XVI.—Moultonia: a New Bornean Gesneraceous Genus.

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We have published recently* an account of a new Gesneraceous genus *Moultonia* discovered last year in Sarawak, Borneo, by Mr. J. C. Moulton, Curator of the Sarawak Museum. The genus presents interesting morphological features, the explanation of which is not yet complete. The dried specimens of the plant hitherto available are inadequate; observations on its habitat, on its vegetative development, on its fruit-structure and especially on the development of its seedling are very much desired. Consequently we gladly accept the opportunity offered by Mr. Moulton of giving the following short notice of the plant and its peculiarities in the Journal of the Sarawak Museum, in the hope that it may guide residents in Borneo who may be willing to help forward the investigation by sending further material or notes of observations on the spot and especially by securing seed. We also give a figure † of a sheet of a dried specimen of the plant, which may be an aid to its identification in the field and will show also how fragmentary is the material as yet received of a type of vegetation which presents inviting problems to both botanist and gardener.

We give first of all a botanical account of the plant so far as we know it and then a summary of the problems which it is hoped residents in Borneo will aid in solving.

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* Notes Roy. Bot. Gard. Edin. xl. p. 349, March, 1915.

† The figure is reproduced by permission from our paper in Notes Roy. Bot. Gard. Edin. xl., in which it first appeared.

Moultonia singularis, Balf. fil. et W. W. Sm.

A stout herbaceous plant with a single leaf; stem above ground none; petiole 30–40 cm. long, 1 cm. or more in diameter, striate, with a limy scurf over the whole surface, channelled above and bearing flowers in the channel; the lamina of the leaf 30–35 cm. long, 20–30 cm. broad, ovate or oblong-ovate with cordate base (apex not seen), entire, in the living state no doubt fleshy, above dark green glabrous, below covered with a rough limy scurf; midrib channelled above bearing numerous flowers throughout almost its whole length, below showing a stout projecting ridge 5 mm. broad or more; the primary nerves 20–30, very conspicuous and sub-parallel, 1–3 cm. distant from one another, given off from the midrib at a right angle and much bent on approaching the margin. Peduncles very short, 1–3-flowered; pedicels 3–4 mm. long, lengthened in fruit to 1 cm., covered with a limy scurf; bracts and bracteoles very small, only about 1 mm. long and somewhat fleshy. Flowers small, arising in the furrow of the petiole and in the furrow of the midrib, forming an almost continuous line. Calyx bell-shaped about 4 mm. long, slightly enlarged in fruit, deeply 4-cleft; lobes slightly imbricate, erect, closely appressed in fruit, oblong, more or less obtuse with membranous margins, on the outside with limy scurf, on the inside with a definite limy cushion. Corolla small (no fully developed specimens available for examination); tube short, limb bifid, the posterior lip bifid, the anterior lip (seen only in the bud) undivided, but in the developed flower this lip will probably be trifid. Perfect stamens 4, sub-equal, about 1 mm. long inserted in the middle of the tube; filaments dark coloured, glabrous, about $\frac{1}{2}$ mm. long; anthers all cohering laterally, in shape reniform or almost ear-shaped, scarcely 1 mm. in diameter. Disc cup-shaped, reaching almost to the middle of the ovary. Ovary superior, globose, with a linear style a little longer than the ovary and a small truncate stigma. The lower and seed-bearing half of the mature fruit globose, about $1\frac{1}{2}$ mm. in diameter, with its walls membranous and easily broken, apparently scattering its seeds by an irregular transverse rupture; the upper part of the capsule forming a narrow cone suggesting somewhat the top of a moss capsule, about 4 mm. long and at the base about 1 mm. broad, solid, and at maturity protruding a little from the enclosing segments of the calyx. Seeds very numerous, ovoid or rounded or sometimes more or less quadrate and

angular, of a dark brown tint with an areolate seed-coat; they are scarcely ¼ mm. in length.

