The Origin of Monocotyledons from Dicotyledons, through Self-adaptation to a Moist or Aquatic Habit.¹

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1. INTRODUCTION.

N EARLY twenty years ago (1892), I pointed out that there is a large number of coincidences between the morphological and anatomical characters of Monocotyledons and Aquatic Dicotyledons, sufficient, in fact, to justify the conception that the former class had been evolved from the latter. Beyond a limited extent in experiments upon adaptation, the

¹ Supplementary Observations and Experiments to 'A Theoretical Origin of Endogens from Exogens, through Self-adaptation to an Aquatic Habit'. Journ. Lin. Soc. Bot., xxix, 1892, p 485.

'theory', as I then called it, was not experimentally verified. Several corroborative experiments, however, have been made since; which prove incontestably that the special and hereditary, acquired characters residing in the roots, stems, and leaves of Monocotyledons are precisely the same as those which arise in Dicotyledonous plants, when responding to an aquatic environment, whether seen in Nature or in artificial experiments at the present day. Therefore, one need not entirely rest satisfied with Induction, or the accumulation of a very large number of coincidences, all of which conspire, more or less independently, to establish the conclusion herein maintained.

Since my former paper was published, numerous other coincidences have been noticed, so that my present object is to supplement that paper, and thereby to strengthen the argument with *addenda*, fortified by experiments.

2. EVIDENCES FROM GEOLOGY.¹

During the last twenty years much new knowledge has been acquired about fossil plants. The researches of Prof. Seward, Dr. Scott, and others have been ably put before us. For instance, Dr. Scott thus writes with regard to the relationship between Monocotyledons and Dicotyledons: 'If the Angiosperms were derived from the Cycadophyta, it would appear to follow that the Dicotyledons were first evolved, for their structure has clearly much more in common with the Cycad type than that of Monocotyledons. The latter would thus be regarded as a branch line of descent, diverging, no doubt at a very early stage, from the main Dicotyledonous stock. This view has been maintained, on other grounds, by various modern botanists. So far, however, as the palaeontological record shows, the two classes are of almost equal antiquity, both appearing for the first time in Lower Cretaceous rocks.'²

The reason of our great absence of knowledge of plant life during the Secondary Epoch is because the Liassic and Oolitic series of strata are almost entirely marine; so that countless ages passed, during which we know comparatively little of the land floras.

As exceptions to this statement, the 'Dirt-bed' of the Purbecks, which I investigated many years ago, is very rich in plant remains; and Dr. Scott reminds me of the American deposits which are extraordinarily rich, being contemporary with our own Oolites. Still, taking all the plant beds known of the Secondary Epoch, they do not amount to very much in

¹ See loc. cit., p. 486. Similar references are always to my former paper.

² Studies in Fossil Botany, Pt. II, p. 660.

comparison with what must have been the whole land surface of the globe during that prolonged period.

That Monocotyledons should have arisen nearly contemporaneously with Dicotyledons is not surprising if my contention be true; because rivers and lakes as well as morasses, we may be sure, abounded in all ages.

It has been suggested that the most primitive plants were aquatic, and that some took to land and became terrestrial. Unfortunately, Geology has revealed nothing to support this theory or the reverse; but that all Dicotyledons now existing have been evolved from xerophytic Gymnosperms is generally admitted, and that Monocotyledons, as now limited, were derived from the former is becoming generally accepted. There are about a dozen genera of the order Naiadaceae, all of which are aquatic plants, most of them living in the sea; but that they are *degradations* and not primitive is obvious. No existing order of either class can be said to be primitive, because of their simple structure; for this, in all cases, is the result of degradations. The same must be said of fresh-water plants.

3. DISTRIBUTION AND PERCENTAGES OF THE NATURAL ORDERS OF MONOCOTYLEDONS AS COMPARED WITH THOSE OF DICOTYLEDONS.¹

If it be asked where Monocotyledons were evolved, the present distribution of this class may perhaps indicate the region. Of the thirty-two orders described by Bentham and Hooker in the 'Genera Plantarum', twenty-one are chiefly found in the Tropics and warmer regions of the Temperate Zones; whereas only six have species reaching the Arctic and Antarctic regions.

Sir J. D. Hooker, in his Introductory Essay to the 'Flora of Tasmania', tells us that there are the following proportions between Monocotyledons and Dicotyledons:—

<i>Temperate Floras.</i>		
Europe.	Monocotyledons : Dicotyledons	1 : 5·2
Russian Empire		1 : 5·1
British N. America		1 : 3·8
South Africa		1 : 4·2
Australia		1 : 5·0

<i>Tropical Floras.</i>		
W. Tropical Africa		1 : 3·6
Ceylon		1 : 3·1
India		1 : 3·8
Tropics generally		1 : 3·0
Australia		1 : 3·5

This table, therefore, illustrates the same phenomenon.

¹ loc. cit., p. 487.

Now if the order Cycadaceae, represented by the Bennettiteae, perhaps a very characteristic group of the Secondary Epoch, gives us any clue as to climate, then it might be inferred from the present distribution of the Cycadaceae that Monocotyledons arose in the warmer regions of the world.

4. DEGENERACY OF MONOCOTYLEDONS.

Professor Sacco draws the conclusion from Palms being almost entirely restricted to the tropics, that they cannot adapt themselves to cooler temperate climates, either morphologically or physiologically.¹

This would seem to apply, however, to the great majority of Monocotyledons in different degrees, and the explanation of the fact, I would suggest, is, that having become degenerate in structure by having lived originally in water, they cannot now, as land plants, recover to the full the power necessary to construct such tissues as are found in Dicotyledons capable of resisting the injurious effects of a cold climate. Moreover, having lost the power of making massive timber of concentric cylinders of wood—really girders in combination—they cannot support large trunks.

The degraded condition of all Monocotyledons is also insisted upon by Prof. Hugo de Vries. He says:² ‘Monocotyledons are obviously a reduced branch of the primitive Dicotyledons. In Orchids and Aroids, in Grasses and Sedges, reduction plays a most important part, leaving its traces on the flowers as well as on the embryo of the seed.

‘The whole evolution of Monocotyledons from the lowest orders [?] of Dicotyledons implies the seeming loss of cambial growth and many other qualities.’

‘Retrogression is everywhere so active, that it can almost be said to be the prevailing movement. Reduction in the Vegetative and Generative organs, in the Anatomical structure and growth of the stems, and in sundry other ways, is the method by which the Monocotyledons, as a group, have originated from their supposed ancestors among the lower [?] dicotyledonous families. Retrogression is the leading idea in the larger families of the group, as for instance in the Aroids [especially their allies Lemnaceae] and Grasses. Retrograde evolution is also typical in the highest and most highly differentiated family, the Orchids, which have but one or two stamens.’ Prof. de Vries might have added the rudimentary condition of their ovules and seeds, and consequently the difficulty in securing the germination of Orchids.

Prof. de Vries, like other writers, fails to see that water has been the *cause* of degeneration in Monocotyledons; though all the *now* ter-

¹ L'Évolution biologique et humaine, p. 201.

² Species and Varieties, their Origin by Mutation, p. 15.

restrial species have acquired sufficient adaptations to maintain an aerial existence.

The degeneracy of Monocotyledons is seen in every organ, as e. g. in the exhausting process of flowering and seeding. Thus bulbs, so characteristic of certain orders, which throw up a central flowering stem, perish with the completion of the reproductive process. Larger plants, as *Agave* and *Aloë*, die in the same manner. Lastly, Palms sometimes follow suit. Thus is it with *Corypha umbraculifera*, the Talipot Palm of Ceylon and Southern India. It has enormous leaves, a single blade, it is said, being large enough to cover a whole family. In about seventy years it is then able to flower; but the entire tree perishes immediately after the effort has been made.¹

Miss Sargent observes that: 'The reduction in structure so characteristic of aquatic species is very strongly marked in their young seedlings. . . . Ancestral features have commonly disappeared or become obscure in the general loss of differentiation. Thus, the fact that terminal leaves seem characteristic of aquatic embryos suggests very strongly that their peculiar position is due rather to *suppression of the axis* than to any reminiscence of a stemless period in the history of the race.'²

'Considerable reduction of structure commonly occurs in *the embryo and seedling* of aquatic and semi-aquatic plants'³ [my itals.].

The above quotations apply as well to Monocotyledons generally.

Miss Sargent elsewhere notices how 'the petiolar tube of cohering cotyledons is accompanied by a thickening, or at least much shortened hypocotyl', and adds that it is 'commonly very short in Monocotyledons', the thickening leading to bulbs, corms, &c. This is what might be anticipated from the subsequent tufted condition of the leaves of so many of that class, as well as in perennial dicotyledonous hygrophytes and hydrophytes, in which not only the primary internode or hypocotyl, but the subsequent ones are suppressed.

