fig. 1. For the most part the terminal portions had been broken off. In the single apex investigated there were remains of a *root-cap*. Although the pieces of uninjured roots were of considerable length, there were *no traces of haustoria*.

(1) The root is clothed externally by a single layer of cells with thin walls which represents the piliferous layer. There are *no root-hairs*. This layer soon becomes disintegrated and replaced functionally by—

(2) The *exodermis*, which takes the form of a single layer of cells with thin suberized walls. No passage-cells were to be seen. This layer is succeeded by—

(3) Four to five layers of cortical parenchyma the cells of which have walls of cellulose. Most of these cells contained *coiled mycorrhizal hyphae*, even so far as the endodermis.

The central cylinder is very small.

(4) The *endodermis* forms a characteristic layer of cells of the C-type with greatly thickened, stratified, and suberized inner walls (Fig. 5). The cells are elongated in the direction of the long axis of the root. There are no passage-cells; and it is obvious that liquids cannot pass easily into the central cylinder from the parenchymatous cortex.

(5) The *pericycle* forms a single well-defined layer of longitudinally elongated cells with lignified walls of average thickness. In longitudinal sections the nuclei are seen not to be elongated longitudinally, but more or less square.

With the meagre supply of material, it was difficult to establish any clear facts as to the arrangement and differentiation of the narrow constituents lying within the pericycle.

(6) *Phloëm* (?). In transverse sections, at about four points, there were minute groups, each including three to four very narrow cells with thin walls of cellulose (Fig. 5, *ph*). They were all elongated longitudinally; and some, at least, possessed very long strap-like nuclei. I did not succeed in detecting sieve-tubes.

Excepting these phloëm-cells(?) all the remaining tissue within the pericycle is lignified.

(7) *Xylem*. There are clearly marked conducting constituents represented by narrow tracheides with oval or slit-like bordered pits, or loose reticulate thickenings. Fig. 5 shows that midway between the supposed groups of phloëm, the cells abutting on the pericycle are smaller and more isodiametral than the cells contiguous to the phloëm(?); they probably represent the small outer extremities of the rudimentary radial groups of xylem: for in longitudinal sections tracheides are seen in direct contact with the pericycle, as are also cells with oval nuclei.

(8) The larger central cells, with lignified, simply pitted walls, have nuclei and are elongated longitudinally and represent the conjunctive tissue.

II. *The Stem*—A. *The Rhizome.*

(1) The *epidermis* consists of elongated cells with fairly thin walls and a distinct cuticle. *No stomata occur.*

(2) It is succeeded by about four layers of *cortical parenchyma*, the cells of which have thin pitted cellulose-walls. Within lies—

(3) A *general sclerenchyma-sheath* about four cells in thickness. The cells composing it are sclerenchymatous fibres. The outermost layer is tolerably regular and simulates the endodermis of the root. The remaining three layers of cells have evenly thickened pitted walls, and possess only small lumina.

(4) The *vascular bundles* are arranged close within the general sheath and are numerous.

Each full-sized vascular bundle is still small but possesses well-marked phloëm- and xylem-portions (Fig. 6).

The *phloëm* is constituted of narrow sieve-tubes with transverse plates, and elongated parenchyma-cells in which no differentiation of companion-cells was visible.

The *xylem* has long tracheides with transverse pits, fibres, and a protoxylem of a few narrow loose spiral vessels about which lie elongated narrow parenchyma having thin walls, with wide shallow pits. The intercellular spaces around the spiral vessels are very small.

(5) The *pith* consists of broad parenchymatous cells with thin pitted lignified walls. The cells are elongated in the direction of the axis. The conjunctive tissue connecting the pith with the general sheath is constituted of cells which gradually change from the typical pith-cells to sclerenchyma-fibres as they approach the sheath.

B. *The Scape.*

The structure of other parts of the stem is in all essentials identical with that of the rhizome. Ascending the axis, the cells decrease in size and number. The outermost layer of the general sheath loses its likeness to the endodermis, and as the leaves decrease in number the vascular bundles naturally become fewer.

