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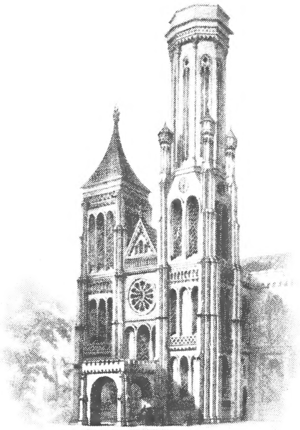

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THE PRINCIPLES OF PLANT-TERATOLOGY

BY

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VOLUME I

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PREFACE.

Dr. M. T. Masters' work on 'Vegetable Teratology' was issued by the Ray Society in 1869. It was a decided success, and a standard work on the subject for many years. It is certainly now out of date, as the mode of treatment of the subject-matter is too much that of an encyclopædia, and too little that of a scientifically-arranged, connected account of plant-abnormalities. Moreover, it is naturally at this date exceedingly incomplete, for, during the last forty-five years our knowledge of abnormal structures has increased enormously.

The present work is intended to present the subject in more scientific fashion, and in quite a new form, both as regards the mode of treatment and the large number of additional facts. While this is the case, the writer is certainly, in some degree, indebted to Dr. Masters for facts and ideas, and to him will always attach the honour of being the pioneer on the subject in this country.

In the present work the subject-matter is treated of under the headings of the various main organs or parts of the plant, *e.g.* root, stem, leaf, and flower, with the exception of the section on Fungi, where the matter is classified under the types of abnormality, as is the case with the whole of Masters' work. At the end of each important section a bibliography of works referring to the subject or subjects treated of is appended. These bibliographies do not pretend to absolute completeness.

The first volume contains a glossary and introduction, and treats of the Fungi, the Bryophytes, and the Root, Stem, and Leaf of the higher plants. The Algæ are not included, as exhibiting too few abnormalities to make description worth while. An historical account of previous memoirs on the subject is not given, as most of the main ones were brought forward by Masters, and since the publication of his work only one teratological treatise of real importance has appeared, *viz.* Penzig's encyclopædic work, 'Pflanzen-teratologie' (of which a new edition is in preparation). But references to earlier publications will be found in the general bibliography following the introduction.

It will be seen that many of the illustrations are taken from the works of other authors. This is quite unavoidable, for if the opportunity of an original sketch or photograph had in every case been waited for, the work would never have been written.

It will be completed in a second volume dealing with the Flower.

The writer is indebted to the Director and other members of the staff of the Royal Gardens, Kew, for the ample facilities afforded for his study of this subject, making all necessary investigations, and for the supply of a considerable amount of material. He desires to thank all those in different parts of the country (too numerous for individual mention) who have so kindly given him interesting specimens during a number of years; no small proportion of these has been obtained at the meetings of the Scientific Committee of the Royal Horticultural Society. He has also to thank Messrs. G. Massee, L. A. Boodle, F.L.S., W. T. Saxton, F.L.S., E. S. Salmon, F.L.S., and W. H. Hammond, for some beautiful photographs. To Mr. Boodle he is also indebted for some important suggestions and discussions bearing on various subjects treated of in the work.

Also to Mr. John Hopkinson, F.L.S., Secretary of the Ray Society, for a great deal of assistance in compiling the details of the bibliographical references.

W. C. WORSDELL.

7th October, 1915.

"It is not enough for the scientific definition and characterization of a body to take account of the properties which it exhibits under normal circumstances. Rather must these circumstances be artificially altered, until they offer occasion for the manifestation of qualities usually latent."—Du Prel, 'The Philosophy of Mysticism.'

CONTENTS OF VOL. I.

LIST OF THE PLATES.

NON-VASCULAR PLANTS.

FUNGI.

PLATE

I.—Fig. 1.—*Tricholoma grammopodium.* Fig. 2.—*T. sordida.* Figs. 3, 4.—*Armillaria mellea.* Fig. 5. —*Tricholoma sordida.*

II.—Figs. 1, 2.—*Lentinus lepideus.* Fig. 3.—*Agaricus Aueri.* Fig. 4.—*Polyporus squamosus.* Fig. 5.—*Lentinus holumbrinus.* Fig. 6.—*L. lepideus.* Fig. 7.—*Aleuria vesiculosa* (*Peziza*). Fig. 8.—*Lactarius torminosus.* Fig. 9.—*Agaricus nanus.* Fig. 10.—*Coprinus stercorarius.* Figs. 11, 12.—*Tubaria furfuracea.*

BRYOPHYTES.

III.—Fig. 1.—*Schistostega.* Fig. 2.—*Andreæa nivalis.* Figs. 3, 4.—*Hypnum serpens.* Fig. 5.—*Molendoa Hornschuchiana.* Fig. 6.—*Bryum pendulum.*

IV.—Fig. 1.—*Ptilium crista-castrensis.* Fig. 2.—*Blyttia Lyellii.* Fig. 3.—*Lunularia vulgaris.* Fig. 4.—*Mnium undulatum.* Fig. 5.—*Orthotrichum Lyellii.* Fig. 6.—*Preissia quadrata.* Fig. 7.—*Buxbaumia viridis.* Fig. 8.—*Bryum argenteum.* Fig. 9.—*Marchantia polymorpha.*

VASCULAR PLANTS.

THE ROOT.

V.—Figs. 1, 2.—*Hedera Helix.* Fig. 3.—*Phaseolus vulgaris.* Fig. 4.—*Vanilla planifolia.* Fig. 5.—*Selaginella Kraussiana.*

THE STEM OR SHOOT.

VI.—Fig. 1.—*Cheiranthus Cheiri.* Fig. 2.—*Asparagus plumosus.*

VII.—Fig. 1.—*Asparagus officinalis.* Fig. 2.—*Pinus Pinea.* Fig. 3.—*Allium Cepa.*

The Leaf.

ILLUSTRATIONS IN THE TEXT.

NON-VASCULAR PLANTS.

FUNGI.

BRYOPHYTES.

VASCULAR PLANTS.

THE ROOT.

THE STEM OR SHOOT.

THE LEAF.

GLOSSARY.

Abaxial, of appendages.—That portion of them which is on the side farthest from the main axis.

Abortion.—A state of imperfect development.

Acicular.—Needle-shaped.

Adaxial, of appendages.—That portion of them which is on the side nearest the main axis.

Adnation.—Union of organs of different nature, or of organs of the same nature but of different grades.

Adventitious (adventive).—Arising out of the normal place and time.

Alveolar.—Relating to the honey-comb-like, superior hymenium of *Morchella* and similar forms.

Anaphyte.—A segmented leafy shoot, built up by a succession of individuals or phytons, each of which consists of leaf-blade and leaf-base.

Androgynous.—Bearing both kinds of sexual organs in different parts of the same inflorescence.

Antheridiophore.—A differentiated branch of the thallus which bears antheridia.

Antheridium.—Male sexual organ of Gymnosperms and Cryptogams.

Antherozoid (= spermatozoid).—The motile male fertilizing body.

Antithetic.—The type of alternation of generations in which the sporophyte is intercalated and inaugurates a method of growth, tissue- and organ-formation, different from those of the gametophyte; a discontinuous type of generation-succession.

Apogamy.—The formation of the sporophyte, or parts of it, directly from the vegetative tissues of the sexual plant, the sexual organs being eliminated from the life-cycle.

Apogeotropic.—Relating to axial organs which grow vertically upward.

Apophysis.—The outgrowth on the adaxial surface of the ovuliferous or other scales in the Abietineæ; the basal swollen portion of the capsule of mosses.

Apospory.—The formation of the sexual plant directly from the sporangium or vegetative tissues of the sporophyte, spore-formation being eliminated from the life-cycle.

Archegoniophore.—A differentiated branch of the thallus which bears archegonia.

Archegonium.—Female sexual organ of Gymnosperms and Cryptogams.

Ascidium.—A pitcher-shaped leaf, or portion of a leaf.

Atavistic.—Reverting to an ancestral condition.

Auricle.—A small, imperfectly-formed, more or less rounded, leaflet or segment occurring on the rachis of a pinnate leaf, either between or below the pinnæ.

Awn.—The extension of the midrib beyond the lamina of the glume in certain grasses.

Axile.—Of shoot-nature.

Axillary.—Seated in the angle formed by the insertion of a leaf on the axis (really on the leaf-base).

Bifid.—Divided half-way down into two.

Bifurcation.—Forking.

Bipinnate.—Of a pinnate leaf in which the leaflets are themselves pinnate.

Bisexual.—Possessing both kinds of sexual organs.

Botrytic.—Branched like a bunch of grapes.

Bract.—The leaf which subtends an inflorescence or a flower.

Bracteody.—The change into a bract.

Bracteole.—A small leaf borne on a peduncle or pedicel.

Bulb.—A structure consisting of an excessively shortened axis bearing fleshy, food-storing scale-leaves, and a central rudiment of foliage-shoot and inflorescence; a modified vegetative shoot.

Bulbil.—A small, axillary shoot, having the general structure of a bulb, but which is probably a modified flower.

Callus.—Parenchymatous tissue formed by the cambium for the purpose (usually) of covering wounds.

Calyculus = epicalyx.

Calyptra.—The old withered neck of the archegonium which becomes carried up on the apex of the sporogonium.

Cambium.—The meristematic generative layer which gives rise to new tissues.

Capsule.—A dry, dehiscent seed-vessel.

Carpellody.—The change into a carpel.

Caulome.—The category to which all organs of shoot-nature belong.

Cladode (= *phylloclade*).—A green, leaf-like shoot.

Cleistogamous.—Relating to self-fertilized, non-expanding flowers; also to moss-capsules which never open to shed their spores.

Cob.—The fruiting inflorescence of the maize.

Coleoptile.—The first plumular leaf in Monocotyledons, ensheathing the young succeeding leaves.

Collateral (of axillary buds).—Occurring side by side in the transverse plane.

Columella.—The central axis of sterile tissue in the capsule of Bryophytes.

Concrescent.—Grown together to form a single structure.

Congenital.—Occurring before birth.

Cotyledon.—The seed-leaf.

Cresting.—The many-graded forking of an organ, or of its divisions.

Crisping.—Copious marginal incision of a leaf.

Decurrent.—Of a leaf-base which is fused, for some distance downward, with the stem.

Decussate.—Of successive leaf-pairs alternately inserted at right angles.

Definite variation.—A non-fortuitous change in a determinate direction.

Depauperization.—Impoverishment.

Dermatogen.—The layer which gives rise to the epidermis.

Dichotomy.—Apical division of an organ, its main body being concerned, into two equal or unequal parts of equal rank.

Diœcious.—Bearing the two kinds of sexual organs on distinct plants.

Distichous.—Having leaves arranged in two rows (one-half phyllotaxis).

Dorsiventral.—Relating to an organ with differently-constituted upper and lower surfaces.

Emargination.—A notching of the leaf-apex.

Emergence.—An outgrowth from leaf or stem, involving both epidermal and cortical tissues, and which does not, as a rule, develop into a definite organ.

Enation.—An outgrowth from the surface.

Endogenous.—Having an embedded origin from the internal tissues.

Endorhizoid.—A rhizoid springing from the foot of the seta of a moss and growing downwards within the tissue of the gametophyte (= the root of the sporophyte).

Entelechy.—Individualising causality (Driesch); the regulative agent within the cell.

Epiascidium.—An ascidium whose inner surface is morphologically the upper one of the leaf.

Epicalyx (= *calyculus*).—The calyx-like structure occurring either immediately below, or intercalated with, the ordinary calyx, but which is of a different morphological nature.

Epicotyl.—The portion of the seedling-axis above the cotyledons.

Epigæal (of cotyledons).—Appearing above the ground.

Epiphyllous.—Occurring on the leaf.

Epiphyte.—A plant which grows upon the surface of the stem or leaf of another plant, but obtains its food-supplies independently.

Erosion.—The deep, rounded marginal incision of a leaf, as if bitten out.

Etiological.—Relating to causes.

Exogenous.—Having a non-embedded origin from the external tissues.

Extra-axillary.—Relating to a branch arising on the stem away from an axil.

Fasciation.—Multiple forking of an axis; ribbon- or fan-growth of an axis.

Fission.—Splitting, division.

Foveolar.—Furnished with pit-like cavities.

Gametophyte.—A plant of the sexual generation.

Gamopetalous.—Having the petals congenitally united.

Gemmæ.—Vegetative reproductive buds which become detached from the parent and grow into independent plants.

Geophilous.—Having a short, squat stem bearing relatively large dominating leaves.

Germ-plasm.—Non-specialized protoplasm which is capable of giving origin to a new individual plant.

Gland.—A secretory structure of the nature of a hair, or an emergence.

Glumes.—The scarious bracts and floral leaves of the grasses.

Haulm.—The shoot of a grass.

Haustorium.—A root modified for the purpose of absorption from the tissues of another organism.

Heliotropic.—Turning towards the light.

Hermaphrodite.—Possessing both male and female sexual organs in the same flower or on the same thallus branch.

Heterophylly.—The phenomenon in which more than one type of foliage occurs in the same species.

Homogenic.—Of the same essential nature because of identity of proximate descent.

Homologous.—Of the same essential nature because of common origin from the same ancestral organ.

Homophylly.—The phenomenon in which only one type of foliage occurs in the species.

Hymenium.—That part of the fungal tissue which is modified to produce spores.

Hypertrophy.—The excessive development of an organ or part.

Hypoascidium.—An ascidium whose inner surface is morphologically the lower one of the leaf.

Hypocotyl.—The portion of the axis of a seedling intervening between cotyledons and radicle.

Hypogæal (of cotyledons).—Remaining below the ground.

Imparipinnate.—Of a pinnate leaf with a terminal leaflet.

Inflorescence.—In the higher plants, a part of the stem differentiated to bear flowers; in Bryophytes, a portion of the thallus differentiated to bear the sexual organs.

Interfascicular.—Occurring between the vascular bundles.

Internode.—The region of the stem between any two nodes.

Invagination.—An infolding of tissues towards the centre.

Involucre.—The aggregation of bracts below the congested inflorescence of Compositæ, Umbelliferæ, etc.

Knaur (burr).—The swollen excrescences occurring on the trunks of some trees.

Laciniation.—Lateral splitting or division.

Lamella.—The gill of an Agaric; the thin laminar outgrowth from a leaf-surface.

Lamina.—A leaf-blade.

Lenticel.—The breathing-pore of a stem or root.

Ligule.—An outgrowth from the upper surface of the leaf-base.

Lobing.—Leaf-division not extending half-way down from the apex nor half-way to the midrib from the lateral margin.

Mangrove.—A plant inhabiting a tropical sea-swamp and possessing air-breathing roots.

Mechanistic.—Relating to machine-like activity in organization and function, without regard to purpose and utility.

Median.—(1) Relating to the main axis (in proliferation); (2) fore and aft (position of leaf-pair of axillary shoot).

Medullary.—Belonging to the pith.

Meiomerous.—Having a small number of parts or organs.

Meristem.—Undifferentiated tissue from which the various kinds of tissue arise.

Metamorphosis.—Transformation.

Monarch.—Having a single protoxylem-group in the stele.

Monœcious.—Bearing the two kinds of sexual organs in distinct flowers on the same plant.

Monopodial.—A type of branching in which the branches are subsidiary to, and therefore in a lateral position on, the main axis.

Morchelloid.—Resembling *Morchella* (morel) in the type of hymenium.

Morel (*Morchella*).—A toadstool having a superior hymenium of the alveolar type.

Morphological.—Relating to the nature and origin of an organ or other structure.

Morphology.—The study, usually comparative, of the nature and origin of plant organs or other parts.

Multifoliolate.—Of a compound leaf with many leaflets.

Multiplets.—Individuals resulting from multiple partition of the ovum.

Mutation.—A form of definite variation in which an entirely new character suddenly arises.

Mycelium.—Vegetative fungal threads of the substratum, = root of toadstool.

Needle.—The xerophytic type of foliage-leaf found in Coniferæ and some other plants.

Node.—The region of the stem where a leaf or leaves are produced.

Nucellus.—The inner portion of the ovule containing the embryo-sac, enwrapped by the integuments.

Ochrea.—The membranous tubular structure, of stipular nature, which encloses the shoot immediately above the leaf in Polygonaceæ.

Ontogeny.—The history of the individual plant or organ from its birth onwards.

Oophyte (= *gametophyte*).—The sexual plant.

Operculum.—The lid or circular covering at the apex of the moss-capsule, above the peristome-region.

Pampinody.—The change into a tendril.

Papilla.—A small rounded outgrowth.

Paraphyses.—Hair-like growths occurring amongst, and protecting the sexual organs in Thallophytes.

Parenchyma.—Soft-walled, non-conducting, living tissue.

Paripinnate.—Of a pinnate leaf devoid of terminal leaflet.

Peduncle.—The stalk bearing an inflorescence.

Peltate.—Shield-shaped.

Perianth.—(1) A floral envelope in which calyx and corolla are alike in colour and texture; (2) the floral envelope generally.

Periblem.—The layer or layers which give rise to the cortex.

Perichætium.—The "perianth" of mosses, *i. e.* the leaves surrounding the sexual organs.

Periderm.—Cork.

Peridium.—The outer envelope of a fungal fructification.

Peristome.—The circle of teeth at the apex of the moss-capsule which regulates the exit of the spores.

Petalody.—The change into a foliar organ having the colour and consistency of a petal.

Petiole.—Leaf-stalk.

Petiolule.—Stalk of leaflet, or subdivision of leaf.

Photophilous.—Growing in the light.

Phyllode.—A foliage-leaf devoid of leaf-blade, and in which the petiole has become flattened and more or less leaf-blade-like.

Phyllody.—The change to a foliage-leaf.

Phyllome.—The category to which all foliar organs belong.

Phyllotaxis.—The leaf-arrangement on the stem.

Phylogeny.—The evolutionary development of the race.

Physiological.—Relating to the life-functions of the organism.

Phyton.—The unit, composed of leaf-blade and its basal part or stalk, which is the fundament of stem-structure; on the "phyton-theory" every stem is essentially built up of a sympodially-developed succession of phyton-units. The phyton is the true *Individual.*

Pileus.—The cap, or spore-bearing part; = flower or fruit of toadstool.

Pinnate.—Lateral incision of a leaf to form two or more leaflets.

Pinnatifid.—Of a leaf, laterally incised half-way, or rather more than half-way to the midrib.

Pinnatisection.—Marginal incision of the leaf as far as the midrib.

Placenta.—The region in the ovary on which the ovules are inserted.

Pleiomerous.—Having a large number of parts or organs.

Pleiotomy.—Multiple apical division; formation of multiplets.

Plerome.—The layer or layers which give rise to the central cylinder.

Plumule.—The portion of the embryo and seedling developed above the insertion of the cotyledons.

Podosyncarpy.—In which the double capsule of a moss has one half fully developed and the other half abortive.

Pollen-sac.—One of the fertile divisions of the anther, containing the pollen; homologous with a sporangium.

Postgenital.—Occurring after birth.

Primary node.—The region of the axis at which the first-formed leaves or cotyledons are inserted. (Applied to Dicotyledons and Gymnosperms.)

Primordial leaves.—The foliar organs first formed after the cotyledons.

Proliferation or *prolification.*—An extension, in the same or another form, of the organ or of subsidiary parts of it.

Prothallus.—The non-vascular individual of the sexual generation in vascular Cryptogams and Gymnosperms.

Protonema.—The green filament, belonging to the sexual generation, which results from the germination of a spore in mosses.

Pseudo-bulb.—An aërial tuberous shoot borne by epiphytic orchids.

Pseudo-stipules.—The basal segments of a leaf (as in *Cratægus*) which have been derived from the *lamina* and not from the leaf-sheath.

Rachis.—The central axis of an inflorescence or leaf.

Radicle.—The root of the embryo and seedling.

Ramenta.—Membranous, scale-leaf-like outgrowths occurring on the petioles and shoots of some plants, *e. g.* ferns.

Rejuvenescence.—The return to a youthful or ancestral condition.

Reversion.—A return to an older, ancestral condition.

Rhizogenous.—Root-producing.

Rhizoid.—The colourless modification of the protonemal filament in Bryophytes serving to attach the plant to the substratum; in Fungi the mycelial threads which serve the same purpose. In both cases the rhizoid may be regarded as a "root."

Rhizophore.—A highly modified, leafless, downward-growing shoot, producing adventitious roots near its tip; it occurs in the Lycopodiales.

Ring or *Annulus.*—The lower part of the ruptured veil, forming a frill upon the stipe, in Fungi.

Ring-fasciation.—A stem-structure, resulting either from dichotomy or fusion, in which the tissues are composed of two concentrically-arranged sets; an external, normally orientated, and an internal, inversely orientated one.

Rudimentary.—Not having a full and complete development.

Sarcody.—The change to a fleshy consistence.

Scale-leaf.—A scarious or fleshy foliar organ, devoid of chlorophyll, situated on the vegetative axis.

Scape.—A completely or almost leafless peduncle, springing from the centre of a rosette of foliage-leaves and bearing a single terminal flower or capitulum.

Schizocotyly.—The forking and multiplication of cotyledons.

Sclerotium.—The compact resting-mass of fungal hyphæ.

Sepalody.—The change into a sepal.

Seta.—The stalk bearing the capsule in the sporogonium.

Short-shoot.—(Spur), in Coniferæ and *Gingko*; a greatly-shortened branch in the axil of a scale- or primordial leaf, which bears scale- and foliage-leaves, or the latter only.

"*Singular becoming.*"—Mechanical causality (Driesch).

Sorus.—A well-defined group of sporangia or conidia.

Spathe.—The large, usually coloured, bract of Aroids and some other plants, subtending the spadix.

Spawn.—The mycelial matrix from which "mushrooms" and edible "toadstools" are grown.

Spine.—A leaf, part of a leaf, or a shoot or branch which has become radially symmetrical and terminates in a hard prickly point.

Sporangium.—The spore-containing organ of the sporophyte.

Sporocarp.—The fruit of the water-ferns (Hydropterideæ).

Sporogenous.—Spore-producing.

Sporogonium.—The spore-bearing structure of anthithetic conformation resulting from fertilization of the ovum in Bryophytes.

Sporophyll.—A foliar organ which bears sporangia.

Sporophyllody.—The change into a sporophyll.

Sporophyte.—A plant of the asexual generation of Bryophytes and vascular plants which produces the spores.

Spur-shoot = Short-shoot.

Squamiform.—Scale-like.

Squamody.—The change into a scale-leaf.

Stamen.—The "male" sporophyll in flowers, consisting, typically, of a stalk or filament bearing a terminal anther.

Staminody.—The change into a stamen.

Statolith theory.—The view which accounts for the tropic movements of organs by the stimulating influence on the protoplasm of the starch-grains or other contents of the cells.

Stipe.—The stalk bearing the cap = stem of toadstool.

Stipules.—A differentiation of the basal, sheathing portion of the leaf, resulting in a lateral leaflet or segment on either side.

Stolon.—A subterranean, horizontally-growing elongated shoot.

Subaxillary.—Occurring a short distance outside the axil.

Subtending.—Of a leaf in whose axil a branch occurs.

Sucker.—A vigorous shoot springing from the stem-base or the root.

Sympodial.—A type of branching in which the main axis is subsidiary in its development to the lateral branches, each one of which alternately assumes the *rôle* of extending the whole shoot- or root-system.

Syncarpy.—The union of fruits.

Syncotyly.—The union of cotyledons.

Teleological.—Relating to *purpose* and *utility* in organization and function.

Tendril.—A leaf, leaflet, stipule, shoot, or inflorescence modified for a climbing function.

Teratology.—Lit. the science of wonders; the department of morphology which treats of the abnormal forms of organs and tissues.

Ternate.—Of a compound leaf with three divisions.

Tetrachotomy.—Apical division of an organ into four equal or unequal parts of equal rank.

Thallus.—A plant in which no vascular tissue, or indications of such, occur.

Thorn.—A leaf, part of a leaf, or a shoot or branch which has become radially symmetrical and terminates in a hard prickly point.

Torsion.—Twisting, without any movement in space of the organ involved.

Tracheide.—Water-conducting element with closed ends.

Traumatic.—Relating to wounds.

Trichome.—The category to which all organs of hair-nature pertain, *i. e.* a unicellular epidermal outgrowth.

Trifoliolate.—Of a compound leaf with three leaflets.

Trigonal.—Three-angled.

Triplets.—Individuals resulting from tripartition of the ovum.

Truncate.—Presenting the appearance of having an apical portion abruptly cut off.

Tuber.—A swollen root or shoot, consisting almost entirely of parenchyma stored with food-material.

Twins.—Individuals resulting from bipartition of the fertilized ovum.

Umbo.—Apophysis (in Coniferæ).

Vaginula.—The withered basal portion of an archegonium enclosing the base of the sporogonium.

Virescent.—Become green, and more or less foliaceous.

Volva.—The envelope enclosing the cap of a toadstool.

Whorl (of leaves).—Two or more inserted at the same node.

Winding.—A stem-movement due to the bending of the axis out of the vertical direction at every turn, as a result of the unequal rate of growth of the tissues at different points of the circumference.

Xerophytic.—Adapted to withstand drought.

PRINCIPLES
OF
PLANT-TERATOLOGY.

INTRODUCTION.

THE EVOLUTION OF PLANT-ORGANS.—One of the most important departments of botanical study is that of the evolution of the forms of plant-life. A particular form which it is desired to investigate from this point of view may be either that of the entire plant, of one of its organs, or of one of its tissues. The present work is mainly concerned with the phylogenetic (evolutionary) origin of the organs of plants. The chief problem to solve is: From what original organ has this or that form or structure been derived in the course of evolution, and what are the changes through which it has passed in order to reach its present condition?

THE THREE CATEGORIES OF ORGANS.—At an early stage of the investigation it became clear to the present writer that there can never have been, so far as vascular plants are concerned, more than three categories of organs* in the past from which all modern structures have descended, viz., stem, leaf, and root, and that even the first of these, viz., the stem, does not really exist at all, so far as morphological origins are concerned, but is built up solely by

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* *I. e.* three main subdivisions of the plant-body.

the bases of the leaves.* Further, these three categories have always, in spite of many apparent intermixtures and transitions, remained distinct from each other. The diversity of form—the well-nigh endless modifications which these three organs have undergone owing to their equally varied adaptations and uses—has misled botanists into imagining either that there are more than three categories of organs or that no hard and fast line exists between any two of them, so that stems may change into roots, roots into stems, leaves into stems, etc. But no one has ever yet demonstrated the existence of any such transitional forms, *i. e.* forms which, at one stage of their individual existence, can be shown to be of the nature of one of the organ-categories, and at another stage can be shown to partake of the characters of another category, with intermediate steps between the two.

Goebel says: "Formerly much controversy turned on the question as to whether a sporangium or an ovule should be considered as a modified hair (trichome), or whether it should rank as a foliar (phyllome), or axial (caulome) structure. At the present it is regarded as immaterial whether it corresponds in position with any one of these organs; its essential importance is discerned in its spore-producing character, that is, ultimately, its functional property." But, while the function of this sporangium and ovule is of great importance, it is surely of not less importance to trace if possible the evolutionary history and origin of these organs and to discover their homologies with other organs.

THE METHODS OF MORPHOLOGICAL INVESTIGATION.—In order to determine the origin, from one of the three categories of organs, of any structure whose present nature is doubtful, and whose mere appearance is perhaps wholly misleading, there are four methods of investigation from which we may choose.

In the first place there is the study of the *ontogeny*

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* This is the phyton-theory, which is here upheld.

or the history of the individual organ during its present life-time, once very fashionable, and still very much in vogue because it is usually held that the developmental history of the individual is a recapitulation of that of the race. There can be no doubt that, in a great many cases, this is perfectly true, and that therefore for such cases this method is perfectly reliable; *e.g.* in order to determine the nature of the "phyllode" of a mature *Acacia*-tree, it is sufficient to grow a seedling, when it can be clearly shown from transitional leaf-structures that the "phyllode" is the petiole of the leaf and not the leaf-blade or the entire leaf. On the other hand, it is equally true that the ontogenetic method of research is not always reliable, but just as often, or perhaps more often, yields misleading data, and sometimes even takes a path which is the exact opposite to that of the phylogeny, *e.g.* the development of an ovule resembles that of a bud more than anything else, and if the ontogeny was our only guide in the matter, we should take it to be a bud, though of a somewhat peculiar type; but if there is one thing which seems more certain than another, it is that an ovule is *not* a shoot; hence, the ontogeny is shown to be absolutely useless for determining its true nature.

Secondly, there is the *anatomical* method, upon which various observers, notably Van Tieghem, have resolutely relied in the past. Darwin also made large use of it in determining the structure of orchid-flowers. But it is a mistake to suppose that internal organization can be relied on by itself for determining the true nature of a doubtful organ; it is, when the question is adequately considered, an inverted method of dealing with such problems, and the reverse of this is true; for internal tissues, such as the vascular tissue, will always be laid down in accordance with the needs of the organ, and therefore, as a general rule, subsequent in time to its external conformation. As a well-nigh universal rule it may be stated that the anatomical method is of subsidiary value for determining the morphological nature of an organ.

Thirdly, we have the *comparative* method, which is pre-eminently serviceable, for a structure, the nature of which is obscure in a particular species, can often be elucidated by comparison with the appearance which it presents in an allied species or genus.

Fourthly, and surely most important and valuable of all, is the *teratological* method. In very many cases the so-called "freaks" and "monstrosities" represent reversions or harkings-back, in one form or another, to an ancestral condition, but this will always take place in a way which is modified by the structure and idiosyncrasies of the organ which is undergoing change. For example, a vegetatively proliferated rose, whose floral organs change into green leaves and become vertically displaced owing to elongation of the floral axis, tells us better than the facts of its ontogeny would, better than those of its anatomical structure, better even than would any comparison of the flower in its normal state with any other type of flower, that the flower has been derived in the past by congestion and abbreviation of an axis, and by the extreme reduction and modification of leafy sporophylls. But it would be absurd to suppose that the leafy shoots from which our flowers originally sprang in any sense resembled, save in the matter of possessing an elongated axis and leafy sporophylls, those into which our modern flowers so frequently proliferate. Under special conditions of nutriment and moisture, the older tendency to break the bounds which an adaptive evolution has placed upon the flower becomes manifested. This is a very different view from that which regards the proliferation as a mere haphazard and meaningless occurrence.

But floral proliferation is not nearly so instructive and so full of meaning in connection with the ancestry and morphological nature of the parts concerned as are certain other abnormalities such as those occasionally shown by the ovuliferous scale in Coniferæ and the ovule in the Angiosperms. Celakovsky has fully, clearly, and convincingly pointed out the nature and importance of these phenomena.

ABNORMALITIES NOT ALL REVERSIONS.—That *all* teratological changes are not of the nature of reversions is shown by the change which the structure of flowers undergoes from the pleiomerous to the meiomerous condition, for the former must be regarded as the more primitive, also by the cases of connation and adnation of organs, of the change from a bipinnate to a pinnate leaf or segment, etc. Indeed, the majority of the cases of simplification are "progressive" rather than reversionary; but it will be noticed that they represent a small minority. Many of these are of great interest as indicating the changes which have already occurred in allied forms along the lines of normal evolutionary development.

THE VALUE OF ABNORMALITIES.—As regards the use and value of abnormalities generally, all botanists have not by any means held the same opinion. For example, members of the Schleiden-Sachs-Goebel school have always tended to emphasise the facts of ontogeny rather than those of teratology; indeed, they have largely disparaged a study of the latter as of slight importance. Goebel admits that "in many cases teratology serves as a fingerpost for the right interpretation of morphological questions,"* and that "we are enabled to obtain, by the study of these malformations, a deeper insight into the homologies of the organs, and especially those of reproduction of the higher plants."†

But he proceeds to state his view that the morphological problems which can be interpreted by means of teratology "are relatively rare and not of outstanding importance." "We must regard the way in which teratology has been developed hitherto as un-

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* Schenk's 'Handbuch.'

† 'Science Progress,' 1895.

serviceable, and the use of malformations for drawing conclusions with regard to normal structures as a mistaken one." "Its function is not to pick out of these 'manifestations of nature' that which the ontogenetic method is totally unable to do, but to determine the conditions under which malformations have arisen."*

Although the botanists who hold this view are very eminent, their arguments fail to convince one that it is anything but pre-eminently erroneous, and will not for a moment withstand close investigation. The firm opinion may here be expressed, on the contrary, that "malformations" are often of great value for solving morphological problems, as will be seen from what is set forth in the pages of this work.

It is important that Goebel correctly admits that "we cannot say where a normal structure ends and an abnormal one begins, both being connected by the most imperceptible transitions."†

A. St. Hilaire says: "The abnormalities of plants are not, as has so often been said, freaks of nature, bizarre irregularities, brought about by chance causes. They are characteristic modifications, whose explanation may always be referred to general principles, simple results of quite common laws of organization."

And again: "One ought not to look for the characters of the monstrosity outside the general organization of the plant; they are only foreign to the species of plant in which the abnormality is found. The abnormal phenomena exhibited by certain individuals are found as normal characters in other plants, and between two flowers, of which one is monstrous, the other normal, there exists often no other difference than that the same character is exceptional in the one and common in the other."

The great authority of Von Mohl may here also be quoted in support of the value of the study of abnormalities: "In order to dissolve the present doubt (as

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* Schenk's 'Handbuch.'

† *Ibid.*

to the meaning of the parts of an anther), the observation of monstrosities is, as in many other cases, more appropriate than the investigation of normally developed flowers, for in the latter it is but seldom, *e.g.* between the petals and stamens of *Nymphæa*, that a gradual transition occurs from one organ to the other, but usually this transition is sudden, so that the method of transition must be guessed at and bridged by conclusions and analogies which are deceptive, whilst in monstrous flowers frequently a retrogression from the form of one organ to that of the preceding takes place, and thus, by means of numerous intermediate forms which sometimes approach nearer to the one, sometimes to the other organ, a gradual change of one form into the other is seen." "Therefore monstrosities offer the chief data, from Linnæus' time onward, for the construction of the doctrine of metamorphosis, and one may indeed assert that, without observations on monstrous flowers, human sagacity would hardly have been in a position to find the right road towards an explanation of floral structure; it still constitutes in many cases the thread by means of which alone we are in a position to find our way through the morphological labyrinth."

Moquin-Tandon says: "It would be an error to regard vegetable anomalies as freaks of nature, as strange or blind irregularities, resulting from fortuitous causes and leaving on the mind a confused memory of inexplicable deformities. Anomalies are particular modifications which can be brought under common, simple, and exact principles which are themselves but corollaries of the most general laws of organization."

Quotations from authorities like these are surely sufficient to confirm and substantiate the writer's own views as to the importance of the study of this aspect of morphology, and to justify the production of the present work.

TELEOLOGICAL VERSUS MECHANISTIC THEORY.—The object in writing this work was not only to cite facts, *i.e.*

to make an encyclopædia; it was not even to answer the question "how" such and such an abnormal structure came about; but it also lay in attempting to answer the question *why* the "abnormal" changes occurred. The title of this work indicates, in fact, a desire to give both a scientific and a philosophic treatment to the subject. It is well to make this attempt, although the great difficulties met with render it very inadequate.

As it should be held that the perfect way in botany lies in facing the question "why?" as well as the question "how?", it is evidently necessary, in the attempt to give a reason for the various teratological phenomena cited, to adopt the teleological* as opposed to the mechanistic attitude. And this view is supported by the physiologist Pfeffer,† who says: "Owing to our ignorance of the exact causal relationship of the different phenomena observed, a teleological explanation becomes more and more necessary, and if properly used it is in its way not only perfectly justifiable, but also capable of aiding discovery and stimulating enquiry when applied to natural phenomena." And again: "The different changes and processes which go on in a living organism must necessarily have a purposeful character."

While some of the explanations attempted from this point of view extend but little, if at all, beyond the region of conjecture, it is, on the other hand, quite certain that any explanations attempted from the materialistic standpoint would, in most cases, fail far more hopelessly.‡

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* *I.e.* dynamic teleological or vitalistic.

† 'The Physiology of Plants,' p. 9.

‡ For the simple reason that they merely answer the question "how?"; they are concerned with the phenomenon of "singular becoming" (in philosophic parlance), not with that of "unifying causality"; with the play of chemico-physical energies, not with "entelechy." Hence, they can never give a real explanation. Bergson has shown that the *intellect* (which is the faculty almost exclusively employed by the average modern scientist) is concerned solely, as its proper function, with the manipulation of the *inorganic* world. So that we need not be surprised at the failure of modern botanists to understand the living plant and its problems. As Bergson says: "The intellect is characterised by a natural inability to comprehend life" ('Creative Evolution,' chap. ii, p. 174, 1914).

The vitalistic position appears to be the only logical one.* Hence, *any* change which takes place, whether normal or abnormal, is assuredly always of the nature of a *definite* variation which, under normal conditions—*i. e.* as a rule in Nature—takes the form of a purposeful adaptation. In the case of so-called "sports," or "monstrosities," which arise under abnormal conditions, as so frequently in cultivation, the change is not of the nature of a purposive adaptation in the usual sense of that expression; it is often, on the contrary, deleterious, as is shown by the instance of completely double flowers. Here, under the influence of a powerful abnormal stimulus, the plant is constrained to take an unusual course in the development of some of its structures, to readjust itself to exceptional circumstances; but even in these cases, as in double flowers, a fasciated shoot, the complete vegetative transformation of a flower into a shoot, the virescent ovule, etc., there is in a sense a purposive adaptation, for no doubt the plant adapts itself in the best way it can to the abnormal conditions. In any case the vitalistic position must here also be upheld, for these abnormal structures are not of the nature of haphazard, fortuitous variations,† are not the result of the working of mere chemical and physical energies, which are always blind, but are to be attributed, equally with the normal structures found in Nature, to the working of a regulative vital force. As Czapek says: "My conviction is that nevertheless physiology cannot be really identical with the chemistry and physics of living organisms. If we consider the explanation of the fundamental problems of life to be the aim of physiology, physics and chemistry will presumably not be able to fulfil this great task for themselves alone."‡ The able philosophy of Bergson also thus concludes: "Before the complexity of an organism

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* For the philosophic *proofs* of it (three in number) see Driesch: 'The History and Theory of Vitalism,' p. 208, 1914, and his other works.

† "Chance is the greatest enemy of thought" (Driesch, *loc. cit.*).

‡ 'Chemical Phenomena in Life,' p. 7, 1911.

and the practically infinite multitude of interwoven analyses and syntheses it presupposes, our understandings recoil disconcerted. That the simple play of chemical and physical forces, left to themselves, should have worked this marvel we find hard to believe."*

Many abnormalities which are of the nature of *reversions*, as in the case of the forking of the alternate leaves at every node on the shoot of *Ulmus glabra*, seem also to be definite variations, and also, in a sense, purposive adaptations, for, under the influence of abnormal stimuli, whereby the balance of the organism becomes upset, latent ancestral tendencies or traits are brought to the surface, resulting in a form which represents the best response which the plant can make to the unusual conditions.

Hence, the Sachs-Goebel theory of "material and form"† seems to fall, as it assumes that "the differences in the forms of the organs of plants depend upon [*i. e.* are due to or caused by] differences in their material components, and that the variations in the organic forms result from variations in the processes of nutrition. Thus the substances which give rise to the formation of a foliage-leaf are different from those which lead to the formation of a carpellary leaf. If this be so, the causative‡ action of the so-called morphological processes may be admitted, etc." Here the mechanism employed to bring about a result is alone

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* 'Creative Evolution,' p. 263, 1914: How different is this conclusion from that of Farmer, for example, who is one of that school whose views the present work is designed to oppose: "Organic form may be regarded as a necessary outcome of the combination of matter and force, without reference to any teleological consideration of use or the reverse"! ("Stimulus and Mechanism as Factors in Organisation," 'New Phytologist,' vol. ii, 1903, p. 193).

† 'Stoff und Form.'

‡ No causality (in the true sense of the word) can ever be attributed to purely mechanistic processes, such as are involved in all these cases. The purely blind chemico-physical energies must be ruled out as the controlling and regulating agents in organization. Theirs is a much more subordinate *rôle*. The whole problem is outside the true domain of physical science, and cannot be solved by its method; one of the mistakes made by writers like H. Elliot ("A Survey of the Problem of Vitalism," 'Science Progress,' Jan., 1915) lies in supposing that the methods of physical science can be applied to the whole series of known phenomena. The agnostic attitude of Mercier is rather to be preferred.

considered. Surely the true initiating cause resides rather in the innate need or necessity of the organism to form a particular structure under the stress of a particular stimulus, this structure being brought into being by the action of a regulative vital force.

Goebel says that, in the case of the development of double flowers, the "question is one of increase in the quantity of the materials out of which the parts of the flower are formed." But though the heaping up of material may be the immediate stimulus, the formation of a petal in place of a stamen would depend on the presence of a regulative force in the plant. In the same way the change of the direction of growth of a root or stem under some special stimulus is not due to gravity as a regulative cause (*i. e.* the true primary cause), but to this same vital force acting in direct response to the needs of the plant. Here, again, investigators show a tendency (so at least their phraseology suggests) to confuse the mechanism employed for the gaining of a certain end with the true cause of the modification. In brief, any morphological change, whether normal or abnormal, is due to a re-adjustment or re-adaptation on the part of the organism as the result of the reception of some unusual stimulus. Between the reception of the stimulus and the modification of structure there is an interval; the action of the stimulus is indirect; the causal nexus between the two is, so to speak, modified half way, and the intervening factor is the instinct* of the plant, which takes in hand the building of the new structure.

The above paragraph is written merely in explanation of the writer's attitude with regard to the etiological aspect of the subject of this work.

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[*] Informed and guided by the past experience of the race.

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NON-VASCULAR PLANTS.

I. FUNGI.

Only the higher forms of this group will be considered. In these the subaërial portion only is dealt with, and not the chief vegetative portion, the mycelium, growing in the substratum. One regards the "mycelium" of the substratum as the root-system, the "stipe" as the stem, and the "pileus" as the flower or fruit.

In dealing with abnormalities in this group great caution is necessary in the interpretation and classification of the various phenomena met with, chiefly on account of the extreme plasticity and simplicity of the "tissues" composing the plant. Nevertheless we can doubtless employ much the same type of classification of the abnormalities here as is done in the case of the higher plants; for, as a matter of fact, we do meet with true counterparts, in this lowly kingdom, of many of the morphological changes with which we are familiar in the vascular plants; and this, for the reason that, as above pointed out, we see the analogical counterparts in the higher Fungi of some of the main organs of the higher plants, just as will also be seen to be the case in the Bryophytes.

A different method is adopted here from that pursued in later sections of this work. Instead of classifying the phenomena under the heads of the organs concerned, Masters' plan will be followed and headings made of the abnormalities themselves.

1. DICHOTOMY AND FASCIATION.

In these lowly plants there can be only one type of branching, though the changes rung thereon may be numerous, and that is: the dichotomous. Monopodial branching rarely obtains in the lower Cryptogams.

Dichotomy.

The simplest case of this phenomenon is seen where the stipe or "stem" bifurcates into two equal arms, involving at the same time a similar division of the cap (pileus). A good instance is afforded by a *Phallus impudicus* described by Rolland; here the stipe was forked a short way from the apex; the apical plate of the fruit was divided into two, each of which was again partially forked (fig. 1).

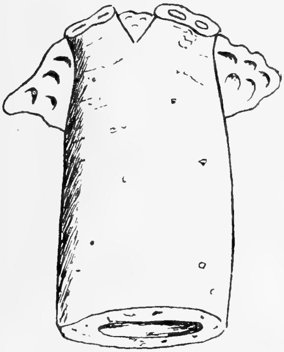

Fig. 1.—*Phallus impudicus*. Imperfect double forking of the apex of the stipe. (After Rolland.)

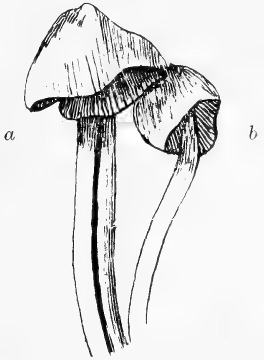

Fig. 2.—*Mycæna galericulata*.
a. Incipient stage of forking.
b. Normal individual.

The writer has seen cases in which, as in the *Mycæna* figured (fig. 2), a median groove along the stipe was the only indication of incipient forking. In another specimen the separation into two equal divisions of the stipe was more pronounced, while two distinct apical knobs occurred on the cap.

Cases of unequal dichotomy into two are more frequent, as in that of *Pratella campestris* observed by Heckel, where the branching occurred at the level of the "ring."

Boudier observed, like Rolland, dichotomy in *Phallus impudicus*, but in this case the branching was very much deeper, and unequal, one of the arms being quite vertical, the smaller one being lateral; both occurred within the same volva. His interpretation of the structure was: fusion, the smaller one being carried up by the larger.

It may here be remarked that it is quite possible that, in some of these cases which look like branching, fusion between two stipes and fruits may be the true cause of the phenomenon; but unless unequivocal evidence of fusion is present, all such cases will be held to be due to forking.

Passing from these cases in which one degree of forking only obtains, we come to those abnormalities whose very remarkable appearance is due to the occurrence of many degrees of forking. The best known instance of this is afforded by *Lentinus lepideus*,* and has been described by many authors, from Aldrovandi in 1671 to Buller in 1906. If grown from the earliest stage onwards *in the dark*, two phenomena occur: excessive elongation of the stipe, and multiple dichotomy thereof, giving rise to a stag's-horn-like structure of the whole fructification (Plate II, figs. 1 and 2). Correlated herewith, the pilei or caps become excessively reduced in size, occurring as tiny knobs at the tips of the ultimate branches, or entirely disappearing as such, rudimentary gills being formed on the sides of the branch-tips. This structure is due entirely to growth in the dark; if light be introduced, pileus-formation and cessation of stipe-elongation at once set in.† A similar case may also be referred to

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* Various names have been assigned to this abnormality in the past, *e.g. Clavaria cornuta, Ramaria ceratoides, Helvella serpentiformis.*

† Not a fortuitous, indefinite variation.

as having been observed in *Agaricus Aueri* by De Seynes (Pl. II, fig. 3).