Obtained by a native collector, working under Mr. J. C. Moulton's supervision, from near Sudan in the State of Sarawak, in February, 1914.

For those to whom botanical terms may present difficulty, the important characters which will aid (apart from the figure) in their search for the plant are:—A stout herb with no apparent stem, a single large leaf 1 foot or more in diameter with a stout stalk at least 1 foot long, and, most characteristic of all, with numerous small flowers attached to the furrow of the leaf-stalk and to the furrow of the midrib of the blade. The plant is so unique in these characters that its recognition is easy. It is, in all probability, a shade-plant in wet forest.

We have described this plant as possessing a single leaf with a leaf-petiole and epiphyllous inflorescence, and the dried material at our disposal sanctions no other course. If we follow convention in this we by no means intend thereby to express our view of the morphological value of the vegetative parts described. The plant seems to us to have special interest from the morphological side, but the true explanation of its parts can only be arrived at by an investigation of the living plant. Meanwhile we may give here the morphological interpretation which appears to us as probably the right one of the parts as we know them.

We suggest that the stalk and broad lamina are the parts of an outgrowth from the primitive protocorm of the plant—the stalk being hypocotyl, the lamina cotyledon—which it will not surprise us to learn has no other vegetative organs. From this protocormic outgrowth which possesses great meristematic activity the flowers arise. The whole construction of *Moultonia* is to us that of a plant showing a permanently embryonic vegetative state.

Let us clearly understand what this means.

Of the egg, out of which every angiospermous plant develops, one-half is devoted to the formation of a body of meristem-cells which is the primitive corm—protocorm—of a future plant; to the other half which forms the suspensor is assigned the primary duty of regulating the position of the protocorm within the seed and of aiding in the feeding of it. The whole product of the egg—suspensor and protocorm—is commonly known as the proembryo,

and is adapted to the intraseminal phase of life of the organism preceding the period of rest incidental to the seed habit. The degree to which development proceeds up to rest varies. As a minimum the suspensor may be no more than a single cell and the protocorm an undifferentiated body of a few meristem-cells. More advanced the suspensor may be pluricellular, even massive, with haustorial outgrowths penetrating far in search of food, and likewise the protocorm becomes a body with haustorial extension in the form of lobes (one in Monocotyledons, two in Dicotyledons)—the cotyledon; so that there is differentiation into a central mass—hypocotyl—and cotyledon one or more. This may be all. But in more advanced states—and these are perhaps the more usual—a primordium of the hypogeous axis of the mature plant is laid down at the basal end of the protocorm as the primary root, and a primordium of the epigeous axis is laid down—at the apical end of the protocorm when there are two or more lateral cotyledons, at the side when there is one terminal one—as the plumular bud. There may be several such primordia. What has to be emphasised here is that the ordinary angiospermous plant, as we see it, is the product of two primordia arising out of the protocorm. The protocorm is the embryonic stage. The root and shoot of the plant are the mature stage. In the former, potential meristematic activity is spread through the whole protocorm, and this is very different from the restricted meristematic activity that is found in the epicotylar shoot. In most Angiosperms the embryonic protocorm, shedding its haustorial cotyledons after they have performed their function during transition of the organism from intraseminal to extraseminal life, loses individuality in its fate as connecting link betwixt the root and shoot of the mature plant.

In the light of what we have just said, we suggest that *Moultonia* is one of those plants which never goes beyond the stage of the protocorm. It never forms primordia of primary root or plumular bud. The vegetative apparatus—long-stalked lamina—is a primitive outgrowth, become assimilating, of the protocorm. That it will have at its base many adventitious absorbing roots we expect, though our material gives no indication of them. The laminar portion we take to be cotyledon. Probably the stalk part of it may be less cotyledon than hypocotyl, but of that we can say nothing definite. We are more certain of the correctness of the suggestion we make that this outgrowth

is persistently meristematic throughout, and in the mid-line of its upper surface at least, for it is there that the flower-buds arise in linear series but not in age sequence from below upwards or from above downwards. Young and old are intermingled throughout the length.*

It may be asked what are the grounds upon which we base the views expressed above. We will explain.