Miss Sargent calls attention to the prevalence of tufted or 'squat' plants on the Alps, and attributes it to the short hot summer following the melting of the snows. Insolation, however, may assist in arresting the axis. In South Africa, she adds, 'parallel conditions are seen in the dry season being followed by the heavy rains of the wet one.'⁴

The following British plants will remind the reader of this correlation between tufted foliage, arising from perennial axial structures, and an aquatic habit. Many Grasses, Rushes, and Sedges, *Iris*, *Eriocaulon*, *Isoëtes*, *Narthecium*, *Toffieldia*, *Stratiotes*, *Alisma*, *Sparganium*, *Hydrocharis*, *Lit-*

¹ Gardeners' Chronicle, vol. xlvii, p. 426, and Supplementary Illustration.

² Reconstruction of a Race of Primitive Angiosperms. Ann. of Bot., xxii, p. 151.

³ Ibid., p. 152.

Theory of Origin of Monocotyledons, &c. Ann. of Bot., vol. xvii, p. 79.

722 Henslow.—*The Origin of Monocotyledons from Dicotyledons, torellia, Drosera, Pinguicula, Menyanthes, Samolus, Primula, and most bulbous plants, &c.*

It must not be forgotten that starvation and strong light can produce the same arrest of the internodes, as seen in plants growing on walls, &c., as *Draba, Sedum, Arabis Thaliana*, and many others. So that this peculiarity of Monocotyledons is not *caused* by the arrested habit, but this itself may be the result of varying degrees of water, or else in consequence of other inducements.

Degeneracy is very obvious where the aquatic form is contrasted with the land form of amphibious plants, such as *Bidens cernua, Ranunculus Lingua, Polygonum amphibium*, &c. As these plants grow equally well in either environment, they retain the capacity for adapting themselves to both conditions; hence neither form is hereditary, so as to develop the characters of any one form when grown in a different environment.

It is only, as a rule, after a prolonged residence of many generations (in water or in great drought, for example) that the acquired characters of adaptation are developed when the seeds are grown in totally different circumstances. Thus *Ranunculus heterophyllus*, the Water Crowfoot, retains the dissected and floating types of foliage on land; and the fleshy Cactaceous plants 'come true' to seed in England.

Miss Sargent observes that 'Monocotyledons may be shown to be on the whole a decadent race, of which some branches have been driven to an aquatic habit to escape the severer competition on land'.¹ Unfortunately, they do not escape it. Rivers, ponds, &c., soon get choked with a mixture of aquatic plants; e.g. Water Crowfoots or *Elodea*. If by 'decadent' she means *prior* to their entry into water, the question arises—What caused the decadence on land? The author does not appear to see that it is *water* itself which has caused the degeneracy in all aquatic plants.

'We may look on living Monocotyledons as a race which has been on the whole unsuccessful in the struggle for existence; and in consequence maintains itself chiefly in situations where the local conditions are exceptionally favourable to its peculiar characters.'² But grasses with 3,200 species in all kinds of soils and climates are ubiquitous; Palms have 1,100; Orchids, 4,000 to 5,000 species, &c. Such do not seem to warrant Miss Sargent's hypothesis.

Degeneracy is well seen in the structure of the stems. The cylinders of wood of a Dicotyledon form a combination of girders, and whether hollow or not, afford ample strength to support the weight of the tree or herb; but the dislocation of the strands in Monocotyledons brings about a mechanical weakness. Hence, palm stems made into walking-sticks are sometimes very brittle. The petiole of rhubarb leaves, naturally a hygro-

¹ Reconstruction, &c., p. 175.

² Reconstruction, &c., p. 176.

phyte, in which the strands are scattered, is equally weak,¹ and snaps across with the greatest ease.

Herr Ph. Eberhardt has shown how even a moist air has a similar effect to water upon woody stems, by greatly reducing the mechanical tissues of support.² Further illustrations will be mentioned later.

5. POSSIBLE AQUATIC ORIGIN OF PALMS.

Certain special resemblances are well illustrated by Palms. Though solid, silicified stems have been found fossil in Cretaceous rocks of America and in the Miocene of Antigua, some were remarkable for having a portion of the ground tissue in the condition of aerenchyma, a truly aquatic character. MM. G. Bonnier and Leclerc du Sablon illustrate this fact by a section of the stem of *Palmoxylon lacunosum*.³ Mr. Drabble has also shown that many living Palms have roots full of lacunae, and names *Kentia*, *Metroxylon*, *Phoenix*, *Caryota*, *Areca*, &c., as well as *Phytelephas*.⁴

Another peculiarity about Palm-roots is the presence of what Jost calls 'pneumathodes'. They are described as *plaques farineuses*, probably from some resemblance to lenticels; they surround the bases of roots. M. C. L. Gatin, who gives an account of Jost's paper, would refer them to something more analogous to what is found on Ferns of the orders Marattiaceae and Cyatheaceae (two of the most ancient kinds of Ferns), consisting of fine trees with noble fronds growing in moist ravines. He concludes his article as follows:—'Il ne me paraît pas sans intérêt au moment où les travaux de l'école anglaise ont remis à l'ordre du jour les importantes questions de phylogénie des grands groupes végétaux, de constater une grande analogie de structure entre les organes respiratoires des Palmiers et ceux des Cyathœacées et des Marattiacées.'⁵

Though most Palms have tall stems *now*, as terrestrial trees, it does not necessarily follow that primitive Palms were not small shrubs.

Of course, pneumatophores are well known as occurring on the roots of hygrophytic trees and herbs, as *Taxodium distichum*, &c.; but they often fail to be produced if the tree grows in dry ground, as is the case with this deciduous Cypress.

¹ The rhizome, used as a drug, is known by the absence of a compact cylinder of xylem, which is replaced by stellate clusters.

² Ann. des Sci. Nat., tome xviii, 1903, p. 61.

³ Cours de Botanique, p. 1214, Fig. 2193.

⁴ The Anatomy of Roots of Palms. Trans. Lin. Soc., 2nd Ser., Bot., vi, p. 427.

⁵ Observations sur l'appareil respiratoire des organes souterrains des Palmiers, par M. C. L. Gatin. Rev. Gén. de Bot., xix, p. 193.

6. LEAVES OF LARGE SIZE CHARACTERISTIC OF MANY AQUATIC PLANTS.

With regard to the foliage, the enormous size to which the leaves can attain is a characteristic feature of certain hygrophytes and hydrophytes. Of the former are the Ferns just referred to, *Gunnera*, *Rheum* (from Rha, the old name of the Volga), *Petasites* (as contrasted with *Tussilago*), &c.

Of the latter may be mentioned the *Victoria regia*. Of Monocotyledons, Aroids, Bananas, and Palms illustrate the same fact, whether they be hygrophytes or not at the present time. On the other hand, the largest trees among Dicotyledons or Gymnosperms, such as *Eucalyptus* and *Sequoia*, have no such leaves.

7. WATER-STORAGE ORGANS.

If plants had been more or less aquatic, and subsequently became xerophytes, it is presumable that they would only be able to sustain life during great and prolonged droughts, by adopting methods of storing water. Such is not infrequent in both classes. Species of *Erodium* and many others utilize various internal structures for storing water in the deserts near Cairo. *Oxalis cernua* does the same in South Africa and Malta, &c. *Poa bulbosa* has swollen nodes in dry ground, but not in moist soil.

Hence, tuberous roots, swollen internodes, bulbs, and corms are often acquired in adaptation to arid conditions on land. The prevalence of them among Monocotyledons, as seen in the orders Orchideae, Iridaceae, Amaryllidaceae, and Liliaceae, would seem to indicate an ancestral aquatic life. I would, therefore, regard the object of providing plants with corms, bulbs, and rhizomes to be threefold, viz. to enable them to be perennials, to be reservoirs of food, and if they be hydrophytes or hygrophytes which became xerophytes, then their third use is for water storage.

8. THE REQUIREMENT OF MUCH WATER BY MANY TERRESTRIAL MONOCOTYLEDONS.

In support of this contention, not only are there still living aquatic members of the above-mentioned families, but under cultivation they all require a fair amount of water during growth, while some, such as Lilies, *Aspidistra*, &c., revel in it.

'*Watsonia*, for example, succeeds best when the saucer is kept full of water.' This genus in cultivation 'requires to be dried off gradually and then to be submitted to a baking in the sun', evidently in adaptation to the South African droughts.