Close under the flowers the axis is triangular in cross-section. The cortical layers are reduced to two or three in number. The general sheath is triangular also in the section, and two to three layers in thickness. Within the three angles of the sheath are three pairs of larger bundles, the bundles lying within the sides of the triangle being smaller.

III. *The Leaf* (Fig. 7).

The leaves are more or less closely pressed against the axis.

Each consists of a lower (outer) and an upper (inner) epidermis, with a certain amount of undifferentiated mesophyll in which runs the single vascular strand which enters the leaf.

The *epidermis* consists of typical cells, and towards the margins its two layers compose the whole thickness of the leaf. *Stomata* occur only in the lower (outer) epidermis, and solely in that portion which covers the midrib.

The *mesophyll* forms a sheath round the vascular strand in the midrib, and suddenly thins off towards each side. So that the greater part of the leaf consists simply of two layers of epidermis with here and there a single or double layer of mesophyll-cells. The walls of all the mesophyll-cells are thin but lignified, excepting in the immediate neighbourhood of the midrib, where the walls consist of cellulose.

The cells in the outer (lower) half of the leaf in this region contain excreta, especially in the form of raphides enclosed in mucilage. The adjacent parts of the axis may be quite devoid of raphides. This recalls the same distribution in

some holosaprophytic Orchids¹, and further suggests that the scales function as excretory organs. The occurrence of stomata also in the same Orchids seems to imply that the leaves function as organs by which any excess of water is excreted.

The *vascular strand* has an incomplete and rudimentary sclerenchymatous sheath which is more strongly developed on the lower (outer) side. It is composed of *phloëm* with sieve-tubes and much parenchyma, and *xylem* with a few narrow spiral tracheides, and a considerable quantity of elongated parenchyma with thin cellulose-walls.

IV. *The Inflorescence and Flowers.*

The flowers are arranged in a corymbose raceme (Fig. 3). In my specimens there were never more than four flowers on one scape. The flowers are actinomorphic, hermaphrodite, and regularly trimerous (Fig. 4).

The *perianth* is composed of two whorls of three segments each. The free portions of the outer three are narrow, and are open in aestivation. The free portions of the inner whorl are much broader and larger, and are valvate in aestivation. The lower portion of the perianth is adnate to the wall of the ovary. In the case of both whorls of the perianth, just below their entirely free portions their margins are distinct and separate from one another, but their inner (upper) faces are fused with the wall of the ovary (Figs. *f, h*). This interesting case is sufficient to prove that, in this instance at any rate, *the wall of the inferior portion of the ovary is partially formed by the perianth*, and that it is not composed simply of the original carpellary tissue together with an adherent excavated receptacle.

The three smaller segments become entirely free at a lower level than do the three broader, and are attached lower down. They therefore represent the outer whorl.

¹ Percy Groom, Contributions to the Knowledge of Monocotyledonous Saprophytes. Read before the Linnæan Society, Dec. 20, 1894.

Androecium. There are two trimerous whorls of stamens, the anthers of which are basifixed, sub-introrse (in the bud condition), and have four pollen-sacs each. Those which represent the *outer whorl* are opposite to the three outer segments of the perianth, and are *inserted on the wall of the ovary*, at a lower level than the *three inner stamens*, which are *inserted on the bases of the inner segments of the perianth* (Figs. *b, c, h, k*).

Gynaecium. The pistil is remarkable in at once showing a transition from an apocarpous to a syncarpous type, and from a free to an adnate ovary. The lower portion of the ovary is inferior, trilocular, with two double rows of horizontal anatropous ovules attached to the axile placentae (Figs. *a-k*).

Above, the ovary separates into three distinct ovuliferous follicle-like portions which gradually pass into three short styles capped by papillose capitate stigmas (Figs. *a, b, c, l*).