Planchon observed in *Agaricus ostreatus*, grown in the dark, an excessive formation of crowded twisted branches, giving rise to botrytic and coralloid forms. Klebahn describes and figures a somewhat similar case in *Tricholoma conglobatum*.

Martelli figures what is perhaps one of the most complex and copiously branched specimens ever seen. This was in *Agaricus coalescens* var. *cladonioides*, in which occurred fasciated branches of all grades, the ultimate branches of all being in the form of small stipes bearing tiny caps. He attributes the form to lack of light and moisture.

This same phenomenon occurs in the Polyporaceæ when subjected to similar conditions. There is a specimen in Kew Herbarium of *Polyporus squamosus* forking palmately at the apex of the stipe, and another one forking in stag's-horn fashion. Buller describes good instances of the latter (Pl. II, fig. 4), and Gillot of *P. umbellatus*.

The darkness in all these cases appears to induce the outward manifestation of otherwise latent ancestral features. For we find these abnormal forms occurring elsewhere in the Fungi as perfectly normal structures, viz., in the Clavariaceæ and Xylariaceæ, and these groups are regarded as simpler and older than the Agaricaceæ and Polyporaceæ.

There is one form, found for the first time in Belgium, the branching of which is *not due to darkness*, as it occurs in the light; this is described by Roumeguère under the name *Boletus ramosus*; it is the *Polyporus imbricatus* var. *ramosus* of Fries. It has many cylindric branches covered with tubes.

FASCIATION.

The occurrence, side by side with simple dichotomy, of the more complex phenomenon of *fasciation* is met with here as in the higher plants * An excellent example thereof has been observed in *Armillaria mellea* (Pl. I, fig. 3). Even cases of this sort have been ascribed to fusion by some authors.

We thus see that the phenomena of dichotomy and fasciation, as they are observed in the higher plants, have their exact counterparts in the Fungi.

2. PROLIFERATION.

This phenomenon may be exemplified by such a case as that described by Roumeguère in *Agaricus mundulus*, where a secondary sessile, normally-orientated cap occurred on the top of the primary one; the tissues of both were continuous and homogeneous. De Seynes saw, in *Lentinus holumbrinus*, springing from the top of a rudimentary cap, five smaller stalked fruits (Pl. II, fig. 5). Voglino describes a case of "superior proliferation" in *Clitocybe cyathiformis* and in *Armillaria mellea;* on the pileus arose three small stipes, one centimetre high, ending in minute fertile caps. He, as also Fermond in similar cases, thought he detected in section of the stipe individualised strands of hyphæ traversing the tissues of the stipe and passing into the secondary stipes above; they thus considered that these were merely cases of the enclosure by a stronger specimen of a number of weaker ones. This seems a far-fetched explanation.

What may probably be regarded as a proliferation are those cases where one or more stalked inverted secondary caps occur on the upper surface of the primary one. Fries figures an excellent instance in *Agaricus denigratus*, with a perfectly-formed stiped inverted fruit, the tissues of which are so absolutely continuous with those of the normal one as to practically preclude the idea that it was carried up when young; the object clearly suggests a proliferation.

Then there is the *Russula vitellina*, figured by W. G.

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* For description of "fasciation" see under "STEM."

Smith, where, on one and the same pileus, were a normally-orientated and two inverted caps with rudimentary stipes. He also figures another case in an Agaric with a perfectly central, single, stalked inverted cap, the whole structure concerned being so symmetrical and even as to suggest proliferation rather than any other phenomenon as a cause.

The reason for the inversion of the cap in these cases lies in the fact that, as a rule, similar surfaces tend to come into contact, so that the secondary cap must have its *upper* surface opposed to that of the primary one and its hymenium and stipe directed upwards.

One of the most interesting abnormalities in Fungi is that described by Chifflot as occurring in *Aleuria vesiculosa* (*Peziza lycoperdioides*). For here we see an instance, with which we are familiar in the foliage of the higher plants and probably in the Agarics just cited, of the working of the law of laminar inversion. There occurred one to three extra caps centrally within the primary one. The secondary cap had its hymenial surface directed outwards, *i. e.* immediately opposed to that of the primary cap. The hymenial surface of the tertiary cap was normally orientated, so that the outer surface of this cap was immediately opposed to the corresponding surface of the secondary cap. There was the commencement of a fourth cap whose hymenium, in accordance with the law, was directed outwards (Pl. II, fig. 7). The simplest case of all was that in which, instead of a secondary cap, a single lamina grew vertically upwards from the centre, with, as might be expected, a hymenium on both its surfaces.

There may here be mentioned an isolated case illustrating a wholly distinct kind of proliferation, viz. that of the entire margin of the pileus. Morot noted, in *Psalliota sylvicola*, the occurrence of two "rings," one within the other. A furrow ran all around the lower surface of the cap a certain distance from the margin, marking the former attachment of the upper "ring."

The margin of the cap had then extended beyond this, forming a new set of gills; hence the presence of the lower "ring."

It was stated above that the abnormal growth in the dark of certain Agaricacæ and Polyporaceæ was often largely due to extreme extenuation of the stipes; this may, in fact, occur without any branching whatsoever. In the case of the Polyporaceæ it would seem, as in the case of the *Ganoderma* described by van Bambeke, that the cap also forms part of the proliferated portion, and represents a persistence of the embryonic condition of the spore-bearing tissue.

Brefeld describes four-foot long proliferations of the stipe of *Coprinus stercorarius* when grown in the dark. Buller also describes proliferation of the stipe, in correlation with non-formation of the cap, in *Lentinus lepideus* (Pl. II, fig. 6). This type of proliferation is obviously the simplest of all. It may be compared with the extreme cases of vegetative proliferation of the inflorescence in the higher plants. It doubtless represents an attempt on the part of the stipe to reach the light.

We must next mention those cases in which proliferation takes place at the reverse end, viz. from the base of the stipe. Where the upper surface of the caps of two individuals become fused at an early stage, owing to their growing in very close contiguity, the stronger of the two sometimes wrenches the weaker, stipe and all, away from attachment to the mycelium in the substratum, and at the same time, owing to the expansion and upturning of the cap of the larger specimen, the smaller one comes eventually into a completely inverted position with its stipe directed upwards (Pl. I, fig. 2).

Now Trog observed, in a case like that just described, in *Agaricus alutaceus*, that from the basal end of the inverted stipe a new cap developed. Hence the curious object presented of three caps one above the other. Biers describes a similar case in *Boletus edulis*, and he ascribes the position even of the tertiary cap to its being carried up.

Morot observed in *Lactarius torminosus* that from the centre of a stipeless inverted cap, on the top of the primary one, grew forth a normally-orientated stiped cap. This is an interesting case, for there is here no question of any of the structures being secondarily carried up, as both the secondary and tertiary ones are due to a congenital, median outgrowth (Pl. II, fig. 8).

A quite different case is cited by Boudier in *Ganoderma lucida.* The cap had been broken off its stipe, when from the apex grew a new normal cap and two smaller, incomplete ones.

3. ADVENTITIOUS BRANCHING.

Under this heading may be grouped, although in some instances arbitrarily, owing to lack of comprehension of the phenomenon, those cases of branching which do not seem decipherable either as forking or proliferation, and this owing chiefly to the peculiar position in which the new branches arise.

Van Bambeke describes, in *Mutinus caninus*, the basipetal formation of three or four apparently adventitious branches, each repeating, on ever dwindling scale, the structure of the parent individual. The first and highest of these arose "outside the median plane of the primary fruit, from about the middle of the part comprised between the outer limit of the gelatinous layer of the peridium and the basal end of the fruit."

The present writer observed in three specimens of *Tricholoma sordida* the complete formation of a secondary individual within the tissues of the primary one, viz. within the upper part of the stipe, which is in that region hollow, this cavity being continuous with it and being caused by the splitting of the tissue of the pileus for a short distance above the gill-tissue. In one case the adventitious individual was quite free within the cavity, in other cases its pileus was perfectly fused and continuous with the upper portion of the split tissue of the pileus of the primary individual. In one specimen the adventitious individual was forked, but its two caps had become secondarily fused together. The caps of the adventitious individuals were more or less rudimentary and the gills were not properly differentiated (fig. 3).

Brefeld describes interesting cases of adventitious branching from the tissues of the stipe in *Coprinus stercorarius*, and here we enter upon the rare domain of experimental investigation in fungi. This author excised the caps of extremely young individuals, which were sprouting from the sclerotia, whereupon new stalked fruits sprouted from the ends of the stipes; a most interesting feature was that, at the point where the stipe joined the top of the old stipe-stump, numerous rhizoids were produced by the former. This we may compare with the rhizoid-formation occurring sometimes at the base of adventitious shoots in the Bryophytes. Brefeld cites this as an instance of fructifications being formed without the intervention of a mycelium.

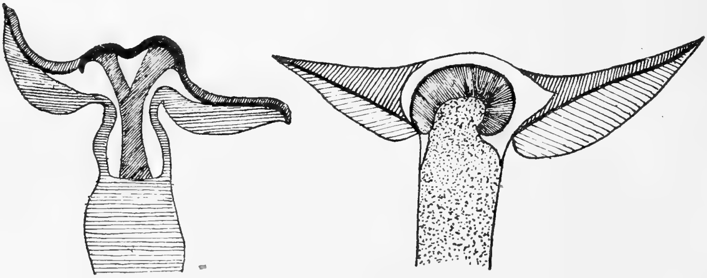

FIG. 3.—*Tricholoma sordida*. Adventitious fructifications arising from the internal tissues.

When the cut surface of the stipe was plastered over, the new individuals were induced to spring from the surface-cells of the stipe. In some cases he caused five individuals to spring from the surface of one stipe; of these one developed ahead of the others, which remained rudimentary.

By successive excision of the caps he obtained three to four generations of individuals, with rhizoid-formation at each point of sprouting. The number of generations was limited only by the duration, prior to exhaustion, of the sclerotia (Pl. II, fig. 10).

Again, young individuals were detached before the stipes had begun to elongate, when, from the cut ends of the stipes thus detached, sprouted new individuals, giving the curious appearance of two caps at either end of a common stipe.

Another form of adventitious branching is seen where the main, and as a rule, immensely larger and stronger stipe bears at different heights from one to many (twenty-five have been observed by Voglino in *Mycæna galopoda*) lateral stipes, each topped by a rudimentary cap. Voglino, who observed this phenomenon also in *Collybia rancida*, amongst others, ascribes it to fusion of several individuals, of which the strongest is represented by the main stipe. De Seynes, on the other hand, who observed a main stipe of *Agaricus nanus* bearing numerous tiny secondary ones near the base, believed it to be a true case of branching (Pl. II, fig. 9). Jacobasch found the same thing in *Marasmius Rotula*, and ascribes it to branching due to rainy weather supervening after a dry period.

Brefeld also found that in the case of the greatly-elongated stipes of *Coprinus* numerous tiny lateral fruits were formed at intervals along the stipe after the latter had ceased to elongate. In some cultures the stipes ceased to form fruits and formed sclerotia instead.

In all the above-cited cases we have to do with adventitious outgrowths from the stipe.

But they also occur in the pileus.

Brefeld found that when the cut ends of the excised stipes were plastered over, adventitious individuals arose from the inner edge of the cap. On the cap being sliced unequally in the longitudinal direction, as many as ten young individuals arose from the cut surface.

Thus he proved that every cell of the stipe, every hypha of the cap, including the gills, may give rise, at every stage of development, to the same hypha-shoots and fruit-rudiments, precisely as in the case of the mycelium of the sclerotium.

He conducted these experiments in order to demonstrate the real vegetative nature of the basidiomycetous fructification.

Wettstein describes three individuals growing from between the gills of *Agaricus procerus* breaking through the edge of the cap, and growing vertically upwards.

Quincy mentions, in *Lactarius pallidus*, the outgrowth, from a furrow on one side of the upper surface of the cap, of a second entire individual.

Trog states that a new cap developed from the upper surface of a triangular piece of the cap of *Agaricus applicatus*, which had broken off and fallen on the ground.

There must next be mentioned the cases of adventitious formation of mycelium, corresponding to the adventitious roots in the higher plants.

The formation of mycelium at the base of adventitiously-arising stipes has already been mentioned. This is quite comparable to the formation of roots at the base of adventitious shoots in the higher plants.

Brefeld cultivated slices of individuals of *Coprinus* which were already differentiated into cap, volva, and stipe, in a decoction of manure, when from every living cell mycelial threads grew out.

He also removed a young undifferentiated fruit-rudiment and soaked it with the manure-decoction, when it grew out into a new mycelium which produced fructifications.

Fully-differentiated caps, when similarly soaked, produced mycelium from all the cells.

4. INVERTED HYMENIUM.

Amongst the most interesting and striking of fungal abnormalities is the occurrence, in the higher forms here dealt with, of the fertile tissue, or hymenium, on the upper as well as on the lower surface of the cap. Its common occurrence and striking appearance are both reasons for attempting an adequate explanation thereof. This will be done when the facts have been cited.

There are two chief forms which this phenomenon assumes. Either (1) the hymenium may uniformly, or in patches, cover the upper surface of the cap, and consist of a foveolar instead of a gill-structure, giving a morchelloid aspect to the whole fruit, or (2) one or more secondary inverted caps may occur on the upper surface.

Superior Hymenium.—The writer has seen an instance of this in *Tubaria furfuracea.* In this case, however, the hymenial tissues were very irregular, constituting a transitional structure between the foveolate and the gill-type (Pl. II, figs. 11 and 12). In *Mycæna luteo-alba* he has seen a much more typical foveolate hymenium which was continuous, by means of an invagination on one side, with the normal gill-hymenium below. W. G. Smith figures forms of *Agaricus furfurascens* which were exactly like morels, and moreover all transitions occurred between them and the normal forms amongst which they grew.

Boudier describes a *Cortinarius*, the surface of whose cap was beset with broad, irregular pores or small alveolæ, 2–4 mm. in diameter and 5 mm. deep, and undulating walls covered with spores. The interlamellar spaces on the lower side of the cap were continuous over the margin with the alveolæ above.

Dumée and Lutz describe a similar *Cortinarius*, but in their case the hymenium only covered a quarter of the cap's surface.

Montague, in Gay's 'Flora of Chile,' cites "*Stylo-*

bates morchellæformis" as a normal form, but it is almost certainly merely an abnormal variation.

Jacobasch describes a *Clitocybe laccatus* whose cap was split into two, and the whole upper surface was covered with gills which were continuous with the lower ones at the split region.

Ferry mentions a *C. nebularis* whose cap was covered with small spheres the surface of which consisted of sinuous, labyrinthiform alveolæ lined with hymenium.

Vuillemin observed in *Hydnum* and *Cantharellus tubæformis* patches of hymenium on the upper surface, due to upturning of portions of normal hymenium and subsequent fusion across of the marginal lobes of the cap, thus cutting off and including the hymenium as islands. In *H. repandum* the cap of one individual became fused on one side to the stipe of another, when that same (upper) side of the cap became covered with fertile projections; hence in this case the latter could not owe their origin to invaginations from the lower surface.

In this same plant Phillips describes the occurrence of several groups of spines on the upper surface, of the same colour and shape as those of the normal hymenium. *The upper part of the stipe* was also covered with similar, but downwardly-directed spines.

Very interesting are the cases afforded by *Polyporus*; this genus seems more susceptible than most fungi to the phenomenon under consideration.

Vuillemin noticed that *P. sulphureus* bore sporiferous tubes on its upper surface when growing in the darkness of tree-hollows. He also observed that in plants growing on roots which were appearing aboveground, disk-shaped and not unilateral caps were formed, with the hymenium directed upwards. A *Polyporus betulinus* was described whose cap was constricted into two portions, one of which was normal, the other with hymenium on *both* surfaces, this being perhaps due to the one half growing out beyond the shelter of the *Polyporus* above. Patouillard has shown that this genus could form abnormal pores on any part of the exposed cap. Jacobasch observed that, on the upper surface of the cap of *P. sulphureus* coming in contact with the moist ground, it produced spores.

Cotton observed that spore-formation constantly ensued on the upper surface of *Sparassis* when it became inverted.

INVERTED CAPS.—There may be left out of serious consideration cases of inverted stalked caps which are obviously the result of a weaker individual being carried up from the ground by a stronger one, after their cap-surfaces had become fused at an early stage (Pl. I, fig. 2).

We are concerned here with a totally distinct phenomenon, which may be divided into two sets, viz., (1) the congenital formation of an inverted cap or caps, from the earliest stage onward, on the upper surface of the primary cap; (2) the formation of the inverted caps by local invagination of the margin of the primary one. It is held, however, that the two sets represent really the same phenomenon, of which (1) represents the final and completed stage of (2), arising congenitally and isolated. In fact, the phenomenon is perfectly analogous to that of ring-fasciation of a flower or capitulum as described in a later section of this work, where we see that the central inverted portion, due in its origin to an invagination of the outer parts, may also arise congenitally, showing no trace of how it came to be there.

The writer has not seen such early stages, but is informed that inverted caps have been seen to arise as small papillæ on the surface of the primary cap, remote from the margin, developing into structures sometimes raised up considerably, on sterile tissue, from the cap-surface, and in the majority of cases not producing a stipe from the centre of the gill-tissue. To this category would belong such a case as that of the *Agaricus fumicola* mentioned by De Seynes, on which there was a central, inverted and stipeless cap which he says could not have been formed by invagination, as there is no sign of any notching of the margin of the primary cap; so he ascribes it to prolification. Here also probably belong the cases observed by Ferry of small, inverted caps, without stipes, on *Clitocybe nebularis*, which arose at first sub-epidermally, and which *he* states were due to smaller individuals being carried up by, and engulfed in the tissues of, the larger one. On the other hand, there may be cases which are intermediate between the two sets of phenomena. Hymenial portions might have become invaginated on to the upper surface at a young stage of the primary cap, and later, by the subsequent fusion across of the marginal lobes, have become isolated, appearing, therefore, in the mature stage of the primary cap as having congenitally arisen in that position. It is just possible that the inverted cap of *Tricholoma grammopodium* shown in Pl. I, fig. 1, may have arisen in this way, as the cap is inclined to one side, which may be that on which the invagination occurred; there was, however, no sign in the specimen of any fusion of lobes on that side, the margin being perfectly even and continuous, so that this also may be regarded as a case similar to those just cited of De Seynes and Fries.

In fig. 4 is seen, in *Clitocybe clavipes*, a good case of imperfectly-formed inverted caps due to invagination at three points of the circumference of the primary cap, for the traces of their origin are obvious. The secondary ones seem to have ordinary gills. In the case of *Tricholoma sordida*, shown in Pl. I, fig. 5, we see an early stage in the formation of an inverted cap by invagination stereotyped and fixed for us in the mature structure; it will be noticed that the most invaginated portion, viz. that nearest the centre of the cap, has a foveolate hymenial tissue, as is also the case with the tiny abstricted portion still further to the inside. This tendency to pass from the gill- to the alveolar structure is, as a rule, characteristic of the inverted caps.

Some of De Seynes' cases are ascribed to invagination.

Ludwig ascribes the inverted caps of *Russula depallens* to splitting of portions of the upper surface; the surface of the wound, instead of cicatrising, formed, during moist weather, gills. If this is so, it is certainly a quite novel and unheard of mode of formation for the inverted structures.

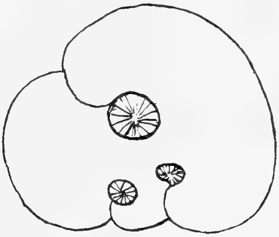

FIG. 4.—*Clitocybe clavipes.* Upper surface of cap, showing three inverted stalkless caps caused by invagination from the lower surface.

Fermond says that the inverted stipeless caps are due to the infolding of the normal hymenial tissue and fusion of the cap-margins behind it; he found all transitions.

Guéguen, on the other hand, appears to regard the phenomenon as due to accident, for he ascribes it to lesion of the edge of the cap.

ORIGIN OF THE PHENOMENON.—The writer may at once state his conviction, surviving in spite of many a protest by mycologists and others, that all these cases of inverted hymenium are the expressions of a partial reversion to an ancestral character.

The most primitive type of fructification is probably that of *Clavaria*, etc., in which a cylindric or club-shaped branch is uniformly covered with hymenium, which extends down the stalk as well for some distance. Buller figures an abnormality in *Lentinus lepideus*, which may be regarded as a reversion to the primitive type (fig. 5). Cases in which the hymenium covers the whole of the upper exposed surface, in the form of a semi-alveolar structure, or labyrinthiform gill-formation, are seen in *Tremella* and *Næmatelia;* and these plants pertain to the Protobasidiomycetes; the Tremellineæ have, according to Maire's classification, branched off laterally from the Auriculariaceæ; and it is from these latter that the Agarics and Polyporaceæ have descended.

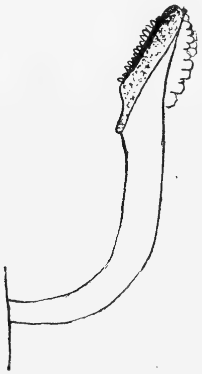

FIG. 5.—*Lentinus lepideus.* Hymenial tissue formed on the side of stipe; cap-formation absent. (After Buller.)

Hence there is some support for the view that the "morchelloid" forms of certain Agarics, described above, are reversions, for this very structure occurs in some primitive forms of the same great group.

The highly differentiated cap of Agarics and Polyporaceæ must be a recent structure, in all probability derived from a "fruit" of simpler construction, in which the hymenial tissue was uniformly and generally distributed.

Abnormal conditions of the substratum, such as excess of food, of the air, or of light, would tend to upset the balance of the organism, and induce a reversion or harking-back of the structure to a simpler form. This involves the transformation of the sterile tissue of the upper surface of the cap into the original fertile tissue. The cap-like form is probably derived from the cylindric by compression, and expansion in the horizontal plane. In fact, we see this original simple structure still retained in the otherwise complex type of *Phallus.* This mode of origin of the "cap" is also clearly shown by such an abnormality as that seen by Buller in *Lentinus* (Pl. II, fig. 1) where the secondary stipes (s^2) are springing from the edges of the rudimentary pileus (p^1) which is here nothing more than the upper, somewhat flattened portion of the stipe. Also the case in the same plant, shown in Pl. II, fig. 4, where gills are arising from the lateral surface of the upper part of the stipe, is very like a reversion to the ancestral condition.

All the cases of invagination of the hymenial tissue on to the upper surface, or the congenital outgrowth of inverted sessile caps, probably represent partial attempts to reproduce, in the midst of, and against the tendency of, the modern structure, the ancestral form. There is too great a tendency nowadays, especially among Continental botanists, to ascribe abnormal structures either to pure accident or to the direct action of the environment without regard to any phylogenetic or hereditary causation. This attitude it seems desirable to oppose.

It is one aptly illustrated by the case of Magnus, whose explanation of the phenomena under discussion was that they represent new formations due to the abnormal habitat. He says that they are not due to splittings of the cap or to invaginations; on the other hand, cases like that of Boudier's *Cortinarius* are to be attributed to modifications of the inner structure: a mutation. In any case, he will have nothing to do with phylogenetic origins.

It is true that in the cases of *Polyporus* cited above the appearance of hymenium on the upper surface was due to the direct action of the environment; but the very ease with which such a change took place points to the fact that the normally sterile tissue is potentially fertile and has once been normally so.

Another ancestral feature which reappears when the recently-acquired sterile tissue of the upper surface becomes changed, by means of the two methods above described, into fertile hymenial tissue, is that in the case of the Agarics the gill-tissue becomes, in that position and in the vast majority of cases, alveolar or pore-producing. Pl. I, fig. 5, shows this very well, where an obvious transition is found; in fact in many cases there obtains a structure which is clearly composed neither of gills nor of pores, but is transitional between the two. Boudier, in speaking of his abnormal *Cortinarius* (above described) states that the change to the alveolar condition is due to the protection which is required for the spores when situated on the upper surface, which a gill-structure would never provide. This is, doubtless, the reason why this structure obtained, and still obtains, in the primitive types which exhibit it, but it can hardly be the explanation of its presence in the abnormal Agarics, which is—a reversion to that primitive condition. The Polyporaceæ and Hydnaceæ represent a more ancestral type, as regards this fertile tissue, than the Agarics. The latter have completely lost the original alveolar or pore-structure. A phenomenon which demonstrates that that is the primitive and the gill-structures are the more recent is shown in the fructifications of *Trametes lobata* and certain species of *Dædalea.* In the development of the cap, the pore-structure, in typical forms, is first produced, later on a transitional structure, and finally (forming the marginal portion of the whole cap) gill-formation entirely supervenes. Here we have, in the ontogeny of a member of the Polyporaceæ, the evolutionary stages which have been passed through in the phylogeny with the Agarics as the result. Some individuals of one and the same species of *Dædalea* have pore-structure only, others have gill-structure only, throughout the lower surface of the cap; others, again, show transitions between the two.

In the evolution of the Agaricineæ we may therefore postulate three changes as having taken place:

1. The production of the horizontally-extended flattened cap-form of fruit from the original cylindric dome-shaped form.

2. The relegation of the hymenial tissue to the lower surface of the cap.

3. The formation of "gills" from the original pore- or alveolar structure.

If the above hypothesis, put forward to account for the abnormal fungi, is not thought plausible, what other cause can be possibly thought of to account for all these abnormal cases? That these are not mere accidents is shown by the fact that W. G. Smith found, on more than one occasion, crops of mushrooms every individual of which bore an inverted cap on its surface. So he concluded that this feature was inherent in the spawn, an observation which surely supports the above general hypothesis.

5. CHANGE OF FORM.

Naturally connected with what was dealt with in the last paragraphs of the preceding section is an abnormality described by Boudier in *Agaricus maculatus*. This consisted in having the majority of the gills cyclically, instead of radially, arranged. There were in this case two sets of normal gills besides the circular ones. Between the outermost circle and the margin there were irregular transverse partitions, often anastomosing, resembling pores. Between the innermost circle and the point of attachment of the stipe were irregular prolongations resulting from fissures in the first circle, and resembling certain *Sisostrema*. The circular lamellæ often anastomose at their base by folds uniting them together. The probable explanation is that the anomaly represents an abortion of the original gills along with an exaggerated development and fusion of the interlamellar folds so frequent in Agarics. This seems probable, and also that this form is a transitional one of a peculiar type. It would appear that the tangential walls of the alveolæ or pores, to which reversion is taking place, have become exaggerated at the expense of the radial ones, except at the margin, where the balanced pore-structure prevailed.

The genus *Cyclomyces* represents a normal stereotyped instance of this very abnormality, but more complete and thorough. It is evidently a transitional type, standing between the Agarics and the Polyporaceæ. Fries places it in the latter, while Léveillé claims it for the former.

Patouillard found in *Psathyra gyroflexa* that the gills throughout the cap were split up into orbicular outgrowths slightly united together. Is this a reversion towards the *Hydnum* condition? W. G. Smith figures an *Agaricus æruginosus* in which the gills were reduced to a regularly-arranged set of teeth, as in *Hydnum*; this, almost certainly, *is* a case of reversion.

Polyporus is particularly liable to change of shape of its fructification. The unilateral bracket-like character is clearly derived from its habitat on the sides of tree-trunks, etc. If grown on a horizontal substratum the cap may be centrally attached to the stipe, as in *Boletus*, etc. Jacobasch observed *incrusted* forms of *Polyporus*, and transitions to these from the normal forms. The incrusted is the normal condition in the section Resupinati.

Morot observed in *Pleurotus ostreatus*, an Agaric which normally has a unilaterally-attached stipe, that the cap was quite circular and regular, the gills hardly decurrent, as in the normal case, and more like a *Clitocybe*.

6. FUSION.

Cases of fusion are very common in Fungi, the hyphal tissues lending themselves extremely readily to this phenomenon. It is by no means always possible to distinguish between cases of fusion and of forking.

Lamotte describes the intimate union of the stipes of two individuals, of which one penetrated the cap of the other.

W. G. Smith observed, in *Geaster fornicatus*, union between the basal part of two plants forming together a single large base.

De Seynes describes in an Agaric the fusion of the bases of the stipes and post-genital lateral fusion of the two caps, the intermediate portion being free.

The remarkable case figured in the 'Gardeners' Chronicle' of 1876 (p. 396) of "twin mushrooms," seems due to the fact that at an early stage the stipe-bases and the central portion of the upper surface of each pileus became intimately fused; later, as growth in length of each stipe proceeded, great stretching took place, causing the stipe-like elongation between the points of union of each cap (fig. 6).

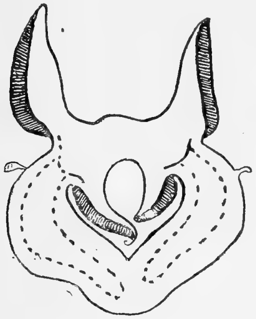

FIG. 6.—*Agaricus campestris.* Longitudinal section showing fusion of two individuals both by base of stipes and centre of caps. (After W. G. Smith.)

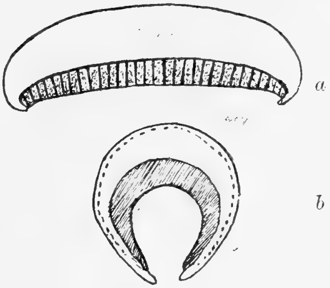

FIG. 6a.—*Agaricus campestris.* *a.* Stalkless fruit. *b.* Young stage showing that the position of the "ring" is at the point of attachment to the ground. (After W. G. Smith.)

7. ABBREVIATION.

This is the opposite condition to that of proliferation. The only case known to the writer which will appropriately come under this heading is that cited by W. G. Smith of a "stemless mushroom" (*Ag. campestris*). The stipe was completely absent. This was due, according to him, to the fact that "the point of attachment to the ground was at the bottom of the veil, at the same point where the veil was ultimately ruptured." This being so, the necessity for stipe-formation seems to have been obviated (fig. 6 *a*).

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II. BRYOPHYTES.

The abnormalities occurring in Mosses and Liverworts will be considered together.

As is to be expected in such a lowly group as the Bryophytes, affording by their simple organization such a restricted field for the occurrence of deviations from the normal structure, the number of different kinds of abnormalities is very limited, and only a small section of this work will be devoted thereto.

1. THE SEXUAL GENERATION.

Vegetative Organs.—*Shoot.*—Dichotomous branching of the stem is very rare in Bryophytes. Hagen figures a remarkable case of multiple forking of the male plant in the moss *Schistostega*, so that the appearance is afforded of a single stem bearing a number of stalked male flowers (Pl. III, fig. 1).

Abnormal branching of the stem was observed by Debat in the moss *Aulacomnium palustre;* as a result of pressure of snow, or other cause, the stem grew *horizontally* instead of vertically, and did not complete its normal development. Lateral, slender branches were given off which grew vertically upwards, and had the general appearance of stolons, bearing leaves of a different shape from the normal. The stem of the liverworts belonging to the Jungermannieæ group is full of resting, growing points; if, as Schostakowitsch found, the stem be wounded in any part, these at once grow out into leafy shoots, affording an interesting case of abnormal proliferation. It was owing to this character that that investigator could not utilize plants belonging to this group for his regeneration experiments.

Von Schoenau has an interesting paper on the branching of mosses. He points out that many mosses have resting, rudimentary, often scarcely-formed, lateral buds. He excised the apex of the stem of several mosses and found that the bud nearest the apex grew out into a branch and gradually pushed over the terminal scar of the excised apex into a lateral, and itself assumed a perfectly terminal position (Pl. IV, fig. 1). The same kind of thing, he points out, occurs normally in species of *Polytrichadelphus*, where the main axis terminates in a sporogonium which eventually becomes pushed over into a lateral position by a new lateral shoot. Sometimes, as the author figures in *Mnium undulatum*, two equal strong laterals appear on either side of the scar of the main shoot, giving the appearance of a forked stem; this becomes still more deceptive when the central scar completely disappears. In other cases, as in *Ptilium crista-castrensis*, lateral buds from the middle and lower regions of the axis developed into shoots when the main shoot remained intact; due to the latter's growth being hindered in some way. Proliferation of lateral branches was also induced in another way: the main shoot of a *Mnium* came, for some reason or other, to lie flat on the substratum, when three vigorous lateral shoots grew vertically upwards therefrom (Pl. IV, fig. 4). He attributes this to the increased moisture and nutrition caused by the main shoot's position. He also caused inhibition of apical growth of shoots of *Polytrichum* by submerging them in water, when numerous lateral branches grew out from no particular region of the shoot. He also made other experiments in connection with the action of light on branch-formation.

The converse phenomenon was observed by Brizi in the moss *Brachythecium rutabulum*, whose buds occurred in the axils of leaves representing shoots whose internodes were quite suppressed and which never elongated, an unusual condition.

Adventitious shoots are very common in Bryophytes.

Necker was the first to induce these shoots by cutting up portions of the thallus of *Marchantia* and *Fegatella.*

Forest Heald found that buds arose directly from detached portions of the stem of the moss *Fissidens*, *i. e.* without the intervention of a protonema.

Goebel found on a detached piece of the thallus of the liverwort *Blyttia Lyellii* that buds arose on the apical portion of the midrib; on a piece of the thallus-wing, *i. e.* devoid of midrib, they were irregularly distributed on the surface (Pl. IV, fig. 2). He made numerous other investigations with the liverworts *Riella* and *Sphærocarpus.* He also describes how in the weak "*Ulvula*" forms of the thallus of *Metzgeria furcata*, whose cells were largely dead, and in which normal growth was suspended, there developed narrow adventitious shoots, without a midrib or rhizoids, which may be even filamentous, representing a kind of reversion to the juvenile form.

Schostakowitsch describes experiments with various liverworts in connection with the regenerative properties possessed by them. In *Preissia commutata* he found that adventitious shoots arose from the surface of the proembryo when placed in semi-darkness. In several others, *e.g.* *Anthoceros*, *Riccia*, and *Lophocolea*, he found that shoots arose on the lower side at the edge of cut pieces of thallus; in some cases rhizoids were first formed, and afterwards, from the same region, young plants sprouted.

Vöchting made numerous regeneration-experiments with liverworts of the Marchantiaceæ-group. He cut off pieces of thallus and placed them on moist sand. As a result fresh thallus-shoots sprouted from the lower side of the midrib at the apical end of the piece, and remained attached to the piece from which they grew. On older pieces, two or three shoots arose. Small bits cut off from the edge of the thallus also produced adventitious shoots, but not so rapidly. An old brownish portion of thallus produced a shoot at the basal end. He obtained the same results as those cited above when he cut off pieces parallel to the surface of the thallus, and also when he isolated bits of the internal parenchymatous tissue. Pieces cut from the upper part of gemmæ-cups also formed adventitious shoots. These experiments were made with *Lunularia vulgaris* (Pl. IV, fig. 3).

Bolleter obtained, with the liverwort *Fegatella conica*, much the same results as those of Vöchting; he found that the adventitious shoots always arose on the lower side of the thallus. He induced artificial production of gemmæ by keeping the thallus for some time in darkness and moisture; they were formed in the same region as that in which the shoots arose.

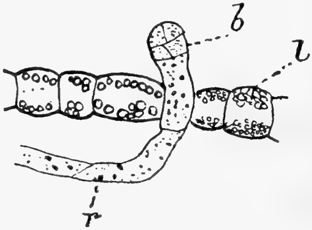

FIG. 7.—*Mnium rostratum*. Transverse section of portion of a leaf, showing origin of a bud from a leaf-cell, together with the previously-formed rhizoid. (After Forest Heald.)

Kreh obtained similar results with several Jungermanniaceous liverworts.

Gemmæ occur normally at the apex of shoots in the liverwort *Cephalozia bicuspidata*.

The above are all cases of adventitous shoots occurring on other shoots.

We next come to those of adventitious shoots sprouting on leaves.

Dozy and Molkenboer describe a very interesting phenomenon in this connection. They observed male plants growing from the upper surface of a leaf of a female plant in the mosses *Macromitrium Blumei* and *M. Braunii.*

Spruce observed in *Jungermannia juniperina* that each of the leaves borne at the top of the stem produced a shoot on its surface; there were no roots formed at the base of the shoots.

Forest Heald found buds originating from the leaves of the moss *Mnium* without the intervention of a protonema (fig. 7).

Massolongo observed buds (with basal rhizoids) arising on leaves of the liverwort *Lophocolea Hookeri* in the position of the two teeth, and evidently replacing them. There was also a smaller bud situated on the leaf-margin (fig. 8). He points out that gemmæ are only known to occur in *L. minor* at all frequently, being rare in other species. This case of Massolongo's differs from those above-mentioned in that the adventitious buds are marginal and not superficial.

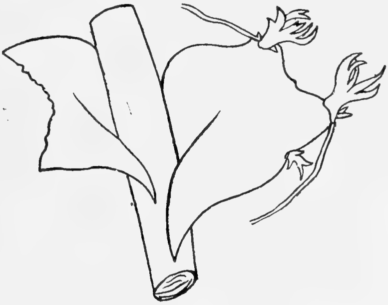

Fig. 8.—*Lophocolea Hookeri.* Adventitious buds arising from the margins of the leaf. (After Massolongo.)

Kreh caused shoots to arise on detached "perianth"-leaves of the liverworts *Scapania nemorosa* and *Cephalozia bicuspidata.*

The *gemmæ*, so frequently occurring in mosses and liverworts, represent special forms of vegetative reproductive organs. They are miniature shoots and may be compared to the bulblets of the higher plants. They are also occasionally formed adventitiously. W. P. Schimper describes the formation of agglomerations of gemmæ at the apex of the leaves of the moss *Orthotrichum phyllanthum;* he also observed them on the leaves of the mosses *Grimmia*, *Syrrhopodon*, and *Calymperes;* in the last-named only the lower part of the leaf developed its parenchymatous tissue in the ordinary way, all the rest being used up for gemmæ-production. They also occur at the apex of the leaf of the liverwort *Diplophyllum albicans.* All these cases are, however, normal for the genera or species concerned; yet they can only represent abnormalities which happen to have become fixed.

Finally, there are the fairly numerous cases of adventitious shoots occurring on the "*inflorescence.*"

Klein, for instance, describes how, in the liverwort *Marchantia polymorpha*, thallus-shoots grew from the "root-furrows" of the stalks of antheridio- and archegoniophores when these were bent down on to the soil; they also occurred on the upright ones, but, in these, were very small and not externally visible. He states that these occur normally as resting-buds.

Bolleter induced shoots to grow from the lower side of the "cap" of both antheridio- and archegoniophore in *Fegatella conica.* None could be obtained from the stalk, the reason of this being that in this plant the stalk is a more ephemeral structure than it is in *Marchantia.*

Vöchting laid the cut-off stalks of the archegoniophores of *Marchantia polymorpha* and *Lunularia*, either entire or in pieces, on moist sand, when in all cases one or two adventitious shoots appeared at the basal end, either on the cut edge or near it. When the "caps" were cut off their stalks and laid on sand, shoots were formed from furrows close to the cut surface on the lower side (Pl. IV, fig. 3 *b* and *c*). If the "rays" were isolated, shoots always arose on them at their basal end. All his experiments were made with inflorescences containing unfertilized archegonia.

Kreh caused shoots to develop from the base of old fertilized archegonia-walls in the liverwort *Aplozia.*

Gemmæ are produced as a normal feature in the position of sexual organs in the moss *Tetraphis;* but besides the gemmæ-producing flowers there are also the ordinary male and female ones. Clos, in a paper the writer has not seen, speaks of male flowers becoming changed into agglomerations of gemmæ, which must mean that the antheridia are replaced by gemmæ, just as ovules in the higher plants are sometimes replaced by shoots.

Leitgeb describes the formation of gemmæ-cups in the place of archegonia in *Marchantia*, as also the occurrence here and there of a completely organized shoot bearing gemmæ-cups, which causes him to suggest that the archegoniophore may represent an entire system of shoots.

Turning now to the sporophyte-generation, Montagne describes the occurrence of gemmæ in the place of spores in the ripe capsule of the moss *Eucamptodon perichætialis*. This is a good instance of apospory in mosses.

A very good example of the same phenomenon in the liverworts has been afforded us by Lang, who induced it artificially in *Anthoceros lævis* by cutting up young unopened sporogonia and laying the pieces on damp sand. From the cut ends grew young thalli which formed rhizoids. He observed that all the shoots arose each from a single cell, and that they mostly had their origin from the subepidermal layer, but that they may arise from any of the wall-layers inwards as far as that which bounds the sporogenous layer. Hence this is a true instance of apospory.

Leaf.—It cannot be said that abnormalities connected with this organ are common in either mosses or liverworts. Brizi records elongation and forking of the leaf in the moss *Homalia lusitanica*. H. N. Dixon cites a leaf of *Funaria hygrometrica* which was forked halfway down. Arnaoudoff describes two cases of leaves in *Mnium punctatum* in which unequal dichotomy of the leaf occurred; in one leaf the lobes were respectively

7 mm. and 6·5 mm. long (fig. 9 *b* and *c*). Györrfy cites similar cases in the mosses *Andreæa nivalis* (Pl. III, fig 2) and *Dicranella varia*. There are a few genera of Bryophytes in which forked leaves are a normal feature.

Under the heading of enlargement and increase of surface of the leaf may be included a phenomenon observed by Potier de la Varde in the moss *Atrichum undulatum*. The seta was surrounded and enclosed by a brown organ resembling a sheathing bract, which he considered to be probably a transformed and modified involucral leaf; the margins of the sheath were united for half its length; it had no midrib, and occurred at the base of the paraphyses; the capsule, perhaps in correlation therewith, was very short and abruptly truncate, and contained only twenty spores (fig. 10).

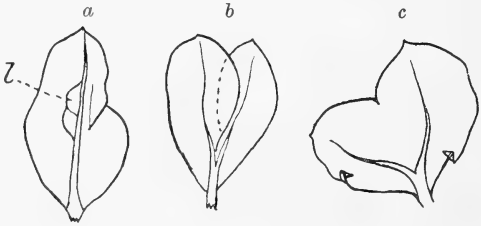

Fig. 9.—*Mnium punctatum*. *a*. Leaf with lamellar outgrowth (*l*) from dorsal midrib. *b* and *c*. Leaves showing unequal dichotomy. (After Arnaoudoff.)

Here also may be mentioned those cases which remind us of the laminar enations on the leaves of the higher plants. Limpricht observed a much smaller secondary lamina arising from the midrib of the lower side of the leaf in the moss *Phascum bryoides*. In the same way Arnaoudoff describes a small lamellar outgrowth from one side of the midrib of the lower surface of the leaf of the moss *Mnium punctatum* (fig. 9 *a*).

Brizi observed two leaves of the moss *Barbula Brebissonii* united halfway along the midrib of the lower surfaces, and in *Orthotrichum leiocarpum* two leaves similarly united by the lower third of their laminæ.

As will be suggested with regard to the same phenomena in the higher plants, the lamellar outgrowths and the union of the surfaces of two distinct leaves may represent one and the same phenomenon exhibiting different degrees of development, or under different forms.

This may or may not be the case. It is not likely to be so if these abnormal outgrowths from the lower surface are of the same nature as the curious lamellar enations from the midrib which occur normally in *Pterygoneura*, *Crossidium*, and *Barbula* on the upper surface of the leaf. In *Polytrichum* they are merely trichomes springing from the epidermal cells. Schimper also mentions the normal occurrence of median lamellæ in *Pottia subsessilis* and *Fissidens adiantoides*.

FIG. 10.—***Atrichum undulatum.*** **Base of seta enveloped by sheathing leaf; paraphyses (*p, p*) at base. (After Potier de la Varde.)**

In contrast to all the above-cited instances of increase of the leaf-surface is that of the leaves of young plants of the moss *Amblystegium glaucum*, which were reduced to their midribs.

Root and Protonema.—In view of their great similarity, these two organs will be considered together. The "root" of the sexual generation is the rhizoid, and this organ would seem to be really homologous with the protonema into which it may change under certain circumstances.

This transformation of the rhizoid into a protonema may therefore be mentioned as one of the main abnormalities which it exhibits. Conversely, the protonema may change into a rhizoid. Kützing placed detached leaves of the moss *Bryum pseudotriquetrum* on sand, when the cells grew out into protonemal filaments which became rhizoids at their ends. Schimper also saw protonema-buds arising from the lower surface of the leaves of the mosses *Orthotrichum Lyellii* and *O. obtusifolium*, which grew into rhizoids (Pl. IV, fig. 5).

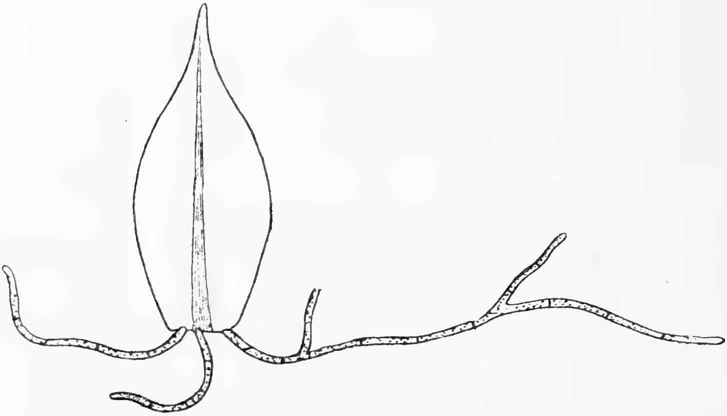

FIG. 11.—*Funaria hygrometrica.* Protonema threads springing from basal end of leaf. (After Schimper, in part.)

Kny describes, in *Marchantia polymorpha* and *Lunularia vulgaris*, a curious kind of pseudo-proliferation of the rhizoid. Secondary and tertiary rhizoids were observed to arise successively within the primary one, giving the appearance of three tubes, one within the other (Pl. IV, fig. 9). In other cases there occurred two or three side by side within the primary one. These supernumerary rhizoids arose from the layer next within that from which the normal ones arise, which shows that the epidermis is not sharply differentiated from the inner tissues. Adventitiously-formed rhizoids are exceedingly common. Vöchting found that when, in *Lunularia*, all the rhizoids were cut off close to their point of origin on the young thallus, new ones grew out from the lower surface.