'Liliaceae, on the other hand, requires an abundance of water, and the genera never like being very dry; so their bulbs should not be taken up.

The finest specimens of *Lilium cordifolium* growing wild are on the shores of lakes, in eighteen inches of water, thus being true aquatics. Hyacinths cannot be grown in this country as in Holland; without doubt this is a question of water. There they get an abundance of it. Tulips require less water than Hyacinths.¹

Mr. N. S. Pillans, the well-known Cape botanist, writes me from Cape Town: 'One question you ask I can reply to, that is whether Cape bulbous plants flourish best when their roots get an abundance of moisture. *They certainly do*, and most species flourish best under those conditions. Some become so luxuriant as to change their appearance, just as some succulents do.'

The leek is a bulbous plant when wild, as in the dry fields of Malta; but under a rich cultivation it has reverted to its, presumably, ancestral bulbless form.

I would suggest that the trunks of Palms, like the Baobab and 'bottle' trees, store water in the ground tissue; for some species resemble the latter at their base. Indeed, a palm may be compared with the bulb without internodes, but with the axis or stem drawn out; just as some Lilies pass gradually from bulbs to rhizomes.

Cycad stems may be compared to Palms, for both living and extinct plants of Cycadaceae and Bennettiteae are palm-like. The large pith of the latter, as seen in *Bennettites Saxbyanus*, was probably adapted for water storage.² Similarly the figure given of *Cordaites*³ shows a strong zone of xylem with a large and discoidal pith, admirably adapted for water storage. These and other features seem to prove that such Cycadaceous plants were *not* hygrophytes or hydrophytes but entirely xerophytes.⁴ It is notorious how the Date-palm craves for water.

9. CYCADS AND MONOCOTYLEDONS.

It is a remarkable fact that Robert Brown, from the study of the embryo, thought he saw an affinity to Monocotyledons in Cycads; so he placed Cycadeae at the end of that class, immediately preceding Dicotyledons. 'In this order,' he says, 'we have at least, in respect of the external structure of the embryo, a *transition* from Monocotyledons to Dicotyledons. The development of the plumule agrees better with that of the former class; for in all these (Grasses and Aroids excepted) the primary

¹ The above facts have been kindly communicated to me by Mr. Rudolf Barr, the experienced cultivator of bulbs.

² Scott, op. cit., ii, p. 563, Fig. 201.

³ Ibid., p. 528, Fig. 190.

⁴ See my paper on the Xerophytic Characters of Coal-Plants. Quart. Journal Geol. Soc., lxiii, 1907, p. 282.

leaves are always scale-like or are mere sheaths; while in all Dicotyledons perfect leaves are developed.' ¹

The primary leaves of the seedlings of *Victoria regia*, however, are similarly more or less arrested in development, and are comparable with those of *Sagittaria*.²

It might be suggested that *Cycas*, like Palms with a similar pseudo-pectinate or compound leaves, was derived from an aquatic ancestor, but now become a strong xerophyte, like *Agave* and *Aloë*, which are comparable in form with *Stratiotes Aloides*. But, on the other hand, intense drought may bring about an imitative result, as in *Hakea* (Proteaceae). This has more probably been the case with *Cycas*. These 'pectinate' leaves of xerophytes closely resemble in form the submerged leaves of *Proserpinaca palustris*.

Ceratozamia is the only known Cycad with only one cotyledon, though the second can be, and has been developed. The ovules are shed shortly after fertilization, so that the cotyledon is not developed until the seed lies on the ground. It arises at one, the lower, side, and gradually enlarging, the margins touch each other with the sheathing base. It thus agrees with hygrophytic and hydrophytic plants of both classes, as well as terrestrial Monocotyledons.

A longitudinal section shows a 'scale' opposite to the cotyledon, just as in the Oat. An inequality in size appears to be not unusual in other Cycads, as it is also in *Nymphaea*.

The reason why the lower cotyledon, i.e. as the seed lay on the soil, was only developed was clearly not in consequence of gravity, which would act equally on the development of both, but lies in the presence of water, whereby the lower one gets more saturated. When arrangements are made so as to equalize the moisture all round the seed, and it is made to germinate on the clinostat, both cotyledons are developed. Rotation is found to retard the growth. According to the figures given the primary root is very slender, and adventitious roots are represented as issuing from the hypocotyl close to the cotyledon.³

¹ 'In utrinque longitudinalis, plus minus obvius, cotyledonum duorum accretionem indicat, earumque separatio interna in regione Plumulae ante germinationem certe conspicuae manifesta est.

'In hoc ordine igitur habemus, saltim respectu structurae externae Embryonis, transitum a Monocotyledonibus ad Dicotyledones. Plumulae autem evolutio cum priori classe magis convenit; in his omnibus enim, Gramineis Aroideisque exceptis, foliola primaria hujus organi semper abortiva et squamiformia, vel merae vaginae sunt; dum in Dicotyledonibus omnibus folia perfecta evadunt. Aliud discrimen forsitan obtinet inter Plumulas duarum classium; in Dicotyledonibus ejusdem foliola primaria cum cotyledonibus alternant [as in *Tamus* and *Asparagus*, which have rudimentary second cotyledons]. In Gramineis et Aroideis contra in quibus solummodo e Monocotyledonum Classi hanc determinare possumus, cotyledoni opponuntur. Cycadeae quantum e re tam minuta judicare liceat, hac ratione cum Dicotyledonibus quadrant' (Prodromus Florae Novae Hollandiae, p. 347).

It will be noticed that Brown wrongly uses the word *cum*. It only means 'with' in the sense of 'accompaniment'.

² loc. cit., p. 515.

³ Morphology of Gymnosperms, by Coulter and Chamberlain, pp. 99 ff., Figs. 75-9; Figs. 187-

The development of the lower cotyledon only is probably analogous to the well-known fact that of two opposite leaves growing on a horizontal branch the lower will be larger than the upper. This is said to be due to gravity; but as the larger leaf requires the most water, it must be upon *that* which gravity acts. If the bough be kept reversed, then the leaves which would have been naturally uppermost, becoming the lower, now grow to be the larger.¹

10. MONOCOTYLEDONOUS DICOTYLEDONS.

In addition to the plants mentioned in my previous paper, *Corydalis solida* may be considered, for although Sir J. D. Hooker, in his Student's Flora, regards it as having connate cotyledons, M. Velenovsky considers it to have one; and he discovered an additional coincidence with Monocotyledons. It consisted in a peculiar adaptation of the hypocotyl and the petiole of the cotyledon, in that these are covered with absorbing hairs and can give rise to endogenous adventitious roots, so that the petiole acts as a true root.

This is not an isolated fact, for M. Gatin had previously observed that among certain Monocotyledons the petiole and cotyledonary sheath are sometimes covered with absorbing hairs, as e.g. in *Trachycarpus Martiana* and *Strelitzia*.²

It may also be noted that *Corydalis solida* has a corm and glabrous dissected foliage; the former may perhaps primitively have been for storage of water and the leaf submerged. In *Ranunculus Ficaria* and *Carum Bulbocastanum* the embryo is greatly arrested in the ripe seed; so that germination in both alike is very slow, features due to degeneracy which water can account for.

Miss Sargent, quoting from Hegelmaier's observations, shows that the development of the cotyledon is in a crescent-shaped ridge which thus agrees with the Water-lily, thereby acquiring a sheathing base. 'Hegelmaier and Schmid consider one possibility only—the formation of a single cotyledon from the original pair by suppression of the second.'³ Miss Sargent also refers to *Corydalis cava*, as having an 'embryo monocotyledonous from the first. . . . From the researches of Dr. Schmid, we know that no traces of the

194 (p. 155); Fig. 462 (p. 429); quoted from The Embryo of *Ceratozamia* by H. A. Dorety. Bot. Gaz. xlv, 1908, pp. 412-16, Figs. 1-7.

¹ Influence des agents extérieurs sur l'organisation polaire et dorsiventrals des plantes, par M. L. Kolderup Rosenvinge. Rev. Gén. de Bot., vol. i, Figs. 12, 13, p. 131. See Author's experiments, Origin of Plant Structures, p. 205.

² La morphologie de la germination et ses rapports avec l'anatomie, par M. C. L. Gatin. Rev. Gén. de Bot., xx, p. 273.