To do this we recall the well-known features of germination exhibited by other genera of Gesneraceæ. Let us begin with *Streptocarpus*.† Taking in the first instance *S. polyanthus*, Hook., we find within its seed at the period when it is ripe the protocorm of the embryo as an elongated ovoid body showing towards the apical end two lateral outgrowths of equal size—the cotyledons. There is no trace of a primordium of a primary root, nor of a plumular bud, and there never is. When germination takes place, the whole surface of the protocorm becomes covered with absorptive hairs. One of the cotyledons is arrested in growth, the other elongates and growing rapidly by basal intercalary growth forms in time a broad green lamina without stalk. Soon a series of adventitious roots develop from the hypocotyl and also from the cotyledon base. The top of the hypocotyl where the cotyledons are does not in this species show much growth in length, and the cotyledons remain about the same level. Soon the smaller

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* A cotyledon is often like a leaf in its later stages of life, and is perhaps most commonly spoken of as a leaf. But a leaf is an organ of the epicotylar axis proceeding from the plumular bud. The leaf arises as a lateral structure from one of its nodes. A cotyledon as an extension of the embryonic protocorm may proceed from the end of the protocorm or from its sides, and does not present in its evolution the fundamental criteria required by the foundations of morphology for being reckoned the homologue of an epicotylar leaf. Entering this caveat, we are content in our systematic description to speak of the vegetative body of *Moultonia* as a leaf with a petiole and having epiphyllous inflorescence.

† Crocker, "Notes on Germination of Certain Species of Cyrtandreæ" in Journ. Linn. Soc. v. (1861), 65, t. iv.; Dickie, "Note of Observations and Experiments in Germination" in Journ. Linn. Soc. ix. (1867), 126; Dickson, "On the Germination of *Streptocarpus caulescens*" in Trans. Bot. Soc. Edin. xiv. (1883), 362, pl. xiv.; Hielscher, "Anatomie und Biologie der Gattung Streptocarpus" in Cohn's Beiträge iii. (1883), 1, tt. i.–iii.; Fritsch, "Ueber die Entwicklung des Gesneraceen" in Ber. d. deutsch. Bot. Gesellsch. (Gen. Versamml.) xii. (1894), 26.

Crocker was foreman of the Propagation Department, Royal Gardens, Kew, and was the first to record the features of germination of *Streptocarpus*. His observations were exact, and he distinctly states that there is an absence of all trace of plumule. His figures found their way into the botanical text-books of the period. We mention this because his work, as well as that of Dickie and Dickson, is ignored by Hielscher, who is quoted in most modern German books as if he were the observer who first made known the facts.

arrested one withers and dies off, so that the whole vegetative organisation of the plant is an enlarged green cotyledon with a basal portion of hypocotyl and adventitious rootlets. Year by year the intercalary growth of the cotyledon proceeds and further rootlets are formed. That is the whole mature vegetative plant. If at an early period the enlarging cotyledon be removed, the arrested one opposite to it on the protocorm may develop into the same form. Here there is never a vegetative epicotyl, never a primary root. The vegetative body is a persistently growing extension of the embryonic state. A like explanation covers the case of *Lemna* amongst Monocotyls—only there the embryonic form repeats itself in successive branchings.

This is the type of what in systematic works is named the "Unifoliate" Streptocarpi.

At flowering period the inflorescence takes origin in the hypocotyl within the sinus at the base of the enlarged cotyledon, and develops a scapose axis or scapose axes with many flowers in biparous cymose branching. It never spreads over the laminar area. Meristematic activity seems to be located in the hypocotyl at the base of the cotyledonary lamina. How exactly the flower-axis arises has not been really observed in this species. We do not yet know whether the apex of the hypocotyl forms a primordium which can be interpreted as a postponed plumular bud with destiny of flower production only, or whether the origin of the inflorescence is spread over a wider linear or broader area of the hypocotyl. The figure of *Acanthonema strigosum*, Hook. f., in the *Botanical Magazine* (1862), t. 5339, indicates a like history of development in that species.