Forest Heald induced rhizoid-formation, in *Mnium rostratum* and *Funaria hygrometrica*, from both sides of detached leaves in both light and darkness; he found that nothing short of complete separation of the leaf from the stem would induce rhizoids to appear. Fig. 11 shows adventitious protonemata springing from a separated leaf of *Funaria*. In *Funaria* portions of stem torn away with the leaves also produced protonemata. He found that protonemata or rhizoids were only formed from special cells of the leaf-base in *Barbula*, *Brachythecium*, and *Funaria;* and only from special cells of the ventral leaf-surface in *Atrichum* and *Polytrichum;* on the other hand, from *all* leaf-cells in *Mnium*, *Bryum*, and *Phascum*. In *Bryum*, *Barbula*, *Brachythecium*, and *Phascum* protonemata only were formed in light, and rhizoids only in the dark; in *Atrichum* and *Polytrichum* protonemata only were formed in both light and darkness.

Westerdijk caused protonema-formation from leaves, stem, or rhizoids (fig. 12) of mosses by means of mutilation.

Correns also describes numerous cases of adventitious protonema-growth.

Pringsheim found that protonemal threads grew from the cells of the cortical region in cut pieces of the stem of certain mosses.

Goebel observed protonemata growing from the inner side of the calyptra in the moss *Conomitrium Julianum*, and Limpricht found the same thing in detached calyptræ of *Phascum*.

Schimper states that in the moss *Oncophorus glaucus* the perichætial leaves form masses of "proembryonic rhizoids" in their upper part, and that in *Buxbaumia* the marginal cells of the leaves elongated into similar rhizoids. Both cases are normal.

We will now turn to the formation of adventitious protonemata in the *sporophyte generation.*

Stahl experimented with the moss *Ceratodon purpureus;* he placed sporogonia, whose capsules were nearly mature, but with still unripe spores, under a bell-glass in diffuse light on moist earth. He found that protonemata grew from the chlorophyll-cells at the cut ends of the seta. In the case of capsules the chlorophyll-cells of the third and fourth layer from the surface grew out into protonemal threads.

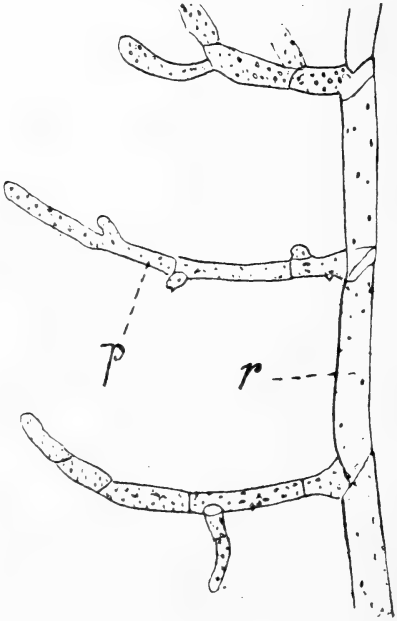

FIG. 12.—*Tortula muralis.* Protonemæ (*p*) growing directly from rhizoid (*r*). (After Westerdijk.)

The classical researches of Pringsheim also are interesting. He induced protonema-formation from chopped-up pieces of the setæ of mosses. He found that it will only take place from cells lying between the peripheral cortex and the central conducting-strand, as this region contains most reserve-stores (Pl. III, figs. 3 and 4). The region in the seta from which the protonemal threads arise corresponds to the zone in the capsule situated between the columella and the wall in which the spore-mother-cell layer occurs. In the case of the vegetative stem it is from an analogous region. The reason, he says, why the peripheral cells of the seta do not form the threads is because they become mature sooner and lose their formative power.

These phenomena observed by Stahl and Pringsheim constitute interesting examples of apospory. But they do not appear to possess any significance so far as affording support to the hypothesis of homologous alternation of generations. As Celakovsky points out, the vegetative sporogonial-tissues of the moss have, with the exception of the peripheral layer of cells, been sterilised, in the course of evolution, from purely sporogenous tissue, so that it is not surprising if many of the cells still possess the potentiality of protonema-formation. This may be, in fact, regarded as a kind of reversion to an ancestral condition, surely a rare statement to make with regard to adventitious-growths in the vegetable kingdom. The real reason why Pringsheim could not induce protonema-formation from the peripheral cells is because this layer has never been sporogenous, like all the internal tissues have been.

There may here be introduced a phenomenon which is of sufficient rarity to be regarded as an abnormality, although it may in reality be normal for the particular species in which it is found.

Goebel has described, in the mosses *Diphyscium*, *Buxbaumia*, and *Eriopus remotifolius*, the emission of tubes from the surface-cells of the foot of the seta which is embedded in the tissues of the gametophyte; the tubes become divided into cells by transverse walls, and may also branch. Györrfy observed that the setal foot of the moss *Molendoa Hornschuchiana* emitted a rhizoid for a distance of 225 μ into the gametophytal tissues; it grew, not straight downwards, but in a very sinuous course, and consisted of several cells, and was quite unbranched (Pl. III, fig. 5). We see that in these isolated cases the sporophyte has a root-system of its own. And this must be regarded as an evolutionary step onward towards a higher differentiation and greater independence of the sporophyte.

INFLORESCENCE.—Coker mentions a kind of fasciation in the archegoniophore of the liverwort *Preissia quadrata*, which was forked above (Pl. IV, fig. 6).

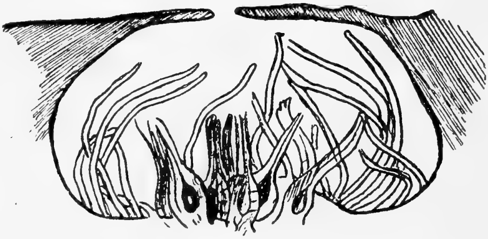

FIG. 13.—*Lunularia vulgaris.* Sessile group of archegonia situated at base of cavity of thallus. (After Miano.)

Proliferation of the flower into a second vegetative shoot, reminding us of the same phenomenon in the higher plants, appears to be of very common occurrence in *Polytrichum commune.*

Bescherelle describes a plant of the moss *Webera annotina* which bore stalked or sessile lateral flowers. In some cases all the flowers were lateral and sessile and the stem terminated in a tuft of leaves. When stalked the flower-stalks were either leafless or leafy. He attributes the occurrence of lateral flowers to branching of the normal terminal one, as they possessed much fewer antheridia and perianth-leaves; the fact that all the flowers were ripe at the same time supports this. He also observed that in some specimens the perianth showed a tendency to split up into subsidiary ones. Sansom appears to have seen a case of division of a flower into two in *Polytrichum commune*, as the two setæ springing from the apex of the stem were each surrounded by a distinct perichætium.

Following on these cases of branching of the inflorescence, we meet with a case of "abbreviation." Miano observed in *Lunularia vulgaris* sessile archegonia occurring in pockets of the thallus in which normally archegoniophores occur, thus approaching the normal condition of *Aytonia* and *Clevea* (fig. 13). He also observed archegonia situated laterally on a wart-like excrescence, suggesting the condition of *Corsinia*; also on short-stalked archegoniophores, but still included within the pocket. Ekstrand mentions the fusion of female flowers in *Nardius hæmatosticta*.

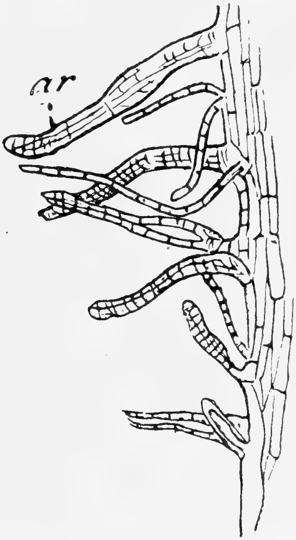

FIG. 14.—*Mnium undulatum*. Archegonia (*ar*) growing laterally on the stem. (After Westerdijk.)

Westerdijk mentions a curious case of either reduction or displacement, probably the latter, in *Mnium undulatum*, in which he noticed archegonia occurring in a lateral position on the stem; it was not the result of wounding (fig. 14).

The changes due to *metamorphosis* and *hermaphroditism* must be next considered.

Cutting noticed a curious condition of affairs in *Marchantia palmata.* In the archegoniophore there was an outgrowth from the lower side of the disk or cap; the upper surface of this outgrowth was directed downwards and bore antheridia, while its stalk bore archegonia at the base. This case is remarkable owing to the fact that a new male branch is formed long after the whole inflorescence has been definitely differentiated as a female one (fig. 15 *a* and *b*).

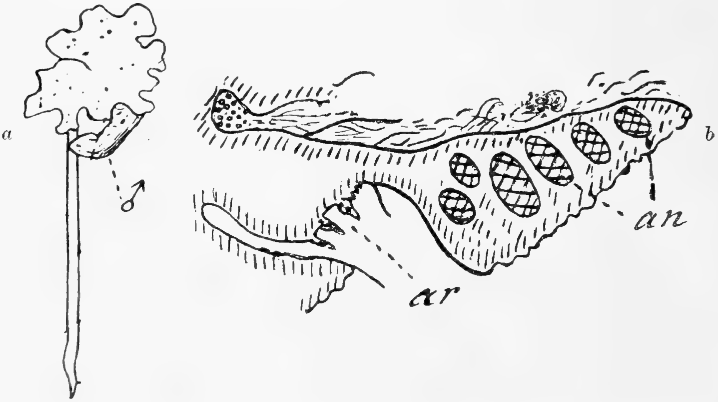

Fig. 15.—*Marchantia palmata.* *a.* Archegoniophore showing a male outgrowth. *b.* Hermaphrodite branch from an archegoniophore. *ar.* Archegonia. *an.* Antheridia. (After Cutting.)

Ernst observed mixed inflorescences in the liverwort *Dumortiera*, both in the diœcious *D. velutina* and the monœcious *D. trichocephala.* Goebel found in the liverwort *Preissia commutata* that the abnormal androgynous inflorescence bore antheridia on the upper surface of the front side, and archegonia on the lower surface at the back. He does not, however, consider it a reversion to an ancestral monœcious condition.

In the same plant Townsend found antheridia present in what, from its shape, was undoubtedly an archegoniophore in the first instance.

In *Physcomitrium eurystoma* each plant had three kinds of shoots: male, female, and hermaphrodite, according to Ruthe, who found antheridia at the base of the archegonia in the female shoots.

C. Müller found, in *Leucobryum giganteum*, the archegonia transformed into "branchlets," and no paraphyses present, while the perichætium was exuberantly developed. Antheridia occurred on these female plants. He had never previously found male flowers anywhere. The plant is normally diœcious.

Lindberg found in the moss *Brachythecium erythrorhizon* transitions from archegonia to antheridia.

Limpricht also observed transitional structures between antheridia and archegonia in the liverworts *Jungermannia Kaurini* and *Cephalozia Gottschei.*

Ekstrand describes the transformation of a male branch into a vegetative shoot in the liverwort *Harpanthus Flotowianus.*

Marchal made the very interesting observation that the moss-plants which were produced by regeneration of the sporophyte of diœcious forms were hermaphrodite.

All these phenomena clearly suggest that, firstly, the hermaphrodite condition is the original, primitive one, and secondly, that there is no essential or real distinction between the two kinds of sexual organs, just as is also apparent from transitional structures observed in the higher plants. Marchal's observation seems to show that the mode of origin of moss-plants by regeneration of sporophyte-tissues upsets the balance of the organism and causes it to revert to an ancestral condition.

The final subject which will be treated of in connection with the sexual generation is that of the *multiplication* or *reduction of the sexual organs.*

The former phenomenon appears to be rare. Warnstorf mentions a case of a second much smaller antheridium branching off from the base of another immediately above its short stalk in the moss *Fontinalis antipyretica.*

Brizi mentions several cases of reduction. In the moss *Eurhynchium circumnutans* the antheridia were reduced in number in the male flowers, while the female flowers were sterile. In the moss *Hypnum triquetrum* the archegonia of the female flowers were aborted. In *Brachythecium velutinum* the female flowers were devoid of archegonia.

2. THE SPOROPHYTE GENERATION.

"DOUBLE" SPOROGONIA.—This is undoubtedly the commonest abnormality met with in the sporophyte generation. Moreover, no abnormality in Bryophytes, with the possible exception of apospory, has given rise to a greater number of theories to account for its cause or meaning.

Schimper was one of the first to record "syncarpy," as it was called, in a number of different mosses. In these the capsule gave the appearance of being forked in varying degrees, sometimes only slightly at the apex, sometimes halfway down (fig. 16 *b*), in other cases again to the extreme base, this last producing the phenomenon of twin capsules borne on a common seta (fig. 16 *a*). He ascribes the phenomenon to the fusion of two sporogonia arising from two different archegonia which have come into contact in the receptacle, *i. e.* in the apex of the vegetative stem. Györrfy observed unequal forking of the capsule on a common seta (Pl. III, fig. 6) in a species of *Bryum*.

Le Dien, who observed much the same thing in the moss *Trichostomum rigidulum*, says that it is due to the formation of two capsules belonging to the same archegonium and subsequent fusion of their pedicels.

Bescherelle agrees with Schimper, but emphasises the point that both archegonia which have fused must have been fertilized or no "syncarpy" could have occurred.

Durieu de Maisonneuve observed a double capsule on a common seta situated within a single calyptra, which seems to point to origin from one archegonium. This was in *Sphagnum contortum.*

Györrfy observed in *Plagiobryum demissum* two capsules on one seta; both arose from a common "neck" at the apex of the latter. He cites Bruch's observation of two setæ of *Polytrichum alpinum* occurring within the same calyptra. He concludes that the phenomenon is due to abnormal development of the same ovum and not to fusion of two adjacent archegonia. He also observed in *Dicranum Blytii* that the seta was forked into two unequally-long arms, each bearing a normal capsule. Ballé saw the same thing in *Pogonatum,* in which one arm was larger than the other.

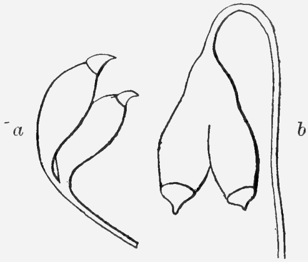

Fig. 16.—*a. Bryum cæspiticium. b. Brachythecium plumosum.* Double capsules. (After Schimper.)

Gottsche observed two to three capsules on a common stalk.

Györrfy observed in *Buxbaumia viridis* two sporogonia springing from the same vaginula, quite distinct from each other; one of them was shorter, and bore a rudimentary, sporeless, transparent capsule (Pl. IV, fig. 7).

Mönkemeyer observed in *Bryum argenteum* all stages of forking of the capsule; it is interesting to note that in this case he was able to trace the phenomenon to insect-bites at the apex during the young stage of the capsule (Pl. IV, fig. 8).

Leitgeb, whose paper is not at present accessible to the writer, ascribes the phenomena of "double" sporogonia to the fact that the growing point of the developing sporogonium had become injured by some external agency such as frost, as a result of which lateral cells assumed its *rôle*.

Györrfy gives the following brief summary of the views held on the origin of "double" sporogonia of Bryophytes, which are amplified here and there by remarks within brackets:—

1. Entry of two antherozoids into one archegonium [giving rise to formation of two capsules and subsequent fusion of their setæ].

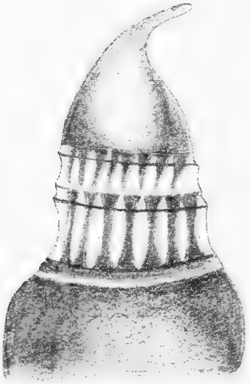

FIG. 17. *Bryum saxonum.* Apex of capsule showing three tiers of peristome teeth. (After Mönkemeyer.)

2. Development of two egg-cells in one archegonium (Brongniart) [Hofeneder] (Le Dien).

3. Fusion of two sporogonial embryos belonging to two different archegonia (Schimper, Bescherelle).

4. From one egg-cell (Pfeffer, Leitgeb [Györrfy] [Mönkemeyer in *Bryum argenteum*]).

In connection with the second and fourth theories it may be mentioned that two egg-cells in a single archegonium have been described by Coker in *Mnium*, by Bliss in *Polytrichum juniperinum*, and by Hofeneder in *Bryum cæspiticium*.

Hypertrophy, etc.—A few curious cases of hypertrophy or development of extra structures in the capsule must now be referred to.

Mönkemeyer describes in the moss *Dicranella varia* two sets of mutually inverted peristome-teeth as occurring between the main part of the capsule and the operculum. In *Bryum saxonum* there were three sets: two as in the previous case, and a third uppermost one arising from the edge of the lid and projecting free into the peristome-cylinder below (fig. 17); in all three sets the peristome-teeth are much shortened.

Brizi observed, in the moss *Homalothecium sericeum*, lateral hypertrophy of the apothecium, which was full of starch and other granules.

The final abnormality which is worth while mentioning is the occasional occurrence of cleistogamous capsules observed by Mönkemeyer in *Bryum saxonum*. Györrfy also describes capsules of *Splachnum sphæricum* which consisted of an apophysis only, no fertile portion being present, this being attributable to injury.

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VASCULAR PLANTS.

I. THE ROOT.

The root is less prone than any of the other organs to deviate from the normal form, which is probably due to its usual location in the comparatively uniform environment of the soil, where the factors which induce variation are very much less numerous and varied than they are above-ground. Most examples of abnormal roots occur above-ground.

The abnormalities in roots may be grouped under four headings: (1) Branching; (2) Fusion; (3) Change of Direction; (4) Adventitious.

1. BRANCHING.

MONOPODIAL.

Those plants which have tap-roots, representing the later development of the radicle of the seedling, usually produce lateral roots of relatively insignificant development which becomes still more marked when the tap-root is swollen and fleshy. Owing to abortion of or injury to the tap-root, or part of it, in the carrot (*Daucus Carota*), several of the lateral roots may become very greatly developed, equalling in thickness the original mother-root and often giving rise to fantastically-shaped structures. Trécul describes in the beet (*Beta vulgaris*) a lateral root which, owing to its puncture by an insect, became greatly hypertrophied. Caspary figures a root of the rape (*Brassica Napus*) whose rootlets had developed as fleshy tubercles.

Lateral roots which, under normal circumstances, are but little or not at all developed, can be induced to do so by artificial mutilation, as by excision, of the apex of the main root. Goebel describes and figures a case in the Ternstrœmiaceous plant *Norantea guianensis* in which a species of sympodial branching was induced in the long branchless descending aërial roots by the excision of the apices of the main root and the successively-formed lateral roots; and he describes the same kind of thing for the aërial roots of *Vanilla* (Pl. V, fig. 4) and *Monstera*, and in the root of the broad-bean seedling. Miss Chandler describes aërial roots of *Tibouchina* whose tips died away, causing a sub-apical profuse formation of lateral roots, and sometimes a fasciation-like flattening of the tip.

Forking and Fasciation.

The various cases known of palmately-divided tap-roots, in the carrot, turnip (*Brassica Rapa*) (fig. 18), radish (*Raphanus sativus*), and parsnip (*Pastinaca sativa*), would seem, from their appearance in the mature condition, to be due to fasciation (see *infra* under Stem), as the thick basal portion of the main root is divided up at the apical end into a number of branches. But this condition might quite well have been brought about by the early abortion or dying away of the main root, causing the rapid and equal development of a number of lateral ones, the original mode of growth becoming obscured in the mature structure.

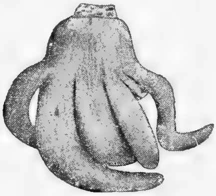

Fig. 18.—*Brassica Rapa*. Abnormal lateral branching, probably due to abortion of the main root.

Fermond describes forked roots in the turnip, fennel (*Fœniculum vulgare*), and salsify (*Tragopogon *porrifolius*). One cannot say whether this is true forking or a case of abortion of the main root with hypertrophy of the two lateral roots; either phenomenon might yield the same appearance.

The tuberous roots of *Orchis* and *Ophrys*, with their apical division into a number of separate tips, may be regarded as normal examples of fasciated roots; the vascular structure supports this, for in the tuber-lobes there may be present more than one vascular cylinder.

The apogeotropic, coralloid respiratory roots of Cycads must probably also be regarded as instances of normally fasciated roots.

Miss M. Rathbone sent the author some aërial roots of the ivy (*Hedera Helix*) from Neston, Cheshire, which showed, better than he has seen elsewhere in the vegetable kingdom, examples of dichotomy or forking and of fasciation, with gradual transitions between the two phenomena. Caspary in 1882 observed the same phenomenon in this plant and gives a beautiful figure of it. At the point of its attachment to the stem the root is quite narrow and apparently cylindrical in contour; but Caspary, in studying the development, found that the section of the root at this point was really oval in outline, and that the zone of tissue in the stem from which it arises is exceptionally broad in the tangential direction, the root thus arising from the first as a more or less flattened organ; however, as growth proceeds the root expands more and more in fan-like fashion. It may subsequently fork neatly into two equal arms, one of which may grow more rapidly than the other and fork again equally; or successive dichotomies may take place, one arm, often, apparently, on the same side, developing ahead and expanding in fan-like fashion, until at the apex it appears to branch simultaneously into a number of various-sized short branches; at the same time the whole root, owing to unequal rapidity of growth on the two sides, becomes slightly twisted (fig. 19). Some roots merely reach a club-shaped condition, swollen towards the apex, but quite unbranched and unflattened; such represent transitions between the simply forking and the fasciated condition (Pl. V, figs. 1 and 2). The forking and fasciated roots bear a number of lateral branches which represent the weaker arms of each successive forking which have been left behind, the same phenomenon which occurs in forking stems and leaves; a normal case of this is well seen in the stem of *Selaginella*.

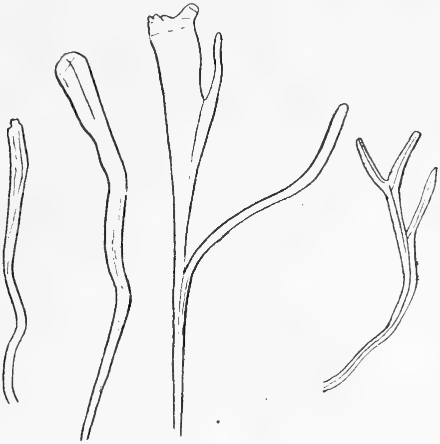

Fig. 19.—*Hedera Helix*. Roots showing incipient forking and fasciation.

The extreme fasciated condition yields a structure greatly resembling the thallus of the Alga *Zonaria*, even having the same zone-bands (Pl. V, fig. 2).

Interesting cases of fasciation of aërial roots in the orchids *Aërides crispum* and *Phalænopsis Schilleriana*, as also of the roots of aloe, have been figured or described in the 'Gardeners' Chronicle.' These showed conspicuous spiral curvature, and in the case of the aloe, similar transitions between simple dichotomy and fasciation to those above-described.

Fermond gives cases of fasciated lateral roots in *Phaseolus multiflorus*, one of which was 24 millimetres long and 7 to 8 millimetres in breadth, and terminated in four rootlets of variable length.

In *P. vulgaris* slight fasciation of some of the lateral roots was induced by excising the radicle of the seedling at an early stage of its development. This is a counter-phenomenon to the fasciation of the lateral branches induced by excision of the main plumular axis (Pl. V, fig. 3).

2. FUSION.

Postgenital.

The facts which are known of the union by natural grafting of two roots belonging to two distinct plants, such as that of two carrots figured by Masters, has, of course, no morphological significance. The same may be said of the similar grafting which occasionally occurs between two bark-forming roots of the same or of two distinct plants as in *Ficus scandens*, beech, spruce, pine, etc., in which by mutual pressure the union occurs as deeply as the cambium, so that eventually bast and wood common to the two roots is laid down.

In the ivy and the asclepiad *Hoya carnosa* it frequently happens that two aërial roots of the same stem may arise very close together and during growth outside the mother-stem may become pressed and flattened against each other along the greater part or the whole of their length; tangential and radial divisions occur in the epidermal cells of the uniting sides of each root forming a pseudo-parenchymatous tissue common to the two roots. In a case like this the union does not extend more deeply than the cortex. In view of the crowded arrangement of the roots of the ivy on many parts of the stem, union between any two roots is not a surprising phenomenon.

Congenital.

Franke made an interesting observation of this type of union with regard to the aërial roots of the Virginian trumpet-flower (*Tecoma radicans*), and also in the roots of *Rhus radicans.* The roots occur in rows of four or five. There is at first a common rhizogenous meristem out of which the separate root-apices become differentiated, and these form the common dermatogen- and periblem-tissues of the compound root.

There is thus a congenital union of the dermatogen to form a common root-cap and a similar union of the periblem to form a common cortex; there are, however, three distinct plerome-tissues giving rise to three separate vascular cylinders. The presence of separate apical meristems and of separate vascular cylinders is an indication that we are here dealing with a congenital fusion of distinct roots (fig. 20).

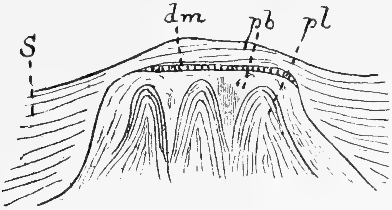

Fig. 20.—*Rhus radicans.* Three congenitally-fused rootlets with the plerome of each distinct. (After Franke.) *S*, tissue of mother-stem. *pl*, plerome. *pb*, periblem. *dm*, dermatogen.

On becoming freed from the mother-stem the individual roots tend to separate mechanically, each growing thereafter greatly in length. Fermond seems to have observed a similar phenomenon in the willow (*Salix*), where three rootlets were seen to emerge from the same lenticel on the parent-root; they were congenitally fused.

Conclusions.—The abnormal cases of root-branching above described are obviously all due to hypertrophy. When the main root is absent or poorly formed, the lateral roots, by correlative growth, develop in such a way as to supply its place. The fasciated roots represent merely a particularly luxuriant mode of growth, from what cause we do not know. All that will be said in regard to the morphological explanation of fasciation in the stem will apply equally to the root; the phenomenon is the same in both; hence this explanation will be deferred until the stem is treated of.

The cases of fusion described are of much value, for they show us clearly the difference between post- and congenital union and fasciation of organs. In the *Tecoma*- and *Rhus*-roots the congenital union, Franke points out, is comparable, not to the development of a gamopetalous corolla where the free tips are the first parts to be formed, but rather to the leaf-sheath of *Equisetum* in which the separate teeth are formed subsequently to the common ring-wall. The structure in *Tecoma* and *Rhus* is clearly of a compound nature, as the presence of three plerome-cylinders indicates; a fasciated root is always a single, uncompounded structure, dividing above, and at the base possessing but a single plerome-cylinder. It is of importance to distinguish between these two phenomena.

3. CHANGE OF DIRECTION OF GROWTH.

In the majority of plants the tap-root grows vertically downwards and the lateral roots grow obliquely downwards or horizontally. There are plenty of plants, however, in which the roots take quite other directions; in this connection one need only mention the apogeotropic roots of cycads, of mangroves, and of *Taxodium distichum*, which grow vertically above the surface of the soil for the purpose of obtaining a better supply of air. Roots can, for the most part, be induced to grow in any direction by artificially changing the nature of the medium in which they grow; *e. g.* roots will always grow away from a dry and towards a moist medium in whatever direction it may be advisable for them to do so. Baillon observed the roots of *Monstera deliciosa* growing vertically upwards away from the heated atmosphere caused by the warm stage on which he had placed the pot.

The manner in which some modern physiologists write about gravity is distinctly misleading; one gets the impression from their treatises that they regard it as a primary stimulus comparable, for example, to that of light, and one is led to suppose that roots grow downward under the influence of gravity in the same way as stems, under the influence of light, grow toward the source of light. Nothing, however, can be further from the truth; gravity, as a primary cause, has nothing whatever to do with a root's movements. Light, however, is a primary cause of heliotropic movement because the plant receives a direct benefit from the rays striking its leaf-surface at a certain angle.

The true cause of root-movements resides in the habit and needs of the plant, built up upon the past experience of the race; and according to its needs, of fixture, moisture, food, aëration, temperature, water-currents, etc., will it cause its roots to grow in this or that direction: vertically upwards just as readily as vertically downwards. Gravity only comes into play in connection with the minute mechanism by which the main movement is accomplished; it acts on the cell-contents, thereby stimulating the cells and tissues.*

4. ADVENTITIOUS ROOTS.

Included under this heading are all roots which occur out of their normal position, or at a period, or under circumstances, exceptional for them. Adventitious roots may occur (1) on *roots*, (2) on *stems*, (3) on *leaves*, (4) on *floral organs*, (5) on *prothalli*.

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* As a matter of fact scientific study is not concerned with the true primary cause at all, but solely with the proximate mechanical one. The teleological aspect of the subject belongs to the domain, not of science, but of philosophy.

(1) On Roots.

If the tap-root or radicle of a bean-seedling be cut off at or near the tip, it is possible, as Goebel illustrates, to induce very large numbers of lateral roots to grow out which otherwise would never do so; and, unless one adheres unnecessarily closely to the ordinary academic use of the term, these roots may be styled adventitious.

The tubers of *Dioscorea* are, it may well be assumed, merely modified roots. Goebel figures an excised piece of a tuber of *D. sinuata* which, on the anterior side, produced numbers of adventitiuos roots, and on the posterior side, shoots.

(2) On Stems.

These occur normally in Nature as a very widely-spread phenomenon. They often, as in grasses, bulbous Monocotyledons, and *Selaginella*, constitute, at least in the mature state of the plant, the only existing root-system. Originally roots, and roots only, formed the seat of origin of other roots; their formation by the tissues of the stem must be a secondarily-acquired character. When the normal root-system has been in some way hindered from functioning properly, a compensatory system of roots may arise from the stem-tissues, as in the case of the vine and willow mentioned by Masters. As a result of natural injury to the stem, roots may arise near the injured portion, as in the trunk of the elm cited by the same author, in which the roots grew downwards in the hollow centre. The writer observed in a stem of the Cycad *Encephalartos Altensteinii*, growing wild in Zululand, that, as a result of external injury, great numbers of adventitious roots had arisen in the cortex, some of them nearly an inch in thickness, and were running down vertically through the outer portion of that tissue. This is comparable to the normal passage of adventitious roots in the stem of some Marattiaceous ferns.

In *Selaginella* the roots are normally adventitious in origin, arising laterally from the rhizophore (a stem-structure) near its tip. In some shoots of *S. grandis* sent by Mr. Compton, of Cambridge, which had grown in abnormally moist conditions, the rhizophores were excessively (*i. e.* a few millimetres) short, bright green and glabrous; the single adventitious root was from half an inch to an inch long, covered with dense white hairs, and arose terminally on, and as a direct continuation of, the rhizophore; the terminal position and exogenous mode of origin are due to the precociousness and exceptionally strong development of the root. Bruchmann describes similar very short rhizophores as a normal feature in the seedling. In the abnormal shoots their constant position at the base of a stem-fork shows them to be rhizophores and not roots; moreover, in this genus roots are never normally formed directly on the stem.

Adventitious roots may be induced to form freely by artificially mutilating the stem. The method of propagation of plants by means of cuttings rests on this root-forming faculty of the stem; in the case of many plants the mere placing of the cut end of a stem in water or moist air or soil is sufficient to cause root-formation from the callus formed by the cambium; as a rule, such roots are more readily formed from the nodal than from the internodal region.

If the tips of the rhizophores of *Selaginella* (which the writer has recently demonstrated to be morphologically of shoot-nature) be cut off, new roots can be induced to form out of the callus at the apex. It is a very interesting fact that if young pieces of the leafy shoots of *Selaginella* be cut off and placed in sand, roots can be induced to form directly from the base of such a cutting. Goebel and Bruchmann both describe and figure such cases (Pl. V, fig. 5).

Goebel figures a tuber of *Corydalis solida* which, on being cut in two, developed roots from the lower cut surface of the upper half.

In some cases roots may be caused to form without the aid of mutilation, as in the stem of *Myriophyllum* figured by Goebel, a portion of which was bent under water, when roots developed abundantly from the convex, but hardly at all from the concave side.

In some shrubs, *e.g. Ribes*, *Jasminum*, *Viburnum Opulus* var. *nanum*, which form very dense growth, inducing a tendency to suffocation, curious gall-like structures arise immediately below most of the nodes, which are due to the formation of a mass of adventitious roots; these do not grow out into the air, hence the gall-like appearance.

(3) On Leaves.

Adventitious roots are not infrequently produced in the axils of the leaves of the water-cress (*Nasturtium officinale*) under normal conditions, doubtless induced by the aquatic habitat. But they are in most if not all cases merely the forerunners of adventitious shoots and perhaps were attached to rudiments of these which are still within the tissues of the leaf. Mr. Howard sent a carnation from the Agricultural College at Wye which had evidently been grown under very moist conditions, as adventitious roots had been emitted, not only all the way up the stem, but also all along the lower side of the midrib of the leaves. Irmisch mentions roots arising from the stalk of the cotyledon in *Carum Bulbocastanum*, and Masters saw the same phenomenon in the mango.

Roots are most usually emitted by leaves as a result of mutilation. If leaves of *Bryophyllum calycinum* are detached from the plant, each marginal notch may produce a single root (fig. 21); this must be regarded as the first root of the adventitious bud whose rudiment has not as yet appeared outside the tissues of the leaf.* Goebel figures cases of root-formation on

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* *Cf.* the mode of appearance of the first leaf in the lateral buds of *Lycopodium Selago*.

leaves of the celery (*Apium graveolens*), *Hibiscus*, and *Streptocarpus* which had been cut, but not severed from the stem. Very many plants, more especially *Begonia*, *Gloxinia* (to mention merely two well-known cases), have the power of emitting roots from their leaves after these have been taken off, incised in various ways, and laid in a damp situation.

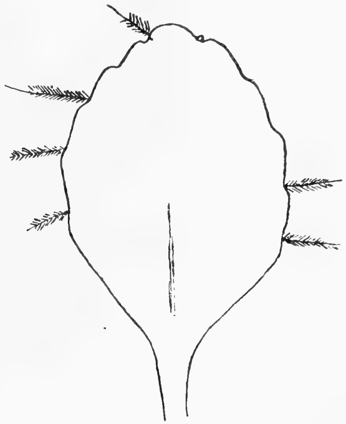

FIG. 21.—*Bryophyllum calycinum.* Adventitious roots each growing from a leaf-notch. (After Goebel.)

(4) ON FLORAL PARTS.

Dr. Rendle showed the writer an ovuliferous scale of a cone of the spruce (*Picea excelsa*) which had been lying in a very damp place; from its surface quite a long root had grown out.

(5) ON A PROTHALLUS.

Lang induced in prothalli of the hart's-tongue fern (*Scolopendrium vulgare*), which had been grown under artificial conditions, the production of roots such as are normally developed by the sporophyte; this must be regarded as a stage in the formation of an adventitious bud.

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II. THE STEM OR SHOOT.*

Included under this heading are, firstly, the ordinary leafy stem and its branches such as we see it, *e. g.* in any ordinary plant, and secondly, the hypocotyledonary stem (hypocotyl), viz., that portion of the axis which intervenes between the cotyledons and radicle in every seedling. All other structures which technically come under this heading, but which have become involved in the building up of the compound organ known as the flower, will be treated of under the heading of that organ.

Many and varied are the forms and other characters of the stem even in quite normal circumstances, and many of these, as will be seen in the course of the following pages, offer an interesting parallel to the variations which occur as a result of abnormal tendencies.

The stem or shoot may become abnormal either as regards its form or its position.

There will now be described the different types of abnormal tendencies exhibited by this protean organ. These may be distributed under four main headings, viz.: (1) Differentiation; (2) Simplification; (3) Change in Direction of Growth; and (4) Adventitious Origin.

1. DIFFERENTIATION.

The abnormal growth assumes the form either of lateral branching or of an extension of the vertical growth of the main shoot.

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* Latin *caulis.*

Fasciation.*

1. Ordinary Fasciation.—This is one of the most widely-spread phenomena in the vegetable kingdom, occurring most commonly amongst cultivated plants, but also from time to time in Nature.

A "fasciated" shoot, whether it be the main stem of the plant or an individual branch thereof, may be described as follows. The shoot affected is, in the majority of cases, if not in all, more vigorous and stouter than the normal ones amongst which it may be growing. At the base, and for a varying distance upwards, it has the usual cylindric contour; sooner or later, however, this becomes more and more flattened, until, in the upper part of the axis, a band-shaped structure is assumed which is due to the great increase in diameter of the stem in one plane only, all the tissues being concerned in this formation, so that in transverse section of the stem the central vascular cylinder would present the appearance, according to the degree of fasciation, of a drawn-out oval instead of the circle which it normally assumes.

Fasciation may affect the main stem only, all the lateral branches being normal; or some of the lateral branches, viz., those situated in the plane of the fasciation may be affected like the parent stem, while others, emerging from the latter at right angles to the fasciation, are quite normal. Often individual branches or portions of such are fasciated, while the main stem is perfectly normal, as in the case of many trees, *e. g.* the ash and sycamore.

In nearly all cases the fasciated shoot branches above, giving rise to a complex system of secondary fasciated axes, which in their turn may again branch, and so on, sometimes *ad infinitum.* This branching of the fasciated stem at the apex is of the primitive type known as dichotomy or bifurcation (forking), such as characterizes many Vascular Cryptogams, *e. g.* the

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* Latin *fascia*, a banding.

club-moss (*Lycopodium*), *Selaginella*, etc., in which the main body of the shoot divides into two equal or unequal parts; it is distinguished from axillary branching, which is the normal type for Phanerogams, by the fact that in the latter the main axis does not divide at all, and subsidiary shoots arise laterally in the axils of the leaves.

This is the only criterion of difference between the two types of branching which is here recognized. A study of fasciated shoots has led independently to the same conclusions as those of Velenovsky and Schoute,* viz., that a contemplation of the mature structure is ample for distinguishing between dichotomy and monopodial branching, and that, as Schoute has pointed out in detail, a reliance on developmental data for the determination of what is, or is not, true dichotomous branching, as, *e.g.*, whether there is division of the apical cell or not (the artificial criterion of the orthodox text-book), is entirely misleading.

A dichotomizing or bifurcating stem and a fasciated stem represent essentially one and the same phenomenon. Many cases of each are known in Angiosperms. A bifurcated shoot is merely one which has reached the first stage in the direction of fasciation. Its axis divides into two, not necessarily equal parts only; while in the fasciated shoot the axis may divide into several parts at the apex, which is the commonest case; or the ribbon-stem may undergo no apical splitting whatever.†

Abnormal dichotomy (simple forking) has been observed in the stem of the Jerusalem artichoke (*Helianthus tuberosus*), in *Mæsa ramentacea* (fig. 22), the wall-flower (*Cheiranthus Cheiri*), and the stone-hore

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* See his splendid treatise on the branching of *Hyphæne*.

† The ordinary text-book definition of "dichotomy" cannot be accepted, viz., a division involving the bisection of the apical cell into two equal halves; this should be regarded as merely a special instance of the phenomenon; it would not cover the cases of stem-forking in *Lycopodium* and the Phanerogams, which possess no apical cell. "Dichotomy" should be defined as a division of the organ, from the apex downwards, into two parts of equal rank, although not necessarily of equal size or development.

(*Sedum reflexum*), amongst Dicotyledons. Celakovsky has clearly and beautifully demonstrated another interesting type of true dichotomy in *Lonicera Periclymenum* (fig. 23); but many other plants will show the same phenomenon under similar circumstances. Where a leaf dichotomizes deeply, its axillary bud follows suit, so that, as a result, two leaves, each with its axillary bud, appear, where before there was only one (fig. 23 *a* and *b*). In the case of the leaf different stages between apical forking and its complete division into two leaves are all present on different shoots, or on different parts of the same shoot, as mature structures; in the case of the bud only the final stage, viz., that of its complete division into two buds, is represented. But it is obvious that this is a case of congenital dichotomy of a single shoot in its youngest or bud-stage. The ontogeny would never have revealed this, but would simply have told us that two collateral buds arise in the axil of a deeply-divided leaf. Only by the comparative method of investigation can we definitely determine that dichotomy of a single

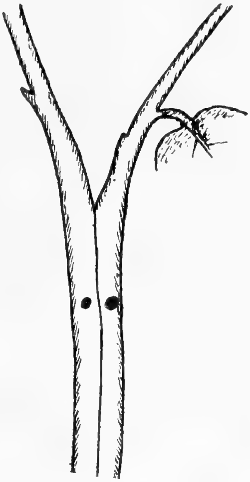
FIG. 22.—*Mæsa ramentacea.* Dichotomy of the stem.

bud has (congenitally) occurred. It is thus seen that dichotomy is not at all uncommon in Dicotyledons: as an abnormal phenomenon, it is true; but we have yet to learn what is the essential distinction between the normal and the abnormal. In Monocotyledons it was seen in an orchid of trigeneric hybrid origin (*Brasso-Cattlælia* × *Fowleri*) in which the pseudo-bulb forked into two; the cladodes of the butcher's broom (*Ruscus aculeatus*) quite frequently exhibit it (fig. 24).

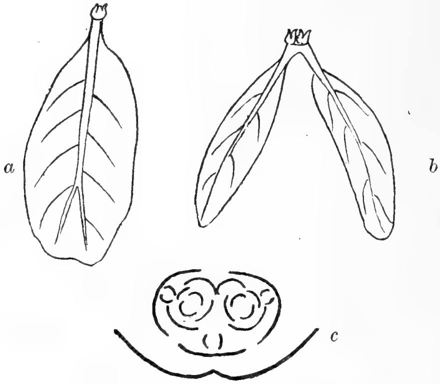

FIG. 23.—*Lonicera Periclymenum.* *a.* Leaf beginning to fork; bud still undivided. *b.* Leaf and bud both dichotomized. *c.* Diagram of leaf and axillary bud, each of which has just dichotomized. (After Celakovsky.)

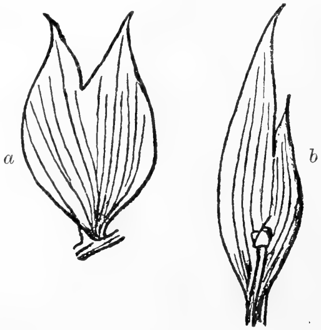

FIG. 24.—*Ruscus aculeatus.* *a.* Cladode showing equal dichotomy. *b.* The same showing unequal dichotomy. (After Celakovsky.)

Milde observed abnormal forking in the rhizome of *Botrychium*.

Schoute observed true dichotomy of the stem, *as a normal feature*, in *Hyphæne*, an African palm. This is the first discovery of the kind in Phanerogams. It arose as follows: "The apical meristem ceased to grow, and in place of it, at equal lateral distances therefrom, two new ones appeared." From this it is obvious that there was no division of the apical meristem into two, and yet true dichotomy is present: because the two lateral branches did not arise owing to injury to the stem-apex; because they are not axillary to any leaves; and because an "angle-leaf" is present opposite the fork precisely as is the case in dichotomizing stems of Cryptogams. Moreover, the two branches bore lateral buds in the axils of every leaf. Velenovsky has also established by personal observation that true dichotomy occurs in *Chamædorea Martiana*.

Fasciation or multiple dichotomy is such a widespread phenomenon, occurring in all groups of vascular plants, that particular instances need hardly be specified, but the case may be briefly mentioned of a plant of the feather asparagus (*A. plumosus*) whose main shoot was fasciated, some of the minor branches being affected in the same way, becoming "crested," thus still further adding to the normal fern-like aspect of the plant (Pl. VI, fig. 2).

There may also be cited the case of the potato var. *Hoornkens*, figured in the 'Tribune Horticole,' whose tuber was palmately branched.

In those cases of fasciation in which no apical splitting occurs it might be thought that no comparison could be instituted between such a fasciation and the dichotomous shoot; but a little investigation and reflection will reveal that in reality a fasciated or ribbon-shoot consists *ipso facto* of a number of independent growing points embedded in a common matrix, *i. e.* still linked together in linear fashion within the body of the parent axis and which have not as yet given rise to individually distinct axes; this unbranched condition is well seen in the fan-shaped type of fasciation met with occasionally.

Precisely the same phenomena, viz., of dichotomy and fasciation, which are generally abnormal in the Phanerogams, occur normally in the Cryptogams. In *Lycopodium*, *e. g.*, dichotomy constitutes almost the only method of branching of the stem, the main body of which divides into two equal parts. Again, dichotomy and both types of fasciation, viz., the band- and fan-shaped varieties, occur in the thalli of Algæ and Fungi (fig. 25 *a* and *b*). Such a structure of the thallus can also be regarded as a latent condition of multiplex forking which in many cases resolves itself at the apex of the thallus into actual forking.*

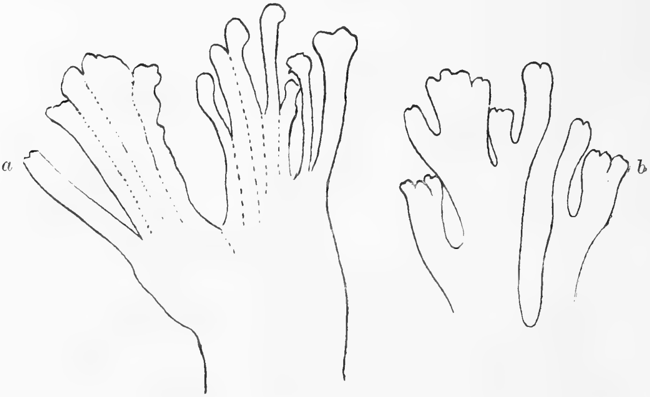

FIG. 25.—*a*. Fasciated shoot of pine. (After Masters.) *b*. Portion of thallus of the Alga *Halidrys siliquosa*.

The mechanical causation of the phenomenon may

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* All the phenomena above considered are merely variants of a single one, viz., dichotomous branching, of which the two extreme forms are, respectively, simple forking and the band- or fan-shaped undivided fasciation. The cases of multiple forking, which link these two extremes together, may be separated into two classes: (1) those in which the apical branching is successive (each newly-formed branch forking subsequent to its formation), and (2) those in which it is simultaneous (the forkings, few or numerous, arising congenitally as such). In (1) the forking occurs at different levels; in (2) at the same level.

be here briefly referred to. It appeared to be the case that the fasciated organ represents in itself from birth onwards the equivalent or potentiality of two or more organs of which at the earliest stage there was no sign, and that, owing to the inherent tendency for these "latent" organs (if they may so be termed) to assert themselves, the subsequent branching gradually, as shown by the appearance of furrows and ridges and the band-shaped expansion of the organ, ensued; these furrows and striæ are not due to postgenital union of several shoots, as Masters and others supposed, but represent the first signs of partition of a single shoot.