³ The Reconstruction of a Race of Primitive Angiosperms. Ann. Bot., vol. xxii, p. 157.

original bicotyledonary structures are to be found in the early history of the embryo.'¹

Miss Sargent gives a list of Pseudo-monocotyledons, under five orders—Fumariaceae, 3; Umbelliferae, 3; Primulaceae, 1; Lentibularineae, 2; Nyctagineae, 3—and observes they are 'also characterized by the early formation of tubers [or corms], or at least by the development of a much shortened squat axis'.²

The following is Darwin's observation on *Abronia* (Nyctagineae):—'In *A. umbellata* and *A. arenaria* one of the cotyledons is quite rudimentary and destitute of a petiole. At first it stood opposite to the larger cotyledon; but as the petiole of the latter grew in the *same line with the hypocotyl* [i.e. making it to be falsely terminal] the rudiment appeared in older seedlings as if seated some way down the hypocotyl. . . . In both these species the hypocotyl is so much enlarged, especially at a very early age, that it might almost be called a corm. . . . In *Cyclamen persicum*, the hypocotyl, even while still within the seed, is enlarged into a regular corm. . . . With several Cactaeae, the hypocotyl is from the first much enlarged, and both cotyledons are almost or quite rudimentary, as in *Cereus Landbeckei*, *Rhipsalis cassytha*, &c. So, too, is it in *Stapelia sarpedon*.'³ Darwin reasons as to the cause of the enlargement of the hypocotyl, in its being correlated with the arrest of one or both the cotyledons, and suggests the necessity of storage of *food*. At the early stage it would seem to be more probably *water*, whether in plants descended from aquatics or habitually living in *drought*.

The *Cyclamen* is another genus which has usually only one cotyledon, though a second has been seen. From the late Dr. M. T. Masters' investigations the genus agrees with Monocotyledons in the following details:—

1. The early disappearance of the primary root.
2. One cotyledon is normally absent.
3. The cotyledon acts as an absorbing organ for consuming the endosperm, just as in *Trapa* and Monocotyledons.
4. The first leaf is over the site of the missing cotyledon, and the second nearly over the existing one. Hence the phyllotaxis begins as $\frac{1}{2}$, as in nearly all Monocotyledons.
5. If four leaves occur there is an attempt to return to the $\frac{2}{5}$ divergence with the persistent quinary arrangement of the flower.
6. The development of the large corm is analogous to those of Iridaceae.
7. The glabrous, cordate leaf is paralleled by that of *Ranunculus Ficaria*, *Nymphaea*, *Limnanthemum*, and *Hydrocharis*.

¹ Theory of the Origin of Monocotyledons, &c. Ann. of Bot., vol. xvii, p. 69.

² Ibid., pp. 76–8.

³ Movements of Plants, p. 95 ff. (abridged; my italics.).

Miss Sargent, in her paper 'On the Origin of the Seed-leaf in Monocotyledons',¹ takes the present prevailing view that this class was not precedent to, but descended from Dicotyledons, and says, with regard to *Allium*, 'the second half of the root-stele might originally have been supplied by the trace of a second cotyledon opposite the first.'² She also suggests that the two bundles of the cotyledon and hypocotyl of *Anemarrhena* may be traces representing the two distinct cotyledons of some ancestor. If this view is justified the 'cotyledon' of *Anemarrhena*, and probably that of all Monocotyledons, must be equivalent to both the seed-leaves of Dicotyledons.'³ Miss Sargent would seem thus to consider that the single 'cotyledon' of Monocotyledons results from a fusion of the two, characteristic of Dicotyledons; but there is some ambiguity in her use of the term 'cotyledon'. Thus, in this sentence: 'Three bundles from each cotyledon [meaning the *blade*] enter the petiolar cylinder.'⁴ But elsewhere, speaking of *Eranthis hiemalis*, she says: 'The partial union of two cotyledons [meaning the *petioles only*] is undisputed.'⁵ Again, 'The two cotyledons of Primitive Angiosperms have united to form the single member in Monocotyledons.'⁶ This change in the use of the term is a little confusing. *R. Ficaria* has been thought to indicate a fusion because its single cotyledon has often an emarginate blade, supposed to consist of two united; but it sometimes has none, or again two sinus. Miss Sargent adds that each of the two strands in the petiolar cylinder of *Eranthis* gives rise to three just before entering the blade. But those of *Anemarrhena* supply none. This countenances the view I have expressed elsewhere, and maintained by certain botanists in 1875, that the ordinary so-called 'leaf' of Monocotyledons with parallel venation is really homologous with the petiole only.⁷ Others, as Sachs, regard the *blade* as arising directly from the sheath; but no mention is made of the parallel venation, which, to my mind, decides the question.

I would summarize my position as follows:—

What is suppressed in the embryo of Monocotyledons consists of—

1. The *blade* of the existing so-called single cotyledon, this being homologous with the petiole.

2. Both the *blade* and the *petiole* of the missing cotyledon.

What is retained consists of—

1. The petiole only of the existing cotyledon.

2. The single bundle of the petiole of the missing cotyledon (if present).

¹ New Phytologist, i, p. 107.

² op. cit., p. 109.

³ op. cit., p. 110.

⁴ Origin of the Seed-leaf in Monocotyledons. New Phytologist, vol. i, p. 111.

⁵ op. cit., p. 113.

⁶ Reconstruction, &c. Ann. Bot., xxii, p. 183.

⁷ M. D. Clos mentions de Candolle and Treviranus, in Des éléments morphologiques de la feuille chez les Monocotylés. Mém. de l'Acad. des Sci. Toulouse, 1875.

This is then 'caught' within the broad or sheathing base of the single petiolate cotyledon.

This retention of the bundle from a lost organ may be paralleled by those of the five lost stamens being retained within the perianth segments of the flowers of Orchids.

This does not alter the fact that the organs, the cotyledon, and the stamens are suppressed.

Moreover, one cotyledon may be suppressed, but it does not *necessarily* follow that its representative strand should pass into the sheathing base of the one developed.

The rudiments of abortive cotyledons remain in *Ceratozamia* and *Trapa*, and also in the Oat; but no cord belonging to the lost one enters the developed cotyledon.

In *Ranunculus Ficaria*, Irmisch figures the petiole of the single cotyledon, showing the sections of the midrib and two marginal strands characteristic of most dicotyledonous leaves.¹ *Bunium* is simpler in having only one central strand.² *Anemone apennina* has the two blades of the cotyledons *sometimes* coherent half-way up. Then the two strands are included, but diverge as midribs.³

With regard to *Ranunculus Ficaria*, I have noticed some other features than those mentioned in my former paper as indicative of an ancestral aquatic habit.⁴

Both the upper (as on floating leaves) and lower epidermis are provided with stomata; while the cells of the lower have a wavy or indented outline, each has a cluster of chlorophyll granules in it. The cells on the upper have much less irregular walls, and are devoid of chlorophyll. The guard cells of the stomata are provided with chlorophyll.

The leaves have been described as 'opposite' (Hooker), but while the first two leaves on the flowering stem appear to be a pair of leaves, i. e. one opposite to the other, the sheathing base of one *overlaps* that of the other. Other leaves on the same stem are single.

The phyllotaxis, therefore, is $\frac{1}{2}$. This arrest of an internode between the first two leaves on a vigorously growing, erect stem is perhaps, the result of a habit not yet quite abandoned, when the stem was enabled to grow, on the plant becoming terrestrial. The leaves were doubtless originally crowded together, as is more generally the case now, arising from a very short thick 'stock', giving the 'squat' habit to the Lesser Celandine, growing, as it usually does, in damp soils.

¹ Beiträge zur vergleichenden Morphologie der Pflanzen, Parts I and II (1854).

² Irmisch, op. cit.

³ Miss Sargent mentions *Ranunculus chiensis*, *R. repens*, *Phlomis*, *Urtica*, &c., as having been found with the two blades of the cotyledon more or less united, but it is in all cases exceptional or 'monstrous'.

⁴ loc. cit., p. 495.

Professor Hugo de Vries¹ has shown by experiment that there are three causes which give rise to annuals; that is, they hasten the production of the central stem, viz. freedom of growth, by the absence of crowding, insolation, and a rich soil. Conversely, we may assume that crowding, shade, and a poor soil, besides water, may be expected to produce 'tufting' rosettes and a 'squat' habit.

The phyllotaxis of the Lesser Celandine suggests the origin of the three sepals and eight or nine petals, as the normal numbers. The absence of fives being accounted for by the single cotyledon and the $\frac{1}{2}$ arrangement of the leaves, these alone *cannot* give rise to the $\frac{2}{5}$ arrangement.

It has also been noticed that the fibrovascular bundles or strands are 'closed' as in Monocotyledons. This will be referred to again, as recorded by Professor Vines.