Nectaries (Figs. *b, c, e-h*). There are three septal nectaries which open opposite the segments of the inner whorl of the perianth, slightly above the highest point at which the latter are coherent to the wall of the ovary. They are three simple unbranched sacs, extended radially, and reaching down not quite so far as the chambers of the ovary. They are lined by a single layer of palisade-like secreting cells, which have densely staining contents and conspicuous nuclei. The cuticle of these cells is raised even in the bud-condition of the flower. No mechanical cells strengthen the nectariferous tissue.

Fruit. The free portions of the gynaecium dehisce like three follicles, and allow the escape of the seeds from the lower part of the ovary also.

Seeds. These were described under the name of *Petro-savia*¹: they are ribbed, albuminous, and with a very minute undifferentiated embryo.

¹ Percy Groom, loc. cit.

GENERAL REMARKS ON PROTOLIRION.

A. *Vegetative Structure.*

The structure of the roots tends to show that *Protolirion* is not a parasite. No connexion between them and other plants could ever be seen, nor any trace of the existence of haustoria. On the other hand, the root structurally agrees with that of a saprophyte (cp. Burmanniaceae; *Triuris* and some species of *Sciaphila*; Gentianaceae) in the following points: (1) absence of root-hairs, (2) presence of a well-developed cortex, containing endotrophic mycorrhiza, (3) small size of the central cylinder, and the minuteness of the vessels. The whole central cylinder of these relatively long roots is less in size than is one single fair-sized vascular bundle of the rhizome, which suggests, not conduction of nutritive solutions along the cylinder, but a general absorption taking place over the whole surface of the root.

B. *Flowers.*

Beccari gives the following generic characters as characteristic of *Petrosavia*, and I have italicised those which do not agree with *Protolirion*: 'Perigonium trigonum 6-partitum, persistens coloratum, *inferum*, phyllis inaequalibus, 3 exter. minoribus angustioribus basi omnibus connatis. Stamina 6, phyllis opposita et *eorum basi inserta*: filamenta subulata; antherae biloculares apici acutiusculae basi bilobae, basifissae, introrsae. *Ovaria tria*, perigoni phyllis angustioribus opposita, *ex ima basi libera* sessilia follicularia erecta; *stigmata sessilia vix incrassata*, papillosa; ovula horizontalia, anatropa, placentis 2, latis, marginalibus et ventralibus bi-triseriatim adfixa. Fructus trifollicularis, folliculis siccis, horizontalibus, sutura ventrali hiantibus Prae-floratio valvaris.' The rest of the description agrees, as far as it goes, with the parts represented in *Protolirion*.

The peculiar transitional state of the gynaecium (apocarpous, adnate-free) is of interest. From this it is impossible to form any idea as to the affinity of the plant. Beccari placed *Petrosavia* amongst the Liliaceae which typically have separate styles and often follicular fruits (old order Melanthaceae). *Protolirion* is still more like such forms as the Veratreae and Tofieldieae, in that the pistil is not completely apocarpous. In the Veratreae there are forms with half-adnate ovaries (*Stenanthium* and *Anticlea*).

The structure of the wall of the adnate portion of the ovary shows that the adnation is in this case caused by actual fusion of the floral whorls with the wall of the originally free ovary. The free basal margins of the adnate portions of the perianth further suggest that the plant is derived from forms with superior ovaries rather than a degenerate type of some family of plants with inferior ovaries.

Protolirion agrees in habit and structure of its seeds with Triuridaceae and Burmanniaceae; and it is interesting to note that it stands midway between them in the character of its gynaecium. This coincidence is the more striking when it is remembered that some systematists (Eichler and others) view the Burmanniaceae as forms lying between the Liliaceae-Amaryllidaceae and the gynandrous family Orchidaceae. In *Protolirion* there is a commencement of the gynandrous condition, for the three outer stamens are attached to the wall of the ovary.