The writer is indebted to Dr. A. H. Church,* of Oxford, for the concrete and definite concept of "growth-centres." He says that in the normal shoot "growth is distributed at the apex of a shoot in such a manner that its transverse-component may be expressed by a plane circular construction around a central point (the growth-centre)" and that "the circular section of the vast majority of plant-axes is evidently the outcome of such a regular and symmetrical distribution from the growing-point . . . In the 'fasciated' system the centric distribution around a point (the single growth-centre) is changed for an attempt at similar distribution around a number of such centres . . . or around a longer or shorter series of such points constituting a line, with the result that great disturbances ensue, owing to the impossibility of normal uniform growth expansion in such a system." He says further: "A growing system might evidently have one such a centre or more than one. One is the simplest case, and as a matter of observation is the general rule; on the other hand, the case of multiple growth-centres is included under the botanical title of '*fasciation phenomena*.'"

In many cases there appears to be an immense

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* Fermond elaborates a complicated mechanical explanation of fasciation which need not be here entered into.

number, even an infinity of growth-centres involved or latent within the organ, which continuously and successively assert themselves as the organ increases in age, so that, as in the case of a fasciated wall-flower shoot observed, the ultimate branches produced are very numerous and finely subdivided, eventually becoming resolved into foliage-leaves pure and simple (Pl. VI, fig. 1).* Further, owing to the fact that in almost all "fasciations" some growth-centres are weaker than others, giving rise to branches which, while equal in grade or value to the others, are smaller in diameter and less rapidly elongating, the curious phenomenon of winding of the shoot is produced, which is an almost invariable concomitant of fasciation. It is the same phenomenon as is seen in the twining of climbing plants, its essential characteristic consisting in the bending of the axis out of the vertical direction at every turn (Pl. VI, fig. 1). This may, in some cases, become so pronounced that the axis becomes completely inverted (Pl. VII, fig. 1). This winding of the axis must not be confused with the phenomenon of torsion or twisting, which is a totally different one in which the axis never leaves the vertical direction of growth. It will be referred to later.

If we suppose the normal single "growth-centre" to be replaced by (*i. e.* to become segmented into) two only, and these two to be equally balanced as regards strength and development, the branching to which they give rise would be an approach to dichotomy,† as defined in the text-books.

2. Trigonal Fasciation.—There may be further mentioned those cases where the transverse extension of growth is not in one, but in two dimensions. Peduncles of the cowslip (*Primula veris*) were observed so strongly developed as to represent a three-fold organ; in transverse section the organ would appear three-lobed, and if branching could have occurred

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* *Cf.* the "phyton-theory."

† Nestler regarded the tip of a fasciated shoot as composed of a continuous row of apical cells ('Vegetationslinie').

above, a trichotomy in two dimensions would have resulted. Nestler also found a stem of *Amaranthus* sp. which was trigonous instead of band-shaped.

3. Ring-Fasciation.—There is another type of fasciation which has been termed "ring-fasciation." The shoots showing this phenomenon are less flattened and more cylindric than is the case with those belonging to the other types. In such a stem, which gradually increases in diameter from below upwards, there appears in its upper portion a central cavity whose diameter increases upwards with that of the stem. Arranged concentrically around the cavity are all the various tissues of the stem in inversed order, *i. e.* the epidermis lines the cavity while the protoxylem of the central cylinder lies face to face with that of the normal cylinder of the stem; hence all the tissues of this peculiarly-constructed stem occur in two

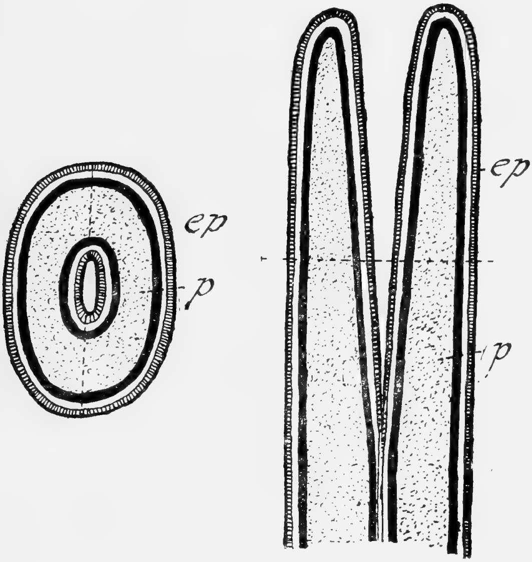

Fig. 26.—Diagrams of transverse and longitudinal sections of a stem to show construction of "ring-fasciation." The dotted line in the latter shows the region of the transverse section; and in the former, where, theoretically, splitting should occur to cause bifurcation. *ep*, epidermis; *p*, pith.

concentrically-grouped sets: an external, normally-orientated, and an internal, inversely-orientated set (fig. 26). This phenomenon, which is not an uncommon one, occurs in the stem of the so-called "mummy pea" (*Pisum sativum* var.) in which the fasciated condition always comes true from seed. Boodle, also, has noted it in shoots of the hollyhock (*Althæa rosea*), and Conard in those of the yam (*Dioscorea Batatas*). Schoute has also observed it in the stems of some abnormal palms. Somewhat more complicated instances have been noted in the scape of the dandelion (*Leontodon Taraxacum*) by Reichardt, Michelis, Cramer, and others. In the case of Reichardt's specimen the scape bore four capitula around the apex, in the centre of which an aperture gave entrance to the central cavity of the scape, which gradually narrowed below, ending blindly some way down. Besides the normal central cylinder of the scape, there were two inner rings of bundles, the innermost of which ended blindly (passing from below upwards) in the solid core just below the narrowed termination of the cavity. Unfortunately this author says nothing about the orientation of the bundles composing these rings: a most important feature. He regards this remarkable phenomenon of the abnormally swollen scape, with its four capitula, central cavity, and three vascular cylinders, as due to a fusion of five scapes, a central rudimentary and four peripheral ones; and he gives an ingenious reason for his belief; but this explanation is on a par with that of fusion, so often ascribed to the phenomenon of ordinary fasciation, and is not really adequate (see below).

What is said with regard to the interpretation of the general phenomenon of fasciation may be so far forestalled by stating that ring-fasciation, like ordinary fasciation, may be regarded as an attempt on the part of the cylindric organ to effect a multiple dichotomy. In many cases, possibly in all those which concern cylindric structures, this is primarily induced by an apical invagination (what the Germans term "Einstülpung") of the organ, comparable to the turning inside out of a glove-finger, as is indicated by the fact that in most cases the cavity ends blindly before reaching the base of the organ, and, as in such instances as the mummy pea and the dandelion, by the terminal aperture. This is the morphological explanation of the phenomenon; as the formation of the cavity by this means is congenital, there is, of course, no indication thereof in the ontogeny. This will at once explain the set of inverted tissues adjacent to the cavity. If now we imagine a number of pairs of constrictions to occur (each pair consisting of a constriction on the outer and one on the inner surface), the tissue between the pairs of constrictions rounded off, so that the normally- and inversely-orientated parts of each such region become one cylindric whole (see the diagrams, fig. 26), a number of subsidiary terminal shoots will be produced, as in the mummy pea or the dandelion described by Reichardt. The innermost of the three vascular rings ascribed by him to the central of the five fused scapes might belong to a tissue representing the resurgence of the downwardly-invaginated scape-tip.

The two internal scapes, occurring side by side, found by Michelis in the dandelion, could be explained by the presence of two apical invaginations. Adventitious proliferation of the stem within the base of the scape is the probable explanation of the instance in which Michelis observed a third capitulum-bearing scape within the others, as it probably also is of other similar cases mentioned in the literature.

Ring-fasciation is thus seen to be a very remarkable method of effecting a dichotomy of the stem.

CAUSES OF FASCIATION.—As regards the causes underlying the phenomena of fasciation, two main views on the subject have been held.

a. Fusion-Theory.—Some authors, *e.g.* Linnæus ("Fasciata dici solet planta cum plures caules connascuntur, ut unus ex plurimis instar fasciæ evadat et compressus"), Hincks, and Masters held that, owing to the stimulus of superabundant nourishment, a number of buds arise in close proximity, which, as growth proceeds, exert such a mechanical pressure upon each other that they become grafted together to form a single shoot. It has been maintained that the longitudinal striæ which fasciated shoots exhibit represent the lines along which the presumed postgenital fusion has occurred.

b. Expansion-Theory.—The precisely opposite view, fitly represented by the able writer Moquin-Tandon, maintains that fasciation is due, not to the mechanical, postgenital union of several separate shoots, but to the flattening, *i.e.* to the growth-expansion in one plane, of a *single* shoot. This view is strongly supported by Blaringhem who has had wide practical experience of fasciations.

The objections raised by Moquin-Tandon against the idea that fasciation is due to postgenital union of several shoots have never yet been adequately met. One of these was as follows: that if fasciation was due to such a cause the single elliptical medullary canal which is usually found on transversely cutting a fasciated shoot, could never occur, but, on the contrary, two or more such canals would always and inevitably be met with, and one may add that the neat elliptical contour of the vascular cylinder as seen in transverse section of such a stem could hardly be brought about by the mere *postgenital* union, however intimate, of stems; traces would always occur of the originally separate cylinders. Moquin rightly further objects that it is quite unlikely that a number of buds would become united in one plane only. Masters says that the buds are in one plane from the first. But it may be asked: how and why is this the case? Again, Moquin says that in the majority of fasciated stems all the other branches which should be present are to be found; not one is wanting as would have been expected had fusion occurred. But a typical fasciated stem is too finished a structure, too compact and concentrated a whole to be due to a mechanical union of a number of separate shoots. Every appearance afforded by the phenomenon suggests a single structure in itself.

Nestler says: "Fasciation cannot be a fusion of several axes, but only an expansion of a single normal cylindric axis which from hitherto unknown causes has arisen from a peculiar modification of the growing point." Takobasch believed that it arose in consequence of an incipient forking of the stem. With these views the writer fully concurs.

c. Pleiotomy-Theory.—Moquin's definition, however, does not cover the whole ground, nor fully explain the phenomenon. The basic principle governing the latter is expressed in the following quotation from Blaringhem: "Fasciations result, not from the union of young organs which remain coherent for a longer or shorter period, but from the absence of individualization of the cells or tissues into independent buds. Fasciation results from a retardation in the dissociation of the parts." That is, apparently, during the ontogeny no fusion between two or more individuals has ever occurred, but where now only one individual has been developed, two or more were always, since the period of fertilization of the ovum, potentially present, and the multiple dichotomy (actual or latent) in which fasciation consists, represents the imperfect formation of multiplets, just as trichotomy represents that of triplets, and dichotomy that of twins.

If a vertical first division occurred in the fertilized ovum, causing the separation of two distinct cells, the result would be the formation of twin-embryos, as observed in *Rhizophora conjugata*. Treub describes a case in which in *Loranthus sphærocarpus*, the fertilized ovum divides by a vertical wall, but the sister-cells develop together into a single proembryo, consisting of a double row of cells. The case of imperfect twins, in which the lower part of the structure is undivided while the upper is separated into two similar parts, represents at once the simplest case of fasciation in existence and also the phenomenon which most easily and clearly explains it, illustrating as it so well does the result of the compromise between the two tendencies towards unification and separation respectively. It is a by no means uncommon phenomenon for two embryos or young seedlings to appear more or less intimately fused together. De Candolle figures cases of this sort in the sun-spurge (*Euphorbia Helioscopia*) and *Sinapis ramosa* in which the fusion occurs from the insertion of the cotyledons downwards. In the phenomenon as observed in *Eremostachys laciniata*, the union was in the region of the primary node only, the cotyledons and radicles being quite free: a veritable Siamese twins of the vegetable world! (Pl. IX, fig. 4). Morris describes a very similar case to this in *Widdringtonia cupressoides*.

All cases of dichotomy in Angiosperms represent, therefore, imperfect twin-formations; one could even apply the same statement to all normal cases of dichotomous branching in Cryptogams. Fasciation is the imperfect formation of a number of offspring (multiplets) by partition, and is a result of the compromise established between the forces making for unity and fission respectively. The fasciated shoot is a unity, a single individual structure, as is clearly evidenced by its homogeneous cylindric base. Its expansion in one plane of the diameter proportionately to the increase in stature is due to the tendency on the part of the shoot to dichotomize, this being equally balanced and neutralized at every moment by the opposite tendency, viz., that to cohere as a unity; this alone is the *vera causa* of the ribbon-growth with which we are so familiar.*

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* In an interesting case of this in *Sterculia alata* from Wallich's collection, the collector says of it: "Two embryos seemingly from one nucleus, soldered together, with only two cotyledons to both conjointly above which separation has taken place naturally."

In the light of what is written above it would seem that Plot, in his 'Natural History of Oxfordshire,' comes nearer the mark than anyone else when he regards "fasciation" as due to the ascent of too much nourishment for one stalk and not enough for two; though he probably ascribes too absolute an influence to the external factor of nutrition.

d. Physiological Causation.—As regards the physiological cause of fasciation it is probably a pathological condition. In the majority of cases it is doubtless stimulated to appear by the presence of superabundant nutrition which produces a subtle diseased condition, thus giving rise to a hypertrophied growth which destroys the balance of the organism.

The proof that fasciation is often due to the flow of superabundant nutriment to the organ affected is directly afforded by some of the experiments which have from time to time been made in which artificial mutilations of one part of the plant, causing a hindrance to the normal flow of sap in a particular direction, have induced an over-rapid and abundant flow into other unwonted channels inducing an excessive multiplication of these channels to take the excess of sap: hence the fasciated shoots. For instance Sachs and also Lopriore produced at will fasciated shoots in the axils of the cotyledons of the scarlet runner (*Phaseolus multiflorus*) by excising the main axis of the plumule at an early stage; if this mutilation is performed at a later stage no fasciation results. The writer has repeated these experiments of Sachs and Lopriore with marked success, great numbers of seedlings producing fasciated shoots in the axils of the cotyledons. In every case the shoot was only affected at the base, a normal growth being formed above (fig. 27). Blaringhem, Lopriore, and others have published interesting accounts of cases of fasciation induced by artificial mutilations of various kinds.

In other cases the attacks of insects constitute the cause of fasciation, and here again the phenomenon is doubtless to be ascribed to an abnormal flow of nutriment into the organ or organs concerned.

Yet it seems fairly clear that the environmental factor is not the only one involved; for fasciated stems appear as isolated cases amongst others which are perfectly normal and where both are growing apparently under precisely similar conditions. It would appear, therefore, that the idiosyncrasy of the individual organ or plant itself is another, if not the chief factor, which must not be left out of consideration. Variability of constitution causes variability of reaction to the environment.

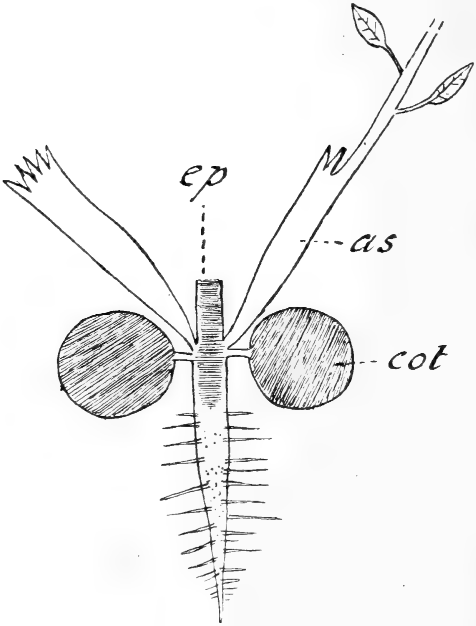

Fig. 27.—*Phaseolus multiflorus.* Axillary shoots (fasciated at base) formed after excision of plumule (*ep.*). *as,* axillary shoots; *cot,* cotyledons. (Semi-diagrammatic.)

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PROLIFERATION.

Under this heading are included all those cases of shoots, belonging to the various categories, which are extended beyond the limit of growth which is normal to them. This is often the result of extraordinary vigour due to over-nutrition, but it is more than doubtful if this factor can be always traced.

1. MEDIAN.—As regards the case of rosettes in a cowslip (*Primula veris*), the main vegetative axis was seen to have proliferated, while at the same time becoming congenitally united with the scape, and had produced at the apex a second rosette of foliage-leaves. In other plants which normally possess a suppressed

vegetative stem and a basal rosette of leaves, the former may develop its internodes and grow into an elongated leafy axis, as in the daisy (*Bellis perennis*) forming the variety sometimes known as *B. hybrida.*

The same is true of other rosette-forming plants, *e. g. Carduus* (*Cnicus*) *acaulis:* in this case the "flowers," normally sessile in the midst of the rosette, become seated on an elongated shoot.

The tendril of the Ampelidaceæ in the normally-growing plant arises laterally on the stem on the side opposed to the leaf-insertion, and apparently affords a case of an extra-axillary branch; morphologically, however, the whole shoot is constructed sympodially and the tendril really represents a modified inflorescence-axis which has become displaced from its original terminal position on the axis by the relatively much stronger development of the axillary shoot at its base. As the plant grows the same thing happens congenitally each time a tendril is formed, so that the main axis of the plant consists of a concatenation of axillary shoots. Now, abnormal cases occur from time to time in which the relative strength of development as between tendril and axillary branch, as we usually see it, becomes reversed, and the tendril grows out into a vigorous terminal leafy shoot or inflorescence while the axillary shoot becomes much more weakly developed and relegated to a lateral position. This is an excellent instance of reversion to an ancestral condition. Cases of this kind have been observed both in the vine (*Vitis vinifera*) and the Virginian creeper (*Ampelopsis hederacea*).

Bulbs occasionally proliferate. Gay describes a bulb of the snowflake (*Leucojum æstivum*) which, owing to the swelling of the internodes, produced the appearance of two or three bulbs one above another; Irmisch observed the same phenomenon in *L. vernum* (fig. 28), and it has been cited in the snowdrop (*Galanthus nivalis*), and also in the onion (*Allium cepa*) and other plants.

There must now be mentioned one of the most remarkable abnormalities which have ever come under the writer's notice. Messrs. Little & Ballantyne of Carlisle forwarded to Kew three bulbils of *Lilium tigrinum* var. *Fortunei*, each of which was proliferating directly into a flower, whose parts, with the exception of the ovary, which was scarcely developed, were fairly normal; no other organs intervened between the scale-leaves of the bulbil and the sepals of the flower. This seems to be a very rare case, and is the only instance mentioned in this work of median proliferation resulting directly in flower-formation.

FIG. 28.—*Leucojum vernum.* Formation of a second bulb above the normal one. (After Irmisch.)

In the pines the short-shoots or spurs normally bear, according to the species, two, three, or five "needles" seated very close beneath the apex of the shoot, and practically terminal; below these are a few scale-leaves. In the Scotch fir and stone-pine, owing to the suppression, by injury or otherwise, of the axis of the main branch, some of the short-shoots proliferate, separating the two "needles" widely apart in the transverse direction and producing above them an axis bearing scale-leaves which may produce short-shoots in their axils (Pl. VII, fig. 2). Normally the apex of the shoot between the two needles is either quite suppressed or else in the form of an insignificant papilla. This phenomenon is merely another example of correlation of growth. But it is also frequently caused by fungus-attack, and, as F. E. Lloyd and R. B. Thomson have recently shown in *P. radiata* and *P. Tæda*, by copious water-supply.

In the stone-pine (*Pinus Pinea*) a proliferated short-shoot bore large numbers of spirally-arranged "needles" instead of the normal two opposite ones, these "needles" then partaking more of the nature of the "primordial leaves" borne by the young plant in its early stages of growth than of that of the typical "needles." This interesting phenomenon represents, both as regards the elongation of the shoot and the character and increase in number of its leaves, a reversion to the ancestral condition. Hence it is of extreme interest to compare this abnormality with the case of the fossil plant *Prepinus* discovered by Jeffrey in the Tertiary rocks of New Jersey in which the short-shoots are elongated and bear a considerable number of spirally-arranged "needles." Here, at any rate, is a case where the indications afforded by an abnormality in a modern plant are fully confirmed by the facts of palæobotany.

In this place may be mentioned the important discovery made by Von Mohl concerning the "double needle" of the umbrella pine (*Sciadopitys verticillata*). He showed that its origin is precisely the same as that of the seminiferous scale of the Abietineæ, viz., from the first two leaves of a secondary axillary shoot which have become fused by their inner and posterior margins; as a result of which the ventral surface of the organ is directed outwards. In this way the eccentric orientation and structure of the "double needle" is readily explained. Masters and Carrière described an abnormality in which the "needle" was deeply forked and from the fork sprang a short axis bearing a whorl of "needles." Masters regarded the "needle" as of axial nature; but this abnormality is probably best interpreted as the result of the elongation of the otherwise suppressed axis of the short-shoot bearing the two leaves fused by their posterior margins, causing a separation of the leaves, while the axis remained for part of its length fused with one of its two leaves, and after becoming free higher up, produced fresh leaves. The "double-needle" represents two leaves of a short-shoot which has become much more reduced than in the case of *Pinus*, with its equipment of both scale-leaves and needles. In *Sciadopitys* the axis has become entirely suppressed.

The rhizophore of *Selaginella* is an organ occurring either on the upper or lower surface, or both, at the point of branching of the (usually) dorsiventral stem. It elongates into a root-like organ which grows downward to the soil on reaching which it emits roots near the apex which fix it in the soil. The question arises: What morphological value has the rhizophore? It must surely either represent a root, a shoot, or a leaf. For obvious reasons it cannot be a leaf. It is therefore either a root or a shoot.

On this point the following has appeared in the 'New Phytologist,' vol. ix, pp. 247–249. It "resembles the root of the same plant in the anatomical structure of its vascular parts, for it has a monarch structure of the stele with central protoxylem. Like a root, it is completely devoid of any lateral appendages in the form of foliar organs. Like a typical root it grows *downwards* to the soil and absorbs water through its tissues in a direction the reverse of that in which it has grown. It produces lateral endogenous roots. These characters are, in my opinion, not sufficient to warrant us placing the organ in the root-category. On the other hand it resembles a stem or shoot in the fact that it arises *exogenously* from the tissue of the leafy shoot at the region of forking; but this in itself is not conclusive evidence in favour of its stem-nature, for exogenous roots are known in various plants. But as Bruchmann points out, the *definite* place of origin of the rhizophores at the place of forking, growing in a plane at right angles to that of the stem-fork, the whole forming a cross-like four-armed branching-system at that point, speaks strongly in favour of these organs being shoots.* The absence of a root-cap is another

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* In some specimens of *S. grandis*, grown under abnormally moist conditions, which were sent by Mr. R. H. Compton of Cambridge, there occurred tetrachotomously-branching shoots: at the base of the fork of a vegetative shoot, and, in other cases, of a cone, a leafy shoot of (at least in its lower part) radial symmetry arose on both the dorsal and ventral side.

character speaking in favour of its shoot-nature. The leafless character affords no argument against this idea; several cases are known of shoots which have, for the purpose of some special function, lost the power of forming leaves, either over the whole or a part of their length, *e. g.*, the rhizomes of Psilotaceæ, the inflorescences of Cruciferæ, the shoots of *Trichomanes membranaceum.*"

"Pfeffer has placed on record some most interesting observations in which rhizophores of certain species (*e. g.*, *S. inæqualifolia*) develop spontaneously into *leafy shoots*.

"I have myself recently observed the same phenomenon in the case of the above-mentioned species in the Fern-house at Kew. In the case of one shoot which I may take as a typical example, of the two rhizophores at one fork of the stem, that on the lower surface was perfectly normal and elongated, and with the usual dark-brown colouration, the upper one was very short and changed into a leafy shoot; at the next node the upper rhizophore was a leafy shoot and growing almost horizontally: at the next the lower rhizophore was much elongated, growing downwards, and with leaves somewhat sparsely scattered along its whole length; the tip was becoming green, the rest being dark-brown, and it was just beginning to bend upwards, while at intervals along its course it bore a short leafy branch (this rhizophore represents an interesting transitional form between the normal organ and the rhizophore transformed into a leafy shoot); at the next node the lower rhizophore is a very short leafy shoot and there is no upper one; at the next the only rhizophore present, viz., the lower one, is a leafy shoot which at first began to grow downwards but soon bent upwards sharply; it therefore also represents a more or less intermediate stage of transition.

"On other shoots the transformed rhizophores were much less half-hearted; many of them at once grew quite vertically upwards into typical leafy shoots, each arising at the point of forking of the normal stem; the extreme base of these 'rhizophore shoots,' for a distance of 2 or 3 mm., is dark-brown and leafless like the normal rhizophore. This dark-brown colour *gradually* merges into the green of the typical normal shoot [fig. 29 and Pl. VIII].

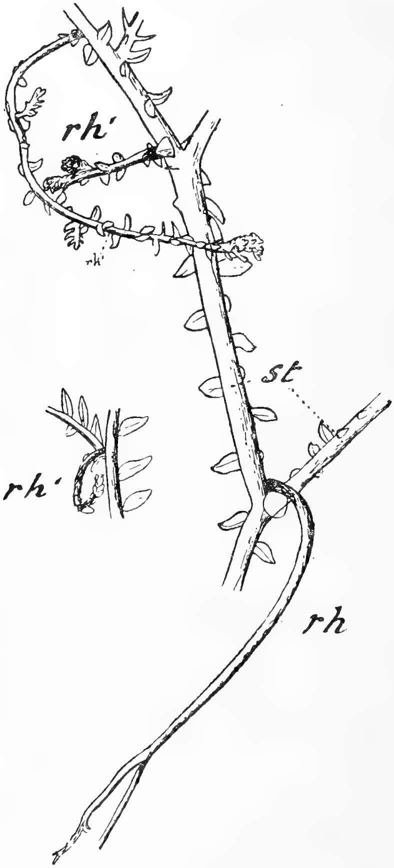

Fig. 29.—*Selaginella inæqualifolia.* Portion of shoot showing rhizophores arising at points of forking. *rh.* normal; *rh'.* abnormal rhizophores.

"In a panful of *Selaginella Mettenii*, A.Br. (a garden hybrid) I noticed that in most, if not all, the plants normal rhizophores were only formed in the *lower* part, where the plant was moist and shaded; in the upper part the rhizophores were invariably replaced by typical leafy shoots which appeared always on the upper surface of the stem; I saw no transitions between them and rhizophores, but their position showed clearly that they represented the latter.

"I have also observed rhizophores in the form of leafy shoots in the following species, besides the two above-mentioned: *S. Wildenovii* Baker, *S. canaliculata* Baker, *S. serpens* Spring, and *S. grandis* Moore. In the first-named I saw a rhizophore in the form of a branched leafy shoot quite a foot high; in the last-named (*S. grandis*) they are in the form of small, flower-like structures, as described by Goebel."

"Bruchmann found in the case of *S. Kraussiana* A.Br. that by cutting off the two arms of the stem-fork at an early stage of the development of the rhizophore, . . . the apical cell of the rhizophore becomes that of a leafy shoot and the latter becomes the direct continuation of the former. . . . I myself performed a similar experiment to that of Bruchmann with stems of *S. inæqualifolia* and *S. Mettenii*, and with similar results.

"From all the above-cited facts it is clear that the leafy shoot in these cases . . . is itself a rhizophore; the appearance suggests unequivocally that the phenomenon before us is *not* a case of a normal rhizophore being first formed which then gives rise, by transformation of its apex, to a leafy shoot; on the contrary, it is clear from direct observation that there is only one organ here present. The cases of *Neottia*, *Listera*, and *Anthurium* are not to be regarded as parallel, for in these there was a clearly-defined organ, viz., the root present in the first instance, whose tip developed suddenly into a leafy shoot, without any transition between the latter and the root; it is most obvious that there are two distinct organs present; the terminal shoot in these cases is almost certainly an adventitious structure which, at first in its origin lateral, has encroached ever more nearly to the apex until it has entirely usurped it. No interpretation of this sort can be placed on the phenomena in *Selaginella* above described. My observations seem to prove unequivocally that the normal rhizophore has the morphological value of a shoot." (For further details and remarks on this subject the reader is referred to this memoir.*)

2. AXILLARY.—Some individuals amongst plants which as a rule produce no shoots in the axils of certain of their leaves are observed to form them more or less abundantly.

Referring firstly to the DICOTYLEDONS, there is an interesting example of this in the foxglove (*Digitalis purpurea*), all parts of which were more or less virescent. In the axils of all the foliage-leaves on the flowering-stem were short leaf-bearing shoots, in correlation with which character the main axis was abnormally low in stature.

It sometimes happens that the potato bears tubers in the axils of the foliage-leaves, whereas normally they occur in the axils of scale-leaves on the subterranean shoot.

In the 'Gardeners' Chronicle' of 25th October, 1856, is figured a broccoli (*Brassica oleracea* var. *botrytis*) with six perfect heads on one stalk.

Long ago Sachs made some interesting experiments with seedlings of the scarlet runner (*Phaseolus multiflorus*). The writer has lately repeated these with similar results. At a very early period, viz., before the plumule had emerged from between the hypogæal cotyledons, it was excised; this had the result in a large percentage of seedlings, although not in all, of causing strongly-fasciated shoots to grow out from the axils of (usually) both cotyledons, where normally, if the plumule had developed, no such axillary shoots occur, or only in the form of small, undeveloped buds (fig. 27, p. 96). Hence this is a good instance of

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* Worsdell, 'New Phytologist,' vol. ix (1910), pp 242–249.

growth-correlation, and is merely a striking example of a very common phenomenon.

Harris describes and figures shoots of *Gleditschia triacanthos* which produced two axillary thorns above the insertion of many of the leaves; this being due to a second primordium developing below the first one (fig. 30).

There is described and figured in the 'Gardeners' Chronicle' a very rare case in which a tendril of a passion-flower (*Passiflora*) produced a lateral shoot in the form of a flower (fig. 31). As the tendril is to be regarded as a modified peduncle or rachis of an inflorescence, this case is a very interesting reversion to the ancestral condition.

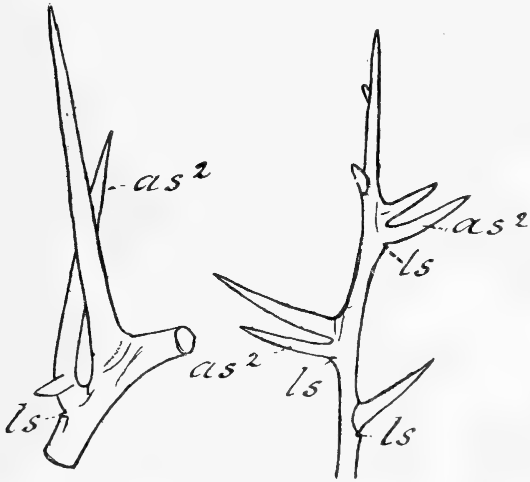

FIG. 30.—*Gleditschia triacanthos.* Development of second axillary shoot (*as*^{2}) below the normal one. (After Harris.) *ls*, leaf-scar.

Turning to the MONOCOTYLEDONS, in a seedling plant of the palm *Pinanga maculata*, grown in the Royal Gardens, Kew, the plumule was forked down to the extreme base; the two resulting branches were of equal length and thickness and were subtended by a common basal sheath; each bore two or three scale-leaves and a terminal foliage-leaf which was forked.

Mr. H. N. Ridley, F.R.S., late Director of the Royal Botanic Gardens, Singapore, who has great experience and knowledge of palms, and to whose interesting paper in the 'Annals of Botany' the reader is referred, informs the writer that the phenomenon is probably due to proliferation of branches from the axils of two uppermost scale-leaves which overtopped and extinguished the apex of the main stem. He says that he has never yet met with a case of true dichotomy in the palms. This may be the correct explanation, but if so, how is one to explain the basal sheath which is common to the two lateral branches? If the sheaths, which probably represent the scale-leaves in whose axils the lateral branches arose, have become *congenitally* united, as is obviously the case, it follows that the extinction of the apex of the main stem by the lateral branches was also congenital, and

FIG. 31.—*Passiflora*. Proliferation of (normally suppressed) lateral bud into a flower. (From 'Gardeners' Chronicle.')

this would amount to a dichotomy of the apex in the sense in which the term is used in this work, while the two branches would yet be axillary and hence lateral. But it is also possible to regard the basal sheath as resulting from the fusion of two uppermost scale-leaves which do not subtend any axillary branches, and in that case the phenomenon would be one of true dichotomous branching.

Martius describes and figures several instances of branching in palms of several kinds. Pulny Andy describes it in the fan-palm (*Borassus flabelliformis*) in which both "dichotomy" and the production of three or four apical branches occurred, and mentions also a case of "dichotomy" in the coco-nut (*Cocos nucifera*). Mr. Ridley informs the writer that branching, whether from the rhizome, or high upon the aerial stem, is the normal feature for the majority of palms. In only a comparative few is it an abnormal feature, as in the coco-nut, and *Areca Catechu;* in other species of *Areca* it is normal. When branching does occur it is never due to injury to the apex, either in normal or abnormal cases, as has been by several writers supposed. A lateral branch may appear late some way down on the aerial stem, and eventually, by rapid growth, reach the height and thickness of the main stem and thus give rise to an appearance of dichotomy. Branching is probably an ancient feature (*cf.* Pandanales); hence the abnormal cases thereof may be regarded as reversions.

Amongst other cases of the formation of axillary shoots where under normal circumstances none such existed, may be mentioned that of a tulip which produced a bulb in the axil of one of the foliage-leaves through whose sheathing base it had completely burst, leaving behind its brown outer coat; the bulb was shortly stalked (fig. 32).

Dietz describes a tall maize-plant (*Zea Maïs*) which, normally unbranched in its vegetative parts, in this case produced long branches, one of which, in its turn, bore five branches, one from each succeeding node, and each of these bore a terminal cob, the stalk of each cob being abnormally long.

Again, K. Müller describes cases in the same plant in which the main shoots had been cut off, causing lateral shoots to spring from the "root-stock."

Blaringhem found that artificial torsion of the main stem causes the production of a number of shoots bearing female spikes or cobs, and he regards this as a reversion to the primitive condition, for the female spike of maize has all the characters of a lateral "fasciated" inflorescence of *Euchlæna mexicana* (*Reana*).

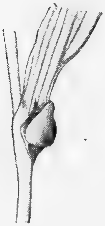

FIG. 32.—Tulip. Axillary branch, in form of a bulb, bursting through sheath of its subtending leaf.

De Vriese observed in *Ixia lutea* and *I. carmosina* long-stalked axillary out-growths bearing small terminal bulbs; these represented abnormal elongations of the stalk of the normal young axillary lateral bulbs. Pl. VII, fig. 3, shows an onion-bulb producing fourteen or fifteen young ones in the axils of the outer scales.

Wirtgen describes a bulb of *Gagea arvensis* from whose scale-axils, in the absence of the terminal stem or inflorescence, single flowers were produced. It has been observed in *Lilium candidum* that occasionally single imperfect flowers arise in the axils of foliage-leaves; the same thing has been seen in *Paradisia*.

As regards the GYMNOSPERMS, in *Cycas revoluta* it is very common, indeed almost a normal feature, for small lateral branches to arise at intervals along the main stem from among the dead leaf-bases; these have been described as adventitious, but they are probably retarded axillary shoots.*

CONCLUSIONS.—With the exception of the proliferated bulbs in *Leucojum*, etc., all the cases of median proliferation above-described are to be regarded as

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* See page 133.

reversions to the more ancestral and original condition in which the shoot was very much less modified in function and therefore in form, and much less reduced in length, than it is at the present day. As we shall see later to be the case with the inflorescence and the flower, the evolution of axile organs has involved a vast amount of stereotyping, and reduction in one form and another, for the benefit of the plant as a whole. Practically none of the cases of axillary proliferation can be regarded as ancestral, for they nearly all exhibit peculiar forms which are not likely to have occurred in the ancestors of the plant concerned, and are generally, moreover, due to the influence of very special stimuli. They represent special adaptations to the abnormal conditions, and they all show what the potentialities of the plant in this direction are, under certain conditions of the environment. The cases of *Passiflora* and *Cycas* are exceptions in this respect.

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2. SIMPLIFICATION.

This comprises the abnormal forms of shoot in which the main axis is abbreviated, or in which all branching is absent or reduced in extent; also all cases of fusion of one axis with another; further, those rare phenomena in which the surface-area of the shoot becomes reduced, representing, in one sense, the opposite of the fasciated condition.

SUPPRESSION.

1. OF THE MAIN AXIS.—The converse condition to that of proliferation of the main axis, viz., where it has become shortened or suppressed, is, for reasons which will be mentioned later, a rare phenomenon. For instance, Fermond describes specimens of the nipplewort (*Lapsana communis*) in which the axis was hypertrophied, *i. e.* much thickened, and, correlated doubtless therewith, much shortened owing to the internodes between the foliage-leaves being greatly reduced, so that these leaves came to be arranged six to seven in a false whorl. He also mentions a similar case in the evening primrose (*Œnothera biennis*).

This same phenomenon (so far as regards the false whorls formed by suppression of internodes) occurs as a perfectly normal thing in many species of *Lilium*.

The abnormal maize-plant described by Lœsener is interesting; the stem was exceptionally short and thick-set, and the leaves occurred close together in four decussate rows instead of the normal two rows, a direct result probably of the extreme shortening of the internodes, when, to avoid too great overcrowding of the closely-contiguous leaves one above the other, they became rearranged, as above described, according to the opposite-decussate type of phyllotaxis.

James cites a depauperised plant of *Rudbeckia hirta*, which, in place of an elongated leafy stem, exhibited, owing to extreme and general internode-extinction, merely a basal rosette of foliage-leaves from which arose a leafless one-flowered scape. Again, the counterpart of this phenomenon occurs normally in the same order. In most species of thistle (*Carduus*) the flower-heads are formed on tall leafy shoots, but in *C. acaulis* the main axis of the plant is reduced to a basal rosette from the axils of whose leaves the sessile flower-heads arise.

Gates observed among his cultures a plant of *Œnothera Lamarckiana* × *grandiflora*, whose stem, although forming a considerable number of leaves, remained as a rosette, without elongation of its internodes, for fifteen months, after which it elongated and bore flowers.

Again, Klebs, by placing the plant under special conditions, induced both the runner and the flowering-stem of *Ajuga reptans* to become changed into rosettes of foliage-leaves.

Asparagus possesses underground, thickened rhizomes and aërial elongated stems. Grevillius mentions a very rare case in which many of the basal branches of the aërial stems in *A. Sprengeri* became, for some distance above the level of the ground, transformed into quite short, thick, tuber-like rhizomes.

Internode suppression occurs normally in all rosette-forming plants.

2. Of Axillary Shoots.—The converse condition to that of abnormal axillary branching is that of the complete or partial suppression of lateral axillary branches. In the spruce (*Picea excelsa*) and silver-fir (*Abies pectinata*) individual trees have been found in which the formation of lateral branches was entirely suppressed; another variety, termed by Caspary *virgata* and by Carrière *denudata*, possesses lateral branches of the first order only which extend horizontally from the main stem and give the tree somewhat the habit of an *Araucaria imbricata*. The branchless condition in the above cases is pretty obviously due to the unfavourable situation of the trees concerned, as in the midst of a dense plantation, where the necessary supply of light and air, and therefore of nutrition, would be wanting. Yet, in order to account for the fact that single individuals only are affected in this way, a part of the cause must doubtless be ascribed to some peculiarity in the constitution of the plant.

Annual herbaceous plants, under ordinary conditions branched, may through malnutrition develop no branches at all.

Klein describes a remarkable instance of this phenomenon in the allspice (*Calycanthus*) and marigold (*Calendula*), where, an axillary shoot being completely suppressed, its first pair of leaves became laterally concrescent, thus affording an instance of one leaf being axillary to another leaf (*cf.* ovuliferous scale in Coniferæ).

FUSION.

The union of two or more shoots may be either postgenital or congenital, as has been already explained in a previous section. It may occur between shoots of the same morphological nature or between those of different nature; between main shoots or between a main shoot and its axillary branch. There may be no external sign of fusion, or there may be more or less pronounced sutures present, indicating to the observant the lines of fusion between the two shoots.

1. POSTGENITAL.—Well-known instances of this are the H-formations in large trees due to the intimate cohesion of the tips of two branches growing in opposite directions towards each other; here the fused organs belong to quite distinct individuals. An excellent instance of this was observed in the case of *Eucalyptus salmonophloia*: two cross-bars occurred, one close above the other; a very rare case. The "Arbre aux cent chevaux" on Mount Etna is a chestnut, 52 metres in circumference, the thickness being the result of the fusion of several trunks growing from the same root. Legrand saw in the Ardennes an oak which was formed by the fusion together of four trunks which became free again above; the oak bears the name of "Arbre des quatre fils d'Aymon." Moquin-Tandon observed two shoots of asparagus which were free and distinct at the base, in contact about the middle, and

fused together to a single apex above. Sénébier found the haulms of two distinct grasses united together to form a single stem whose apex bore wheat on one side and rye on the other.

2. Congenital.—No instance of this kind of union between two or more main shoots appears to be known.

But it is common between the main shoot and an axillary branch. When this phenomenon occurs, of which instances will now be given, the appearance is presented of an extra-axillary branch; as it is, however, very rare in Nature, it must always be ascribed to fusion of the two axes and not to displacement of the subsidiary shoot or branch out of its normal position.

In *Ampelopsis Veitchii* a tendril had become split into two; one of the two branches so formed was carried up, by congenital fusion with the strong axillary shoot, to the next node above, where it left the axis immediately below the leaf of that node. In the sycamore axillary shoots, at intervals along one side of the stem only, were seen fused for a certain height with the main axis.

A good instance of it has also occurred in the long-rooted cat's-ear (*Hypochæris radicata*).

De Vries describes and figures all grades of adnation of this kind in *Hypochæris glabra*, the extreme case being that of complete fusion of both the peduncles and the capitula of the main and axillary shoots.

Prof. F. W. Oliver informed the writer of a case in a species of *Polygonum* in which an axillary shoot sprang from the stem close below the node above that to which it belonged; as it, of course, arose congenitally in that position, the ochrea of the node to which it morphologically belonged was not split on the outer side to admit of the shoot's passage, a fact which, of course, would tend to heighten the illusive appearance of the axillary shoot being displaced and not fused with the main axis. It was interesting to note that the ochrea of the node above was split on the same side on which the axillary shoot emerged just below it. This may aptly be compared, as Prof. Oliver suggested, to the disappearance of the posterior stamen in the flower of *Veronica* as a result of fusion of the two lateral posterior petals to form a single median posterior one; but in the *Polygonum* we see a kind of converse case, in which, owing to the approximated and opposed position of the shoot, the congenitally-fused stipules become disunited on the self-same side.

Conclusions.—All the phenomena coming under this section are to be regarded as progressive and not reversionary, for the changes are of the nature of reduction, which appears to have been a main feature of plant-evolution; although, of course, many of the abnormalities mentioned are mere temporary lateral deviations, and in no sense on the main line of evolutionary change; but they are all adaptations to changed conditions, which are in some cases, probably in all, of a purposive nature.

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3. DIRECTION OF GROWTH.

The Various Directions.

1. Horizontal Shoots.—The change of direction which the stem or branches, or both, may assume in their growth is instanced by various phenomena.

The main shoot or its branches may become horizontal in their growth as in a variety of the spruce which is completely prostrate. Goebel describes and figures the tip of a stolon of enchanter's nightshade (*Circæa intermedia*) which had already turned upwards above-ground and was growing in a vertical direction and about to produce foliage-leaves, but was induced to grow downwards again beneath the soil. Klebs grew a plant of the greater spearwort (*Ranunculus Lingua*) in a warm manure-bed, when the apex of the shoot developed a stolon in place of a continuation of the erect leafy stem (fig. 33).

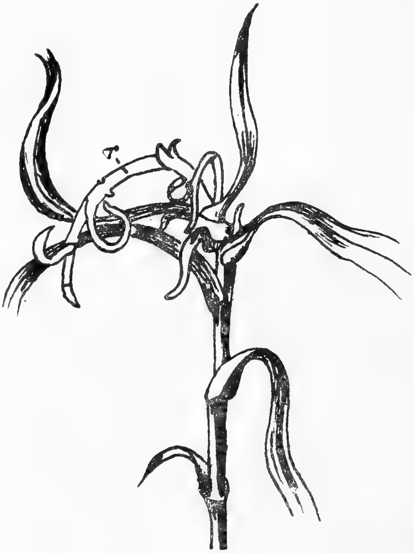

Fig. 33.—*Ranunculus Lingua.* Erect shoot developing into a runner (*r*) at apex. (After Klebs.)

He made a cutting of the inflorescence of the great yellow loosestrife (*Lysimachia vulgaris*) and laid it prostrate on moist soil, when it became changed into a rhizome which grew downwards into the soil.

He also induced the development of a runner at the apex of the inflorescence of the bugle (*Ajuga reptans*) and the ground-ivy (*Glechoma*).

Duchartre gives an account of a plant of *Lilium neilgherrense* whose bulb gave rise to a shoot which at first grew horizontally or slightly downwards in the soil for a certain distance, behaving exactly like a rhizome, bearing scale-leaves and adventitious roots, and eventually grew vertically upwards above the soil in the usual way.

2. Erect Shoots.—The converse case is frequent in which shoots, normally prostrate or creeping, become erect, either congenitally or at a later period of life. In the fastigiate varieties of trees, *e. g.* Lombardy poplar (*Populus nigra* var. *italica*), Irish yew (*Taxus baccata* var. *fastigiata*), and Exeter elm (*Ulmus montana* var. *fastigiata*), all the lateral branches grow erect and parallel with the main stem. There is a variety of the spruce (*Picea excelsa*) in which on a strong lateral shoot a number of erect daughter-shoots arise; the Germans call this form "Harfenfichte" (harp-spruce). There are other forms again which have many "leaders" instead of one.