In allusion to *Ranunculus Ficaria*, *Corydalis cava*, and *Carum Bulbocastanum*, Miss Sargent observes that 'the embryo of all these species is very little developed in the ripe seed. A long period of maturation is necessary before germination can take place. In each, the single cotyledon was certainly derived from two; the ancestral genera certainly had two.'

'The actual process in all three forms bears a strong resemblance to the development of the embryo in *Tamus*. The cotyledon appears on the flattened apex of the pro-embryo as a peripheral ridge [this also occurs in *Castalia*, &c.]. At first it is circular, but it soon becomes crescent shaped by the rapid growth of one side. The stem apex is often late in appearing. It is always formed in the central depression outlined by the circular ring. Very soon the stem-bud is completely dominated by the lateral member, which embraces, and at last arches over it. This lateral member is, of course, the single cotyledon which becomes apparently terminal in the mature embryo, for it manages to push the stem apex to one side. In the interpretation of their results, Hegelmaier and Schmid consider one possibility only—the formation of a single cotyledon from the original pair by suppression of the second.'²

II. THE EFFECT OF WATER UPON ROOTS.

An ordinary dicotyledonous seedling growing in moist soil develops its primary root normally, and frequently to a great length, as under cultivation, the presence of water acting as a stimulus. Thus a turnip root, finding its way into a field drain-pipe, elongated to an extent of upwards of six feet.

If, however, seeds of Dicotyledons be grown in a net over water, as soon as the radicles penetrate it, they perish. Adventitious roots now appear from the hypocotyl. This arrest of the axial root is characteristic

¹ Alternating Annual and Biennial Habit : The Mutation Theory, vol. ii, p. 291, P. 25.

² Reconstruction, &c., pp. 156-7. See refs. in Miss Sargent's References to Literature, op. cit., p. 183.

of all aquatic Dicotyledons and of all Monocotyledons, whether aquatic or terrestrial. This was known to Richard and Poiteaux in 1808.

This difference, as well as others, is well seen in dicotyledonous amphibians, such as *Bidens cernua*.¹

It has long been recognized that a characteristic feature of Monocotyledons, in addition to the arrest of the primary root, is to have the root-cap together with its formative tissue distinct from that of the root behind it.²

Numerous experiments with seedling Dicotyledons germinating in water, not only invariably showed the arrest of the primary root, with the evolution of secondary or adventitious ones; but as one of the latter grows from a lateral papilla, with a common meristem, this latter contracts, as it were, often appearing as pointed, with the calyptra of about four layers, more or less perfectly distinct from the root. If the complete separation is not always fully secured at first, the tendency to divide the merismatic tissue is always present. If sufficient time be allowed before examination, the calyptra becomes distinct.

Miss Sargent calls attention to the '*Absence of a true epidermis in the root above the root-sheath in Monocotyledons*'. This character of the root is so far as we know universal among Monocotyledons, but not confined to them. It is found in the Nymphaeaceae.³ Since the degradation of the epidermis to the epithelioid state is characteristic of all submerged plants, the above loss is probably a further instance of the original effect of water.

12. ORIGIN OF THE FORMERLY CALLED 'ENDOGENOUS' ARRANGEMENT OF THE CAULINE BUNDLES OF MONOCOTYLEDONS.

Professor Vines observes⁴: 'In Schizostely the single primitive stele breaks up into as many distinct strands as it possesses vascular bundles... each schizostele being invested by its own segment of the endodermis. This obtains among Phanerogams in the Nymphaeaceae, some species of *Ranunculus*, as *R. aquatilis* and *R. Lingua*, &c., and in the Monocotyledons *Hydrocleis* and *Limnocharis* (Alismaceae).

'Stems with cauline bundles may be monostelic or polystelic; monostelic stems with cauline bundles are generally gamodesmic, having a solid vascular cylinder, e. g. *Lycopodium*, some aquatic Dicotyledons, e. g. *Utricularia*, *Aldrovanda*, *Callitriche*, *Myriophyllum*, *Ceratophyllum*; some aquatic Monocotyledons, e. g. *Elodea*, *Hydrilla*, &c.'⁵

¹ I have described and figured the two kinds of roots in this plant, the Bur-Marigold, in my *Heredity of Acquired Characters in Plants* (Murray).

² *loc. cit.*, p. 507.

³ *Theory of the Origin of Monocotyledons, etc.* Ann. Bot., xxvii, p. 83.

⁴ *Students' Text-Book of Botany*, i. 152.

⁵ *Ibid.*, p. 173. It will be noted that the above quotations only prove that water affects Dicotyledons and Monocotyledons alike. But the object of this paper is to show that precisely the same results are now to be seen in *terrestrial* Monocotyledons, whose aquatic ancestors have returned to land.

Professor Vines adds: 'Some few Dicotyledons have closed bundles, i. e. without cambium in the stem, e. g. *Adoxa*, *Ranunculus Ficaria*, *Nymphaeaceae*, *Myriophyllum*, *Utricularia*, &c.' Such, of course, agree with all Monocotyledons.

With regard to the similar and the usual condition of monocotyledonous stem-bundles, MM. G. Bonnier and Leclerc du Sablon observe: 'Chaque faisceau est entouré d'une gaine continue de fibres à parois épaissies et lignifiées *qui ont la même origine que le parenchyme qui les entoure*. . . . Les faisceaux offrent une disposition analogue dans certaines Dicotylédones, telles que les Ranoncules, *Thalictrum*, beaucoup d'autres plantes de la famille des Ranunculacées et quelques autres encore.'¹

Podophyllum peltatum has been described by Mr. Holm,² who notes the following facts. The petioles of the cotyledons are united into a long tube. Such is characteristic of many geophilous plants with a moist soil, as species of *Anemone* and other genera of Ranunculaceae. The vascular system of the stem recalls that of a Monocotyledon. The radical leaves are net-veined, but their petioles are expanded at the base into a sheath, from which many traces enter the subterranean stem.³ This gives rise to the dispersed strands in the stem. The traces in the erect stem have lost their cambium and are 'closed' like those of a Monocotyledon. Cambium, however, is found in the bundles of the rhizome; these are arranged in a single circle, but without interfascular cambium.

This species of *Podophyllum* grows in swampy woods in the Southern States of North America. It has a 6-leaved perianth.

The origin of the coherent petioles may perhaps be traced to the ring found on the axis, whence the cotyledons arise, the two crescents of which cohere by their edges. This crescent or ring, as stated, is seen in *Nymphaeaceae*.

Though the rhizome of *Nymphaea* first suggested the similarity to the scattered bundles of Monocotyledons, it is by no means confined to submerged rhizomes. Mr. Worsdell, for example, figures the flowering stems of *Anemone rivularis*, *Caltha palustris*, *Podophyllum peltatum*, and *Hydrastis canadensis*.⁴ To these petioles may be added those of *Thalictrum flavum* and *Rheum*.

As the 'closed' bundles of Monocotyledons and of certain Dicotyle-

¹ Cours de Botanique, pp. 182-4 ff.; Figs. 258, 259 (Monocotyledons), Fig. 260 (B) *Thalictrum*.

A slight discrepancy seems to be noticeable between Vines's and Bonnier's descriptions in the words I have italicized in the account of the latter botanist; for while Vines regards the bundle sheath as due to the *endoderm*, which it certainly is in many cases, Bonnier attributes it to the medulla or *ground tissue* of the root. I would venture to suggest that both cases may occur in different plants.

² Bot. Gaz., xxvii, 1899, p. 419.

³ See my paper, On the Origin of the Sheathing Petiole, p. 499.

⁴ A Study of the Vascular System in certain Orders of Ranales. Ann. of Bot., xxii, Pl. 32, 33.

dons, chiefly aquatic plants, are mostly *without* cambium, so, on the other hand, *traces of cambium* are to be found in Grasses and Sedges.

Mr. A. Chrysler thus writes:¹ 'A well-marked, though generally short-lived cambium occurs in the bundles just above the node and near the base of the leaf-sheath in certain Grasses.' This fact is considered by him to lend support to the view that 'Monocotyledons have been derived from some group possessing a cambium, probably the Dicotyledons'.

'A cambium² is present also in the bundles at the nodes of *Scirpus cyperinus* and other species. These features indicate that the Cyperaceae is one of the most primitive groups of Monocotyledons. The view which derives this class from an essentially dicotyledonous ancestry receives further support.'

In my former paper³ I drew attention to the series of concentric circles in *Nelumbium*, apparently indicating the first stage of their dislocation from a primitive and more compact zone of fibro-vascular bundles. Miss Sargent observes that the 'regular orientation—xylem inwards, phloem outwards—suggests that the leaf-traces were formerly linked together by a cambium.'