The occurrence of septal glands collaterally throws light on the affinities of *Protolirion*. Such nectaries are known only in the Monocotyledons, and solely in Liliaceae, Haemodoraceae, Iridaceae, Amaryllidaceae, Bromeliaceae, and Scitamineae¹. As we cannot judge the affinities of *Protolirion* by its embryo, and the absence of a cambium might be merely a degenerative change, there would be nothing to prove that *Protolirion* was not a trimerous Dicotyledon. But the presence of septal glands, with monocotyledonous floral characters,

¹ Grassmann, Flora, 1884, pp. 113-134.

makes it certain that the plant is a Monocotyledon. Septal glands are not present in the flowers of all the genera in the families mentioned ; as far as observation has gone they are notably absent from those Liliaceae which have three styles or a branched style (Melanthaceae). So the apocarpous condition of the upper portion of the pistil of *Protolirion* may be a partial reversion from syncarpy to apocarpy, associated with the peculiar habit of the plant (cp. modified flowers of parasites amongst Dicotyledons).

Affinities of Protolirion. It is difficult to decide where to place this simple form. On the one hand its incipient gynandry may be but an unimportant and casual factor, which will be found to recur in some other forms which have a half-inferior ovary. Yet it may be of deeper significance in suggesting that the Orchidaceae are more closely allied to plants with a superior ovary than to forms with an inferior ovary—in particular that they were derived rather from the Liliaceae than from the Amaryllidaceae. In habit, structure of the seed (no doubt partially the effect of its saprophytism), and in the partially apocarpous condition of its pistil, *Protolirion* vividly recalls the Triuridaceae. The latter have diclinous flowers, and indefinite one-ovulate separate carpels : but though diclinous, rudiments of the gynaecium and the stamens are frequently present in the male and female flowers respectively. And dicliny appears in the Liliaceae, particularly in the Veratreae, some of which are polygamous. So no great stress can be laid on this difference. The distinction as regards number of carpels, their structure and ovulation, finds analogies in Ranunculaceae and Nymphaeaceae : and the semi-adnation is repeated in syncarpous Veratreae.

But the flowers, fruits, and seeds of *Protolirion* taken together resemble those of the Veratreae, and particularly the Tofieldieae, more than they do those of any other plants.

So *Protolirion* may be regarded as closely related to the archetype of the Liliaceae, and connecting the modern Liliaceae with the Triuridaceae. The transition between

these two families is even more completely illustrated if *Petrosavia* has indeed an apocarpous pistil; and one would feel inclined, in spite of its monocliny, eumery, and multi-ovulate carpels, to include *Petrosavia* in the Triuridaceae.

This investigation has been carried out in the Botanical Laboratory of the University of Oxford, and I desire to express my appreciation of the facilities which have been placed at my disposal.

Mr. H. N. Ridley has been good enough to prepare the following technical description of the plant, based on observations of his own as well as on mine, and to append a brief note:—

Protolirion, gen. nov.

Herba saprophytica parva perennis, omnino pallide ocreo-flava, rhizomate gracili sublignoso 1–3 pollices longo, 1 mm. crasso. *Caules* 1–7 laterales erecti graciles teretes saepe flexuosi. *Folia* squamiformia, ad basin caulis congesta, superne remota, inferiora 2 mm. longa, vaginis teretibus oribus integris, laminis lanceolatis obtusis caule appressis, carinatis; superiora vaginis multo brevioribus internodia 5 mm. longa haud tegentibus, laminis angustioribus acuminatis acutis $3\frac{1}{4}$ mm. longis. *Racemus* corymbiformis ad sexflorus. *Flores* parvi flavi patentes, pedicellis 10 mm. longis suberectis. *Bracteae* singulae lanceolatae obtusae bifidae. *Sepala* anguste linearia-lanceolata acuminata parva. *Petala* majora ovata obtusa alterna. *Stamina* 6, tria epigyna, tria epipetala, petalis breviora, filamentis teretibus crassiusculis superne attenuatis, antheris oblongis basifixis loculis ad basin divergentibus, in marginibus dehiscentibus. *Nectaria* tria petalis opposita. *Pistillum* basi inferiore perianthio adnato syncarpo, superne superius liberum, apocarpum, carpellis 3 distinctis patentibus follicularibus in stylis brevibus attenuatis stigmatibus capitatis papillois. *Placentatio* axillaris. *Ovula* in seriebus duabus anatropa. *Capsulae* ovoideae recurvae patentes in margine superiore dehiscentes. *Semina* in carpello utroque 12 elliptico-

oblonga nodulosa brunnea albuminosa, embryo minuta. Alabastra ovoidea, praeefloratione valvata.