In many trees, as in the Coniferæ, it is easy, by excision of the leader, to cause a lateral, normally dorsiventral branch to assume an erect terminal position and radial symmetry.

Main trunks which have fallen over and lie prostrate often produce on their upper side lateral shoots which grow vertically upwards as their parent stem did previously. Many trees and shrubs whose lateral branches are normally of dorsiventral character, with distichously-arranged leaves, can be induced, by excision of the "leader," or, as in the case just cited, by changing its position, to form lateral shoots of radial symmetry bearing scattered leaves.

The varieties *conglomerata* and *minima* of the ivy (*Hedera Helix*) produce, instead of the dorsiventral creeping shoots, erect ones of radial symmetry, with distichous phyllotaxis.

The rhizophores of *Selaginella*, in their abnormal condition, are very striking examples of this phenomenon. From the almost vertically descending they change to the vertically ascending or erect direction (Plate VIII).

3. Inverted Shoots.—A hyacinth-bulb, owing to injury at the base, produced adventitious bulbous shoots which grew vertically downwards in one and the same line as the normal shoot at the other end. To grow thus was doubtless the best plan they could adopt in order to obtain the necessary light and air. The bulb was growing in a vase of water.

A good example of this is afforded by the "weeping" varieties of trees, such as the elm and birch, in which the branches, or their terminal portions, are directed vertically downwards. This is the normal feature in the case of the rhizophore of *Selaginella* (which has here been shown to be a shoot), and in that of the early stages of the growth of certain rhizomes and runners which at first grow vertically down into the soil before assuming their usual horizontal or oblique direction of growth.

4. Winding Shoots.—The winding of fasciated shoots has already been mentioned; it is often wrongly called "contortion." Other cases, in which the shoot similarly departs from the vertical direction, are afforded by the flexuous, tortuous shoots of the rush (*Juncus*), varieties of the hawthorn (*Cratægus*), and others. It occurs also in herbaceous plants, *e. g.* chicory and snapdragon.

Conclusions.—The majority of the phenomena coming under this heading are progressive, and not reversionary; they represent new departures in the life-history, as in the case of "weeping" and fastigiate varieties of trees.

There are two cases mentioned which are, however, obviously of reversionary nature, viz., when the dorsiventral climbing shoot of ivy becomes erect and radially-symmetrical, and when that highly modified organ, the rhizophore of *Selaginella*, becomes changed into a leafy shoot.

Further, it is evident that shoots may grow in any direction, the sole criterion being the particular needs of the shoot concerned. There exists no rule or law, however general, according to which a shoot grows away from the centre of the earth under the influence of gravity. The statolith theory does not provide the regulative cause of the direction of growth, but only a reminding stimulus which is subsidiary to, and, in origin, cannot be coeval with, the primary cause, which is the habit of the shoot, ingrained in its substance, to grow in this or that direction; but if the normal external stimuli, *e.g.* moisture or light, are wanting or greatly modified, that will necessarily cause a modification of the growth-direction, simply because the shoot then meets with conditions to which it is unaccustomed.

The misleading way in which most modern physiologists write about the influence of gravity is well illustrated by a sentence which may here be quoted from a recent text-book. After speaking of the way in which unicellular Algæ move towards a source of oxygen, and in which spermatozoa swim towards the ovum under chemical influence, the author says: "The growth of roots towards the centre of the earth and of shoots away from it is due to a perception of the direction of the gravity-pull." * Any ordinary student reading this would surely conclude the author's meaning to be that the root as a whole and the shoot as a whole are influenced directly by the gravity-stimulus in the same way as the Algæ and the spermatozoa previously cited are directly influenced by the oxygen and chemical substances respectively. This, of course, is not so.

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* Stevens, 'Plant Anatomy in its Relation to Development and Function.'

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4. ADVENTITIOUS SHOOTS.

Adventitious organs are those which arise at a later period than their usual time of origin, out of their normal position, and in what one would regard from the *à priori* standpoint as unexpected places. And this is a correct way of envisaging the phenomenon, for, phylogenetically, the three essential organs, shoot, root, and leaf, have a definite mutual relation and origin which are maintained in all ordinary circumstances; but here and there specific changes in the environment and in the constitution of the individual have led to the abnormal production of certain organs which we call "adventitious." Adventitious shoots are exceedingly common and of many kinds. They may be classified according to the organs on which they occur. A shoot is produced normally from another shoot as a branch in the axil of a foliar organ. This shoot, however, is not always strictly in the axil, but sometimes occurs either on the leaf-base or on the main axis a short way above the leaf-insertion. Following Celakovsky in regarding so-called "axillary" shoots as always occurring on the leaf, it is evident that they represent normal adventitious shoots definitely stereötyped as regards their position on the leaf. As can be clearly seen in some Coniferæ, the leaf has both a decurrent and an ascending foliar base; where an axillary branch arises it does so from the surface of the enlarged ascending portion of the leaf-base. "Axillary" branching can thus be best explained by assuming that in all, or most, axes the leaves possess ascending foliar bases and that lateral branches are produced upon these.*

We will consider adventitious shoots according as they arise on root, stem, leaf, and floral organs respectively.

ROOT-SHOOTS.

These are exceedingly common and widely spread. Amongst the commonest are the well-known suckers which arise from the roots of the plum, the elm, the balsam-poplar, etc. (Pl. IX, fig. 5); the willow (*Salix*) and *Sisymbrium Alliaria* will also form them very readily under certain circumstances. Gardeners propagate many plants by means of root-cuttings. Such have been produced in *Drosera hilaris*. The roots of the bird's-nest orchid (*Neottia Nidus-Avis*) produce root-buds almost as a normal character; these usually arise laterally; occasionally, however, they arise at the apex and congenitally replace the real root-apex. This phenomenon has evidently misled some morphologists, causing them to regard it as a case in which the root develops directly, at the apex, into a shoot, demonstrating thereby the essential identity in morphological nature of the two organs. This conclusion is here regarded as erroneous: the above is merely a case in which the adventitious lateral shoot has arisen so close to the apex and so strongly that it has completely absorbed and replaced it; for all that, it remains the same adventitious shoot. A similar

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* On the phyton-theory, which is here held, the stem is really built up entirely of leaf-bases; hence axillary shoots can *only* arise on leaves in any case. The development of the sporangium in *Selaginella* occurs in a way which indicates the presence of an ascending foliar base; and this will entirely abolish the anomalous idea of its arising on the stem.

phenomenon has been observed in some other plants, *e.g.* the lesser twayblade (*Listera cordata*) (Pl. IX, figs. 1 and 2), *Anthurium*, *Lycopodium cernuum*, and in the ferns *Diplazium* and *Platycerium*.

For the numerous other cases of shoots arising adventitiously on roots, the reader must be referred to the literature on the subject.

Fig. 34 shows a shoot arising endogenously from the root-tuber of a dahlia.

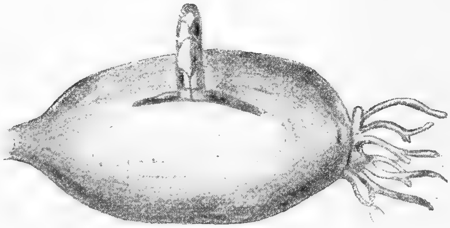

Fig. 34.—*Dahlia.* Adventitious shoot developing endogenously from a root-tuber. (After Carrière.)

STEM-SHOOTS.

Describing those, in the first place, which arise from the more external tissues, there are very few cases where these arise from the leafy stem, unless this has been injured or artificially mutilated. In the club-moss (*Lycopodium Selago*) great numbers of bulbils or buds are formed exogenously near the apex of the stem in the same position as the leaves; they are clearly not in the leaf-axils; they drop off and thus reproduce the plant. This is a normal character of the species and may have arisen as a "sport" in the past. Again in *L. aloifolium* adventitious buds grow out at the base of the stem. In both these cases the shoots must be regarded as occurring on the leaf-bases, as the whole stem is probably clothed with these. The shoots of *Begonia phyllomaniaca* are often covered with small buds.

Adventitious shoots on stems are usually formed as a result of mutilation.

The phenomenon of "witches' brooms" is due to the excessive local production of branches on a twig. The Germans call them "Hexenbesen." They occur on many kinds of trees, perhaps as often as any on the common birch, resembling large birds' nests. They are in all cases due to stimulation caused by a subtle attack, at a very early period, on the tissues by a mite (*Eriophyes rudis*) in some cases, in others by that of a fungus (*Exoascus alni*). The wound caused by either mite or fungus induces an excessive flow of nutriment to the affected spot and this expresses itself in hypertrophied branching.

Tubeuf describes structures resembling "witches' brooms" produced on the Conifer *Thujopsis dolabrata* in Japan under the influence of the mycelium of *Cæoma deformans;* they "consist of leafless non-chlorophyllous axes, dichotomously branched, and with each branch ending in a disc"; the fungal sori are formed under the epidermis of the terminal disc. We see here that the infection induces a reversion to the ancient dichotomous type of branching.

The large "knaurs" or "burrs" which appear from time to time on elms, oaks, and other trees, in some cases are caused by the lopping off of branches, in others their origin is obscure.

In the case of an elm which had been grafted in the Jardin des Plantes at Toulouse there was observed to arise below the graft an enormous cushion which produced more than a thousand closely-approximated branches interlaced together.

At Montpellier a branch of *Broussonetia* produced within an area of a few centimetres several hundred shoots. The same thing was seen in a mulberry in Toulouse botanic garden.

From the exposed cut surfaces of stumps of forest-trees, such as the beech or poplar, young regenerative shoots usually arise in numbers from the cambial zone.

Coulter and Chrysler describe the formation of shoots from the vascular ring after decapitation of the stem, and from chips of the cortex in the Cycad *Zamia*.

Goebel figures a case in *Streptocarpus Holstii* whose axillary shoots had been removed, and from each such axil an adventitious shoot arose bearing leaves in whorls of three instead of two.

The faculty which some plants, under artificial injury, exhibit for the formation of these adventive shoots has been made use of by bulb-growers; for instance if a hyacinth-bulb is slit in a certain way at the base through that portion which morphologically represents the stem, great numbers of small bulbs will be formed along the edges of the slits.

Fig. 35.—*Solanum tuberosum* (potato). A system of young tubers sprouting from the pith of the primary one. From a photograph.

Again Goebel figures and describes a portion of the parasitic stem of *Cuscuta glomerata* in which a number of endogenous adventitious shoots had arisen in the immediate neighbourhood of the haustoria, and he also states that such were produced artificially by cutting off the upper and lower portions of the stem.

He also figures a tuber of *Corydalis solida* which was cut in two: from the cut surface of the lower piece shoots sprouted.

The "Crown Gall" disease, now known to be caused by *Bacterium tumefaciens*, gives rise in certain plants to the formation of a dense aggregation of adventitious shoots all round the stem-base; each shoot is a slender structure bearing rudimentary leaves. This curious phenomenon has occurred in two species of mullein (*Verbascum nigrum* and *V. pyramidatum*).

Then there is the phenomenon of shoots arising from the pith. In a decapitated stem of the Cycad *Stangeria paradoxa*, from the centre of the pith grew out a young leafy shoot.

Berkeley figures a similar case in the sea-kale (*Crambe maritima*) where a number of buds were springing from the pith.

A figure is given on the previous page (fig. 35) of adventitious shoots bearing tubers springing from the internal tissue (the pith) of a potato, and bursting through to the outside. Various authors also describe this phenomenon, which seems to be usually ascribed to the rubbing off of the external buds or eyes. Carrière also induced it by removal of the external surface. Hence it would seem that in this case also mutilation, accidental or purposive, is the cause of the phenomenon.

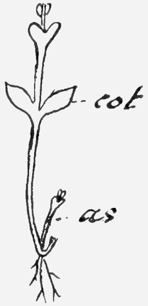

Fig. 36.—*Linaria arenaria*. Adventitious shoot (*as*) growing from hypocotyl. (After Bernhardi.) *cot.*, cotyledons.

Instances are also known of shoots arising from the hypocotyl. There are several species of *Linaria* which regularly multiply by the development of shoots growing directly out of the hypocotyl; these at first form an elongated leafless portion resembling the hypocotyl itself before giving rise to leaves and flowers (fig. 36).

Jensen describes the formation, as the result of injury to the epicotyl, of buds from the hypocotyl of *Jatropha curcas*.

Leaf-Shoots.

These also are of extreme frequency. Just as adventitious shoots on roots have become, in such cases as the plum and elm, a normal, constant feature of the plant, in the same way in certain plants adventitious shoots on leaves have become a fixed and normal characteristic, as in *Bryophyllum calycinum* and the orchid *Malaxis paludosa*, where they occur all round the margin of the foliage-leaves; in other species of the first-named genus they do not occur; in one species a shoot was observed seated in the notch at the tip of one of the cotyledons; another occurred on the top of the petiole; on neither of the two young foliage-leaves already formed were any buds present.

The ladies' smock (*Cardamine pratensis*) is well known to form great numbers of adventitious shoots on its foliage-leaves at the base of the leaflets; several other species of the genus do the same. They are also well known to occur in other members of the section Arabideæ, *e.g.* in the water-cress (*Nasturtium officinale*), and in a species of rock-cress (*Arabis pumila*). With the exception of the last-named, all these plants grow in moist habitats, and the environment has probably something to do with the anomaly.

In *Tolmiæa Menziesii* adventitious shoots are often, and apparently as a normal feature, formed in the sinus at the base of the leaf-blade, a character which appears to become accentuated under cultivation. In all three of the British species of sundew (*Drosera*) such shoots are frequently developed on the upper surface of the blade (Pl. IX, fig. 3). But by far the most remarkable case of this sort is afforded by *Begonia phyllomaniaca* (probably a cross between *B. manicata* and *B. incarnata*) in which the surface of the blade and petiole is thickly sprinkled with buds in all stages of development. In one of the parents, *B. manicata*, as also in some other species, the surface of the blade and petiole along the veins is clothed with brown scale-leaves; the formation of such a scale-leaf may perhaps be regarded as the first arrested stage in the development of an adventitious shoot, which has become a fixed character of the species. It is a similar phenomenon to that found in *Lycopodium Selago* during the development of the bulbils on the stem, in which a basal leaf is formed before any other organ makes its appearance; yet in both these cases the precocious foliar organ must be regarded as being attached to as yet undifferentiated tissue of the axis of the bud; in *B. manicata* this never develops further and becomes merged in the tissue of the leaf-vein. Transitional stages between these epiphyllar emergences of *Begonia* and foliage-leaves have been observed, a fact supporting the view expressed above.

In this connection must be mentioned a most interesting account by Dr. Marie Stopes of the normal mode of origin of the lateral branches of *Cycas revoluta*, as observed by her in Japan. The "buds," which may develop into quite large, thick lateral branches, "may arise, apparently, at any time," but the interest of the phenomenon lies in the fact that they originate, not in the axils, but on the upper surface of the scale-leaves of the stem, a short distance away from the axil. At first there is no connection between their vascular system and that of the stem, and in a young stage they may produce one or two adventitious roots. At a later period, however (as, of course, must necessarily be the case), when the buds become well-developed branches, complete vascular connection with the main stem is established.

Now the Cycads are a group intermediate between the Ferns and the Angiosperms; in the former of these two lateral shoots are produced, in the majority, in an extra-axillary position on the stem, or, in other cases, on the petiole, and it is exceptional to find them, as in the Hymenophyllaceæ, in an axillary position; in the Angiosperms they are always axillary. The mode of forming lateral shoots in Cycads would seem to be transitional between that of the other two groups, viz., always adventitious on the petiole a short way from the axil. In view of what has already been stated (see p. 126) with regard to the real position of axillary shoots in Angiosperms, it is highly probable that the subaxillary, petiolar position in Cycads represents the condition from which the truly axillary position in Angiosperms has been derived. Dr. Stopes' observation strongly supports Celakovsky's view of the matter.

Adventitious shoots occur, often as quite normal features, on the upper surface of the blades and petioles of many ferns, such as *Asplenium bulbiferum* and other species, *Aspidium Filix-Mas*, *Athyrium Filix-fœmina*, *Pteris aquilina*, *Gymnogramme chrysophyllum*, and *Polypodium proliferum*. They occur normally on the lower surface in *Cystopteris bulbifera*.

The phenomenon may be correlated with the damp habitat of most ferns. In some cases, however, as in those of *Pteris quadriaurita* and *Aspidium aristatum*, they arise under the influence of the Fungi *Taphrina Laurencia* and *T. Cornu-cervi* respectively.

According to Goebel, the fern *Adiantum Edgworthii* produces adventitious shoots at the actual apex of the leaf whose apical cell divides into two, and from one of the two daughter-cells the adventitious shoot is developed; this, therefore, is exactly comparable to what occurs in the roots of the ferns *Diplazium* and *Platycerium*.

Kupper found that in species of *Adiantum* and in *Asplenium prolongatum* the apical cell of the adventitious bud proceeds directly from that of the leaf. In the former genus the first three leaves of each bud arise from the thickened tip of the leaf quite away from the new vegetative apex; in the *Asplenium* this is the case only with the first leaf. The first roots arise endogenously on the convex side of the apex of the mother-leaf; the later ones on the axis of the bud. In *Aneimia rotundifolia* the leaf-rudiments may arise before the shoot-apex is present; and he found that the first leaves (as many as six) arise quite independently of the shoot-apex, although normally orientated thereto, and in perfectly regular arrangement. This, then, is a quite comparable case to that of the adventitious leaves and shoots in *Begonia* and *Lycopodium* above-mentioned.

Adventitious shoots, in the form of bulbils, are often produced in abundance on both the upper and lower surface, and on the margin, of the leaves of the Cape Star of Bethlehem (*Ornithogalum thyrsoides*), and on the lower side only in *O. longibracteatum* and *O. scilloides*. The writer has seen them formed in abundance along the veins of the upper surface of the "Chinkerinchee" (*O. lacteum*) (Pl. X) and also in the axils of the bracts of *O. thyrsoides*.

FIG. 37.—*Solanum Lycopersicum*. Adventitious shoot (*as*) growing from "axil" of leaf-segment. (After Duchartre.)

In the majority of the examples hitherto cited the phenomenon occurs in a state of nature. Under cultivation, or as a result of mutilation, the instances can be multiplied. In the enormous branching stem-like leaves of the tomato (*Solanum Lycopersicum*) shoots frequently appear in the "axils" of the petiolules of the large leaflets (fig. 37).

Gardeners make abundant use of the capacity possessed by leaves of certain plants to form adventitious shoots in order to propagate such plants by means of leaf-cuttings; for this purpose leaves of *Begonia*, *Gloxinia*, *Streptocarpus*, and many others from a great diversity of natural orders, are cut through here and there in the region of the veins, and at the points of incision new plants are formed when the leaves are laid on moist soil.

For other cases of regeneration induced by artificial treatment the reader is referred to Goebel's book.

But an instance cited by him may be mentioned in which a youthful organ was shown capable of regeneration, but the mature organ quite incapable. Just as the tadpole is able to regenerate amputated limbs, but the frog cannot do so; in the same way it was found that the primordial leaves of *Lycopodium inundatum* are able, but the mature leaves quite unable, to produce adventitious shoots.

From the morphological standpoint no more interesting experiment is known than that recently described by Doyle. "A sprout was grafted on a petiole of *Pelargonium zonale* var. *meteor*, all the other buds and leaves being removed. After a short time the petioles carried large shoots, completely functioning as stems, while the qualities of a stem, viz., indefinitely active cambium, the appearance of interfascicular cambium, considerable secondary thickening, periderm-formation, were all taken on by the petiole." This may be regarded as a case of an adventitious shoot growing on a leaf, but placed there by direct artificial means, instead of arising in such a position naturally or as the indirect result of an artificial environment. The position of this shoot, terminal on the petiole, and replacing the whole of the upper part of the leaf, viz., the higher part of the petiole and the leaf-blade, may in some sort be compared with the terminal position of the adventitious shoot on the roots of *Neottia* and certain ferns. In the case of the *Pelargonium* the petiole, in spite of the remarkable internal changes which it undergoes, still remains a petiole, and can only be regarded as changing into a stem from the purely physiological and functional point of view. In the same way as the adventitious occurrence of tracheides, sporangia, or a sporophytic shoot on the prothallus of a fern cannot surely be held to prove an homologous relationship between the prothallus and sporophyte.

Bulb-growers often propagate bulbs, *e.g.* those of the hyacinth, by deeply scooping out the base of the bulb so that the fleshy scale-leaves are cut through, when, at the margins of the cut surfaces abundant young bulbs are formed. Some bulbous plants, *e.g.* *Lilium* sp., are propagated from single bulb-scales; in the same sort of way as the fleshy leaves of some species of *Sedum;* and, doubtless, other Crassulaceæ will also produce young plants when isolated and placed in sand.

A bulb of hyacinth affected with the crown-gall disease (caused by *Bacterium tumefaciens*) was greatly hypertrophied, due to the abundant formation in all parts of the bulb-scales of small bulbils, more or less irregularly and imperfectly formed. Just the same kind of structure has occurred in a bulb of *Scilla* sp., but in this case the hypertrophy may be attributed to a mite which was found in plenty on the affected part.

A bulb of the wild hyacinth (*Scilla festalis*) was also seen to have proliferated to form a second bulb at a considerably higher level. As this second bulb consisted entirely of thickened scale-leaves and was devoid of a central axis, the lateral bulblets formed by it, instead of arising, as in the lower bulb, in the usual axillary position, were obliged, owing to the absence of the axis, to arise adventitiously on the outer scale-leaves, through which they sent their roots.

A very remarkable case of adventitious bud-formation on foliage-leaves recently came under the writer's notice. Amongst the basal leaves of a plant of *Verbascum nigrum*, affected with the "Crown Gall," from whose "collar" sprouted a great mass of small shoots, was one leaf whose margin was studded all round with adventitious buds giving the leaf an unusual appearance.

Beusekom gives a most detailed account of the developmental formation of endogenous adventitious buds near the tips of the leaves of *Gnetum Gnemon.* They were induced both by the depredations of an insect (*Aspidiotus*) and by minute needle-wounds.

OVARY-SHOOTS.

Adventitious buds also occur on floral organs, especially in the pistil. Peyritsch has described vegetative buds sprouting from the placentas, *e. g.* in *Sisymbrium Alliaria*, and apparently thereon replacing the ovules, and the same phenomenon has also been observed in the winter-cress (*Barbarea vulgaris*). Celakovsky describes interesting cases in *Sisymbrium Alliaria* in which the buds appeared in most cases on the virescent inner integument of the ovule either on its upper surface, when the integument was in the form of an expanded leaflet or a pitcher, or on its lower face (on outer surface of pitcher), in all cases at or near the base of the organ (Pl. XI, fig. 1). Penzig figures and describes buds growing on the virescent ovule, but it is not quite clear upon which integument they occur; they either grow out side by side with the elongated nucellus, or from the tissue immediately underneath the nucellus which then becomes raised up and borne at the apex of the leafy bud. In all these cases of adventitious buds occurring in the ovary, even where the buds occur in the exact position of ovules, replacing the normal ovules, there can surely be no question at all of the buds representing metamorphosed ovules for the simple reason that no transitional forms or stages between these buds and ovules, or between the bud-leaves and virescent integuments, have ever yet been met with, and it is these alone which could prove the homology between the two. The buds are obviously entirely new structures and bear no more homogenic relationship to the ovule than do adventitious buds to the foliage-leaves which bear them.

Some have supposed that the adventitious shoot arising on the inner surface of the inner integument represents the nucellus; but apart from the fact that cases, as above stated, are known in which both occur on the same integument, Celakovsky always found, in *S. Alliaria*, that, while the nucellus occurred fairly high up on the upper surface, the shoot always occurred at the very base.

A similarly new formation, in the above sense, is the adventitious shoot produced, as described by Goebel, in the place of a sporangium on the upper surface of the sporophyll of the quillwort (*Isoëtes lacustris*). (For formation of flower-buds adventitiously see under "Flowers.")

Adventitious plants, in the form of embryos, arise normally from the nucellus in *Euonymus*, *Citrus*, *Funkia*, and *Cœlobogyne*.

5. ADVENTITIOUS GROWTHS IN THE SEXUAL GENERATION.

Prothallus-Shoots.

The sexual generation or gametophyte is, as every botanist knows, differentiated as a distinct, independently-growing plant among the Vascular Cryptogams, and is known as the prothallus. A new vascular plant or sporophyte arises from this as a result of fertilization taking place in the female sexual organ or archegonium. This is the normal course. It is now known, however, that in a good many ferns, *e. g. Pteris cretica* (fig. 38), in which the phenomenon was first discovered by Farlow, the prickly shield-fern (*Polystichum aculeatum*) (Pl. XI, fig. 2), the hart's-tongue fern (*Scolopendrium vulgare*) (Pl. XI, fig. 4), and *Nephrodium pseudo-mas* (Pl. XI, fig. 5), adventitious shoots and roots, developing into young fern-plants, may from time to time, under conditions which do not as yet seem to be adequately determined, arise from either the upper or lower surface of the prothallus; usually from the latter, when they appear to develop in the same region as, and to replace, or even to grow out of, the archegonia. This phenomenon, known as *apogamy*, represents clearly, like all other cases of adventive bud-formation, a short cut in the mode of reproduction, and it entirely replaces and supersedes the sexual method.

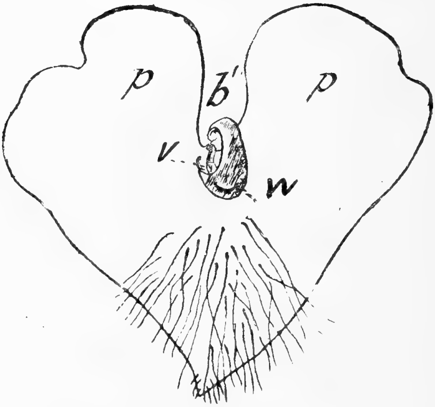

Fig. 38.—*Pteris cretica*. Sporophyte growing apogamously on prothallus. (After De Bary.) *p*, prothallus; *w*, root of sporophyte. b^1, first leaf of sporophyte; *v*, second leaf of sporophyte.

Adventitious Prothalli.

Of great interest is the phenomenon of *apospory* in ferns. It is also an instance of the formation of entire plants on leaves, but the plant in this case belongs to the sexual, the leaf producing it to the sporophyte generation. Druery first described the phenomenon in a variety of lady-fern (*Athyrium Filix-fœmina* var. *clarissima*). Wollaston discovered it in *Polystichum angulare* var. *pulcherrimum*. Bower later investigated the entire phenomenon in these and other ferns, *e.g.* *Trichomanes alatum*. In the first-mentioned and in the bracken (*Pteris aquilina*) (Pl. XI, fig. 3, and fig. 39) the prothalloid growths are formed from the sporangia which become thereby arrested in their development, and never produce spores. In *Polystichum* there are three distinct methods of production of these prothalloid growths: (*a*) from the arrested sporangia; (*b*) from the base of the sorus, *i. e.* quite distinct from the sporangia; in this case also the sporangia of the same sorus are arrested in their development; these prothalli may be in part plate-like and in part filamentous; (*c*) from the pinnule of the frond, *i. e.* quite independently of both sporangia and sorus, viz. from the vegetative portion of the frond; of this category there were prothalli which sprang from the surface of the pinnule in the region of a vein, and others which arose from the margin as a direct continuation of its growth; a case of this

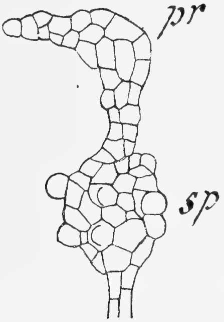

FIG. 39.—*Pteris aquilina.* Prothallus (*pr*) growing aposporously from sporangium (*sp*). (After Farlow.)

kind may be represented in fig. 40, where the tissue of the pinnule gradually merges into that of the prothallus, a case which reminds one of the adventitious shoots of *Neottia*, etc., terminal to the root and a direct continuation of its apex, as also of the formation of adventitious shoots in ferns as a direct outgrowth of the leaf-apex. In *Trichomanes* the prothalli arose directly from the pinnule in a similar way. Also Druery observed, in *Nephrodium pseudo-mas* and *Scolopendrium vulgare* var. *Drummondæ*, the formation of prothalli on the margins of the frond (fig. 40). It may be mentioned that in some of these prothalli sexual organs occurred.

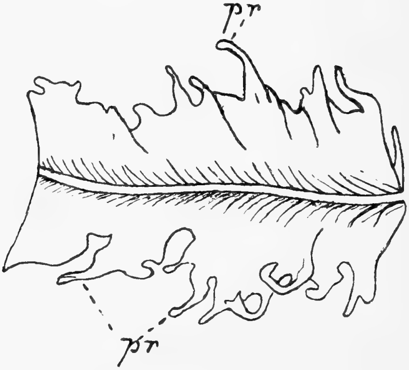

FIG. 40.—*Scolopendrium vulgare* var. *Drummondæ*. Portion of frond showing incipient prothalli formed aposporously. (After Druery.) *pr*, prothallus.

Another phenomenon must here be referred to. Just as the sporophyte may give rise to other sporophytes adventitiously on its leaves, in the same way the oophyte or prothallus may produce secondary prothalli adventitiously. Cramer observed this in *Osmunda* and Goebel in *Gymnogramme*; in the latter they may be formed marginally or on the surface, as the result of injury to the apex of the normal prothallus, or in the absence thereof. Treub observed the same phenomenon in the prothallus of *Lycopodium*.

General Conclusions on Adventitious Shoots.—As regards the formation of adventitious shoots in general, they seem to represent an attempt on the part of the plant to reproduce itself more rapidly (*i. e.* by a short cut) than by the normal method, whether this takes the form of vegetative or sexual reproduction. It would also seem that very often adventitious shoots arise as a result of the presence of some special stimulus, such as excessive moisture or nutriment; in a mutilated organ the accumulation of nutriment near the wound induces very accentuated tissue-growth, the callus-cambium being stimulated to exceed its function of mere callus-formation and to develop a shoot. Where a great accession of nutriment occurs owing to the activity of foreign internal organisms, as in the *Verbascum*-leaf mentioned, unmutilated organs may develop these buds just as freely. Quite as interesting are those cases where the buds have become fixed and stereotyped as a normal character of the plant, and where no special or abnormal stimulus appears to exist to induce their formation; this has simply been found to be a convenient method of reproduction, and being once assimilated into the ordinary life-history, needs no extraordinary stimulus for its production at the proper time and place.

Some botanists have supposed that the production of adventitious shoots by leaves amounts to a demonstration that there is no essential morphological distinction between leaf and shoot, and that in like manner the root is homologous with the shoots which it bears, etc. This appears to be a hasty and inadequate conclusion. The fact that a shoot arises adventitiously from a foliage-leaf, a root, or the integument of an ovule, cannot surely reveal anything as to the capacities and essential nature of the external form of the organ bearing the shoot; the external form and characteristics of the organ as a whole can hardly enter into the question; for in none of these cases are there any genuine transitional stages between the organ producing the shoots and the shoots themselves, and such stages constitute the only evidence in proof of the identity of any two structures. It seems that the explanation of adventitious shoot-formation is rather to be sought in the nature of the internal mechanism of the organs producing the buds, and that it must really be due to a homology between the protoplasmic constituents, or some of them, of these organs, a germ-plasm being present in most parts of the plant.

The same argument may be applied to the cases of apogamy and apospory. The protagonists of the theory of "homologous" alternation of generations have seized upon these phenomena as an apt weapon for use in defence of their cause; if the prothallus, say they, is capable of giving rise directly, by vegetative budding, to a fern-plant, or the fern-plant to a prothallus, this is evidence in favour of the two generations being one and homologous. But this apparently represents the same indefensible position as that of those who maintain the homology of shoot and leaf from the fact of the latter producing adventitious buds. Why may not germ-plasm exist in the prothallus as well as in the foliage-leaf of the fern? On the view above-stated the prothallus is no more necessarily homologous with the adventitious shoot which it bears than is the fern-leaf with the shoot or prothallus which *it* bears. That which would afford proof of the homological identity of prothallus and fern-plant would be transitional forms (each itself maturely developed) between the two, the one gradually merging into the other; but no such phenomenon has ever yet been seen.

It is true that the curious structures induced by Lang in the prothalli of various ferns: cylindrical thallus-lobes bearing ramenta, or sporangia, and containing tracheides, and the prothallus-lobes of ordinary flattened form above but leaf-stalk-like in structure below, the "new growths" as he termed them, are clearly, in one sense, transitional structures between a fern-leaf and a prothallus-lobe, as are also the tips of the pinnules which merge into prothalli; they are not, however, in the morphological sense of the term transitional organs at all; there is no series of forms connecting the two, as *e.g.* there is between a phyllode and a compound leaf; a transition only exists between one portion of the prothallus-lobe and another portion of the same lobe. If there could be shown an actual bud on the prothallus bearing both prothallus-lobes and leaves or structures combining the characters of these two organs, then we might believe in the possibility of a transition between a prothallus and a sporophyte shoot. The real explanation of the abnormal structures so happily discovered by Lang appears to be as follows. If we consider, for the sake of comparison, the formation of an adventitious shoot upon, say, a *Begonia*-leaf, it is obvious that, in order to form the shoot at all, transitional stages of growth must be gone through representing the passage between the tissues of the leaf at that particular spot and those of the shoot; these are passed through so rapidly, however, as to be unnoticeable. The same is true of many of the buds formed on the prothallus and of the prothallus formed on pinnules. But, for all that, these intermediate stages, representing the adaptation of the tissues of the leaf or prothallus respectively to the formation of those of the shoot, must exist, however unnoticed. On the other hand, the "new growths" on the prothallus appear to owe their existence to the fact that in many cases the transitional stages between the tissue-formation of the prothallus and that of the shoot are not sudden, but, on the contrary, long drawn-out, and often, moreover, interrupted; the attempt on the part of the prothallus-tissue to form sporophytic shoot-tissues is also often half-hearted and incomplete, often resulting in failure, when a reversion to the formation of prothallus-tissue once more supervenes. Phenomena of this kind naturally give rise to such pseudo-transitional organs as Lang describes. The phenomenon of adventitious buds on the fern-prothallus is seemingly comparable to that of similar buds on the *Begonia*- or fern-leaf and does not in any sense imply a homology between the shoot and the leaf or thallus bearing it; the same germ-plasm exists throughout the whole plant in both its generations.

The present mode of alternation between the two generations is clearly antithetic, for the simple and only reason that for the production of the sporogonium or fern-plant, etc., from the oospore, a totally new method of growth of tissue and organ-formation is inaugurated. Why should not the present antithetic method of sporophyte-development have always prevailed? Why try and devise a new, unheard-of method, based entirely on abnormal and exceptional phenomena?

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III. THE LEAF.

Goethe was the first to recognize that the numerous and varied foliar organs of the plant are all modifications of the same original organ. He says: "The secret relation subsisting between the different external organs of plants, such as leaves, calyx, corolla, and stamens (which are developed in succession, and, as it were, out of one another), has been long acknowledged by naturalists in a general way; indeed, much attention has been bestowed upon it, and the title Metamorphosis of Plants has been given to the operation by which one and the same organ presents itself to us under various disguises." He imagined a typical leaf of which all leaves are variants, which surely is the root-idea of modern comparative morphology. But he had no conception of a transformation of foliar organs by descent from some common ancestor, or that his type-leaf had a real existence in the past. He describes only the modifications which appear in the foliar organs during the development of the plant from the cotyledons up to the flower. Alex. Braun put forward much the same kind of view. But the treatises of both authors are profound and valuable so far as they go. Goebel's view is that every foliar rudiment is that of a foliage-leaf, but according to circumstances it may develop into any other type of foliar organ. He gives no reasons for holding such a view, and it is difficult to know exactly what his meaning is. If, however, it is meant that all other foliar organs have been derived from foliage-leaves in the past, he is no doubt correct.

In the light which recent palæontological data have afforded, it would seem that the factor of reduction, both in the number and size of organs, has played a large part in evolution in the past; this becomes clear when we consider the derivation of the Cycads from the ancient Pteridosperms (Cycadofilices). In these the foliage-leaves were large and fern-like; in their descendants they are reduced in size and in complexity of organization. It is possible, although we know nothing of the ancestry of Angiosperms, that in these also reduction has played a large *rôle*. In this section of the work it will be assumed that a well-developed foliage-leaf is the type or ancestor from which all other kinds of vegetative foliar organs of the present day have been derived, and so far this view agrees with that of Goebel, although he cannot surely have any right to assume that foliage-leaf nature inheres in every rudiment, for the modification into bract, scale-leaf, etc., must in most cases be congenital.

Now, if it be a true theory that the foliage-leaf is the original ancestor of all other forms of vegetative leaves, we should expect to find here and there tendencies to reversion to the parent-form. And this is what we actually find.

All leaf-abnormalities may be grouped under three main headings: Retrograde Metamorphosis, Progressive Metamorphosis, and Change of Position.

1. DIFFERENTIATION.

The reduction in size and complexity of organization, and the alteration of consistence, have produced many and various forms of vegetative foliar organs which have become fixed and stereotyped in the life-history of the plants producing them; and it requires an exceptional disturbance either in the individual plant or organ, or in the environment, or both, to obtain a release from this fixity, and a reversion, partial or complete, towards the ancestral form.

1. Phyllody of Bracts.—Bracts are the leaves which subtend a flower or an inflorescence. They may be

foliage-leaves, in no way differing from those on other parts of the plant either in size or complexity, as in some Cruciferæ, but are more usually much reduced and scale-like in consistence. Under the stimulus of excessive flow of nutriment or moisture the scale-like bracts may develop congenitally into foliage-leaves resembling those of the plant, as in the case of the bracts subtending the spike of the plantain (*Plantago major* and *P. lanceolata*) (Pl. XII, figs. 1 and 2). Or the bracts subtending all the flowers of the spike may become similarly changed, while at the same time the internodes of the axis become suppressed and the flowers remain undeveloped; this gives rise to the "rose-plantain" (Pl. XII, fig. 3). This is obviously an example of correlation of growth. In many Compositæ, *e. g.* the daisy (*Bellis perennis*), the bracts of the involucre may develop as foliage-leaves; the same is also true of many Umbelliferæ, *e. g. Daucus Carota.*

Schmitz observed in abnormal inflorescences of the cypress spurge (*Euphorbia Cyparissias*) that the involucre was no longer represented by a whorl of five small bracts alternating with crescent-shaped glands, but had become resolved into spirally-arranged small foliage-leaves, each bearing a gland on either margin such as is borne not uncommonly by the normal foliage-leaves of Euphorbiaceæ.

Velenovsky describes virescent catkins of *Salix aurita* in which the bracts of the flowers became leafy and were sometimes also furnished with stipules as in the case of the normal foliage-leaf.

The three small bracts immediately below the flower of *Hepatica triloba* sometimes develop as foliage-leaves.

The spathe of the cuckoo-pint (*Arum maculatum*) has been seen transformed into a stalked foliage-leaf, thus approximating to the normal condition of *Spathiphyllum.* The same change has been seen in the sheathing-bracts of the "cob" of Indian corn.

In the Conifers, concomitant with the other remarkable changes occurring in the cones, to be described later, the bract subtending the seminiferous scale in the female cone may become leafy.

The most reduced and modified form of bracts to be seen in the vegetable kingdom is that in the horse-tail (*Equisetum*) in the form of the "collar" subtending the inflorescence. In *E. maximum* and *E. arvense* this structure has been seen resolved into a whorl of ordinary leaves united into a sheath at the base.

All the phenomena just mentioned under this heading are to be regarded as cases of reversion to that which represents more or less perfectly the ancestral condition of the organ concerned, viz., a foliage-leaf; concomitantly with other parts of the reproductive region, the bracts have, in the course of evolution, undergone simplification. In *Equisetum* the normal leaves have undergone excessive reduction as compared with those of their ancestors; hence, if still further degeneration is to occur in order to give rise to the bracts or involucre of the cone, we could hardly expect any better-developed structure than the "collar" to result. In the Calamarieæ of the Coal Period the foliage-leaves were larger and also free, not being united into a sheath, and the bracts were of equal development.

In all the above cases the change consists in a more complete development of the foliar organ involved, viz., the superadding of a blade or lamina to the modified stalk or petiole of which alone the majority of bracts may be supposed to consist.

2. REAPPEARANCE OF BRACTS OR FOLIAGE-LEAVES.—It is a very exceptional thing for a shoot to be wholly devoid of foliar organs for any considerable portion of its length. Scapes afford such an instance, and the inflorescence of most Cruciferæ. In many Cruciferæ it it is by no means rare for the bracts, which for some unknown reason have been lost, to reappear, as in the wallflower (*Cheiranthus Cheiri*), stock (*Matthiola*), and rock-cress (*Arabis*); such cases are reversions to the normal state exhibited by several genera, *e.g. Porpyhrocodon*, *Dipterygium*, and *Selenia*, in several

of which the bracts are very well developed and foliaceous.

The observation by Velenovsky and Domin of the reappearance of leafy bracts (accompanied by virescence and other changes in the flowers) in the winter-cress (*Barbarea vulgaris*) is interesting, for in one species, viz., *B. bracteosa*, bracts occur as a normal feature.

In *Cephalotaxus* the writer observed, in slightly proliferated female flowers, the abnormal occurrence of two superposed pairs of small foliar organs situated in the transverse plane immediately below the two ovules (fig. 41 *c*). It is probable that, owing to lack of adequate space, a median whorl or two, which might otherwise have developed, has been suppressed. It is highly probable that these basal scale-leaves represent the reappearance of structures which were once present in the flower of *Cephalotaxus* before it became so greatly reduced, and that they correspond to the two to three pairs of scale-leaves (bracts) which occur normally on the floral axis below the ovules in *Taxus* and *Torreya*.

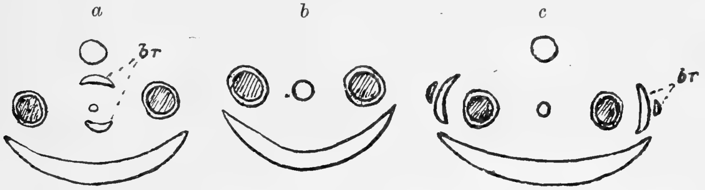

FIG. 41.—*Cephalotaxus drupacea.* Diagrams of a normal flower (*b*) and two abnormal "flowers" (*a* and *c*).

The articulation in the axis of the male flower of *Euphorbia*, probably, as Celakovsky points out, marks the position of bracteoles which have become suppressed. In some abnormal cases these have been found to reappear. Abnormal specimens of the dandelion (*Taraxacum officinale*) and daisy exhibit scapes bearing one or more foliar organs; the same has been seen in a species of *Leontodon* and in the lily-of-the-valley (*Convallaria majalis*), etc.; in this connection it is to be noted that in the autumnal hawkbit (*Leontodon autumnalis*) tiny involucral bracts extend a long way down the scape; in the *Leontodon*-scape figured by Masters the abnormally-placed leaves are foliaceous. The ancestral state of the shoot must have been a leafy one, and the naked condition has arisen owing to some special adaptation. All the above are clearly, therefore, cases of reversion.

It is probable that in those plants in which a marked difference obtains between the shape of the radical and that of the cauline leaves, this is a secondary phenomenon, and that originally the leaves borne on different parts of the axis were much more alike, or that there was not such a well-marked basal rosette as there is at present; hence we may regard as a species of reversion the case described by Goebel of a hare-bell (*Campanula rotundifolia*) which bore all up its flowering-stem the semi-orbicular leaves normally occurring at the base only.

3. SARCODY OF SCALE-LEAVES.—There was described in the 'Gardeners' Chronicle' a rare abnormality in *Crocus* consisting in the transformation of the brown, membranous scale-leaves at the base of the aerial stem into fleshy scale-leaves like those composing the bulb of a lily or hyacinth. The change was the more remarkable from the fact that *Crocus* does not normally possess such fleshy bulb-scales. In correlation with their formation in this case the foliage-leaves were small and the flower was imperfectly developed.

4. PHYLLODY OF SCALE-LEAVES.—The transformation of scale-leaves to foliage-leaves is a very much rarer phenomenon. In the axils of foliage-leaves of the potato, owing to prevention of the normal underground tuber-formation (but also occasionally when this is not thwarted), small tubers develop bearing small foliage-leaves and transitions between these and the ordinary scale-leaves.

A very good instance of the phenomenon is afforded by a plant of a butcher's broom (*Ruscus androgynus*) observed by Dickson, which was growing in a pot and produced a weak leafy shoot. To these two facts is attributed the anomalous formation of well-developed radical foliage-leaves, they, of course, being regarded as transformed scale-leaves which alone are produced in the normal plant. These foliage-leaves, to some extent resembling the cladodes in size, shape, and venation, differed from them in (1) the possession of a distinct midrib; (2) the venation being convolute; (3) being long-stalked; (4) having the stomates on the morphologically lower surface. These facts suffice to show that these leaves were quite distinct organs from the cladodes. Askenasy also observed the same phenomenon in *Danäe racemosa*, where well-developed foliage-leaves were seen to follow on the green-tipped sheathing scale-leaves at the extreme base of the shoots sprouting from the rhizomes. That the foliage-leaf represents the ancestral organ and the tiny colourless scale of the cladode-bearing stem a later modification is evidenced by the facts of ontogeny, for the seedling always develops a number of ordinary foliage-leaves subsequent to the cotyledons. There is no doubt that cladode-formation stands in correlation with the development of the leaves and bracts as minute scale-leaves, and that the appearance of true foliage-leaves represents a reversion to the condition of the plant before it possessed cladodes.

The runners or stolons of an enchanter's nightshade (*Circæa intermedia*) and a mint (*Mentha aquatica*) were found, as described by Goebel, to develop small foliage-leaves on exposure to light instead of the minute scale-leaves normally formed underground. Yet the runners of the moschatel (*Adoxa moschatellina*) under similar treatment could not be induced to form foliage-leaves.

The scale-leaves at the base of the stem of *Anemone Pulsatilla* often develop a green blade and so become foliage-leaves.