Take now the case of *S. Rexii*, Lindl., as described by Dickie (with which that of *S. primuloides*, Dickie, conforms). Here the development starts as in the preceding case, but the top of the hypocotyl on the side next and below one of the cotyledons grows out for a short distance so that the two cotyledons are separated by a length of hypocotyl. The cotyledon left behind is the arrested one. The other enlarges, and a cursory examination of a seedling at this stage might suggest the presence of two cotyledons: one sessile small, and one petiolate large. The apparent petiole—and it is so called by Hielscher—is really the hypocotyl. When *S. Rexii*, Lindl., flowers it forms one-flowered scapes, and these take origin close to the sinus of the cotyledonary lamina from the hypocotyl

meristem tissue in a "simple tangential row." Here we have the case of *S. polyanthus* over again, only that the elongation of the hypocotyl has created the appearance of a petiole, and so the flower-axis seems to come from where an apparent petiole joins a lamina. This is not all, however. In *S. Rexii*, Lindl., there appears at the cotyledonary sinus a cluster of stalked leaf-like structures. These form a sort of rosette and are characteristic of the "Rosulate" Streptocarpi. The published accounts of their origin are vague in terms, and their relation to the inflorescence is not clear. They are said to come off alternately from a whole series of centres, whilst the inflorescences are developed in a simple basifugal row. We are in no better case here than with *S. polyanthus*, Hook., for the determination of the morphological relationship of these later vegetative structures and of the inflorescence to the protocorm. All we can recognise is that there is a vegetative organisation superposed upon the condition that is permanent in *S. polyanthus*, Hook. For its reconciliation with normal plumular development further investigation is required.

Then we have a state of further differentiation in *S. caulescens*, Vatke, as Dickson showed, typical of the whole series of "Streptocarpi Caulescentes." Here the same general lines of early development of the protocorm are followed, and there is an elongation of the hypocotyl between the cotyledons, the upper of which is the larger. This upper cotyledon does not reach extravagant size; it has quite the appearance of a petiolate cotyledon coming off from the hypocotyl. From the hypocotyl and in apparent upward continuation of it ascends an axis like an ordinary epicotylar noded axis bearing foliage-leaves which are like the larger cotyledon in form. How this axis arises, if from a plumular bud or no, is not described. Its appearance suggests such normal evolution as occurs in many other Gesneraceæ.

The suggestions conveyed in the construction of these Streptocarpi have led us to the interpretation we have predicated for *Moultonia*. One may suppose that the hypocotyl below an upper enlarged cotyledon has grown out to form the stalk with the lamina of the cotyledon at its end, and that the inflorescence meristem, instead of being strictly limited to an area at the base of the cotyledon, is spread along the hypocotyl and also along the lamina.

As an intermediate condition we may bring into the case the evidence offered by *Monophyllæa*.

We have pointed out that *Moultonia* is allied to *Monophyllæa*. This genus we only know from the description and figure given by Clarke.* Clarke suggests, we think rightly, that the *folium unicum* of his plant is a cotyledon. There appears to be in *Monophyllæa* a single stalked leaf—to speak conventionally—as in *Moultonia*, but the stalk is shorter and at the junction of lamina and stalk scapose inflorescences arise. At the summit of the scapes the flowers are disposed in a unilateral, spicate raceme which curls over circinately. We should interpret all this construction as that of a hypocotyl elongated in the form of a petiole and bearing at its extremity a cotyledonary lamina. We should expect in the young protocorm to find a second smaller arrested cotyledon. At the point where cotyledonary lamina and hypocotyl join, the inflorescence arises from the hypocotyl. The meristem for the inflorescence is localised at this region.