Sp. unicum, *P. paradoxum*.

Loc., Malay Peninsula, in dry hill woods at an altitude of from 1,000 to 3,000 feet on the Larut Hills, Perak, and on Kedah Peak in Kedah. Coll. H. N. Ridley.

I published a short account of this plant in the Journal of the Straits branch of the Royal Asiatic Society, No. xxiv, pp. 170-2 (dated 1891), under the name of *Petrosavia*, thinking at the time it was identical with the plant described under this name by Beccari. Beccari's plant, however, though in many respects resembling this, is in some most important details very distinct, as shown in the preceding remarks by Mr. Groom. It is very difficult to refer *Protolirion* to any order; possibly it is most nearly allied to Triurideae.

H. N. RIDLEY.

EXPLANATION OF FIGURES IN PLATE III.

Illustrating Mr. Groom's paper on *Protolirion*.

p^1 = outer perianth-segments. p^2 = inner perianth-segments. s^1 = outer stamens. s^2 = inner stamens. sg = stigma.

Fig. 1. Whole plant. ($\times 3$. Winkel.) $m.a.$ = main axis. a'' = axis on $m.a.$ a''' = axis arising on a'' .

Fig. 2. Portion of the scape above ground. ($\times 15$. Winkel.)

Fig. 3. Inflorescence. ($\times 5$. Winkel.)

Fig. 4. Flower, after fertilization of the ovules. ($\times 15$. Winkel.)

Fig. 5. Transverse section of portion of central cylinder of root. (Zeiss $\frac{1}{2}$ immers. Oc. 2). ph = phloëm (?). xy = xylem-rays (?). end = endodermis. pc = pericycle.

Fig. 6. Transverse section of a vascular bundle and portion of the general sheath of rhizome. (Zeiss 3. DD.) $g.s.$ = general sheath. ph = phloëm. px = protoxylem. Arrow points radially inward.

Fig. 7. Transverse section of leaf embracing rhizome. ($\times 9$. Winkel.)

Figs. a, b, c . Longitudinal sections of flower. ($\times 20$. Winkel.)

Figs. $d-l$. Transverse sections of flower. n = nectary.

58 *Groom.—On a New Saprophytic Monocotyledon.*

Fig. *d.* Through the base of flower, showing loculi of ovary. ($\times 25$.)

Fig. *e.* Higher up showing septal glands, loculi of ovary, and vascular bundles. ($\times 25$.)

Fig. *f.* Higher than *e*, shows commencement of outer perianth. ($\times 25$.)

Fig. *g.* Higher than *f*, shows outer perianth free from ovary-wall. ($\times 25$.)

Fig. *h.* Higher than *g*, shows inner perianth, and outer stamens appearing. ($\times 20$.)

Fig. *k.* Higher than *h*, shows both perianth whorls free, outer stamens free, and inner stamens appearing, nectaries disappeared, and carpels commencing to be distinct from one another. ($\times 25$.)

Fig. *l.* Section high up flower, through three styles. ($\times 25$.)

Groom del.

Groom del.

GROOM.-ON A NEW SAPROPHYTIC MONOCOTYLEDON.

University Press, Oxford.

Groom, Percy. 1895. "On a new saprophytic monocotyledon." *Annals of botany* 9, 45–58. <https://doi.org/10.1093/oxfordjournals.aob.a090733>.

View This Item Online: <https://www.biodiversitylibrary.org/item/233478>

DOI: <https://doi.org/10.1093/oxfordjournals.aob.a090733>

Permalink: <https://www.biodiversitylibrary.org/partpdf/318365>

Holding Institution

Smithsonian Libraries

Sponsored by

Biodiversity Heritage Library

Copyright & Reuse

Copyright Status: Not in copyright. The BHL knows of no copyright restrictions on this item.

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>.