Miss Sargent also observes:⁴ 'Traces of a cambium in the vascular bundles of monocotyledonous seedlings have been recorded by several observers, as in *Zea*, *Typha*, *Lilium*, *Dracaena*, and in the hypocotyl of *Yucca arborescens*, &c.'

She quotes Professor Quéva as saying: 'The persistence of a cambium zone in the bundles of certain Monocotyledons shows that we may logically consider them as derived from the more primitive Dicotyledons, by means of the early disappearance of the cambium, and an increase in the number of traces from each leaf.'⁵

In addition to the above, Mr. Chrysler observes that 'something similar occurs in the development of the central cylinder of Araceae and Liliaceae.'⁶ The simple siphonostelic stage persists in *Acorus* for several internodes, and the stem looks much like that of a Dicotyledon; higher up some segments of the stele become amphiasol (*sic.* amphivasal?), and this may be regarded as the first appearance of a monocotyledonous character.'

Again, in speaking of the central cylinder, he adds: '*Medeola* and *Lilium* show the effect of long internodes combined with extended gaps in breaking up the central cylinder into several strands arranged in the circumference of the circle.'⁷ 'The plan of the young stele,' continues Mr. Chrysler, 'as, e. g., in *Smilacina*, bears a close resemblance to that of Dicotyledons, and differs from the older state of the latter only in the absence of cambium. These considerations lead to the conclusion that the

¹ Bot. Gaz., xli, p. 11 ff. (Jan. 1906).

² Rev. by A. B. Plowman, Ann. of Bot., xx, pp. 1-33, Pl. I, II, 1906.

³ loc. cit., p. 512.

⁴ Reconstruction, &c., p. 144.

⁵ op. cit., p. 145.

⁶ Bot. Gaz., xxxviii, pp. 161-4.

⁷ ibid., p. 177.

Monocotyledons are *not* an ancient group, but that they have branched off from the Dicotyledons, or that both groups have sprung from a stock which resembled the modern Dicotyledons more closely than it did the Monocotyledons.'

Mr. Chrysler, like the other writers quoted, does not appear to see that this close connexion is really due to a common cause, viz. degradation through an aquatic habit of life.

13. THE FORMS AND STRUCTURE OF AQUATIC LEAVES ARE THE RESULT OF THE DIRECT ACTION OF WATER.

In my former paper¹ I suggested that the 'gashes' of some Aroids, as well as 'fenestrations' (e.g. *Anadendrum Monstera*, *Caladium*, *Pothos*, &c.)—recalling those of the lattice-leaved plant (*Ouvirandra fenestralis*), such also occasionally occurring in our pond-weeds—were formerly due to water, and that they are now hereditary in terrestrial species.

The pinnate or palmate forms of the leaves of some Aroids and, perhaps we may add, Palms, the marginal incisions being quite unlike those of a Dicotyledon, may have been acquired in their days of antiquity when submerged.

In support of this contention I can now add that the dissected type of foliage when submerged has been proved experimentally to be due to the degenerating effect of water upon the protoplasm of the stem. Mr. MacCallum succeeded in showing this by setting up osmosis artificially. He dissolved certain nutritive salts in the water in which he grew plants of *Proserpinaca palustris*. The result was just what he anticipated, namely, that the superfluous water, with which the protoplasm of the stem was saturated, was withdrawn, so that the plant was now enabled to bear, and produced subsequently fully developed leaves of the aeriform, pinnately nerved, lanceolate type.²

In the case of *Ranunculus heterophyllus* the dissected type of leaf has been proved, both by Nature and my own experiments, to grow equally well in air after being sown in a border, and is thus hereditary, though it is a character entirely acquired by the *soma*. Sowing the seeds of *Ranunculus heterophyllus* in a garden border, they all came up and developed dissected leaves, but perfectly in adaptation to air. Subsequently the floating type appeared, as if the stem had reached to the surface of imaginary water, and finally the flowers were borne. This heredity of the acquired characters of the foliage lends countenance to the view that the pinnate and palmate characters of Aroids and Palms are due to the same cause, as well as all their other permanent aquatic types of structure.

¹ loc. cit., p. 522.

² Bot. Gaz., xxxiv, p. 106. I have described and figured this more fully in my Heredity of Acquired Characters in Plants, pp. 34 ff. (Murray).

Another common feature of nearly all Monocotyledons and aquatic Dicotyledons is the total absence of hair, 'glabrous' being the characteristic feature of nearly all alike.

14. THE RETICULATED VENATION OF SOME MONOCOTYLEDONS IS ONLY IMITATIVE OF THAT OF DICOTYLEDONS.

An important fact must be noticed. The reticulated leaves of certain Monocotyledons are *not identical* with, but only *imitate*, by approximating the structure of, those of Dicotyledons. The typical monocotyledonous leaf being really homologous with a petiole only, and therefore phyllodinous, has parallel strands. If such be an aquatic plant, it may be so only in comparatively deep water, as *Sagittaria*. If it bear floating leaves, the usual change is to widen the intervals at the upper end by curving the strands so as to make a curvinerved or elliptical blade. This now introduces transverse cross-bars, thereby strengthening the whole. If the blade becomes aerial considerable changes take place; the first is for the two outermost strands to curve downwards, so that the blade assumes a spear-head or hastate shape. By the prolongation of the downward points it becomes like an arrow-head or sagittate. These points may be rounded off and so a cordate form is acquired, being specially adapted, according to Mr. Hiern,¹ for resisting the strain of running water when floating.

The last change or advance is to form tissue between the lower points or fill in the cordate gap. The blade then becomes peltate, as in *Alocasia* and *Nelumbium*, as well as our own *Hydrocotyle*.²

The minuter venation changes with these forms; the first appearance of an irregular network is seen between the small divisions of the first described. The veins, primarily at right angles to the longitudinal strands, become oblique; the number of main strands may be reduced even to three, so that plenty of space is allowed for more uniform reticulations. The blade then closely resembles an ordinary one of a Dicotyledon, but a prominent midrib, like that of a Dicotyledon, is absent in Monocotyledons; for when the leaf is large, as in *Caladium*, &c., a cluster of strands become crowded together, but as their ends successively diverge obliquely across the blade, becoming reticulated, the median cluster is reduced to nothing towards the apex of the blade.

We thus discover that aerial reticulated leaf-blades of Monocotyledons are not *identical*, but only *imitative* of the fibro-vascular system of an ordinary dicotyledonous leaf. The change is very well seen by comparing the small elliptical blades which first arise from the tuber with the subsequent sagittate ones of *Arum maculatum*.

Indeed, one is tempted to speculate upon this fact. For no Monocotyledon would seem to possess a decidedly aquatic form resembling an aerial

¹ Proc. of the Cam. Phil. Soc., Oct. 1872.

² loc. cit., pp. 515 ff.

leaf-blade of a Dicotyledon. Conversely, a submerged leaf of any aquatic plant of this class rarely, if ever, agrees with a Monocotyledon. Thus the ribbon-like form of *Lobelia Dortmanna*¹ and others has really a midrib with lateral ribs branching from it at the base. They subsequently run parallel, *imitating*, but are not *identical* with, say, those of a grass blade or *Sagittaria*. *Hippuris* has a single midrib without lateral ones, and thus is degraded to a very simple condition.

Could, therefore, Monocotyledons have arisen so early as to have *preceded* the reticulated venation of Dicotyledons? The earliest kind of branching venation appears to have been dichotomous, as seen in Ferns (*Adiantum*) and the *Ginkgo* of to-day; but in *Cordaites laevis*, as figured by Dr. Scott² after Renault, the leaf is represented of the simplest kind with parallel venation.

Something of that sort, perhaps, supplied the original type of leaf of Monocotyledons, now represented by the petiole only. This, however, professes to be no more than guess-work and a suggestion only. At all events, as Miss Sargent notes, the cotyledons of Monocotyledons would seem to carry the two strands, one being the relic of a lost cotyledon, with no *third* strand in the place of a true midrib as in Dicotyledons. In some cases, as *Eucomis nana*, according to her description, the two cotyledonary strands approach so as to make a pseudo-midrib 'exactly opposite to the first leaf'.³ It also occurs, she adds, in *Lilium* and *Allium*.

15. REPRODUCTIVE ORGANS.

In the section with this heading⁴ I omitted to allude to the degraded flowers of some aquatic Dicotyledons. Thus the Halorageae, apparently derived from Onagraceae, exhibit several instances of aquatic genera having much reduced flowers, both in size and number of parts, such as in wanting a corolla and being unisexual. Elatineae, again, affords another instance. *Hydrocotyle* has no vittae, in accordance with the well-known fact that oils and resins are much reduced or absent from plants growing in moist regions.