Now *Monophyllæa* is of special interest to residents in Borneo, as that country contains at least three of its known species—some ten in number. The study of its morphology from the seedling stage would be full of value and would throw much light on the problems raised by *Moultonia*. We therefore hope that those interested will try to secure specimens and seeds of both genera. *Monophyllæa* can be recognized among the Gesnerads by its single large leaf, presenting a similar appearance to that of *Moultonia* but with the inflorescences, as indicated above, distinct from the leaf-stalk and midrib.

Of the allied *Epithema* we have insufficient knowledge to allow of our making a suggestion of interpretation.

The following morphological series within the plants named issues from what we have said:—

Streptocarpus polyanthus, Hook.—Hypocotyl not elongated, cotyledon sessile, scapose inflorescence with open biparous branching developing from hypocotyl base of cotyledonar lamina.

Streptocarpus Rexii, Lindl.—Hypocotyl shortly elongated, giving apparent stalk to cotyledon, scapose

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* C. B. Clarke, Cyrtandreæ in De Candolle Monogr. Phanerog. v. (1883–87), 181, t. xx.

inflorescence (one flower) developing from hypocotyl at base of cotyledonar lamina.

Monophyllæa.—Hypocotyl much elongated, giving apparent long stalk to cotyledon, scapose inflorescence with unilateral racemes developing from hypocotyl at base of cotyledonar lamina.

Moultonia.—Hypocotyl very much elongated, giving apparent very long stalk to cotyledon, inflorescence disposed in umbels originating along middle line on upper surface of whole length of elongated hypocotyl and on midrib of lamina (but not showing special relation to the primary veins).

We do not overlook other explanations that might be given of the construction in *Moultonia*. Thus, in absence of all evidence of the seedling condition, it might be held that in both *Moultonia* and *Monophyllæa* the *folium unicum* is really an epicotylar leaf with which the inflorescence is more or less "congenitally concrescent." In such a view, the unilateral disposition of the flowers on the scapes in *Monophyllæa* might be regarded as a stage towards the complete fusion of scape with leaf in *Moultonia*. To us such concrescences do not appeal.

A more illuminative comparison may be made with what is seen in *Chirita hamosa*, R. Br., of which, however, we have not yet the clear explanation. In Plate III. is a figure of this plant when in flower. The opposite leaves are petiolate, and the flowers arise in a line upon the upper surface of each petiole. They are epipetiolar. The buds on the petiole are not, however, all flower-buds; some are foliage. The sequence is irregular. The position of the inflorescence partially recalls that of *Moultonia*. There is no concrescence here; simply foliar evolution of flower and buds. The seedling of *Chirita hamosa* has cotyledons differing in size and separated by a hypocotylar elongation. The upper is the larger, becomes stalked, and has quite the form of the adult leaf, but it never bears flowers or buds. Possibly, then, what we have been describing in *Moultonia* as a protocorm outgrowth may be after all an epicotylar leaf with epiphyllous inflorescences more extended than in *Chirita hamosa*.

The flower-structure of *Moultonia* is not without special interest. The gynæceum is closed at the top by a solid cone like a style supported upon a stylopod, and this seems

to separate as an operculum from the lower portion of the capsule which remains enclosed in the calyx. For a clear understanding of the mechanism of dehiscence better material than that at our disposal is necessary.

Explanation of Plates II. and III.

Illustrating Professor Bayley Balfour and Mr. W. W. Smith's paper on *Moultonia*.

(The Plates are taken from photographs by Mr. Robert M. Adam.)

Plate II. *Moultonia singularis*, Balf. fil. et W. W. Sm.

,, III. *Chirita hamosa*, R. Br. Plant in flower in the Royal Botanic Garden, Edinburgh.

MOULTONIA SINGULARIS, Balf. fil. et W. W. Smith.

CHIRITA HAMOSA, R. Br.