Lloyd cites a very interesting case in the yellow pine

(*Pinus ponderosa*). When the staminate shoots were pruned, the scale-leaves, scattered on the stem, became hypertrophied and developed as foliage-leaves, resembling, though not quite identical with, the primordial leaves of the plant, and comparable to the scattered leaves occasionally produced on young shoots of the larch (*Larix*). He regards them as atavistic, and the twigs bearing them may be compared to the permanent condition such as obtained in *Leptostrobus* and *Laricopsis*, ancestral forms found in a fossil condition in Siberia and the Potomac, the former standing in the ancestral line of the Pines and the latter in that of the Larches.

5. Phyllody of Tendrils.—The tendril of the Leguminosæ, Fumariaceæ, and some Cucurbitaceæ affords an instance of a foliage-leaf which has become greatly reduced in area of surface and otherwise modified for climbing purposes. Reversions to the original condition are sometimes met with. Penzig observed leaves of the narrow-leaved everlasting pea (*Lathyrus sylvestris*) in which some or all of the tendril-branches had become changed into leaflets, giving rise to imparipinnate leaves. In the yellow vetchling (*Lathyrus Aphaca*) there are normally no leaflets formed, these being replaced by the tendril. Morière and Vetter describe a form *unifoliolatus* in which the tendril is replaced by a small linear-lanceolate leaflet. Mann induced artificial foliation of the tendrils in the garden pea (*Pisum sativum*). The tendrils of the bryony (*Bryonia dioica*) are also cited as occasionally changing back into foliage-leaves. Naudin describes and figures very interesting transitional forms between tendrils and foliage-leaves in Cucurbitaceæ, which prove, in the best possible way, what their real nature is (fig. 42 *a* and *b*).

6. Phyllody of Thorns.—The development of thorns and spines is in the majority of cases the result of, and an adaptation to, a dry habitat, and at the same time probably a protection against animals; it is, in

other words, a xerophytic character. One has only to visit such regions as the Cape Peninsula and the Karroo, or a desert, to perceive that one of the numerous modes of adaptation to the waterless condition is that of a thorny leaf-structure. In our own country we see the same phenomenon (which is more difficult to account for, and seems to be better explained as a protection from browsing animals) in the furze (*Ulex europæus*) where the entire leaf is transformed into a thorn, and in the holly (*Ilex aquifolium*) where the leaf-teeth are developed as such. Now it has been found by experiment with certain plants, *e. g.* the furze and thorn-acacia (*Robinia*), that, if grown in a rich soil and in a very moist atmosphere, the thorns are entirely replaced by trifoliolate leaves and the spiny stipules disappear, which seems to indicate that poorness of soil and dryness of air are at any rate factors in their formation. In the barberry (*Berberis*) De Candolle mentions transitional forms as abnormally occurring between the foliage leaves of the short shoots and the thorns of the long shoots.

FIG. 42.—*Cucurbita* sp. *a*. Normal tendril. *b*. Transition from a tendril to a foliage-leaf. (After Naudin.)

In a shoot of *Acacia horrida*, owing to the infection of the twig by a fungus, *Æcidium ornamentale*, the thorny stipules were stimulated by an inordinate flow of nutriment to develop as green laminate leaves. A form of *Ulex europæus* (var. *inermis*) has been described which is entirely devoid of spines, which were, therefore, presumably replaced by leaves.

There can be no doubt that all these cases are due to reversion to the primitive condition.

7. Bracteody of Glands.—Velenovsky observed the gradual transformation (by means of division, along with displacement and enlargement of the products) of the normal posterior gland in the flower of the withe-tree (*Salix aurita*) into two transversely-placed scale-like bracteoles (fig. 43). This is a reversion, for in the Juglandaceæ and the female flower of Myricaceæ (to which order Salicaceæ are closely allied) these two bracteoles occur as a normal feature. In the course of evolution of the modern *Salix*-flower they have become not only fused together into a single organ occupying a median posterior position, but also reduced to a glandular structure.

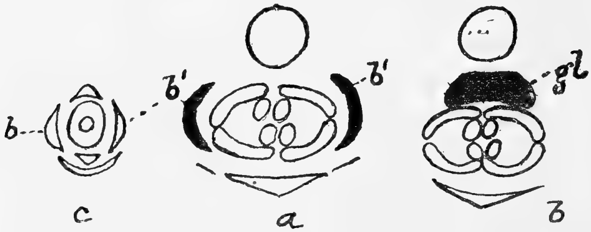

Fig. 43.—*a*. Abnormal flower of *Salix aurita*. *b*. Normal flower of the same. *c*. Female flower of *Myrica cerifera*. (After Velenovsky.)

8. Petalody of Scale-leaves.—A very remarkable abnormality has recently been described by Miss M. L. Green, and which the writer had the pleasure of investigating with her. It consisted in the partial proliferation and transformation of some of the bulbils of a tiger-lily (*Lilium tigrinum* var. *Fortunei*) directly into

flowers, these being more or less imperfect in their organization. The main feature of the phenomenon consisted in the presence of transitional structures between bulbil scale-leaves and perianth-leaves, and even stamens, for in some cases both of these two last-mentioned organs had dark-coloured swollen bases which are obviously of scale-leaf nature. It would appear that the axis of the bulbil elongates somewhat, the lowermost scales remain unaltered, while the uppermost become changed wholly or partially into floral organs. The ovary in such flowers was either absent or excessively undeveloped. The plant was otherwise uninjured and normal (Pl. XIII, fig. 1).

Now the bulbils of Liliaceæ have hitherto been regarded as, from the morphological point of view, reduced vegetative shoots, owing to their resemblance to miniature bulbs, and to the fact that, after falling to earth, they grow out into a vegetative shoot. But a little consideration will probably show that they can hardly be such, and this for more than one reason. Firstly, the production of lateral vegetative branches* is unknown among the herbaceous members (the vast majority) of the order; hence it is highly unlikely that such branches, in whatever form, should suddenly appear in this isolated way among a few scattered representatives of the order. Secondly, bulbils in this order of plants do not occur as a rule in the position of vegetative branches, but practically always in that of flowers, viz., at the base of the inflorescence or the highest part of the stem, a short way below the latter in the axils of bracts or leaves transitional between bracts and foliage-leaves, as in *Lilium bulbiferum* and *L. tigrinum*; never, or very rarely, in the axils of the typical vegetative leaves.† In *Allium* sps. they constantly and often normally replace flowers. In the yellow star of Bethlehem (*Gagea*) they are known to do the

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* Miss Green, in her paper, draws attention to these points.

† The fact that bulbils occasionally occur in this position can be understood when the further fact is recognized that flowers have been known to occur in the very same position.

same, and Wirtgen observed very interesting cases in abnormal plants of *G. arvensis* in which they appeared in the position which normally flowers occupy in the axils of bracts at the base of the inflorescence-axis, and occasionally replacing flowers in the smaller ramifications of the inflorescence; in the same positions on different plants he found normal flowers, more or less abortive flowers, and bulbils. In one case he observed a bulbil bearing terminally a stalked flower at the base of the inflorescence-axis. Thirdly, the fact that the bulbils of *L. tigrinum* var. *Fortunei* became, without any unusual or apparent stimulus, metamorphosed directly into flowers (the comparatively late stage at which this took place alone prevented the lowermost bulbil-scales becoming changed into perianth-leaves), is quite incompatible with the view that they represent vegetative shoots, and before the true nature of bulbils was realized these abnormal ones presented an altogether anomalous phenomenon.

It follows, from the above considerations, and from the fact of the gradual transformation (as shown by the transitional structures above-mentioned) of the bulbil of *L. tigrinum* var. *Fortunei* into a flower, that the bulbil as found in the Liliaceæ represents a modified flower, specially changed for purposes of vegetative propagation. And inasmuch as only isolated members of the order produce bulbils, this modification must be a comparatively recent one. The fact that bulbils, on being placed in very damp situations, as on the soil, grow out into vegetative shoots, is no argument against this conclusion, for under unusual stimuli of moisture and nourishment even typical flowers will often proliferate into vegetative shoots.

That the bulbil of the Liliaceæ is a modified flower would seem to be a new discovery, for the slightest hint of such an idea cannot be found in any of the text-books on morphology. Hesselman, who has described the same abnormality as the above in *L. bulbiferum*, considered the bulbil to be a vegetative shoot and not a flower; this he deduces chiefly from their collateral position in the axils, their late development as compared with that of the flowers, and the fact that they do not appear in the place of the flowers when these happen to be absent. These facts are not, however, of weight in overthrowing the view above propounded. Lack of space alone prevents their refutation in this place.

9. Staminody of Scale-Leaves.—As above stated, bulbil-scales of *Lilium tigrinum* var. were observed reverting to stamens; the swollen bulbil-like bases of the latter clearly showed the homology between the two kinds of foliar organs, and that bulbil-scales have been derived from stamens in the past.

Renner describes "hermaphrodite flowers" in *Juniperus communis.* The scale-leaves on the axis below the seminiferous scales became changed into stamens; occasionally, between the uppermost of these transformed scales and the seminiferous scales is a whorl of small sterile scales. This abnormality may be regarded as a reversion to the condition in which bisexual axes always obtained.

10. Sporophyllody of Scale-Leaves.—Christ cites the curious case of scale-leaves of the epiphytic fern *Stenochlæna* becoming sporangiferous; this probably represents a partial reversion to the condition in which all the leaves were both vegetative and assimilating.

11. Division of Simple Leaves.—Leaves, normally simple or undivided, frequently become in various degrees incised or divided.

a. Lateral Fission or Laciniation.—Leaves of the horse-radish (*Cochlearia Armoracia*) may become deeply pinnatifid (Pl. XVI, fig. 1). De Candolle describes leaves on a branch of a sumach (*Rhus Cotinus*) whose lobes were so narrow and fine that they resembled the foliage of Umbelliferæ. Laciniate leaves are produced in several forest-trees which normally have entire or only slightly-lobed foliage; these occur either throughout the tree or only on certain branches.

They occur in the oak (*Quercus Robur* var. *filicina*), birch (*Betula alba* var. *dalecarlica*), alder (*Alnus glutinosa* var. *laciniata*), hazel (*Corylus Avellana* var. *laciniata*), laburnum (*Cytisus Laburnum* var. *quercifolium*), beech (*Fagus sylvatica* var. *heterophylla*), and oak-leaved foliage of the honeysuckle (*Lonicera Periclymenum*) which has grown in shady woodland.

All these cases are probably due to depauperization, or reduction in the available assimilating surface of the leaf; and may be, as almost certainly in the case of the honeysuckle mentioned, and possibly also in that of the forest-trees, due to absence of sufficient sunlight. On the other hand, it is possibly a reversionary phenomenon, for in some of the genera concerned, incised or lobed leaves are a normal feature of certain species, *e. g.* in the Turkey oak (*Q. Cerris*), Japanese honeysuckle (*L. japonica*), and snowberry (*Symphoricarpus racemosus*).

Again, other kinds of heterophylly seem to be rather attributable to hypertrophy, *i. e.* to an effort on the part of the leaf to increase its area and to reproduce itself. Possibly some of the above-cited cases of laciniation may come under this heading. The most remarkable instance is afforded by certain varieties of the common polypody (*Polypodium vulgare*), *e. g.* the variety *cornubiense* in which the usually entire and simple lateral lobes elongate and themselves become pinnately divided, giving the whole frond a beautiful and elegant appearance; either all the lobes of the frond or only some of them may be affected in this way. The hart's-tongue (*Scolopendrium vulgare*) is extremely subject to marginal incision of the normally quite simple and entire frond, taking the form of crisping (var. *endiviæfolium*), erosion (*erosum*), lobing, or pinnatisection. There are certain fixed and ornamental varieties of the cabbage (*Brassica oleracea*) known as borecole or kale in which the leaves are crisped at the margins owing to their being abundantly, though not very deeply, incised. The same phenomenon occurs in the parsley (*Petroselinum sativum*) and in a remarkable form of *Begonia manicata*.

Further, the leaf of the greenhouse cyclamen assumes a weird aspect when its margin becomes curiously divided up into, as it were, little dissected leaflets, apparently repeating the same freak often met with in the petals of this plant.

These phenomena of "crisping" appear to have no morphological significance.

Fig. 44.—*Ulmus glabra* var. *pendula*. Showing leaflets formed at base of main blade.

Simple leaves may become compound. Leaves of the hazel and elm (*Ulmus campestris*) occasionally cut off a small leaflet at the base. In a weeping variety of the feather-elm (*Ulmus glabra*) great numbers of the leaves on many shoots bore from one to three leaflets (usually stalked) on the petiole below the lamina (fig. 44 *a*); when one leaflet was present, this, which varied greatly in size, was in most cases in the position in which, in the asymmetrically-formed leaf-base, a portion of the lamina is missing. This was also observed in the English elm (*U. campestris*) and the wych-elm (*U. montana*). The phenomenon may perhaps be regarded as a reversion to the complete, symmetrical type of leaf which was probably the ancestral form, and which occurs normally in other species of elm and in other genera, such as *Planera* and *Zelkowa*. In other leaves of *U. glabra* a leaflet occurred on the opposite complete side of the rachis, its presence being due to a portion of the lamina being separated off on that side, whereby the leaf-base, apart from this separated leaflet, became quite symmetrical; in another leaf the presence of a distinct notch near the leaf-base on the same side showed that a leaflet was in process of being cut off. In another leaf both leaflets occurred on the same side, one below the other, while on the other side was a long stretch of leafless rachis; hence on this latter side leaflets had been cut off and completely eliminated, on the other the leaflets still remained. The two (rather smaller) leaves occurring side by side, which resulted from the complete bifurcation of a leaf, had often very long petioles owing to the fact that leaflets had been cut off on both sides of the rachis and completely eliminated. The theory that the normal gap in the leaf-blade of the elm is due to the elimination of a portion of the leaf-blade is rendered probably true by two facts: firstly, as stated above, other species of elm and other genera of the tribe, though not all, have symmetrical leaves and short petioles; secondly, a series was observed in *U. glabra* on the same shoot beginning with a leaf which had a fairly short petiole and an almost symmetrical base, but in which the first indication of a leaflet being cut off on one side was present in the form of a distinct notch a short way from the base; another leaf showed the usual large leaflet excised on one side; another leaf showed in the gap a leaflet of very small size, evidently on the road to extinction; yet another leaf showed the normal asymmetrical base with no leaflet present at all. These abnormalities seem to reproduce for us the stages which have been gone through in the past in the elimination of a portion of the leaf-blade on one side. It may be mentioned that leaves of *U. glabra* frequently occurred bearing three basal leaflets (fig. 44 *b*), two on one side and one on the other, showing that the process of excision of portions of the lamina may occur on both sides of the leaf. Some of these phenomena are therefore probably to be regarded as retrograde or reversionary, viz. those in which leaflets occur, filling, or partially so, the normal gap; others as progressive, viz. those in which the normally complete half of the leaf-base becomes split up or eliminated.

It has been suggested, and probably correctly, that the asymmetrical form of the elm-leaf is due to the dorsiventral character of the shoot and to the economical distribution of the leaf-surfaces to receive as much of the incident light as possible; on these shoots the gap on the lower* side of each leaf is filled by the complete half of the leaf next below it, whereas if the lamina of the lower half of the leaf were also complete it would be shaded and excluded from the light by the leaf next below. Vuillemin suggests that when, as would probably occur in this pendulous and specially vigorous variety, the direction of growth of the shoots became altered, a partial reversion to the symmetrical leaf might occur; or if the shoots became in places abnormally shaded the lamina might become, as a result, more dissected and incomplete than is normally the case, and thus, perhaps, all these various forms of abnormal leaves might be accounted for.

In the specially vigorous, erect shoots of the English elm (*U. campestris*) produced by hedge-clipping, the leaves are nearly always symmetrical.

In some plants of the hollyhock (*Althæa rosea*) the lower axillary buds of the flowering stem had compound leaves consisting each of two perfectly separated, short, roundish leaflets; others were undivided,

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* *I. e.* the side nearest the base of the twig.

but deeply lobed. The leaf of the orange (*Citrus*) normally consists of a petiole bearing a single leaflet; it is a case of a compound leaf reduced to its simplest form; abnormal cases are known, especially in seedlings, in which there are several leaflets present, which is an indication of what the ancestral leaf was like. Other compound leaves are known to become still more compound; in some Leguminosæ it has been observed how simply-pinnate leaves, *e.g.* those of the carob tree (*Ceratonia Siliqua*), become bipinnate, owing to the replacement of all or some of the leaflets by pinnate leaves.

Then again, in some of the Australian acacias in which normally phyllodes, or flattened petioles, only are produced, these, on some twigs, may be replaced by bipinnate leaves. This feature always appears normally in the seedling.

b. Terminal Fission or Forking.—This is in all cases due to a kind of hypertrophy, and an attempt on the part of the organ to reproduce itself. The phenomenon of leaf-forking is one of the most widely-spread in the vegetable kingdom, occurring in nearly all orders of plants. It will be referred to again under the head of Phyllotaxis. Bifurcation of the leaf may be only partial or it may be complete; in the latter case it results in the formation of two leaves where previously there was only one.

Partial bifurcation of the main leaf is beautifully exemplified in the ferns, where we see how common it is for the main frond to be forked more or less deeply at the apex, the forking rarely if ever extending to more than half the length of the frond, *e.g.* in the hart's-tongue. Each of the two portions thus produced may themselves become forked, and the products forked again, and so on, until the "crested" form is attained (Pl. XIV, fig. 1).

Forking of the sterile portion of the frond has been observed in the moonwort (*Botrychium*), but it is a rare phenomenon in the Ophioglossaceæ.

No cases are known of forking in fern-leaves resulting in the formation of two distinct leaves.

Forked leaves occur perhaps most commonly in plants with their leaves arranged in an opposite-decussate manner. Celakovsky describes a most interesting series of cases in the honeysuckle (*Lonicera Periclymenum*), in which all stages between a perfect and entire leaf and the formation of two distinct leaves by means of forking occur (fig. 45 *a–c*). In the Labiatæ they are of common occurrence, and have also been seen in the teazel (*Dipsacus*), the Japan allspice (*Chimonanthus fragrans*), the oak, and *Cardamine pratensis*; also in the pitcher-plant (*Nepenthes* sp.), in which one leaf bore two pitchers, the forking having thus affected the pitcher and the extension of the midrib bearing it; in another leaf the green blade was also forked for a short distance. Fig. 46 shows an elm-leaf in which the midrib is completely forked into two, the lamina only partially so.

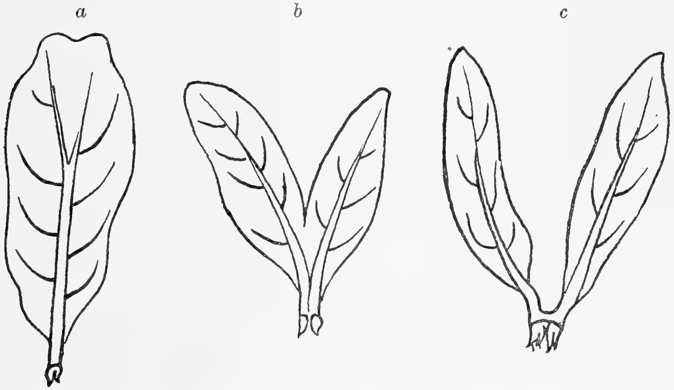

Fig. 45.—*Lonicera Periclymenum.* Three stages in the division of a leaf by terminal forking. (After Celakovsky.)

The same phenomenon occurs in the leaflets of compound leaves in many plants, *e.g.* in the scarlet runner (*Phaseolus multiflorus*). The terminal leaflet had, by forking, added a fourth leaflet to the usual three. The same author who mentions this also figures a leaf of the strawberry (*Fragaria vesca*) in which four leaflets were formed by splitting of one of the two lateral leaflets, and there is a quinquefoliolar variety of *F. grandiflora*. The leaf of various species of clover, *e. g. Trifolium pratense* and *T. repens*, is known to produce not infrequently four leaflets instead of three (Pl. XV, fig. 1), and more rarely five (fig. 47 *a*), six, and even seven leaflets. Of this case there seem to be two types: (1) in which the seven-fold leaf is obviously derived by fission of the three normal leaflets, which are arranged in groups of three each in the position

FIG. 46.—*Ulmus* sp. Forking leaf with midrib but not lamina completely divided. (G. S. Saunders.)

in which they were formed; in (2) the leaflets are scattered along a developed rachis and constitute an imparipinnnate leaf, so that the exact mode in which they arose by fission is no longer clear (fig. 47 *b*). It is stated that the Dutch clover (*Trifolium repens*) may occasionally produce pinnate leaves with as many as ten leaflets. Pinnate leaves may also occur in other genera with trifoliolate leaves belonging to the same tribe, as in lucerne (*Medicago sativa*), melilot (*Melilotus alba*), and bird's-foot trefoil (*Lotus major*). In *Fragaria elatior*, *F. collina*, and *F. virginiana*, Magnus and others describe the appearance on the leaf-stalk, some distance away from the large normal leaflets, of several small auricles, representing the same imperfectly-developed lateral leaflets as occur normally in the avens (*Geum*), silver-weed (*Potentilla anserina*), agrimony (*Agrimonia Eupatorium*), and meadow-sweet (*Spiræa Ulmaria*).

The leaflets of *Trifolium* may not be evenly divided into two; De Vries figures a case in *T. pratense* in which the terminal leaflets had excised a lateral smaller leaflet on either side.

Many pinnately-leaved ferns, such as the male fern, besides having the tips simply forked, or "crested," may exhibit a similar phenomenon in each of the pinnæ (Pl. XIV, fig. 1).

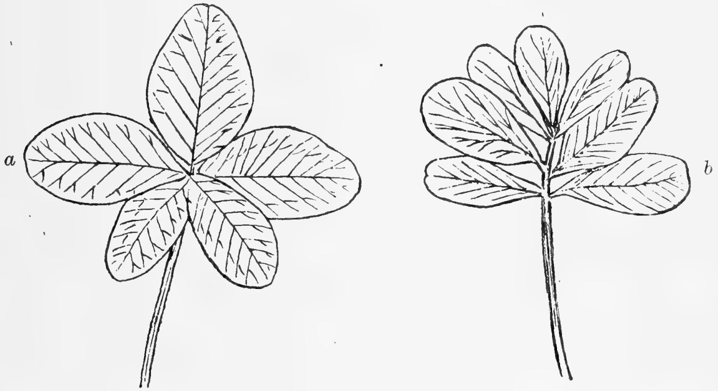

Fig. 47.—*Trifolium pratense*. *a*. Leaf with five leaflets. *b*. Leaf reverted to ancestral pinnate structure. (*b*. After De Vries.)

Bifurcation also occurs either in the terminal or lateral leaflets of multifoliolate pinnate leaves, *e.g.* in the false-acacia (*Robinia Pseudo-acacia*) and crown-vetch (*Coronilla varia*). Now, if complete partition of the leaflet occurs in the terminal leaflet of a compound imparipinnate leaf, a paripinnate leaf, devoid of terminal leaflet, would result, *e.g.* in *Robinia* and *Gleditschia;* and if this occurs in the terminal leaflet of a trifoliolate leaf it would afford a transition between trifoliolate and pinnate leaves, although the former may be regarded as merely a pinnate leaf reduced to one terminal and two lateral leaflets. On the other hand, an unequal division of the terminal leaflet of the nature of that above-mentioned in the purple clover would not modify the imparipinnate character of the leaf.

In various species of *Fragaria* and *Potentilla* the leaves of the epicalyx or calyculus, representing, according to the usual view, the stipules of the sepals fused in pairs, may become divided and the original ten stipules restored. The stipular theory seems proved by an observation made by Velenovsky in flowers of *Fragaria vesca* in which some of the sepals appeared as simple green foliage-leaves and the divided calyculus clearly as stipules. Domin observed in *Potentilla canescens* small foliar organs similar to the calyculus-leaves occurring scattered to the number of two or three, on or immediately below the receptacle; in *P. verna* he occasionally saw a leaf of the epicalyx developed as a foliage-leaf; which facts lead him to think that the calyculus may represent five bracts which have been carried up from below; but they are probably consistent with the former view.

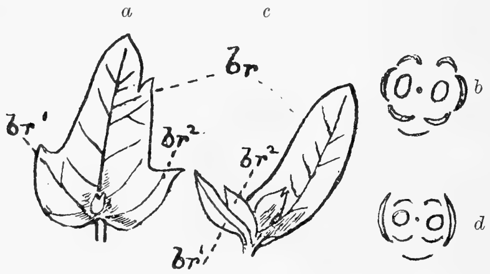

Fig. 48.—*Carpinus Betulus*. *a*. Normal compound bract. *b*. Its diagram. *c*. Bracteoles dissociated from bract. *d*. Diagram of same. (After Celakovsky.) *br*, bract; *br*¹ and *br*², bracteoles.

In the madders (*Rubia peregrina* and *R. tinctorum*) and the crosswort (*Galium Cruciata*) the usually fused stipules may become divided, thus yielding, instead of four, six leaves in a whorl.

Velenovsky observed in *Salix* the splitting of the median gland of the flower into two, representing the reproduction of the ancestral pair of bracteoles (fig. 43, p. 160).

Celakovsky describes abnormal inflorescences of the hornbeam (*Carpinus Betulus*) in which the two bracteoles, normally fused laterally with the bract, were quite free (fig. 48, *a–d*). Both this and the above-cited cases of stipules are obviously reversions to a primitive condition.

CONCLUSIONS ON LEAF-DIVISION.—Apart from those few cases of leaf-division which may be attributed to depauperization and leaf-forking in Angiosperms, the phenomenon should be regarded as entirely a reversionary one, *i. e.* a modification in the direction of an ancestral character. We find in fact that simplification or reduction has played such a large part in the evolution of plant-life that abnormal tendencies in the opposite direction seem to be best interpreted as reminiscences (to use a Platonic word) of features long left behind. In other words, compound leaves are to be regarded as more primitive than simple leaves. Most botanists would hold that the simple leaves of certain Leguminosæ, *e. g. Rafnia*, *Podalyria*, *Borbonia*, and Judas-tree (*Cercis*) have been derived from simplification and reduction from ancestors with compound leaves, seeing that these are typical of the vast majority of Leguminous plants, and few would deny that the leaves of the pennywort (*Hydrocotyle vulgaris*) and the hare's-ear (*Bupleurum*) are modified and more recent in type than those of the vast majority of Umbelliferæ.

The two types of reversion which we meet with are: (1) an increase in complexity of the leaf, and (2) an increase in number of the leaves. Such cases as those of simple leaves becoming compound come under (1); for reasons which will appear later all cases of dichotomy are preferably placed under (2). The multifold dichotomy of leaves, *e. g.* those of ferns, known as "cresting," may be regarded as a case of fasciation, of precisely the same nature as that met with in the stem, where we also find all transitions between simple dichotomy and typical fasciation.

Forking of the leaf is a normal feature in some ferns, *e.g. Schizæa, Dipteris, Platycerium,* and some species of *Ophioglossum,* and was possibly much more prevalent in the past; hence the abnormal dichotomy of ferns, which in a normal way are monopodially branched, is probably a reversionary phenomenon, as in the adder's tongue (*Ophioglossum vulgare*) whose abnormally-forked frond perhaps harks back towards the primitive type, of which the normally-forked leaf of *O. palmatum* represents a more accurate reflexion. Forking in fern-leaves is probably rendered more frequent owing to their prolonged apical growth. As will be seen below, it is not of the same morphological nature as the forking of leaves of Phanerogams.

On the other hand the forking of cotyledons should be regarded as not a reversionary, but a progressive phenomenon, as also that of many cases of forking of opposite-decussate foliage-leaves.

But a full discussion of these phenomena of forking will be reserved until the subjects of Phyllotaxis and the abnormalities of the flower are considered.

As regards the change from simpler to more compound leaves, this is almost certainly a reversion towards ancestral conditions. The normal clover-leaf is probably merely a reduced form of the pinnate leaf found in so many other Leguminosæ, and the transformations it undergoes, as described above, are changes in the direction of more advanced pinnation. The abnormal leaves are often formed as a result of mowing the first-formed leaves off, and the rapid and vigorous formation of new leaves thus caused seems to induce the change; also these leaves are more often formed during the more vigorous growth of early summer than during the later months of that season.

The appearance of bipinnate leaves in place of phyllodes in certain Australian acacias is a very clear instance of reversion to the primitive condition. The ontogeny of the seedling of these acacias exhibits these bipinnate leaves at a certain stage. And all the

South African species produce them normally in the adult plant.

The appearance in various species of *Fragaria* and in *Potentilla thuringiaca* of auricles on the petiole, thus reproducing in these plants abnormally what is a normal and fixed character in other members of the order, is a most important point. In view of the fact that in the two closely allied orders, Rosaceæ and Leguminosæ, pinnate leaves are so widely spread and are more common in the tribes Potentilleæ, Spiræeæ, Poterieæ, and Roseæ than are ternate leaves; and remembering also how great a *rôle* reductive processes have played in the course of evolution, this phenomenon in *Fragaria*, etc., may be regarded as a case of reversion. But these extra leaflets are not produced by fission of any of the normal leaflets, but arise independently on that part of the petiole where it may be supposed that the leaflets have completely vanished in the past.

As regards the appearance of the leaflet in the basal gap of the elm-leaf described above, this is probably a reversion; on the vigorous vertical shoots produced as a result of lopping branches of the common and wych-elms, the large leaves are usually, or very often, perfectly symmetrical, of a character which is probably correlated with the vertical direction of growth of the shoot. It is well-known that vigorous shoots, produced as a result of lopping, tend, in many plants, to develop foliage exhibiting ancestral characters.

12. Rejuvenescence of Foliage.—In many plants the foliage-leaves produced during the early period of life are different from those produced during later life. This we see in the contrast between the "primordial leaves" and the "needles" in the pine and the larch, where they differ both in their form and their position. After the second or third year the primordial leaves cease to be formed, their place being taken by scale-leaves and needles. However,

abnormally, they may become permanent, as in a specimen of a stone-pine (*Pinus Pinea*) observed by Gubler, in which throughout the plant primordial foliage only was developed. Also shoots bearing these primordial leaves only may be induced to reappear as a result of artificial mutilation, as, *e.g.*, by cutting back mature needle-forming shoots of the stone-pine; and these juvenile shoots in this case represent proliferations of the short-shoots (Pl. VII, fig. 2). In several genera of the Cupressineæ (*Juniperus*), cypress (*Cupressus*), *Callitris*, *Chamæcyparis*, and arbor-vitæ (*Thuja*) the contrast between the juvenile and mature foliage is marked. The former consists of spreading needles (Pl. XVI, fig. 3), the latter of needles which are almost wholly concrescent by their upper surface with the shoot (Pl. XVI, fig. 2). In the common juniper (*Juniperus communis*) the juvenile form constitutes the only type of foliage of the mature plant. In male plants of *J. chinensis* many twigs bearing the juvenile foliage constantly appear among those bearing the mature type, so that it is practically a normal feature representing an inherent tendency towards reversion. Quite large plants may be grown from cuttings taken either from the juvenile shoots on the mature plant or on the young plant; such forms, whether their origin be from *Juniperus*, *Cupressus*, or any of the other genera, have been assigned by horticulturists the name of *Retinospora*, *e.g.* *R. squarrosa* and *R. plumosa*, so well-known as handsome garden shrubs, represent merely the juvenile stage of *Cupressus pisifera*; the shrubs known as *R. dubia* and *R. ericoides*, etc., are but youthful forms of *Biota orientalis* and *Thuja occidentalis*. *Cryptomeria* "*elegans*" is the fixed juvenile condition of *C. japonica*. Giard observed a twenty-year old *Biota* whose leaves had all been devoured by insects; as soon as new shoots were formed they were all cylindric instead of flattened, and bore, instead of squamiform leaves, the acicular ones of *Retinospora dubia*.

In *Selaginella* the seedling-shoot bears at first leaves symmetrically arranged around the axis, and all of one kind; later on this more primitive type of shoot changes into the dorsiventral heterophyllous type. The same kind of thing has occurred in certain abnormal shoots of *S. grandis* which arose in the place of rhizophores on either side of the point of forking of the stem, and also in those which arose as proliferations of the cones; in each case the shoot showed at first radial symmetry of growth and leaves of one kind; but eventually as they grew in length they adopted the normal dorsiventral conformation.

FIG. 49.—*Convolvulus arvensis.*—Foliage of mature shoot showing conformation typical of cotyledons. (After Siracusa.)

An especially interesting case is that observed by Siracusa in the field bindweed (*Convolvulus arvensis*). All the leaves of a particular shoot of this plant which grew prostrate on the ground had the bilobed form of the cotyledons (fig. 49). Now the foliage-leaves of the tropical *Ipomæa Pes-Capræ* have normally this bilobed form, and the plant, moreover, is normally prostrate in its growth; hence in the abnormal *Convolvulus* the bilobed form of the foliage-leaves and the prostrate habit of the shoot would seem to be directly correlated; and this particular form of leaf is probably an ancestral one in the order.

G. P. Burns describes an adult and a juvenile form of leaf in *Proserpinaca palustris.* The entire adult form is produced under good vegetative conditions, the divided juvenile form under adverse ones; the environment does not appear to have any effect.

Rejuvenescence of foliage consists of an intercalation, into the life-cycle of the adult, of phases and stages of that of the seedling plant. As the foliage of the latter, where it differs from that of the adult, represents an ancestral type; in the same way, whenever the juvenile foliage appears, normally or abnormally, upon the mature plant, the phenomenon must be interpreted as of a reversionary nature, and as a break or interruption in the progressive evolutionary development.

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2. SIMPLIFICATION.

The phenomena included under this heading are much rarer than those belonging to the previous section. Many of them must be regarded as progressive in nature, others, again, as retrogressive. Under the latter may possibly be included the enations and ascidia of foliage-leaves, and the staminody of foliage-leaves in *Pinus* and *Gingko*; the last-named may have been derived from ancestors which were at once reproductive and assimilating foliar organs. (The relation between enations and ascidia and anther-structure will be dealt with in Vol. II of this work.) The progressive changes represent steps taken out of the habitual course of the ancestry, and they must, therefore, in most cases, be induced by special stimuli. The changes are, in fact, in the direction of evolution, and not the least value attaching to them may reside in the indication which they possibly afford as to the mode in which characters, varietal or specific, may have arisen in the past.

1. SQUAMODY OF FOLIAGE-LEAVES.—Goebel observed in *Circæa intermedia* that if the overwintering stolons are stimulated to further development in the winter by cultivation in a higher temperature, "the point of the shoot which ought to be an inflorescence becomes a stolon, which again pierces the soil, and this may take place after the shoot has attained a height of many centimetres and formed a number of well-developed leaves. The appearance of the shoots above the ground also may be quite suppressed, and the shoot, instead of forming a photophilous shoot with foliage and flower, may continue its growth as a stolon." In such cases those foliar rudiments on the shoot which would under normal conditions develop into foliage-leaves or floral organs, in the subterranean habitat of the shoot develop as scale-leaves.

Duchartre describes how in *Lilium neilgherrense* some of the shoots emitted by the bulb, instead of growing up vertically above-ground and forming foliage-leaves, grow horizontally for a considerable distance in the soil, producing scale-leaves only, before finally turning upwards.

2. PAMPINODY OF FOLIAGE-LEAVES.—This occurs rarely, as in *Lathyrus sylvestris*, where the two lowest leaflets were transformed into tendrils. And in the common vetch (*Vicia sativa*) in which not only (as normally

occurs) was the terminal leaflet developed as a tendril, but all the lateral leaflets as well.

Noll observed a well-nigh inexplicable transformation in the canary-creeper (*Tropæolum aduncum*) in which one of the leaves, viz., the fifth, was changed into a tendril, the more remarkable inasmuch as this plant has no tendril-forming relatives whatsoever; the petiole, however, possesses the power of twining round supports, and if we suppose the leaf-blade to become reduced to *nil*, a tendril-like organ would be the result.

3. BRACTEODY OF FOLIAGE-LEAVES.—A rare phenomenon. In the arum lily (*Richardia æthiopica*), *R. Elliottiana*, and the cuckoo-pint (*Arum maculatum*) one or two extra spathes may occur, a phenomenon due to the transformation of one or more foliage-leaves and the insertion of these at a much higher level on the stem; the extra spathes may exactly resemble the normal one, or may be partly coloured and partly green and leaf-like, and either of the same size as the normal spathe or intermediate in size between that and the leaf (Pl. XVII, fig. 3).

In *Narcissus biflorus* a foliage-leaf became fused with the scape along the latter's entire length; half of the leaf was membranous in consistence, viz., that portion of it which helped to ensheathe the flowers.

Under this heading may be cited the conclusions which Velenovsky and Danek have reached with regard to the terminal portion of the fertile cladode of *Ruscus*, viz., that it represents the anterior of the pair of bracts which has become fused with the two projecting wings of the cladode, and at the same time much enlarged and cladode-like. If this is so, this bract may be regarded as having become foliaceous. Both authors observed abnormal cases in which this bract (according to their view) had become scale-like, altogether like the normal posterior one, both in size, consistence, and position. It is doubtful, however, if this interpretation of the fertile cladode is correct.

4. PETALODY OF FOLIAGE-LEAVES.—Quite as peculiar

a case is that cited by Masters of a rose-leaf of which two of the leaflets "were brightly coloured like the petals, the others being of their ordinary green colour." Then there is the case given by Morren of an exceptionally large foliage-leaf of *Gesnera Geroltiana* occupying the position of the inflorescence and being at the same time brightly coloured. Thomas also observed the partial transformation of a foliage-leaf, on a purely vegetative shoot, into a petaloid organ having the structure and colour of a normal petal, in *Rhododendron ferrugineum.*

5. SPOROPHYLLODY OF FOLIAGE-LEAVES.—This also is not of common occurrence.

Büsgen describes more or less complete transformation of the leaflets of *Marsilia hirsuta* into sporocarps (Pl. XIII, fig. 3); in one leaf the lowest pair of leaflets were in the form of closed fruits, the upper pair in the form of mussel-shaped open bodies.

The following phenomena may be included here, although it is merely the foliage-leaf-like portion of the sporophyll itself that is affected. In the different species of the royal fern (*Osmunda*) transitional forms between sterile and fertile pinnæ of the frond constantly occur; *e.g.* in one pinna all the pinnules of one side may be fertile, the other sterile; in *O. regalis* certain portions of the frond which are normally sterile may become fertile, or sporangia may occur on all the pinnæ of the frond, thus recalling the normal condition of *O. japonica* in which sterile and fertile fronds are quite distinct.

The sterile portions of the fronds of *Aneimia* produce sporangia on some of their segments occasionally.

In the Ophioglossaceæ, also, certain segments of the sterile portion of the sporophyll occasionally produce sporangia.

6. STAMINODY OF FOLIAGE-LEAVES.—A very remarkable instance is recorded in *Pinus sylvestris*, in which one or more pairs of needles on the short-shoots were changed into stamens: an interesting transformation

seeing what totally different types of foliar organ the needle and stamen of the pine are; and, as Penzig points out, the stamen has always been regarded as analogous to the scale-leaf of the main shoot.

Not less striking are the pollen-sac-bearing foliage-leaves on some of the short-shoots of the maidenhair-tree (*Gingko biloba*) observed and described by Fujii. These are borne on the margins of the leaves, they vary in number, and always involve more or less reduction of the leaf-surface which bears them, which in many cases may be almost entirely replaced by pollen-sacs; they are not arranged in any definite manner to form sori (Pl. XIII, fig. 4); "sometimes when an entire leaf is transformed into a stamen, the reduced lamina of the leaf assumes the form and position of the terminal scale" of the normal stamen. "The petioles of leaves bearing pollen-sacs are often much reduced in length and thickness." These abnormalities show that "the knob-like terminal scale" of the normal anther "is the reduced portion of the lamina of the staminal leaf."

7. CARPELLODY OF FOLIAGE-LEAVES.—Fujii also observed a precisely similar phenomenon on the female plant of *Gingko*, and what has been said with regard to position of the pollen-sacs, and the relative development of fertile and sterile tissue, will also apply here. "The ovule is partially enclosed at the base in a cup-shaped swelling just as in the normal ones, and this swelling gradually passes into the lamina of the leaf." "Often elongated outgrowth of the tissue is formed, instead of ovules or pollen-sacs of any definite form, mostly in the margin of the leaf for some length along the course of the veins of the leaf" (Pl. XIII, fig. 5). The following are some of Fujii's conclusions drawn from a study of these interesting abnormalities:—"The ovule is an organ of foliar nature, and the cup-shaped swelling at its base is the reduced portion of the lamina of the carpellary leaf. The ovules of *Gingko* are marginal formations of sporophylls." "The normal seed-stalk is the

floral axis, whose apical bud is usually suppressed, and which bears only two rudimentary carpels. The elongated stalklet of the ovule of *Gingko* occasionally developed is not simple outgrowth, as has been considered by some authors, but is the petiole of the carpellary leaf developed alternately along the floral axis." "The formation of ovules upon the foliage-leaves of *Gingko* reminds us of the carpellary leaves of *Cycas*, and the ovules are in both genera marginal formations of the sporophyll." These generalizations and comparisons may certainly be accepted.

In both these phenomena, viz., staminody and carpellody of the foliage-leaves, we see an excellent instance of the flood of light which abnormalities often throw on the real nature of certain structures which is otherwise, under normal conditions, utterly obscure.

Lutz observed and figured a very rare case, viz., foliage-leaves of a crocus (whose flowers and bracts were unusually affected by carpellody) bearing each a stigma at its tip (Pl. XIII, fig. 2). Many botanists would explain this by supposing that, the balance of the plant being upset, the primitive potentiality resident in the protoplasm of all its parts to form any kind of organ at any time, became raised into actuality when certain abnormal conditions afforded the required stimuli. It is preferable, on the other hand, to hold the view that no organ can assume the characters (or some of them) of another organ unless it has had, with that organ, a common origin in the past. Apart from that common origin there is, owing to the stereotyped morphological and physiological nature of the (in time, position, and function) widely-separated organs, no likelihood of their exhibiting similar features. The abnormal crocus-leaf, *i. e.* assuming the observation to be correct, may be explained by postulating a fern-like foliage-sporophyll as the original common ancestor of both foliage-leaf and carpel, of which we see, in the case before us, a dim reminiscence, expressed, of course, according to the idiosyncrasy of the particular plant concerned. This also is the most likely explanation of the antheriferous and ovuliferous foliage-leaves of *Gingko*.

8. BRACTEODY OF SCALE-LEAVES.—Under this heading must be placed the curious abnormality which Wilhelm observed in the spruce in which the apex of a vegetative shoot became transformed into a cone; in such a case two main changes are implied, viz., excessive shortening of the axis, and transformation of scale-leaves into bracts.

9. SEPALODY OF BRACTS.—In the wood-anemone (*Anemone nemorosa*) and in several other species the foliaceous bracts may, one or other of them, assume the form and colour of the sepals. Such a case as this reminds one of those normal instances where bracts are always brightly coloured, as in Bromeliaceæ, *Poinsettia*, etc.

FIG. 50.—*Picea nigra*. Bracts of lower part of cone changed into stamens with abortion of ovuliferous scales: upper part of cone normal.

10. STAMINODY OF BRACTS.—The "bract" ("Deckschuppe" of the Germans) which subtends and supports the "seminiferous scale" in most Coniferæ, has been variously interpreted as a true bract or as a carpel. In proliferated cones, *e.g.* in *Larix europæa* and *Picea nigra*, transitions have been observed between this "bract" and stamens, the extreme modified form of the organ bearing pollen-sacs on its dorsal side (fig. 50). This phenomenon, of course, does not decide either way as to the morphology of the organ. Its bract-nature, however, being convincing, its consideration is included here. It is this phenomenon which gives rise to the hermaphrodite cones. Usually these modified "bracts" occur in the lower region of the cone. Keissler observed an androgynous cone of the spruce in which a similar change had taken place in the upper part of the "inflorescence," thus reminding one of the usual condition in the "flower" of *Selaginella* in which male sporophylls occur in the

upper and female sporophylls in the lower part of the cone.

Licopoli observed, in flowers of *Melianthus* in which calyx and corolla were absent, bracts taking their place, and that these were antheriferous.

11.—Carpellody of Bracts.—C. Schimper observed leafy bracts of the cabbage which bore ovules.

Œrsted describes the occurrence of an ovule or ovules on the lower side of a bract in a female cone of *Picea nigra* (Pl. XIII, fig. 6).

Lutz found in *Crocus* stigmatiferous bracts.

12.—Simplification of Foliage.—Instances of this phenomenon are much rarer than the converse one: the change from simple into compound leaves. And this fact constitutes one of the pieces of evidence in favour of the view that the latter is reversionary in character, for it is a pretty-generally admitted fact that disturbances in the organism tend to cause the re-emergence of otherwise latent ancestral characters.

The bipinnate leaves of the honey-locust tree (*Gleditschia triacanthos*) may become either wholly or partially pinnate; in the latter case a portion of the frond may be bipinnate, the other portion simply pinnate. Or, the simplification may proceed still further: division of the leaf may totally disappear and the leaf become completely simple. Or again, there may be a compromise between the two extremes; half the leaf on one side of the rachis may be bipinnate, and the other longitudinal half consist of a single unsegmented lamina. Perfectly simple leaves have also been seen in *Robinia Pseud-acacia.*

In the same way the ternately-compound leaf of *Phaseolus* may be replaced by a simple one; and this also occurs in similar leaves of plants of other orders, *e. g.* the strawberry (*Fragaria vesca*) giving rise to the variety *monophylla*, originally produced in 1761 at Versailles as a seedling-sport.

In some other plants, *e. g.* the ash (*Fraxinus excelsa*) and the elder (*Sambucus nigra*), the pinnately-compound leaves may become trifoliolate, or the still greater change may occur, and a large simple leaf be produced, showing no sign of dissection. In the ash an entire tree may exhibit none other but these simple leaves; it is known as the variety *monophylla* or *integrifolia*. The simple leaf so developed does not represent merely the terminal leaflet of the normal pinnate leaf, but stands rather for the whole leaf in which a congenital fusion of all the leaflets must be assumed to have occurred. The simple-leaved variety of *Sambucus nigra* has its counterpart as a normal feature in certain forms of *S. javanica* where the leaves are perfectly simple.