Similarly the degradations of the flowers of Grasses, Sedges, *Lemna*, *Zostera*, and many others are very obvious. On the other hand, as long as the flowers of aquatic plants are visited by insects, there is no reason why they should not resist degeneration in size and attractiveness or number of parts, as is the case in Nymphaeaceae, &c.; though in the Water-crowfoots the flowers are, mostly, considerably degraded.⁵

¹ Bentham spells this *Dortmanni*; Hooker, *Dortmanna*. L. is the authority for both.

² Studies in Fossil Botany, p. 522.

³ Theory of the Origin of Monocots., etc. Ann. of Bot., vol. xvii, p. 19; cp. Pl. I, Fig. 6.

⁴ loc. cit., p. 524.

⁵ See my paper on the Self-fertilisation of Plants, Trans. Lin. Soc., Sec. Ser.—Bot., i, p. 347.

16. CYTOLOGICAL AND EMBRYOLOGICAL INVESTIGATIONS.

Some important researches have been made in the more minute details of embryology, which bear upon this subject.

Messrs. W. Lubimenko and A. Maige have published an article entitled—*Recherches cytologiques sur le développement des cellules-mères du pollen chez les Nymphéacées*.

‘Indépendamment des caractères morphologiques et anatomiques bien connus, certaines particularités cytologiques, comme la grosseur des noyaux et la simplicité de la membrane des grains de pollen, rapprochent cette famille des Monocotylédones. . . . Les études cytologiques faites jusqu’à présent sur le développement du pollen . . . ont permis d’établir des caractères distinctifs assez constants entre les Monocotylédones et les Dicotylédones, et elles peuvent fournir, de cette manière, des documents suffisants pour la comparaison avec les Nymphéacées.’¹

In conclusion the authors add:—

‘Les deux espèces (*Nymphaea lutea* and *Nuphar luteum*) se rapprochent des Monocotylédones par la nature simple du réseau au stade de prosynapsis et par la dissociation précoce des cellules-mères du pollen.’²

Mr. Melville T. Cook has written upon the Embryogony of some Cuban Nymphaeaceae.³ The following is a brief analysis of his paper bearing on the present subject:—

Mr. Lyon, describing *Nelumbo*, considers it should be classed as a Monocotyledon. Cook strengthened his view with *Castalia odorata* and *Nuphar advena*; Schaffner does so by comparing Nymphaeaceae with Helobiae, observing that the number and arrangement of ovules connect the order with Monocotyledons.

The formation of the tube-sac in the embryo-sac is like that of *Saururus* (Piperaceae) (aquatic).

The mention of *Saururus* at once suggests *Peperomia*. Species of this genus have been described by Mr. Hill⁴ and others. Miss Sargent quotes details as follows:—‘There are two cotyledons present in the seed. One is hypogeal and acts as a sucker (comparable with *Trapa*, *Cyclamen*, *Elettaria*, Palms, &c.), the other has assumed the appearance and functions of a foliage leaf. It is geophilous in structure. . . . Its seedlings seem to germinate in the spongy herbage of the locality.’⁵

Mr. Cook calls the ‘tube-sac’ a ‘nucellar tube’. It extends from the antipodal to the chalazal end of the ovule. It originates as a great mass

¹ Rev. Gén. de Bot., xix, 1907, p. 402-3.

² Idem, p. 499.

³ Bot. Gaz., xlii, 1906, p. 376, Pl. 16-18; with Bibliography.

⁴ Morphology and Seedling Structure of the geophilous species of *Peperomia*, together with some views on the Origin of Monocotyledons. Ann. of Bot., xx, 1906, p. 395.

⁵ The Seedling Structure of some *Piperales*. Ann. of Bot., xx, 1906, p. 161.

Miss Sargent discusses the embryology of *P. pellucida* in her Reconstruction, etc. (op. cit., p. 128).

of cells elongated in its direction and rich in protoplasm. These dissolve by disintegration and the tube is formed. The behaviour of the endosperm and nucleus is similar to that of *Sagittaria variabilis*, but this has no nucellar tube.

Mr. Cook refers to Hall as finding resemblances in *Limnocharis*; Strasburger in *Ceratophyllum*; Campbell in *Naias* and *Zannichellia*; all being aquatic plants.

The author calls attention to a probable physiological connexion between the tube and the antipodals in Ranunculaceae, *Sparganium*, and *Vaillantia*, as furnishing nourishment for the embryo. The large lower nucleus formed by a division of the endosperm-nucleus (equivalent to the nucellar-tube nucleus) in *Sagittaria* and Nymphaeaceae showed a resemblance which appeared to indicate a similar function, viz. for supplying food to the embryo through the agency of the endosperm. In *Castalia* (*Nymphaea*) this is done by the 'core' of cells, subsequently by the tube.

With regard to the embryo, there are the following stages of development:—

1. A globular pro-embryo with or without a suspensor, resembling that of *Sparganium simplex* [and *Ranunculus Ficaria*].

2. A cotyledonary 'ridge', nearly circular, enclosing the plumule in the middle. N.B.—This ridge is characteristic of Monocotyledons and is also present in the pro-embryo of *Ranunculus Ficaria*, *Corydalis cava*, *Carum Bulbocastanum*, as also on *Tamus* and *Commelyna*. This ridge represents the commencement of the usual sheathing base of the cotyledon.

3. Two cotyledonary lobes are developed from the ridge, giving the dicotyledonous character.

It may be noted that considerable variation occurs. In *one*, it was so great as to give the appearance of *two equal* cotyledons. [This variety appears to indicate the true dicotyledonous origin, but the ridge being *not quite circular* points to partial arrest of one cotyledon.]

Brassenia and *Cabomba* differ (*a*) in having no cell-walls at first in the endosperm, (*b*) the dicotyledonous character appears very rarely. [Hence these two genera may indicate the more primitive conditions.]

The young embryo of *Nymphaea advena* resembles that of *Lysichiton Kamtschatense* (Aroideae) and of *Ceratophyllum*. Those of other genera are like *Sparganium simplex*, *Naias flexilis* and *Zannichellia*, *Potamogeton* and *Limnocharis*, *Alisma*, &c.

Mr. Cook writes elsewhere upon Nymphaeaceae and *Sagittaria*.¹

In certain Nymphaeaceae the endosperm-nucleus divides into an upper and a lower nucleus, which become separated by a wall formed across the embryo-sac. The upper nucleus forms the endosperm. From the lower

¹ Development of the Embryo-sac in *Castalia* and *Nymphaea*. Bull. Torr. Bot., ch. xxix, 1902.

cell is formed a long tube which grows towards the chalazal end of the ovule, forming a passage by the absorption of the nucellus. It thus plays a nutritive part comparable to that of the antipodal cells in many genera. A similar formation of endosperm has been described in *Sagittaria* by Rendle.¹

The details should satisfy the reader that they are all the result of an aquatic habit of life, thus bringing all Monocotyledons into close connexion with aquatic Dicotyledons.

17. SPECULATIONS ON THE ARREST OF ONE COTYLEDON.

Perhaps the most difficult question to answer is: What were the exact conditions under which one cotyledon was arrested? Such arrest occurs in plants associated more or less with water now, as *Ranunculus Ficaria* and *Pinguicula*, hygrophytes; or which were probably ancestrally aquatic, as all Monocotyledons. But the reduction of the embryo may take place also under other conditions of life, as in parasitism, by drought, &c.

We have seen above that it was clearly proved that the arrest of the intercostal tissue in a submerged leaf is actually due to the weakening effect of water by saturating the protoplasm, so that it is unable to develop a complete blade. From this we may confidently generalize upon the effect of an excess of water upon all parts of aquatic plants.

When we try to connect water with a reduced size of the two cotyledons in the seed or with only one, or again with their total arrest, we are confronted with the fact that existing aquatic Dicotyledons have, as a rule, two cotyledons; but as such aquatic genera or species mostly belong to present terrestrial orders, they are of comparatively modern origin, and we can only assume that heredity has overcome any deteriorating effect sufficient to totally arrest one cotyledon. Still, the size of the cotyledons is not infrequently greatly reduced when in the seed; indeed, they may be arrested in the pro-embryonic condition, so that we seem to see degrees of degradation. Thus:—

1. The embryo may be relatively minute as in Ranunculaceae, in *Dionaea*, *Drosera*, *Gunnera*, and *Eriocaulon*, more or less aquatic plants. On the other hand the xerophytic Holly has a very small embryo embedded in a mass of albumen.