There must next be cited instances of simplification of a leaf which is not compound, but merely deeply segmented. The hawthorn (*Cratægus Oxyacantha*) exhibits great variety in its foliage; the variety *laciniata* has very deeply-incised leaves; other leaves are quite simple and hardly dissected at all; and all transitions occur between these two extremes. In the foliage of *C. sinaica* a most interesting and instructive series of forms was observed. The normal or typical leaf consists of a deeply trifid blade and two very small pseudo-stipules* situated at the base of the petiole and separated from the blade by quite a quarter of an inch. In other leaves the pseudo-stipules were considerably enlarged, the leaf-blade was reduced, correlatively therewith, in size, and pseudo-stipules and leaf-blade were much more closely approximated to each other. In other leaves the pseudo-stipules were in the form of leaf-lobes resembling in every respect the other lobes of the leaf and perfectly continuous with them. In still other much smaller leaves the pseudo-stipules had become completely merged into the leaf-blade, which exhibited no trace of lobing, but was simply dentate, and extended to the base of the rachis as far as the

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* This term is used because Domin has now clearly shown that *true* stipules are in all cases morphologically derived from the leaf-*sheath* and not from the leaf-blade. Good instances of pseudo-stipules are seen in *Cratægus* (as shown above), *Chrysanthemum*, and *Cineraria*; these structures are always outlying segments of the leaf-*blade*.

point where, in the normal leaf, the pseudo-stipules are attached. In this series, then, we see every transition between pseudo-stipules and leaf-segments, a fact which most clearly proves that the pseudo-stipules are merely modified leaf-lobes (fig. 51 *a–f*) and are not true stipules at all, these being always derived from the leaf-sheath.

The much-dissected leaves of *Plantago Coronopus* and the common poppy (*Papaver Rhœas*) are occasionally replaced by perfectly entire ones.

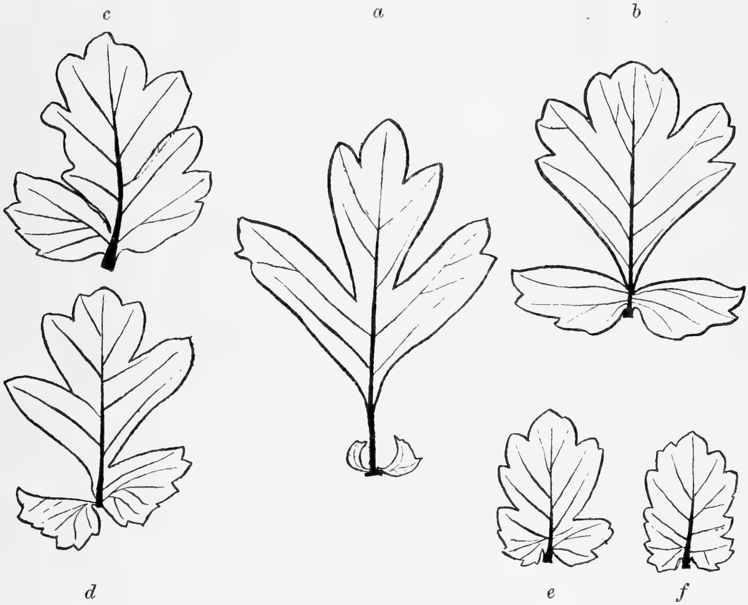

FIG. 51.—*Cratægus sinaica.* Foliage-leaves off the same tree, showing transitions (*a–f*) between pseudo-stipules and leaf-segments.

13. FUSION OF COTYLEDONS.*—This is a common phenomenon in Dicotyledonous seedlings. As a result of it, a single usually forked cotyledon is borne by the seedling in a more or less terminal position, the plumular apex being pushed over to one side. Normal cases of the same phenomenon occur in *Ranunculus Ficaria*, *Anemone apennina*, *Cyclamen persicum*, and *Pinguicula*.

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[*] For a fuller treatment of the subject of Fusion see under "Phyllotaxis."

14. Fusion of Foliage-leaves.—The writer has seen this in *Lonicera thibetica*, *Rhinanthus minor*, *Buddleia Hemsleyana*, and *Marrubium vulgare*. Interesting cases are cited by Klein in *Weigelia*, by Celakovsky in *Ruscus*, and by Braun, Jännicke, Steinheil, and Clos in other plants.

15. Fusion of Scale-leaves.—An apical piece of a shoot of *Pinus Thunbergii*, showing unusual features, was received at Kew from Sir E. G. Loder of Horsham.

"Eight or nine of the scale-leaves in the lower half of the length of shoot bore ordinary two-needled spur-shoots in their axils. The majority of the remaining scale-leaves subtended quite a different kind of axillary shoot, . . .

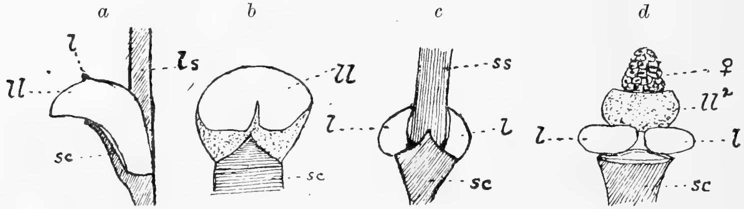

Fig. 52.—*Pinus Thunbergii*. *a.* Recurved fleshy leaf in axil of scale-leaf (lateral view). *b.* Anterior view of same. *c.* Pair of transversely-placed fleshy leaves at base of spur-shoot (anterior view). *d.* Two pairs of fleshy leaves at base of rudimentary female cone. *ls*, long shoot; *sc*, scale-leaf; *l*, fleshy leaf; *ll.* fleshy leaves fused; *ll′*, fleshy leaf of second pair; *ss*, spur-shoot; ♀, female cone. Semi-diagrammatic. × about 2.

"The most frequent form which the abnormal axillary structure assumes is that of a swollen fleshy foliar organ *arching outwards* over or against the subtending scale-leaf. Such structures are aggregated in great numbers towards the apex of the shoot below the group of buds (Pl. XIV, fig. 2). Frequently these bright-green swollen leaves bear a distinct outgrowth on their adaxial surface, sometimes a pair of such outgrowths; and these clearly represent one or two further leaves situated higher up on the axillary shoot, which have become fused with the lowermost recurved one (fig. 52 *a*).

"Another form which the axillary shoot assumes is that of a pair of transversely-placed fleshy leaves, each about half the size of the single recurved leaf above-mentioned, or smaller (fig. 52 *c* and *d*), enclosing between them one or two extra smaller pairs of fleshy foliar organs. All these leaves, from those of the first pair upwards, may be, owing to the very contracted space in which they arise, considerably displaced from the normal position, and here and there irregular fusions may occur, as also correlative modifications in development.

"In several cases the spur-shoots begin with the same transversely-placed pair of fleshy leaves, as in the cases of the axillary shoots just cited, being immediately followed by the usual scale-leaves of the spur-shoot.

"Reverting now to the afore-mentioned recurved fleshy leaves which occur singly (or with extra leaves of the axillary shoot on their adaxial side), in greatest number in the upper part of the shoot, it was determined that this recurved leaf is formed through the fusion, by their *adaxial* margins, of the two transversely-placed leaves which occur in so many of the axillary shoots, with which is incorporated, at least in the basal region, one or two of the succeeding pair of leaves which may or may not undergo (this could scarcely be determined) some revolution in orientation. This mode of origin of the outward-arching scale could only be accurately determined by its anatomical investigation,* for although the slightly bilobed character of many of these scales seems to imply their compound nature, the exact mode of union of the component leaves could only be demonstrated when it was seen that the vascular bundles, forming a row of strands across the leaf, were orientated in such a way that their xylem was directed outwards (*downwards*). In the basal region of the leaf, besides this

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* One of the interesting cases in which the origin and nature of an organ can only be finally settled by the *anatomical* method of investigation.

row of strands, were two others on the *dorsal* (adaxial) side which were irregularly orientated, as if the two foliar organs to which they belonged (represented by two conspicuous ridges), were undergoing a certain amount of revolution or torsion preparatory to their eventual more complete fusion, at a higher level, with the main leaf.

"Particular attention must be directed to the comparison which may be made between these curious recurved leaves of the axillary shoot and the ordinary 'needles' of *Sciadopitys*. . . . The recurved axillary leaves of *Pinus Thunbergii* (albeit abnormal) afford, therefore, another case of *vegetative* leaves being formed in this way, the case of *Sciadopitys* being the only normal one known.

"Strasburger* described and figured a case of fusion by their adaxial margins of the needles of *Pinus Pumilio* [and *P. sylvestris*]; Mr. L. A. Boodle has seen similar fusion of needles [in *P. Laricis* var. *austriaca*]; the present writer has seen the specimens which he collected. The fusion, however, was sometimes by the adaxial and sometimes by the abaxial margins.

"These cases of *Pinus* are not wholly comparable with those of the recurved fleshy leaves of *P. Thunbergii* and with the 'double needle' of *Sciadopitys;* for the needles of *Pinus* are not the first-formed leaves of the axillary shoot, being preceded by a number of scale-leaves; they may be also variously orientated, a fact which will account for the variation in the mode of marginal fusion.

"The best comparison of all may be made between our recurved leaf and the ovuliferous scale of the Abietineæ, for, according to the most popular view of the latter, the mode of origin of the two is precisely identical. In both cases, also, one or two leaves situated at a higher level on the axillary shoot have become incorporated into the double foliar organ; the apophysis or umbo on the adaxial side of the ovuli-

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* Strasburger, 'Die Coniferen und Gnetaceen,' 1872, p. 387.

ferous scale finds its replica in the curious outgrowth (representing the tip of one of the next pair of leaves) occurring in the upper part of the adaxial surface of the fleshy recurved leaf.

"With regard to the physiological meaning and cause of the abnormal condition of the piece of shoot, the equilibrium of the whole has evidently become upset, possibly by the presence of a fungus, which has been ascertained to be present.* The axillary shoots have been stimulated to an exceptional degree and mode of development, but the reason for the particular forms which they have taken is obscure.

"At any rate, the phenomenon of the recurved leaf and its mode of origin lends strong support to the prevailing view of the morphological nature both of the ovuliferous scale of Abietineæ and of the 'needle' of *Sciadopitys*. For it indicates the existence of a tendency in the Coniferæ for the first two leaves of an axillary shoot to unite by their adaxial margins to form a single dominant axillary foliar organ.

"The abnormal shoot under discussion affords, further, a powerful substantiation of the view that teratological phenomena are often of great value in throwing light on the nature and origin of otherwise obscure structures."†

16. Fusion of Bracts.—The involucral leaves of a species of hare's-ear (*Bupleurum junceum*) have been seen united into a saucer-shaped structure.

17. Suppression of Foliar Organs.—In some Leguminosæ, *e.g. Phaseolus vulgaris* and *Vicia Faba*, a leaflet occasionally vanishes completely.

Bracts tend abnormally to disappear sometimes, as was observed by Buchenau in the case of certain two- to three-spurred flowers of *Tropæolum majus*. The absence of bracts is a normal feature in the Cruciferæ.

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* Mr. G. Massee investigated the shoot for this purpose.

† Worsdell, 'New Phytologist,' vol. xiv (1915), pp. 23–26.

18. "ENATIONS" AND ASCIDIA OF FOLIAGE-LEAVES.*—These constitute some of the most remarkable and morphologically interesting teratological phenomena in the vegetable kingdom, as they are also amongst the most difficult to interpret. They are usually regarded as the result of hypertrophy in the development of the organ concerned.

a. Ascidia as Leaf-appendages.—Those, firstly, will be described which are so commonly met with in the cabbage and which assume such varied and interesting forms. Several large leaves were observed which had developed laminar outgrowths of considerable size along the midrib of the upper surface, and also quite small ascidia or pitchers on long stalks in the same position; the surfaces of the enations which were opposed to the (upper) surface of the leaf were morphologically the lower. The enations often assume most curious shapes: elongated structures with but little laminar development very often, and when this occurs, taking the form of semi-pitcher-shaped bodies produced here and there on a vein-like stalk. The enations usually arise from the midrib or from the other larger veins. On one leaf was observed a long-stalked small pitcher or ascidium springing about two-thirds of the way up the midrib, this being unusually thickened below the pitcher's insertion (Pl. XV, fig. 2); the outer surface of the pitcher was morphologically the upper surface, and being opposed to the upper surface of the leaf, it thus obeyed the law of laminar inversion according to which opposed laminar surfaces are similarly constituted (Pl. XVII, fig. 2, and fig. 53 in text).

On other leaves stalked or sessile pitcher-like structures have been seen arising from the lower surface of

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* This phenomenon has been introduced under the section "Simplification" because of the tendency, in the majority of leaves producing ascidia and enations, towards the reduction in size, representing as they do (see *infra*) stages in the formation of anther-structure; and an anther is an exceedingly reduced leaf-blade. It is, at the same time, true that both anthers and the foliage-leaves treated of under this heading are, in their actual structure, more highly differentiated than normal foliage-leaves.

the cabbage-leaf, and this would seem to be a more frequent phenomenon. Sometimes the stalked enation may itself branch copiously and bear numerous pitchers.

A good example has been furnished in the ivy (*Hedera Helix*) of a pitcher arising on a lower surface of the leaf; it arises from the midrib not far from the base; it is not, as are many of those of the cabbage, a symmetrically-shaped structure, but rather resembles a church collection-bag, *i. e.* it is a leaf with a basal pocket; the inner surface of this structure is morphologically the upper surface, the law being thus again obeyed. Eichler gives beautiful illustrations of the same type of structure in *Michelia champaca* (Magnoliaceæ).

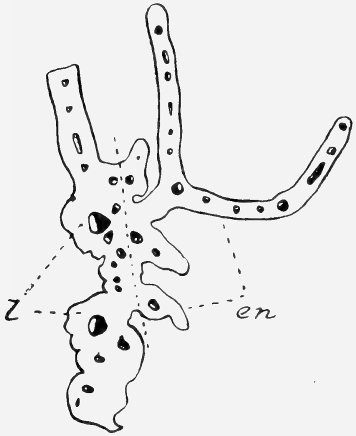

FIG. 53.—*Brassica oleracea.* Transverse section through region of midrib at point of outgrowth of enations (*en*). *l*, midrib of leaf.

To this category belong those cases in which the *greater* part of the leaf is constituted as a pitcher, the part bearing it forming but a small fraction of the whole leaf; such a leaf, *e. g.*, was one of an uppermost pair in a shoot of *Lonicera conjugalis*; the ascidium, which was composed of a lamina with a basal pocket towards the upper surface, was borne on the *lower* surface of the small basal saucer-shaped portion of the leaf

(Pl. XIX, fig. 1). Sometimes, as in leaves of some *Phlox paniculata* which had been attacked by eel-worm at the roots, the small, flat basal portion of the leaf bore on its *lower* surface, not a pitcher, but a long, naked piece of midrib, though in some leaves this had developed a slender strip of blade (Pl. XIX, fig. 2).

In other plants the outgrowth from the lower surface may arise a short distance from the apex as a continuation of the midrib; and this extension of the midrib may or may not expand at its end into a more or less hollowed lamina. There is a variety of "croton" (*Codiæum variegatum*) which exhibits this phenomenon (Pl. XVII, fig. 1).*

It is very interesting to find the same thing precisely occurring in the ferns, *e. g.* in certain varieties of *Scolopendrium vulgare*, viz. *cornutum* and *peraferum*, where the midrib often merely assumes the form of a thorn-like body projecting from the upper or lower surface.

Now, this very phenomenon which we find so frequently in a diversity of plant-groups as a "sport," occurs as a perfectly fixed and normal character in the pitcher-plant (*Nepenthes*), every leaf in all species producing stalked pitchers representing an extension and expansion of the midrib; in most species, however, the extension occurs from the actual and extreme tip of the leaf, as is often also the case in *Codiæum*, but in others it is distinctly from the lower surface a very short distance behind the actual apex; Eichler was mistaken in stating that this latter phenomenon does not occur in *Nepenthes*.

b. Ascidia of the Entire Leaf.—In the first place must be mentioned the case of a cabbage in which was observed such a pitcher consisting of the entire leaf: in this case the inner surface of the pitcher was morphologically the lower (Pl. XV, fig. 3), and in this respect it exactly resembles the extraordinary leaf-formation in "*Ficus Krishna*," a form of *Ficus bengha-*

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* See Celakovsky's beautiful illustrations of this form.

lensis in which all the leaves on the tree without exception have basal pockets, the inner surface of which is morphologically the lower (Pl. XVII, fig. 4). In a leaf of *Glycosmis pentaphylla* the same conformation has been seen.

To all such cases as the above, C. de Candolle has given the term "hypoascidia." To those about to be described he gives the name "epiascidia."

In these cases (the majority) the inner surface of the pitcher is the upper, as in an ascidium of *Pelargonium zonale*,* which was fairly symmetrical in shape; in some such leaves a very small ascidium was developed from one of the veins on the outer (lower) surface; in accordance with the law, the outer surface of this small pitcher was also morphologically the lower (Pl. XVII, fig. 5). A similar formation of a basal pocket formed towards the upper side occurred in a terminal foliage leaf of *Buddleia Hemsleyana*. The same type of pitcher has been observed in *Saxifraga ligulata* (Pl. XVIII, figs. 1 and 4), *Tilia*, and *Ulmus glabra*.

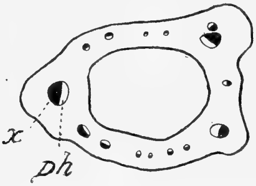

FIG. 54.—*Brassica oleracea.* Transverse section of "hypoascidium" (diagrammatic). *x*, xylem; *ph*, phlœm.

c. Laminar "Enations."—There is a quite different type of "enation" from that of pitcher-formation. The laminar outgrowths from the mid rib of the cabbage-leaf have already been mentioned. *Polygonum cuspidatum* has furnished excellent instances of this phenomenon; in some leaves there was an outgrowth along either side of the midrib for the greater part of its length on the lower surface of the leaf (fig. 55 *a*);

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† Vuillemin states that the rosette-leaves of *Geranium macrorhizum* are normally pitcher-shaped.

similar outgrowths occurred along a portion of the main lateral veins (fig. 55 *b*); in other leaves it was the midrib only which exhibited the phenomenon, the "enation" beginning almost at the leaf-apex and gradually widening towards the base, where it formed, on either side of the midrib by fusion with the leaf-margin, a distinct pocket (fig. 55 *a*). In *Ficus glomerata* similar "enations" on two of the lateral veins have been seen.

In a later chapter the remarkable enations from the lower surface in *Xanthosoma* are referred to.

FIG. 55.—*Polygonum cuspidatum.* Laminar enations from lower surface of leaf.

The case cited by Buchenau of two tobacco-leaves united by their lower surfaces, and a similar case seen in the mango (*Mangifera indica*) in which the two halves of the double leaf so formed are equal in size or nearly so, come under this heading, for one of the two leaves may be regarded as an enation from the other.

An interesting transitional case between a laminar "enation" consisting of an entire leaf (*i. e.* an "enation" equal in development to that of the leaf bearing it) and the subsidiary ones of *Polygonum* and *Ficus*, has been seen in *Janusia guaranitica* in which the enation extended nearly the whole length of the midrib of the lower surface and represented an entire leaf, but of much smaller size than that of its parent.

The same plants of *Phlox paniculata* afflicted with eelworm which bore the dorsal outgrowths from the leaves also produced leaves which bore laminar outgrowths, to the number of one, two, and four, according to the leaf, on the upper surface; these extended some distance along the veins (Pl. XXII, fig. 5); they frequently have little pointed apices of their own, they also, in some leaves, form a pair of basal pockets, as in *Polygonum*. In *Saxifraga ligulata*, besides pitcher-formation on the lower (dorsal) surface, the same type of enation as just described in *Phlox* and *Polygonum*, occurs on the upper surface: the midrib, along its whole length, may exhibit on either side a crumpled wavy outgrowth accompanied often by formation of a pair of basal pockets (Pl. XVIII, figs. 2 and 3). In a later chapter is described the occurrence, on the normal foliage of various species of *Caltha*, of enations on the upper surface.

In the case of a vine the attachment was by the upper surfaces of the petioles only; it was unknown what position on the stem the double leaf so formed occupied.

CONCLUSIONS ON SIMPLIFICATION.—Having regard to the fact that the well-developed foliaceous sporophyll would seem to be the ancestor (so far as our knowledge of plant-evolution at present tends to show) of all other types of foliar organ, we must envisage most of these cases of simplification as, not reversionary, but progressive phenomena, *i. e.* as modifications of an organ which, before it changed, was much nearer the original type. Few will deny that a tendril, a thorn, and a scale-leaf are modified foliage-leaves; therefore, when we see a foliage-leaf or leaflet being replaced by any of these organs the change must be regarded as a forward and not a backward one.

With regard to the bracts, they are for the most part probably modified foliage-leaves, and in the case of the presence of extra spathes in some of the Aroideæ we seem to see the exact process by which the normal spathe arose.

As will be seen more clearly later on, the various foliar organs of the flower are all probably derived from foliage-leaves or leafy sporophylls, hence any change whereby these latter assume the characters of the former must be a progressive one. As regards ferns, it is not at all improbable that the original type of frond, as in so many modern ferns, was both assimilating and spore-producing, and that the differentiation into sterile and fertile fronds on the same plant is a later modification; so that the change of a part of a sterile frond into the fertile condition must be a reversionary one. The case of *Marsilia hirsuta*, however, cannot be wholly reversionary; nor is it, probably, wholly progressive in nature.

All cases of lateral fusion of foliar organs, as also of abortion and disappearance thereof, must of necessity be progressive, and in no sense reversionary.

As regards enations and ascidia, it is difficult to assign an adequate cause for them. The balance of the organ becomes, as it were, upset and the tissue-forming energies materialize in these apparently fantastic shapes; we shall see later, however, when treating of the flower, that all these structures have a definite meaning, and that they are, in a sense, reversionary and probably not to be regarded as progressive in nature. Moreover, as C. de Candolle points out, they are not isolated and exceptional structures, but have their normal counterparts here and there in the vegetable kingdom. We shall find them recurring in certain organs of the flower.

The pitcher or the bladeless extension of the midrib emanating from the lower surface of the lamina must in some instances be regarded as the terminal portion of the leaf whose exceptional position is due to the lateral fusion across the upper face of the leaf of two of its lobes, the result being that the quondam terminal lobe becomes a dorsally-attached structure;[*] and we may probably account for its cup- or ascidium-like form as follows. If the terminal lobe, shifted on to the lower surface, retained its usual form, its upper surface would be opposed to the lower surface of the leaf bearing it, which would violate the law (which appears to exist in spite of some apparent exceptions) of laminar inversion; hence the union of its basal margins across the upper surface is necessary so as to ensure its lower surface being opposed to that of the rest of the leaf. The normal pitcher of *Nepenthes* has probably originated in this way, but has become secondarily shifted (in most species) into a purely terminal position, *i. e.* back again into the original position of the lobe from which the pitcher arose, the latter having been, nevertheless, retained as a useful structure in the economy of the plant. As a natural conclusion from this view of the origin of the pitcher, all that portion of the leaf below the pitcher cannot be regarded as merely a winged petiole; the history of development certainly shows it to be the basal portion of the whole leaf, but in the mature condition it is indubitably the main assimilating part of the leaf; moreover, we cannot allow the developmental history to invariably afford data for morphological conclusions, and no essential distinction can be recognized between a basal and an upper portion of a leaf.

Some of the abnormal leaves of *Phlox* described above show us (Pl. XXII, fig. 5) a very small basal portion bearing the main part of the leaf as its dorsal outgrowth. Normal instances of the same phenomenon are seen in the leaf of the grass with its ligule formed by lateral union of the stipular sheath-lobes across the face of the leaf, in the coleoptile of the grass-embryo and the axillary stipule of *Potamogeton* and other plants, in the glumes of *Bromus* and other grasses with their

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[*] Where a pitcher occurs on the *upper* surface of the leaf, the lateral lobes have united across the *lower* face of the latter.

dorsal awn, all formed in the same way; in all these cases the dorsal surface of the stipular ligule is opposed to the ventral (upper) surface of the leaf, in violation of the law; this, however, may be accounted for by the fact that the ligule in these cases is a mere membranous structure, so unlike the rest of the leaf in consistence and so disproportionately developed that it can exert no influence in determining the facial orientation of the leaf with regard to itself.

One of the most puzzling phenomena amongst leaf-abnormalities is afforded by the enations, in the form of laminar or wing-like outgrowths, with reverse orientation of their parts, which occur on either side of the midrib of the upper or lower surface (usually the latter) of various foliar organs. Only recently has, what appears to be, the real meaning of it transpired.

The foliar outgrowths described above, whether in the form of laminar enations, some cases of pitcher-formation, or entire leaves, really represent an attempt on the part of the organ forming them to reproduce itself, an attempt which is in varying degrees successful. The three main classes mentioned in which they appear all represent essentially one and the same phenomenon under various disguises, viz., that of facial fission of the foliar organ concerned. The type of fission which takes place at right angles to this, viz., marginal fission or forking, we are abundantly familiar with, and it is the most usual method adopted when the leaf proceeds a part, or the whole of the way, towards its reproduction.* In the ferns, apparently, never more than a part of this object is ever attained, for the frond is never completely divided into two, the organ being content with increasing its leaf-surface by simple forking and cresting (*cf.* forked and fasciated shoots, which represent the same phenomenon).

Now, attention may be directed to the various stages which are to be observed in the process of reproduc-

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* C. de Candolle calls these two types "lateral" and "antero-posterior bifurcation" respectively.

tion of the foliar organ by means of facial fission; and it will be seen that the following interpretation will clear up and explain many a bizarre and otherwise inexplicable "freak."

No instance seems to be known in which facial fission has resulted in the formation of two perfectly distinct leaves, but the case of the double vine-leaf described above is a near approach thereto in which attachment obtains by the leaf-stalk only. Then come the cases of the mango, the tobacco-leaf, and those of *Buddleia*, in which the attachment between the two leaves extends for a long distance, or the whole way, along the midribs. This is precisely the condition, and the same structure, which we see in the virescent stamens in which a green lamina is developed along either side of the midrib on the ventral surface of the anther, and which, save for its inverse orientation, resembles exactly the normally-orientated virescent portion.

The next stage is seen in the case of the *Polygonum*- and *Phlox*-leaves, and some of those of the saxifrage, and normally in some species of *Caltha*, in which the ventral or dorsal laminæ extend only part way along the midrib, or never meet above to form an individualized ventral blade, or are very poorly developed as compared with the leaf which bears them. Such laminæ may extend along some of the lateral veins or may unite with the basal margins of the leaf to form pockets. Or, again, a transition may occur, as in the saxifrage, between such a case with two basal pockets and the fusion of these to form a single large basal pocket; here the ventral laminæ, which are basally united with the leaf-margins, extend only a short way up the midrib and unite together across it; or we can picture it more easily, perhaps, by imagining the midrib of the basal pocket of a leaf to become united for a certain distance with the main midrib of the latter, which is the reverse process. In fact, there exists, as is specially well seen in the saxifrage-leaves above described, a series of transitions between a typically-formed pitcher-leaf and a leaf possessing merely laminar outgrowths on either side of the midrib. And further, we are able to reach the striking conclusion, from the consideration of the transitions which exist between these laminar outgrowths and the attachment, either by their midribs or petioles, of two entire leaves, that these two phenomena are really one and the same phenomenon; in other words, a leaf like that of the phlox, *Polygonum*, the saxifrage, or even the virescent stamen, represents merely a leaf in which a second leaf is commencing to detach itself from, as the case may be, the lower or the upper surface by the process of what is above called "facial fission."* This conclusion receives support from such cases as that of the elm-leaf (fig. 44), and the *Syringa*-leaf figured by Celakovsky, in which, by a congenital infolding of the apex or a portion of the margin, ventral laminæ become incompletely formed along the midrib or a lateral vein from above downwards; if this extended to the leaf-base the result would be the formation of two distinct leaves placed back to back.†

In the plants mentioned above we see the congenital, sporadic appearance, for what reason we know not, of isolated stages in the process. It certainly would never have been thought, before envisaging the phenomenon from this view-point, that the ascending or pitcher-like structure, when arising as a modification of an entire leaf and not as a portion of the leaf, represents not, as

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* The infolding and union with the midrib of the ventral side of the pitcher-leaf (*i. e.* a radially-constructed leaf), as in the saxifrage, may be regarded as essentially the same phenomenon as that of "ring-fasciation" in certain capitula and flowers. In both cases it must be held to be a stage in the splitting of the simple organ into two.

† A case of this sort would arise when the two median lamellæ, or their equivalents, on either side of the midrib, remained always distinct and became parts respectively of the two daughter-leaves. These would thus be separated off in a plane at right angles to that of the surface of the mother-leaf. When, however, the lamellæ become united together at either end, this represents a stage in the separating off of two daughter-leaves in the plane of the leaf-surface, and the two lamellæ therefore become part of one and the same daughter-leaf. Emargination or lateral forking of the mother-leaf is, of course, a concomitant of the first process, but not of the second.

we usually suppose, a single leaf whose margins have become congenitally united, but in reality two leaves. This is obvious enough in the terminal pitchers of the *Buddleia* and *Marrubium*, where the normal leaves occur in pairs on the stem below; it is less so in the case of the pitchers of *Saxifraga* and *Pelargonium* which have alternate leaves; but the transitional phenomena observed in the former, and the presence of a marked midrib on the side opposed to that of the normal midrib in the latter, seem to justify this conclusion. The terminal leaf of *Buddleia* with a basal pocket and the pitcher-leaf of *Pelargonium* seem to be precisely similar structures.

The formation of ascidia and of ventral laminæ is, apart from the interpretation of them above given, an absolutely inexplicable and bizarre phenomenon. That an ordinary bifacial, dorsiventral leaf should suddenly appear as a pitcher, or suddenly produce strange laminæ on its surface, is surely incongruous with all we know of the characters of a leaf. This incongruity and inexplicability vanish, however, if the above interpretation of the phenomenon be admitted.

These phenomena have been attributed as a whole to fission, more perhaps for the sake of convenience of description than anything else. But although all are certainly of the same morphological nature, it would be obviously a mistake to attribute them all to fission. Just as in the case of forked leaves, so also here: some must be due to fission, others to fusion (union). In some cases, where we have only detached leaves, without the possibility of observing the leaf-arrangement on the shoot which bore them, as in the case of the mango-leaf, we cannot determine whether the abnormal leaf is due to fission or to union of two leaves. In the case of the saxifrage-leaves, in the absence of any evidence of fusion, we must attribute fission as the cause; the same applies to the *Phlox*-leaves, and possibly to the *Pelargonium*-leaf.

In the case of the double leaf of the *Buddleia*, including the one with a basal pocket, we have indubitably to do with a case of congenital fusion of two opposite leaves by their ventral midribs and basal margins respectively, for the apical portion of the shoot has become displaced in favour of what has now become a single organ. Here, union results in either the formation of a leaf bearing laminæ along the midrib, or in pitcher formation, precisely the same dual aspect of the same phenomenon which becomes induced (probably by the reverse process) in the saxifrage-leaf. In the *Marrubium* it is equally certain that the terminal ascidium is due to fusion of the leaves forming the uppermost pair.

In conclusion, therefore, it may be stated that (1) the presence of laminæ on the leaf-surface, and (2) pitcher-formation of the entire leaf, or of portions of it, may be regarded as two aspects of one and the same phenomenon, viz., the imperfect manifestation in a superficial position of a second leaf.*

The numerous transitional formations exhibited, it is true, not in a single plant or species, but in various genera (not to be depreciated on that account), seem to render this conclusion quite admissible.

It may even be that many of the terminal pitcher-leaves represent reversions to the primitive position of the leaf as indicated by the phyton-theory. And if it be true that the two leaves of a pair have arisen by division of a single leaf, then cases like those of *Buddleia* and *Marrubium* might certainly represent partial reversions.

The normal pitcher or peltate leaves of *Sarracenia*, *Cephalotus*, *Nelumbium*, *Hydrocotyle*, etc., do not appear to represent at all the same phenomenon.

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* Parish suggests that the enations on the abnormal leaf of *Rumex* observed by him may be due to cohesion or fusion of the midribs of two leaves, the blade of the uppermost being reduced or fragmented. This is exactly the idea which is here supported, and an interesting counterpart thereto.

3. ADNATION.

1. Of Foliage-leaf to Stem.—A good example of a normal adnation of this kind is afforded by the adult foliage of the Cupressineæ, in which the greater part of the leaf, which is perfectly free in the juvenile shoots, is fused by its upper surface with the axis, leaving only the tip free. It is simply this fact which causes the striking difference between the two kinds of foliage. Many winged stems owe their peculiarity to fusion of the leaf-base with the axis.

2. Of Foliage-leaf or Bract to Peduncle.—This is not at all infrequent. Costerus and Smith mention that in *Carludovica palmata* the leaf-stalk was fused at the base for a certain length with the stalk of the inflorescence. In a tulip recently seen, the uppermost foliage-leaf, which was equal in size to those at a lower level, was adnate laterally to the entire length of the scape from the insertion of the leaf upwards. The upper part of the leaf was similarly adnate to one of the perianth-leaves. The whole formed a remarkable abnormality.

Normal cases of this abnormality, representing probably mutational departures which have become fixed in the life-history, are quite numerous. The case of the lime is perhaps the best-known, where the membranous bract becomes adnate for a certain distance with its axillary inflorescence-stalk for purposes of seed-dispersal. In *Monotropa Hypopitys* * and *Thesium ebracteatum* * the same fusion occurs. In *Gongylocarpus rubricaulis* * the inferior ovary becomes fused both with its subtending bract and the main axis. Then there are the instances afforded by the *epiphyllous* flowers, *e. g. Phyllonoma ruscifolia*,* *Polycardia lateralis*,* etc. In *Erythrochiton hypophyllanthus* * the flower springs from the lower surface of the leaf; according to Planchon the flower-stalk in this case is fused not only with the lower side of the

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* Of these the writer has seen herbarium material only.

leaf, but also with the whole length of the axis from the axil of the leaf below!

In *Loranthus* the bract is always situated at the top of the pedicel immediately below the flower. This is probably due to an intimate fusion of the lower portion of the bract (which became at the same time exceptionally elongated) with the pedicel.

3. OF FOLIAGE-LEAF TO PERIANTH-LEAF.—This is the case above-mentioned in the tulip where the upper apical part of the foliage-leaf became laterally fused with the entire length of one of the sepals, so that the latter was partly petaloid and partly foliaceous.

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4. CHANGE OF POSITION.—PHYLLOTAXIS.

This is one of the most important, and at the same time one of the most difficult subjects to deal with. Abnormal cases in seedlings will first be treated of.

Cotyledons.

1. Syncotyly.—It is an exceedingly frequent event, of which De Vries figures many instances in his great work on mutations, for the two cotyledons, in plants belonging to a great variety of natural orders, to become more or less intimately fused to form a single organ: a phenomenon termed by him "Syncotyly." De Vries figures such cases in *Mercurialis annuus*

(Pl. XIX, fig. 3*d*), the sunflower (*Helianthus annuus*), the black bindweed (*Polygonum Convolvulus*), and the wild radish (*Raphanus Raphanistrum*) (Pl. XIX, fig. 3*e*); Mr. Dymes has seen cases in the water-milfoil (*Myriophyllum spicatum*), the fringed buck-bean (*Limnanthemum nymphæoides*), and the brookweed (*Samolus Valerandi*); the present writer has seen it in *Gaillardia*, *Eremostachys laciniata* (Pl. XIX. fig. 3*a*), *Salvia amplexicaulis* (Pl. XIX, fig. 3*c*), *Ammi Visnaga*, *Brassica sp.*, and others. It is thus clearly a very common and widely distributed phenomenon. It may assume three different forms. The two cotyledons may fuse by their margins of one side only and assume an apparently lateral position opposed to the first-formed plumular leaf, as in *Salvia* and *Mercurialis*, or, the mode of fusion being the same, the double organ so formed may occupy a terminal position on the axis, as in *Eremostachys;* or, again, the cotyledons may fuse by both margins and form a cup-, salver-shaped, or tubular structure surrounding the plumule.*

There are many plants which normally develop a single cotyledon, *e. g.* the lesser celandine (*Ranunculus Ficaria*), *Anemone apennina*, *Pinguicula grandiflora* and *P. vulgaris*, and *Cyclamen persicum*; in all these the cotyledon is formed in the same way as in the abnormal cases above cited. The single terminal cotyledon normally formed in such cases as *Corydalis solida* and *Abronia* is due to suppression of the other one.

2. Schizocotyly.—Another phenomenon, about equally common, consists in the tendency to multiply the cotyledons, which is, of course, the reverse happening to that just considered. The forking of one or both cotyledons is merely the first stage in the formation of three or four instead of the normal two. The sycamore (*Acer Pseudo-platanus*) very often has three or four cotyledons in its seedlings (Pl. XIX, fig. 4). The writer has seen interesting cases in the wall-flower (*Cheiranthus Cheiri*); in one seedling there were

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* "Amphicotyly."

three cotyledons all of equal size and symmetrically grouped to form a whorl of three (Pl. XXII, fig. 1*d*); in another there were four equal cotyledons, and these were grouped as shown in the figure, the two resulting halves of each divided cotyledon turning through an angle of 90° and coming to lie almost opposite to each other (Pl. XXII, fig. 1*f*). In another seedling one cotyledon only had divided, the two resulting members being each of them much smaller than the undivided cotyledon (Pl. XXII, fig. 1*c*). Yet another case was similar to the last except that the division into two cotyledons was not quite completed, the two organs being still united below; but their free laminæ were directly opposed to each other, as are the two cotyledons in a normal seedling (Pl. XXII, fig. 1*a* and *b*). The normal counterpart of the abnormal phenomenon just described is seen in the seedlings of some Gymnosperms, *e. g.* the pine, in which congenital division of the cotyledons into as many as fifteen occurs. This formation of the cotyledons in the pine seems to be quite analogous to that of the four embryos in the same plant.

Although the cotyledons may increase in number, so that the two opposite ones may be replaced by a whorl of three or four, no cases appear to be known of these organs changing their position in the vertical direction.

Forking and multiplication of the cotyledon is apparently unheard of in Monocotyledons.

FOLIAGE LEAVES.

1. LATERAL.—*a. From Opposite-decussate to Whorled.*—A change in the leaf-arrangement is most commonly met with in plants which have opposite-decussate leaves. In these we have to denote two distinct types of change. In the one case the pair of opposite leaves may become changed into a whorl of three or four, and this takes place by apical fission of one or both of the leaves concerned; and transitional cases occur in which one or both of the leaves is more or less

deeply forked, as in the interesting case of the honeysuckle (*Lonicera Periclymenum*) described by Celakovsky. The same thing has also occurred in *L. thibetica* (Pl. XX, *a*). The extra leaves so formed are not always equal in size to the others; this was the case with the median leaf in a ternate whorl of a hybrid woundwort (*Stachys palustris* × *S. sylvatica*) found by Mr. Sprague. In such a case as this there must have been an unequal bipartition of one of the leaves. In the cornelian cherry (*Cornus Mas*) near the tip of one shoot of the final pair of mature leaves, one of the leaves had become imperfectly divided into three leaves, each of which was four or five times the size of the corresponding undivided leaf of the pair. The bifid character of the leaf, indicating the first stage in the formation of two leaves from one, is very common as an abnormality, especially in plants with opposite-decussate leaf-arrangement.

No instance of a plant bearing normally bifid leaves appears to be known. The case of *Boehmeria biloba* is only in appearance an instance of such a phenomenon; Klein points out that in reality one of the two apparent apices is merely a lateral tooth which has become enlarged so as to equal the terminal part of the leaf in size.

b. From Opposite-decussate to Scattered (*Spiral*).—Displacement, of course, occurs when the whorled or opposite arrangement becomes changed into the alternate. An imperfect change of this sort has occurred in *Buddleia Hemsleyana* (Pl. XXII, fig. 2) at Kew; this plant has opposite-decussate phyllotaxis. In one plant a branch exhibited the following variations at the successive nodes in passing from below upwards: (1) normal; (2) normal; (3) leaves slightly displaced; (4) normal; (5, 6, and 7) sub-normal, but congested together owing to suppression of the internodes, and the leaves of the pairs are not precisely opposite; (8) leaves displaced vertically about half an inch, and not on opposite sides of the stem but rather more approximated on one side; (9) leaves displaced about an inch and the lowest leaf forked so far as the base of the stalk without complete separation into two; (10) leaves nearly opposite, each with an inflorescence in its axil. On another plant a branch representing the stronger of two resulting from a fork, showed the following nodal variations: (1) leaves displaced a quarter of an inch; (2) a single leaf; (3) two slightly displaced leaves, not opposite, but approximated on the side opposed to that on which the single leaf of node (2) is situated at a lower level corresponding to the length of a normal internode; the leaf of (2) may be regarded as having been congenitally displaced downwards from the position of the widest gap between the two leaves of (3) where it would form with them a whorl of three; (4) whorl of three leaves each separated by a quarter of an inch from the other; (5, 6, and 7) whorls of three leaves; then begins the inflorescence. Also on many shoots, especially the suckers, of *Lonicera thibetica* the leaves of several whorls (consisting usually of four leaves) were irregularly displaced; the displacement here is coupled with forking of many of the leaves; it has not proceeded so far but that the scattered leaves can in every case be referred to the whorls they have been displaced from (Pl. XX, *a*). In one branch which bore whorls of three leaves there was one whorl which had two leaves only, not opposite, but widely separated on one side; the next node below had a whorl of three leaves, one of which was forked, and one of the halves so formed was again forked unequally. The cases taken from these two plants represent a very imperfect and half-hearted transition from the opposite-decussate to the alternate or spiral arrangement.

The ash (*Fraxinus excelsior*) frequently exhibits on some of its branches the $\frac{2}{5}$ phyllotaxis without any trace of the opposite-decussate arrangement.

Where the change is much more complete and pronounced it is accompanied, as the internodes lengthen, by a very accentuated torsion of the stem. This is due to the fact that while the leaves composing each pair tend to become separated owing to the stretching of the stem, their bases really remain united, and this occurring along a length of stem including many internodes, inevitably causes the torsion phenomenon. Pl. XXI shows an excellent example of this in the malmaison carnation (*Dianthus Caryophyllus* var.). It is also frequently seen in the teasel (*Dipsacus sylvestris*) (fig. 56) and many other plants with opposite-decussate or whorled leaves. Not only, however, do the leaves of the same whorl remain united, but all the leaves of the shoot, from the base upwards, become congenitally united at the base, a fact which seems common to all plants exhibiting this torsion. This, then, is another instance of the rare phenomenon of leaf-fusion in the vegetable kingdom.

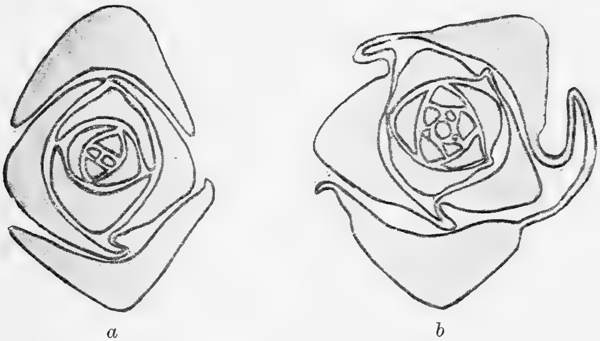

Fig. 56.—*Dipsacus sylvestris.* Ground plan of normal shoot (*a*) and of shoot showing transition to spiral phyllotaxis (*b*). (After De Vries.)

There is another, much rarer, method by which the transition from opposite-decussate to alternate phyllotaxis is effected, viz. by lateral fusion, at one or more nodes, of the opposed leaves of a pair; Alex. Brown observed this in the first pair of foliage-leaves succeeding the cotyledons which, fusing, formed a single leaf alternating with the first leaf of the alternate

FIG. 57.—*Rhinanthus minor.* Shoot showing origin of scattered (spiral) phyllotaxis by fusion of the two leaves at some of the nodes.

series above; he also cites it as occurring in the branches of mature plants, *e. g. Weigelia*, *Calycanthus*, and *Acer dasycarpum.* Steinheil describes a stem of *Salvia Verbenaca* with alternate leaves, which he ascribes to fusion. The writer has himself seen this in the yellow-rattle (*Rhinanthus minor*) (fig. 57). The same thing was figured by Clos in *Stachys maritima* (fig. 58); in this case the alternate leaves were forked, but his conclusion is that they are dividing and attempting to revert to the normal arrangement.

In many of those cases in which the two cotyledons fuse to form a single organ, the phenomenon is the direct cause of the alternate phyllotaxis of the foliage-leaves on the shoot above, where, according to the normal character of the plant, they should exhibit the opposite-decussate arrangement. This has occurred in *Salvia amplexicaulis* and in *Eremostachys laciniata* (Labiatæ). Velenovsky mentions a seedling of *Eucalyptus pulverulenta* in which one cotyledon only was present, as a consequence of which the foliage-leaves above were alternately arranged. It is possible that each leaf in these cases represents a congenital fusion of two, so it is placed under this heading.

c. From Scattered (Spiral) to Opposite-decussate.—This phenomenon of bipartition of the leaf also occurs in plants with alternate phyllotaxis, as in the oak, elm, and rose, but it would appear to be less common in these. In a weeping variety of *Ulmus glabra* shoots for several nodes in succession bore leaves which were completely forked into two distinct leaves, although occasionally a partially forked leaf also occurred; when two distinct leaves thus occurred side by side at one node each bore a bud in its axil; if the forking was incomplete only a single axillary bud was present (fig. 59). On other shoots such nodes in the forking leaves were few and far between. In many of the above cases the change in leaf arrangement does not result in vertical displacement of the leaves, but in the

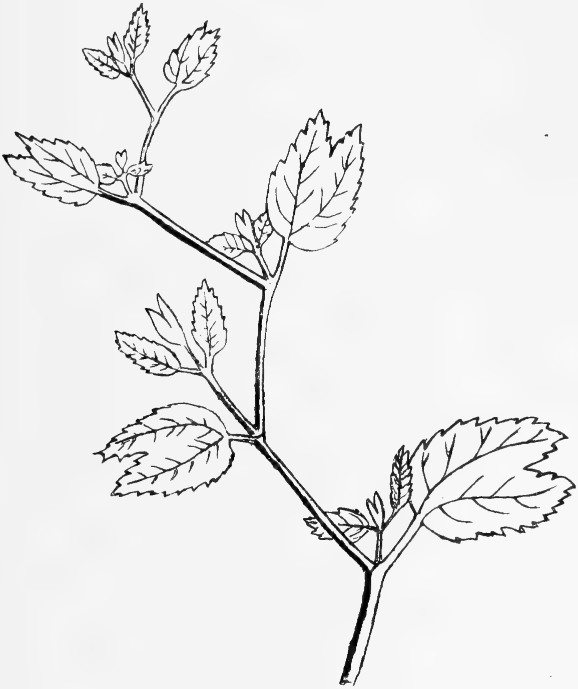

Fig. 58.—*Stachys maritima.* Shoot showing origin of scattered (spiral) phyllotaxis by fusion of the two leaves at each node. (After Clos.)

case of the elm indications thereof were observed, one of the two leaves resulting from the fork being slightly displaced. The meaning of this will appear later.