2. In some seeds the cotyledons are small and arrested as compared with the size of the radicle, e.g. *Pinguicula*, genera of Haloragaceae, *Parnassia*.

3. The embryo may remain in the seed arrested at the pro-embryonic condition of an undifferentiated globular mass of cells, as in *Ranunculus Ficaria*, several species of *Anemone*, *Utricularia*, &c.

4. In the next place there may be an inequality in the size of the embryo, as in *Nymphaea*, &c.

¹ See also Class. of Flowering Plants, i, 163 (Rendle); and Bot. Gaz., xxiii, 6, 260.

In *Ceratozamia* it has been shown above that as a seed lies flat on moist ground, the cotyledon on the *lower* side only is developed; but if the seed be kept uniformly moist all round, then both of the cotyledons become developed.

Now, seeds (provided with a fitting temperature) will not germinate unless water be present, either within the seed or acquired from without; so that whatever may be the differential causes acting on the two cells or groups of cells of the pro-embryo, whence originate the two cotyledons, if *one* receive a trifle *more* moisture than the other, it may, perhaps, determine the development of the former in xerophytes, and the latter in hydrophytes.

Miss Sargent has also shown that the two cotyledonary strands, corresponding to the two cotyledons, one of which is present, but carries the strand of the other, are probably never exactly alike, as in *Eranthis* and *Anemarrhena*. If her figures were drawn under the camera, the *size* of the xylem vessels, expressly concerned in carrying water, are not precisely alike,—and such may, perhaps, make all the difference in deciding which blade shall be arrested, as in all Monocotyledons.

However it may have been brought about in the first Monocotyledons evolved, there are too many collateral coincidences, speaking broadly, between water-effects on Dicotyledons and existing Monocotyledons, in all their organs, to gainsay the probabilities that water was, in some unknown way, the primary cause of the monocotyledonous condition.

Monocotyledons were probably first evolved in the early part of the Secondary Epoch as soon as Angiosperms were established from Gymnosperms; and as we do not even know what the first dicotyledonous Angiosperms were like, one cannot avoid speculating as to the process; for no existing order of Monocotyledons can be pronounced primitive with any degree of safety; because degradations are misleading, if any be selected as such, from being of a more simple type.

18. NON-INHERITANCE, IMPERFECT AND COMPLETE INHERITANCE, OF ACQUIRED CHARACTERS.

Since external conditions may graduate one into another, so that mesophytes are intermediate between xerophytes and hygrophytes, so, too, the same species may find it necessary to adapt itself to soils, &c., of more than one kind. To do this the plant retains the power of response to either condition, and the characters acquired in one are *not* necessarily hereditary in the other, as in the case mentioned of normally amphibious plants.

To become hereditary under *any* change of environment, it is necessary, as a rule, for the species to have lived for many generations under the same conditions as those which produced its special characteristics.

A partial inheritance may last for one or two years; just enough to

prove that acquired characters *can* be reproduced under diametrically opposite conditions of life.

I have shown this to be the case with *Ononis spinosa*, &c.¹ If seeds be sown in a constantly wet soil and atmosphere, the spines are at first present, but reduced, in the seedlings. They grow into leafy branches in the second year. Similarly, if there be a warm, moist spring, the spines of the Barberry will grow out into large leaves. So, too, the Beet, naturally a perennial, under cultivation has become a biennial, this character being now hereditary; but it has not prevented its 'bolting' and so *passing* into an annual. Lettuces, on the other hand, are naturally annuals, but when bolting *return* to this condition.

But, in nature, innumerable instances exist which prove incontestably that acquired characters of plants can be maintained quite irrespective of the environment. This is seen in strong xerophytes with massy fleshy stems, such as of the *Aloë* and *Agave* type, as well as the Cactaceous, and in aquatics; of which *Ranunculus heterophyllus*, described above, is a familiar example. Of course, this also applies to *all* terrestrial Monocotyledons.

According to Weismann, acquired characters, derived by the *soma* from changes in the conditions of life, can only be hereditary, provided they influence the germ cells, which are supposed to exist contemporaneously with the direct actions of the environment. Plants, however, are unlike animals, in passing through a more or less extended period of vegetation from germination, during which those activities are at work upon the plant's *soma*, i. e. *before* any trace of reproductive cells exist. It is not until the vegetative activities decline that certain *vegetative cells* pass over into or become *reproductive cells*. The continuity of protoplasm extending from one daughter nucleus to the other *through* the 'equatorial' cell-plate, may be the means of communicating the effects of external irritations, &c., to the very cells which become reproductive germ cells and sperm cells.

It may be suggested that the movements of the chromosomes to the 'north' and 'south' poles from the 'equator' are the means required for making these protoplasmic strands of continuity, whereby the communications are kept up between the surface and the interior.

Dr. Hugo de Vries' experiments on Mutations clearly prove that marked differences in seedlings (greater than the ordinary 'individual differences') may be permanent from their origin, at least under circumstances in which they appeared; for he does not seem to have tested them in markedly different soils. I notice Professor J. S. Henslow found, in 1827, the same thing to occur with Primulas; varieties came up in his sowings, of which he observed that some were permanent, others reverted, &c.²

¹ Heredity of Acquired Characters in Plants (Murray). See also Origin of Plant Structures, 1895, p. 54.

² Loudon's Magazine of Natural History, iii. 406 and ix. 153.

19. ISOLATION AND NATURAL SELECTION.

It may be observed that I have said nothing about 'Isolation' and 'Natural Selection'. Instead of the former, I prefer to say a *new environment*, however the seeds may have happened to get into it. With regard to the latter phrase, Darwin described it as being only metaphorical.¹

I follow his later ecological explanation of evolution; for I find that in all cases, if a quantity of seeds germinate and grow under new conditions sufficient to cause them to vary, they *all vary alike*, i.e. what he called 'definitely', just as Darwin said: 'There can be little doubt that the tendency [i.e. response] to vary in the same manner has often been so strong, that all the individuals of the same species have been similarly modified without the aid of any form of selection.'²

20. CONCLUSION.

Miss Sargent concludes her long and interesting paper on the 'Reconstruction of a Race of Primitive Angiosperms' as follows:—'The hypotheses which have been considered . . . have led to two phylogenetic schemes only, which attempt to explain the evolution of Monocotyledons from Dicotyledons from a common ancestor. The first is that of Professor G. Henslow. The second is the fusion (of the two cotyledons) hypothesis.'

If the *blades* only be thought to be 'fused' then there is no proof of such being the case, as shown by *Ranunculus Ficaria*. But I understand Miss Sargent to mean by 'cotyledons' solely the *strand* or the vascular bundle of the lost cotyledon to be retained in the sheath and petiole of the one present; as she has shown to be the case in *Anemarrhena*.

All I would maintain is that the strand is the last relic of the cotyledon which has been otherwise totally arrested by water.

The reader will now probably have read enough to perceive, *first*, that there is an immense number of *coincidences* which occur among *aquatic* plants of both classes. *Secondly*, that all *terrestrial* Monocotyledons exhibit the same coincidences, but coupled with re-adaptations for living in air. These coincidences afford an abundance of *inductive evidence* of their having had a common origin in ancestral hygrophytes or hydrophytes among Dicotyledons.

Thirdly, experimental verification now covers the peculiarities of the roots, stems, and leaves of Monocotyledons; proving that water *was* the actual source of what Darwin called 'the direct action of the conditions of life', to which the plant responds. Such acquired, aquatic, structural

¹ Origin, &c., 6th ed., p. 65.

² Ibid., p. 72. The paragraph containing this quotation is *not* in the first edition.

characters have become hereditary, and are still retained in *all* Monocotyledons, whether they be aquatic or terrestrial, now.

In the title of my first paper in 1892, I used the word 'Theory', but judging from the very large amount of *inductive evidence* derived from Morphology and Microscopical Histology, coupled with the experimental verifications now recorded, I feel justified in abandoning the term; for I would maintain that the conclusion has passed the stage of hypothesis and probability only, to that of a *demonstrated fact*.

As a corollary it may be added that all the facts herein stated prove incontestably that the morphological and other characters, which constitute the classificatory distinctions between Dicotyledons and Monocotyledons, have all been acquired by the response of the 'soma'—often long before any reproductive organs exist—to the aquatic conditions of life. Such are now permanent and hereditary.

Henslow, G. 1911. "The origin of monocotyledons from Dicotyledons, through self-adaptation to a moist or aquatic habit." *Annals of botany* 25, 717-744.
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