There must here be introduced the interesting cases in which a single terminal leaf is replaced by a pair of opposite ones. In the umbrella-pine (*Sciadopitys verticillata*), on proliferation of the short-shoot bearing the single "double needle," this organ splits into a pair seated on opposite sides of the shoot, clearly a reversion to the primitive condition. Now in *Pinus monophylla*, which normally bears a single terminal needle, this is not constituted by the fusion of two, as in *Sciadopitys,* but one of the original pair has become suppressed, thus allowing the other to assume sole occu-

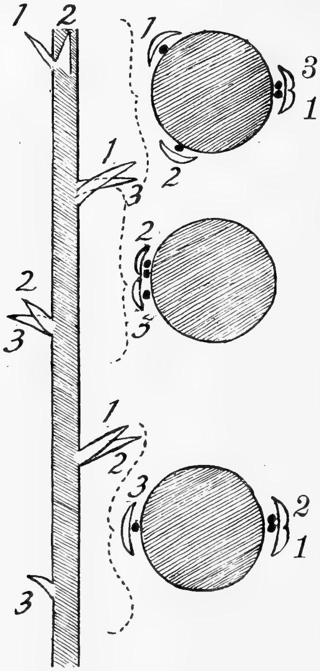

Fig. 59.—*Ulmus glabra.* Diagrammatic representation of mode of origin of opposite-decussate phyllotaxis from the distichous arrangement.

pation of the region of the axis close to the apex which it then completely absorbed; that it is a single leaf, being cylindrical only in its external contour, is shown by the presence within it of a single collateral vascular bundle. The trees of this species at Kew have sometimes short-shoots in which the original two needles had reappeared; one of these was slightly shorter than the other, and both were flattened on the inner side (Pl. XVI, fig. 3). These two plants seem to afford the only two instances known of normally terminal foliage leaves.

d. From Dorsiventral to Radial Symmetry.—In the yew (*Taxus baccata*) the leaves on the primary or main stem have an even and orderly spiral arrangement; on the lateral horizontal or ascending branches, however, the leaves, while still preserving the spiral arrangement (although this may be slightly less regular), become, owing to the twisting of their leaf-stalks, apparently arranged in two rows along the shoot. The fastigiate variety or Irish yew represents a reversion to the primitive type of leaf arrangement. This primitive type is also very frequently induced at the tips of the lateral shoots by the prick of the Cecidomyious insect *Eriophyes psilapsis* (*Phytoptus taxi*), forming a characteristic gall. This would seem to be an interesting case of a traumatic reversion.

2. TERMINAL.—These are of two kinds, viz.: (1) those formed of a single leaf and (2) those composed of two congenitally-united leaves, but transitions between these occur.

(1) *Single Leaf.*—The most remarkable instance of this is that cited by Morren for *Gesnera Geroltiana*[*] where an abnormally large foliage-leaf terminated the axis of the flowering-plant; the structure here is undoubtedly, from its shape, a single leaf, but its unusual size, as well as its position, leads us to suppose that it really represents two leaves. The terminal leaf of *Buddleia Hemsleyana* represented in Pl. XXIII has a basal

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[*] The genuineness of this case is, however, open to doubt.

pocket which has a midrib of its own, and probably represents an imperfectly-formed second leaf; the leaf most probably represents a fusion of two. Terminal cup-shaped leaves have occurred in the garden geranium (*Pelargonium zonale*, fig. 60). In some cases this leaf congenitally arises in a perfectly terminal position and there is no sign of any formation of the real apex; in other cases the leaf is not in the strictest sense terminal, but makes a slight angle with the vertical, and in this case, moreover, the displaced stem-apex can be seen in microscopic section in a lateral position at the very base of the leaf with vascular bundles passing out to it (fig. 60). The pitcher-leaf probably occupies the position of both the terminal inflorescence and the highest axillary vegetative shoot at the same time.

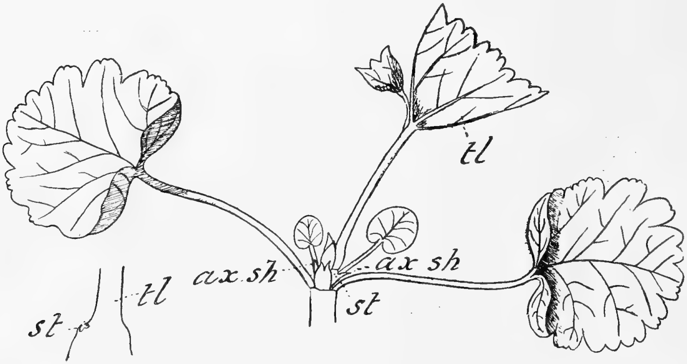

Fig. 60.—*Pelargonium zonale.* Shoot bearing a terminal leaf in form of an ascidium which itself bears a secondary ascidium on its lower surface, with (on left) diagrammatic longitudinal section of base of terminal leaf showing displaced apex. *tl*, terminal leaf; *ax sh*, axillary shoot; *st*, stem.

(2) *Double Leaf.*—In *Buddleia Hemsleyana* the uppermost of the fully-matured pairs of certain branches of a plant growing in Kew Gardens was represented by a single structure composed of the two leaves (one of which, in the case of one branch, was smaller than the other) united by the midribs of their upper surfaces for about two-thirds of their length from below

upwards; it occupied a perfectly terminal position, the uppermost youngest portion of the branch having been pushed over into a lateral position (Pl. XXIV); in another branch the same peculiar double-leaf structure occurred, but here the young, developing portion of the branch had become completely extinct and the double-leaf formed the veritable termination of the branch (Pl. XXV). This congenital union, face to face, of two leaves in the manner described, gives rise to a structure which is almost certainly identical with those above described in *Phlox*, *Saxifraga*, and *Polygonum*, but in a much more developed condition. If we imagine the two ventral laminæ in the *Phlox*-leaf becoming united at their apices and greatly enlarged so as to equal in size, or nearly so, the blade on which they are borne, the result would be a structure quite similar to that in *Buddleia*. Buchenau cites a case in the tobacco-plant of the same phenomenon, but in this instance the leaves were adherent by their lower (dorsal) surfaces, the apical portions being free. The same thing has occurred in the bird's-lip flower (*Strelitzia reginæ*); the two leaves being coherent back to back for the whole length of their blades and petioles.*

This is one type of double terminal leaf in which the constituents are coherent by their (upper or lower) surfaces. In the type about to be mentioned the union is marginal, being similar to the mode of formation of the cup- or salver-shaped double cotyledons which occurs in some plants. De Vries figures seedlings of the snapdragon (*Antirrhinum majus*) in one of which there was such a double plumular leaf succeeding the two normal cotyledons (Pl. XXII, fig. 6 *c*.); in another seedling with three cotyledons the terminal structure consists of a single blade with a basal pocket (Pl. XXII, fig. 6 *a*); it is, in fact, just the same structure as the "single" terminal leaf above mentioned, in

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* The writer is indebted for these leaves to the generosity of Mr. W. H. B. Fletcher, of Bognor.

Buddleia; that both, however, represent imperfectly-formed double leaves is, on comparative grounds, fairly certain. In another of De Vries' snapdragon seedlings the double plumular leaf was of another type, being flat and expanded and only very slightly infolded at the base; it had two distinct midribs (Pl. XXII, fig. 6 *b*). This is comparable to the cases of *Calycanthus* and *Calendula* cited by Klein, where a double leaf, occurring in the axil of another leaf, was formed by the lateral union of the two leaves of the first pair of the axillary shoot, this being itself suppressed.* Klein also figures leaves, usually double, but in one case triple, of *Philadelphus* and *Calycanthus*, which were terminal to leafy shoots, and due to the union, along one of their two margins only, of two or three leaves of the whorl.

In a mature shoot of the horehound (*Marrubium vulgare*) the uppermost pair of opposite leaves was represented by a terminal double leaf (Pl. XXII, fig. 4). On examining this structure anatomically it was found that the collateral vascular bundles constituting the midribs of each opposite side of the cup formed, along with all the confluent lateral veins, lower down in the cup-stalk, a vascular cylinder precisely like that of a stem. In this case there was not the slightest sign of the real stem-apex.

All the cases above described are genuinely terminal foliage-leaves; every one of them, although some are double *in their origin*, are single organs terminating the axis.

BRACTS.

An umbel of *Œnanthe crocata* had a fasciated primary ray, branching above. Bracts appeared at the point of branching, doubtless due to the simulation by the fasciated portion of the peduncle of the inflorescence.

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* *Cf.* origin of ovuliferous scale in Abietineæ.

In *Nymphæa* the apparent fourth sepal in the anterior position has, when compared with that of *Nuphar*, an anomalous insertion, as it covers the two lateral sepals instead of, as in *Nuphar*, being enclosed by them. *Nymphæa* has no bract at the base of the flower-stalk, whereas *Nuphar* exhibits one. Now Caspary observed a most interesting abnormality in various species of *Nymphæa*, viz., the displacement of this apparent fourth sepal into a position at the base of the flower-stalk, showing clearly that it is really the displaced bract, and not a sepal at all, and thus adequately accounting for its covering the lateral sepals. The fourth inner sepal has, owing to this position of the bract, become completely suppressed, and did not even reappear when the bract was displaced into its proper position.* In *Carya*, both the bract and bracteoles are normally displaced upwards to form part of the calyx. In *Loranthus* the bract occurs at the top of the flower-stalk, close below the flower.

General Conclusions on Phyllotaxis.—In the foregoing pages several types of abnormal phyllotaxis have been described. Each of these has its own definite meaning and value whose interpretation has a bearing on the origin of normal leaf-arrangement.

We must regard the spiral type of phyllotaxis as the primitive one. The floral axis is that part of the plant in which least modification and disturbance has, in the course of evolution, taken place, and is hence the region in which we must look for the most primitive type of leaf-arrangement; moreover, the sporophyll-bearing axis must always be at least as ancient as, probably more so than, the purely vegetative axis.

In the more primitive groups of flowering plants the sporophylls are spirally arranged.

But assuredly the best foundation for the view that the alternate, spiral phyllotaxis is the primitive type is that afforded by the time-honoured phyton-theory of

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* See Celakovsky's account of this phenomenon.

Gaudichaud, Schultz-Schultzenstein, Celakovsky, and others, according to which the stem is built up of a succession of segments each one of which is composed of a leaf-blade and a leaf-base; morphologically and primitively, each leaf-blade terminates the whole growth, the succeeding one sprouting from it in a lateral position. The Monocotyledonous seedling shows us this primitive type in actuality, and it is sufficient to contemplate a typical mature Umbelliferous or almost any Monocotyledonous plant to be satisfied as to the probable truth of this theory. For the arguments in favour of it the reader is referred to the literature of the subject and to what has been said above. If true, the Monocotyledonous type of stem, with alternate phyllotaxis (*i. e.* the segmented stems with sheathing leaf-bases) represents the primitive type, and all unsegmented stems are derived therefrom. Both kinds of stem occur in the Umbelliferæ; *e.g.* Domin describes a typical genus, *Didiscus*, with unsegmented stem-structure; in a *single* individual of *D. cyanopetalus* he observed a most interesting reversion to the original segmented condition, for this plant possessed throughout leaves with sheathing bases completely enclosing the stem.

The mode of development of the earliest-formed foliar organs of the seedling has generally been regarded as affording a clue and an indication as to the nature of the foliage-leaves in the ancestors of the plant concerned. This is one of the comparatively rare instances in which the ontogeny is of real assistance in the unravelling of the thread of the phylogeny. In this connection our attention must be directed not only to the conformation of the mature cotyledon or first-formed foliage-leaf, but also to the stages in the ontogenetic history of these organs. Now, in those plants possessing sheathing leaf-bases, the first part to be formed in these early foliage-leaves is the sheathing base, and only at a later stage do the petiole and lamina become differentiated, while in many plants the first-formed leaves consist solely of the leaf-base, as in Cycads.

These facts suggest that the sheathing base represents the most primitive part of the leaf, and that petiole and lamina are a later acquisition. Consequently those groups of plants in which the sheathing base is the most conspicuous part of the entire foliage-leaf, and in which petiole and lamina are not so frequently differentiated as distinct areas, must be regarded as possessing the most primitive type of vegetative stem. As the majority of Monocotyledons exhibit this type they must inevitably be held to be a more ancient group of plants than the Dicotyledons, in which the leaf-conformation is much more highly differentiated. The view that the sheathing leaf-base (and all that it involves) is the result of the geophilous habit of so many Monocotyledons, suggested by Miss Sargant, would appear to be refuted by the fact that the Palms, so primitive in their floral conformation, possess the same sheathing leaf-bases,* although, as tall trees, they represent the very antitheses of geophilous plants. The Palms also, so well-developed in all their parts, constitute a refutation of the modern view that Monocotyledons have been derived from the Dicotyledonous type by reduction. A further important point is this: that the occurrence, although rarely, of dichotomy of the stem as a normal feature in Monocotyledons and never in Dicotyledons shows the former class to be more primitive than the latter, and that the Palms, in which it alone occurs, are, consequently, more primitive than other members of the class.

These then are our clues as to what was the original type of phyllotaxis in the vegetative portion of the axis; for it is probable that in the far-back (fern-like ?) ancestors of Angiosperms there was no great distinction between sporophylls and vegetative leaves either as

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* Here, however, the leaf is differentiated into petiole and lamina, indicating that the Palms have subsequently and independently evolved the higher type of leaf-conformation.

regards their essential conformation and structure or their phyllotaxis.

If this view is incorrect, how are the various abnormal changes from opposite to spiral phyllotaxis to be explained? They would seem to be meaningless. If, however, it be correct, then these changes are easily explicable as reversions to the primitive type, as eruptions from the rigid groove into which evolution has led the type. The opposite-decussate type of phyllotaxis is merely a modification of the spiral $\frac{2}{5}$ type. Baillon observed in a plant of *Chimonanthus fragrans* that the $\frac{2}{5}$ leaf-arrangement prevailed throughout the vegetative axis; as the opposite-decussate type is characteristic of the Calycanthaceæ this isolated exception is not likely to be a progressive, but rather a reversionary phenomenon. The four cortical bundles of the vegetative stem of plants of this order are an indication of the opposite-decussate leaf-arrangement; in the plant of *Chimonanthus* seen by Baillon there were five cortical bundles. Now it is interesting that in the peduncle of both *Calycanthus* and *Chimonanthus* there are six to eight cortical bundles arranged in five sets (*i. e.* at two points the bundles are in pairs). As the presence of five bundles indicates the completed transition from the opposite to the $\frac{2}{5}$ spiral phyllotaxis; so the presence of the extra number shows the gradual transition to a more complicated arrangement which obtains at a higher level, viz., on the floral axis, and is therefore the more primitive type.

The leaf-arrangement in the vegetative stem in plants generally is apparently the result of the mean of two distinct kinds of influence, viz., that emanating from above, representative of the more primitive type, and that coming from below in the cotyledonary region. The former influence makes for spiral, the latter for opposite phyllotaxis. In many Dicotyledons whose phyllotaxy is typically alternate the first few nodes have each a pair of opposite leaves, being formed in correlation with the cotyledonary node. In many other orders all the leaves are alternate, the influence from above being entirely dominant over that from below.* It is significant in this connection that in Monocotyledons, where there is only one cotyledon, opposite-decussate phyllotaxis is excessively rare, occurring only in certain species of yam (*Dioscorea*); it may be only a coincidence, but the Dioscoreaceæ is one of the two orders of this class (the other being the Commelynaceæ) in which the cotyledon is not precisely terminal, and the prominent development of the sheath on the side of the stem opposite to that on which the cotyledon-lamina is developed, along with the very early appearance of the shoot-apex, has caused some botanists (*e. g.* Dutrochet and Beccari) to suppose two cotyledons to be present. It seems that we have to do here with a structure intermediate between one cotyledon and two: hence the strongly saucer-shaped cotyledon enclosing the plumule. In fact, it is probably a comparable structure to the terminal foliage-leaf of *Buddleia* previously described whose basal pocket really represents an imperfectly-developed second leaf. This transitional feature of the seedling would only be a natural concomitant of the other features in Dioscoreaceæ which show them to be transitional between Dicotyledons and Monocotyledons.

It is probably this character of the seedling which causes the frequent appearance of opposite leaves in the order. It is true that in the Commelynaceæ, in which, according to Solms-Laubach, a similar feature of the seedling occurs, the leaves are alternate; but it is to

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* It may often happen that a reversion to alternate phyllotaxis occurs in a portion of the vegetative stem while the opposite type still holds good in the inflorescence above. In that particular plant, therefore, no influence from the inflorescence inducing alternate phyllotaxis could possibly obtain; nevertheless, this influence must be regarded as present in the plant as part of its inherited constitution, for in other members of the genus, order, or cohort the bracts of the inflorescence will be found to be alternately arranged. Once the opposite-decussate arrangement has been adopted by the inflorescence it would appear to be less capable of reverting than is the case with the vegetative axis. Again, for some orders, *e. g.* the Urticaceæ, the opposite-decussate type may be the more primitive, so that the first year's seedlings of the elm, for example, would be producing the original type, the alternate arrangement in this genus being the derived one.

be noted that they are distichous and with very pronounced sheathing bases.

Again, cases have already been cited where, in Dicotyledons, seedlings with a single cotyledon have exhibited alternate phyllotaxis on the shoot above.

On shoots in which alternate phyllotaxis abnormally appears it does so usually in the higher part of the shoot, the lower nodes tending to form the normal pairs of leaves; but this is not invariably the case

The change from opposite-decussate to spiral phyllotaxis which occurs in such cases as those cited in *Buddleia* and *Lonicera* is a very imperfect one. Much more, but still very far from completely, perfect are the reversions exhibited by the contorted stems of carnation, teasel, etc.; in the carnation it was observed that the apical bud (Plate XXI) showed the leaves neatly arranged in a spiral manner; the torsion arises as soon as the internodes begin to lengthen. The same torsion has been observed in some species of horse-tail (*Equisetum*) in which cases it must represent a reversion to alternate phyllotaxis obtaining in ancestors more remote than those we know of in the Carboniferous and Devonian Periods; and it is decidedly of interest that Heer found exactly the same type of torsion in certain fossil Equisetaceæ.

Spiral phyllotaxis can be induced experimentally in plants which normally exhibit the opposite-decussate type; if stems of the horse-chestnut (*Æsculus Hippocastanum*) be cut down, the shoots which subsequently spring up bear leaves arranged according to the $\frac{5}{8}$ type of phyllotaxis; the luxuriant sucker-growth would seem to cause a reversion to a more primitive type of leaf-arrangement. This view is strongly supported by the fact that if stems of *Pinus*, especially *P. Pinea*, be lopped, the short-shoots proliferate and bear primordial leaves (*otherwise produced only in the seedling*) spirally arranged on the axis. Both of these may be regarded as cases of traumatic reversion.

In connection with the generally admitted view that spiral phyllotaxis is primitive, Celakovsky is probably correct in his view that the terminal cotyledon of Monocotyledons is also primitive, and that the two cotyledons of Dicotyledons have been derived therefrom by splitting, which is in direct opposition to the prevailing modern view which regards the Monocotyledonous type as due to reduction from the Dicotyledonous one. If the modern prevalent view is correct we ought surely to occasionally find the single cotyledon of Monocotyledons abnormally forking or else replaced by a pair of cotyledons; but such phenomena are entirely unknown. We have in the short-shoot of *Pinus monophylla* a perfectly parallel case, in which the single terminal leaf results from the suppression of one of the members of the original pair; yet here the reappearance of the missing leaf is not at all an infrequent phenomenon. Why does the same thing never occur in the Monocotyledonous seedling?

On the other hand, the view that the Dicotyledonous condition is secondary and derived is supported by the fact that single cotyledons, due to fusion of two, occur very commonly as an abnormality in Dicotyledons. This may be regarded as a reversion, and this explanation, in the absence of any other, must hold the field.

The reason why the Dicotyledonous seedling offers such frequent "sports" as regards the number of the cotyledons may be attributed to the fact that the Dicotyledonous type of seedling is a comparatively recent variation from the primitive Monocotyledonous type; and the staid and invariable character of the latter is thus explained.

Where a single cotyledon is present in an abnormal seedling, it is invariably followed by a single foliage-leaf, and in plants which normally have opposite-decussate phyllotaxis this is replaced by the spiral type, a fact which again betrays the powerful influence of the cotyledonary node in regulating the leaf-arrangement on the plumular shoot. This phenomenon also shows us another method by which reversion to the primitive spiral arrangement is attained; in this case the transition is complete and perfect from the earliest stage onwards.

Consistently with the view as to the origin of the Dicotyledonous character of the seedling, and having regard to the great influence which the cotyledonary has upon the subsequent nodes, we are constrained to believe that the first one or few pairs of opposed foliage-leaves each arose by fission of a single leaf in the same way as did on this theory the cotyledons, or at least that in many plants this may have been their mode of origin. Higher up on the stem, however, away from the influence of the cotyledonary node, the leaf-pairs probably arose from the extreme shortening and eventual abortion of alternate internodes*; and in cases where the influence of the cotyledonary node is *nil* (and such might occur) internode-suppression would be the sole method of formation of opposite leaves. The cases of fusion of a pair of opposite leaves observed by Braun, Jännicke, Steinheil, Clos, and the present writer support the above view; if these are not reversions how else can they be explained? But the phenomena of displacement are certainly commoner than those of fusion. The alternate phyllotaxis of the stem, immediately succeeding and caused by the single cotyledon resulting from the fusion of two in the abnormal seedlings mentioned, springs into being congenitally and complete, so that we cannot trace the steps by which it arose.

During the displacement which occurs from the opposite to the alternate arrangement it may happen that two leaves, from pairs above and below, may fuse together to form a double-leaf, with distinct apices and two separate midribs; such a fusion would seem to occur for the purpose of economising space on

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* *Cf.* the normal formation of false whorls in *Lilium, Fritillaria, Paris,* etc. However, even in the higher region of the stem the opposite-decussate arrangement may often have arisen by division of the alternating leaves. This also appears to be the view of Velenovsky (see his figure of *Vinca*).

the branch; an instance is figured by Klein in *Weigelia rosea*. Another interesting case of fusion of leaves induced by a change in the leaf-arrangement was observed in *Lonicera thibetica:* of the two whorls already described, the approximation of the two leaves of the uppermost one leaving a wide gap on the opposite side indicates that the third member of the whorl of three is missing from this gap, and the forking of one of the two apices resulting from division of a member of the whorl of three of the lower node indicates that the leaf missing from the whorl above has fused laterally with one of the leaves of the lower whorl; if again separated off it would come to lie immediately under the wide gap occurring in the upper whorl.

Celakovsky cites an interesting case in *Ruscus*: he noted a transition in the phyllotaxis of the scale-leaves from the normal $\frac{2}{5}$ to the $\frac{1}{2}$ type which involved the congenital approximation and fusion of two of the leaves to form a double-leaf.*

Many cases have been cited above of double leaves† which are clearly cases of fusion. Cases of division, however, are seen where one of a pair or group of three cotyledons is forked, or where more than the normal number of cotyledons occur, as in the wallflower and sycamore. In a seedling of the former plant imperfect splitting of one of the cotyledons took place in such a way that the two laminæ so formed were exactly opposed to each other and at right angles to the undivided cotyledon; in another seedling where both cotyledons were completely doubled, the members of each resulting pair were similarly opposed; these

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* Delpino, owing to the fact that he always regarded the phenomenon of double leaves exclusively from the developmental (*i. e.* ontogenetic) standpoint, and never, as he ought to have done, from the teleological point of view, becomes involved in error when he ascribes "multiplication" as the sole cause in every case of double leaves; he excludes "fusion" as a cause for the reason that it would involve a disturbance of the phyllotaxis. He had evidently never come across such cases as that described by Klein in *Weigelia* and by the present writer in *Lonicera*. He also appears to have no conception of the phenomenon of congenital displacement and fusion.

† This term is used for any leaf showing apical division, no matter what its origin may be.

phenomena are cited to show how the origin of the normal Dicotyledonous condition may so easily have come about in precisely the same way.

The forking of the leaves in plants with opposite-decussate phyllotaxis is also, on this view, a case of division representing a stage towards the formation of a greater number of leaves in the whorl than the normal two. In the majority of cases, typified by the Labiatæ, the *Lonicera* described by Celakovsky, the *Buddleia* and *Cornus Mas* (in which latter one leaf of the pair had forked into three, while the other leaf was separated therefrom by a brief internode), the double leaf cannot be explained by fusion, for all the other leaves belonging to the nodes above and below are accounted for, and there is no disturbance of the phyllotaxis. A fact such as the following also supports the forking theory: in a shoot of the *Buddleia* a whorl consisting of four leaves in two opposite pairs was observed; in this case each pair was most clearly derived by forking of each leaf of the pair, as the phyllotaxis above and below was not disturbed, and, moreover, it could not be due to the approximation of two pairs of leaves, for this would involve a horizontal displacement of the pairs, a phenomenon which was never observed on any of the shoots.

A case of unequivocal forking in leaves of shoots with alternate phyllotaxis will now be referred to, viz., in those of the weeping variety of *Ulmus glabra* above mentioned. In this instance also the double leaves or the paired leaves at each node cannot be ascribed to fusion, for the phyllotaxis both above and below is quite undisturbed and all other leaves are accounted for. The explanation of this phenomenon, which is probably the correct one, is that given by Vuillemin, viz., that it represents a partial reversion to the opposite-decussate type of phyllotaxis from which the alternate distichous type of the normal elm-branch has been derived; the former occurs in the first year's growth of seedling elms, and may well be the original type of phyllotaxis in the Urticaceæ. Vuillemin supposes that the alternate arrangement came about by suppression of one of the two leaves of each pair, for this actually occurs sometimes in the seedling stage. This view seems, however, less likely than the view that the alternate arrangement arose as a result of the fusion of the two leaves of each pair; this would certainly best explain the dividing leaves, for each is merely retracing the steps taken in the past, and undoing the act of fusion in order to reproduce the original pair of leaves. This might well be caused by the pendulous habit of the tree causing the branches to grow in a more vertical direction than is normally the case; the distichous arrangement is probably the direct result of the oblique or horizontal direction of growth of the shoots; in the erect-growing first year's seedling the opposite-decussate type prevails. Meehan found that in *U. americana* some individuals exhibited opposite-decussate, others alternate phyllotaxis, and this from the earliest stage.

The phyllotaxis presented by many of the abnormal shoots of this elm suggests that after the production of two leaves by fission of a single leaf, one leaf of the pair becoming pushed over into an anterior or posterior position on the shoot, an internode becomes developed between the two leaves, all of which gives the impression that a $\frac{1}{3}$ phyllotaxis is being incompletely induced, and this may indeed be the case.

Loesener observed a plant of maize in which the leaves were in whorls of three instead of being distichously arranged.

There are thus at least three distinct types of forked or double leaves:

(1) Those which have no direct morphological significance, being comparable to a forked stem, as in ferns.

(2) Those which are due to fusion of two leaves, as in the case of *Lonicera thibetica* and Klein's case of *Weigelia.*

(3) Those which are due to fission and concerned

with a change in phyllotaxis, as in Labiatæ, and in the elm, *Buddleia*, etc.

Celakovsky points out that double leaves are the result of the strife waged during the ontogeny between the two tendencies, viz., towards division on the one hand, and towards fusion on the other.

It is obvious from what has gone before that no general law can be laid down to account for the origin of forked or double leaves. Each case must be decided on its own merits.

Coming to the consideration of terminal leaves we meet in these with a phenomenon which is in direct contradiction to the modern notion that leaves are always lateral appendages on an axis. Instances of normally terminal foliage-leaves and cotyledons have been already cited; other instances of foliage organs which are normally terminal are afforded by the stamen of *Najas* and the carpel of the "bulrush" (*Typha*), and the radially constructed* sterile sporophyll of the cone of *Encephalartos*. The modern view is that stamens and carpels are but modified foliage-leaves, so that in actuality there are plenty of instances of terminal foliar organs. The majority of present-day botanists hold the view, moreover, that the terminal position of the foliar organ, whether it be cotyledon, foliage-leaf, or sporophyll, is a secondary phenomenon, and that the lateral position on the axis is the original one, the growing stem-apex having always, from earliest times, topped the whole. This view should be regarded, however, as a fallacious and artificial one, based as it is on mere appearances, and not on sound data of comparative morphology. It is impossible to discuss the whole matter here. Allegiance to the "phyton-theory" of Gaudichaud, Schultz-Schultzenstein, Delpino, and Celakovsky, may merely be

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* Nearly all terminal foliar organs are radially constructed, at any rate in their external configuration. The leaf of *Gesnera Geroltiana*, cited by Morren, is an exception. On the other hand, radially-constructed leaves are often found in a lateral position, *e. g.*, peltate or pitcher-leaves of elm, lime, *Pelargonum*, etc.

reiterated, according to which the stem of all vascular plants is built up of a number of shoot-segments (phytons) and is in reality a sympodium in the sense that each leaf represents the termination of the stem, each new shoot-segment sprouting from it in a lateral position in the same way precisely as the young stem of *Juncus*, for example, is at first constituted.* It follows from this view that (with the exception of those foliar organs which have been secondarily derived from division of a single organ) the leaves of a shoot are primitively terminal structures and the lateral position is a purely secondary one.

Besides *Juncus*, we have, as Velenovsky points out, in Dicotyledons which in other respects exhibit Monocotyledonous features, viz., *Piper* and *Peperomia*, an instance in which the youngest stage of the seedling shows a complete absence of any stem, the first two or three foliage-leaves sprouting out of one another laterally, and at a point, in each case, some way above the base of the leaf-stalk. These actual facts of seedling organization refute the modern view that an axis is present at every stage of life, and that leaves are lateral appendages thereof. But this view may also be shown to be improbable by the following argument. If the Monocotyledonous structure has been derived by reduction from the Dicotyledonous type, a theory which is entirely bound up with the view that the stem is a primeval feature, then the completely stem-less organization of the seedlings of *Juncus* and Piperaceæ must be regarded as having been derived from that in which a stem is present, a view which, unless the phyton-theory be admitted, is obviously absurd, inasmuch as it involves the recognition of the phytonic structure in these plants, for, apart from the phyton-theory it cannot be imagined that at one end of the scale of development a stem

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* The facts of embryogeny in Bryophytes, Pteridophytes, and Phanerogams are essentially similar in all these groups, and support the view that the sporogonium is the primitive ancestor of the leaf, arising as it does from the same quadrants; hence the leaf is originally a terminal structure.

exists, and at the other end it is absent, although several foliage-leaves are present. But if, on the other hand, the anaphytic organization, such as we see it in the above seedlings, is primitive, the stages by which the Dicotyledonous type of organization (with such a marked contrast between stem and leaf) has been evolved are quite easy to follow. If the phyton-theory be held, then it is *à priori* conceivable that the Monocotyledonous type of organization has been derived by reduction from the Dicotyledonous one; but if it is admitted (as it is on this theory) that the organization exhibited by the above mentioned seedlings was once the primitive one for all Angiosperms, then it seems that by far the most plausible view is to regard the organization of these seedlings as primitive now rather than as representing an exact imitation (arrived at by the process of degeneration) of the primitive organization of the past. The majority of botanists hold that the seedling stages represent those of the phylogeny; why should an exception be made to this almost universally accepted rule in the case of the Monocotyledons? Moreover, one would never expect to see degeneration of embryonic and seedling structures as a universal feature for a whole class of otherwise perfectly organized plants. Monocotyledons are not degenerate.

Such arguments as the above have never been refuted by the upholders of the modern theory; they appear never even to have been thought of. Surely it would have been better to have taken all facts and arguments into consideration before setting forth such a tremendous and far-reaching generalisation as that Monocotyledons have been derived from Dicotyledons by reduction.

If what has been said above be true, there must probably reside within the plant a natural tendency to reassert, under certain conditions, the primitive terminal position of the leaf. And the cases of abnormal terminal leaves above cited may represent an expression of this tendency. The balance of the organism being partially upset, the innate primitive constitution of the shoot asserts itself owing to the absence of the normal restraining conditions of growth, and a terminal leaf, under one form or another, is the result. Hence we may have again to do with a case of reversion.

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ADVENTITIOUS LEAVES.

Adventitious leaves, or those which occur on organs, or parts of organs, where they are never normally produced, are very rare, very much more so than are adventitious stems and roots.

Goebel excised the growing point of some seedlings of *Cyclamen persicum*; this induced the formation of several leaves near the top of the tuberous hypocotyl; these leaves arose independently at different points on the circumference of the hypocotyl, a truly remarkable phenomenon, being a case of leaf-formation quite apart from the meristem of the stem apex (Pl. XXII, fig. 3).

But equally remarkable were the experiments made by Hildebrand on *Cyclamen Miliarakisii* and *C. creticum*. From the stalk of a cotyledon from which the lamina had been removed, sprouted four small stalked leaves in form exactly like the foliage-leaves. When the entire cotyledon was removed the adventitious leaf arose from the epicotyl.

Adventitious leaves occur on the foliage of *Begonia manicata*, *B. phyllomaniaca*, and others in the form of scale-like emergences which may occasionally appear as green leaves. That one leaf should bear another is surely an unheard of phenomenon! This case may be accounted for as follows: each of these scales may really represent the first-formed leaf of an arrested adventitious bud (these buds actually occur very frequently in *B. phyllomaniaca*). If we imagine the lateral buds ("bulbils") of *Lycopodium Selago* to become arrested after the formation of the first leaf (which always appears first before there is any sign of the rest of the bud), we should have a comparable example to what may have occurred in the case of these begonias. This explanation may possibly apply to the case of Goebel's cyclamen whose adventitious leaves may be the precocious formations of otherwise latent shoots; these are known to occur from time to time on the tubers of mature plants.

Ross describes remarkable formations having the character of clusters of tiny leaves with typical internal leaf-structure which arise adventitiously from the layer below the palisade-tissue in the neighbourhood of a vein on the upper side of the foliage-leaves of the Melastomaceous plants *Conostegia* and *Miconia.* They are due to the presence of the eelworm *Tylenchus* in the tissues of the leaf. These structures may be regarded as belonging to adventitious shoots which have not yet come into being. On the lower side of the leaf and arising from the hypodermal layer, he observed clusters of semi-leaf-like structures which he terms "galls," as their internal structure is not leaf-like. They may quite well be leaves in rudimentary form.

In *Aspidium angulare* var. Lang describes single leaves arising on the prothallus, either entirely alone or side by side with a stem-apex: another example of the same phenomenon.

All these facts of precocious and, therefore, dominant leaf-formation tend to support the phyton-theory.

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SUMMARY.

INTRODUCTION.

This work is not a mere descriptive tabulation of interesting and curious "freaks," but is intended as a contribution to the evolutionary origin of plant-organs.

Of these there are three categories only: root, stem, and leaf, although, in reality, the stem is non-existent, being composed of leaf-bases.

Of the four methods of morphological investigation, viz., the developmental, anatomical, comparative, and teratological, the last two are the only reliable ones.

All abnormalities are not reversions, for many are progressive in nature.

As regards the value of abnormalities for the elucidation of morphological problems, the opinion of botanists is divided. The present writer attaches great importance to teratological data for the interpretation of structures of doubtful nature, and cites leading authorities in support of this conclusion.

An attempt is made, wherever possible, to answer the question "why" an abnormal structure is present, as well as "how" it came about. All structures, whether normal or abnormal, are regarded as purposive rather than fortuitous in their origin. They are originated and maintained by the action of a regulative vital force, and not by mere chemico-physical energies. Hence, throughout the work, the dynamic teleological or vitalistic position is upheld as against the mechanistic or materialistic one.

FUNGI.

The subaërial portion of the plant in the higher forms tends to exhibit many of the same types of abnormalities as are met with in the vascular plants.

The phenomena described are: dichotomy; fasciation; proliferation; adventitious branching; the formation of a hymenium on the upper surface of the pileus of Agarics; and the formation of an inverted pileus in the same position, either congenitally or by invagination of the margins of the pileus; the occurrence of gills cyclically instead of radially arranged; fusion of fructifications; and the occurrence of a stipeless cap.

BRYOPHYTES.

Mosses and Liverworts are considered together.

In the sexual generation are described dichotomy, monopodial and sympodial branching, and proliferation of the shoot; suppression of internodes in branches; adventitious shoots occurring on the stem, leaf, thallus, inflorescence, and sporophyte; dichotomy and enlargement of the leaf, laminar enations; union of leaf-surfaces; and reduction of leaf-area.

The root or rhizoid and the protonema are considered together, as they are homologous and interchangeable structures; either may change one into the other. There are described supernumerary and adventitious rhizoids and protonemata on various organs of the plant. Apospory occurs, due to the formation of protonemata from sporogonial tissues, but it is not regarded as affording support to the theory of homologous alternation of generations. Fasciation, proliferation, and abbreviation of the inflorescence; metamorphosis of one sex into the other; hermaphroditism; and multiplication and reduction of the sexual organs are described.

In the sporophyte generation, the main abnormality is that of "double" sporogonia; others are: extra sets of peristome-teeth, hypertrophy of the apophysis, and cleistogamous capsules.

THE ROOT.

The following abnormalities are dealt with:

Branching, including the monopodial type, forking, and fasciation.

Fusion, post- and congenital.

Change of direction of growth; the primary cause of this resides in the habit and needs of the plant, the mechanism employed being the influence of gravity on the cell-contents, which gives the necessary stimulus for the movement.

Adventitious roots, occurring on roots, stems, leaves, floral organs, and prothalli.

THE STEM.

This includes the ordinary leafy stem and its branches, and the hypocotyl.

Under the main heading of Differentiation are grouped the following phenomena:

Fasciation: of this there are two main types: ordinary fasciation and ring-fasciation. The former consists of a multiple forking of the shoot, which may either be latent, *i. e.* without reaching external manifestation, resulting, in that case, in the ribbon- or fan-shaped shoot, or the apex divides, giving rise to a number of branches of equal rank. Ring-fasciation consists of an apical invagination (congenitally-formed) of the stem, thus giving rise to two concentrically-grouped sets of tissues, an external, normally-orientated, and an internal inversely-orientated set, an epidermis-lined central space being formed. The whole may subsequently become split up into two or more cylindric branches, whose point of union below is at the apex of the invagination. Fasciation is a variant of dichotomous branching. Dichotomy is defined as an apical division of the organ into two parts of equal rank, the text-book definition being discarded as inadequate. Dichotomy occurs as a *normal* feature in certain Palms.

The two main views as to the nature of fasciation, held by past authors, viz., the "fusion-theory," and the "expansion" theory, are discussed. The writer's "pleiotomy"-theory is regarded as alone adequate to explain the phenomenon.

The physiological causation is briefly touched on.

Proliferation: this is of two kinds, viz., median and axillary; the former concerns the main shoot, the latter the lateral branches. The phenomenon consists in an extension of the shoot beyond the limit of growth which is normal to it.

Under the main heading of Simplification are included the phenomena of suppression and fusion. Suppression of the main axis is the converse condition to that of proliferation of the same, and is due to internode-shortening and extinction. Suppression of axillary shoots results in an unbranched stem. Fusion of two or more shoots may be either post- or congenital; the latter is always between the main and an axillary shoot, giving rise to the phenomenon of an extra-axillary branch

All the phenomena of simplification are progressive and not reversionary.

The subject of Direction of Growth includes the change of direction which the stem or branches, or both, may assume during their growth. Here are considered: horizontal shoots, erect shoots, inverted shoots, and winding shoots. The majority of these changes are progressive in nature, but the vertical direction of growth of the ivy-shoot and of the rhizophore of *Selaginella* must be regarded as reversionary.

The reason why shoots grow in this or that direction must be sought for in their vital needs, the action of gravity being subsidiary and subsequent to these.

Adventitious shoots are described as occurring on roots, stems, leaves, in ovaries, and on prothalli. The prothallus-shoots constitute the phenomenon of *apo-*

gamy, and the adventitious prothalli occurring on the sporophylls of Ferns gives rise to *apospory;* both of these represent short cuts in the life-history, and can no more be regarded as constituting a support for the theory of homologous alternation of generations in Vascular Cryptogams, than can the occurrence of adventitious shoots on leaves be regarded as showing an identity in morphological nature between these two organs.

The whole series of adventitious shoots and adventitious prothalli stand on precisely the same footing, and must be understood and explained along the same lines. Such shoots are merely those which arise at a later period than their usual time, and out of their normal position.

The Leaf.

The German poet Goethe intuitively recognised the root-principle of modern comparative morphology when he regarded, in his 'Metamorphoses of Plants,' all leaves as variants of a typical leaf, though he missed the idea of their common evolutionary origin. Alex. Braun and Goebel are also cited in this connection.

Leaf-abnormalities are grouped under the main headings of Differentiation, Simplification, Adnation, and Change of Position.

Under "Differentiation" the following phenomena are described: Phyllody of Bracts; Reappearance of Bracts or Foliage-leaves; Sarcody of Scale-leaves; Phyllody of Scale-leaves; Phyllody of Tendrils; Phyllody of Thorns; Bracteody of Glands; Petalody of Scale-leaves; Staminody of Scale-leaves; Sporophyllody of Scale-leaves; Division of Simple Leaves, comprising lateral fission or laciniation and terminal fission or forking; with the exception of some cases due to depauperization and leaf-forking, the phenomena of leaf-division are regarded as reversionary in nature, for simplification or reduction have played a large *rôle* in the evolution of foliar organs; the two types of reversion met with are: (1) an increase in complexity of the leaf, and (2) an increase in number of the leaves; Rejuvenescence of Foliage (of reversionary nature).

The phenomena of Simplification are much rarer than those of Differentiation, for the changes involved are mostly of progressive nature, *i. e.* in the direction of evolution and not retrogressive. They include Squamody of Foliage-leaves; Pampinody of Foliage-leaves; Bracteody of Foliage-leaves; Petalody of Foliage-leaves; Sporophyllody of Foliage-leaves; Staminody of Foliage-leaves (probably reversionary); Carpellody of Foliage-leaves (possibly reversionary); Bracteody of Scale-leaves; Sepalody of Bracts; Staminody of Bracts; Carpellody of Bracts; Simplification of Foliage; Fusion of Cotyledons; Fusion of Foliage-leaves; Fusion of Scale-leaves; Fusion of Bracts; Suppression of Foliar Organs; Enations and Ascidia of Foliage-leaves, comprising (*a*) Ascidia or leaf-appendages, (*b*) Ascidia of the Entire Leaf, and (*c*) Laminar Enations; these are regarded as, in a sense, of reversionary nature; they probably represent (at least from one point of view) cases of incomplete facial fission of one leaf into two, or fusion of two leaves into one, as the case may be, *i. e.* the pitchers and enations of any given leaf are the imperfect manifestation in a superficial position of a second leaf.

Under Adnation is described that of the Foliage-leaf to Stem; of Foliage-leaf or Bract to Peduncle; of Foliage-leaf to Perianth-leaf. All these, of course, are progressive phenomena.

Under Change of Position are described and discussed the subject of Leaf-arrangement (Phyllotaxis). Cotyledons are first dealt with, and the phenomena of Syncotyly and Schizocotyly, *i. e.* fusion and division of cotyledons, described. As regards foliage-leaves which are *laterally*-placed (the usual case), there are four types of change in their position: (*a*) From Opposite-decussate to Whorled; (*b*) from Opposite-decussate to Scattered (Spiral); (*c*) from Scattered (Spiral) to Opposite-decussate; (*d*) from Dorsiventral to Radial Symmetry of the Shoot. *Terminal* leaves are next described, of which there are two kinds, viz., those formed of a single leaf, and those formed of a double leaf. Some cases of the transposition of Bracts are mentioned.

In the discussion of the subject of phyllotaxis, the spiral type is set forth as the primitive one, the best foundation for which view is afforded by the phyton-theory of Gaudichaud, Schultz-Schultzenstein, Celakovsky, and others, according to which each leaf-blade, morphologically and primitively, terminates the whole growth of the shoot, the succeeding one sprouting from it in a lateral position. The Monocotyledonous seedling and stem exhibit the primitive type, which is seen also in some Dicotyledons. The single cotyledon of the former is ancestral, from which the two cotyledons of the latter class have been derived by division. The leaf-arrangement in the vegetative stem of plants generally is apparently the result of the mean of two kinds of influence, viz., that emanating from above, representative of the more primitive type, and that coming from below in the cotyledonary region; the former influence makes for spiral, the latter for opposite phyllotaxis.

The origin of opposite leaves, normally or abnormally, is probably by two methods: (1) By fission of the single leaf at the node, just as in the case of the formation of the two cotyledons in Dicotyledons; (2) by the extreme shortening and extinction of alternate internodes. Alternate leaves also probably arise, normally or abnormally, in two ways: (1) By fusion of the two leaves of a pair; (2) by displacement of these. Forked leaves are due either to division (by far the commonest) or fusion, according to the character of the leaf-arrangement above and below. The *terminal* leaf, of which *normal* instances are cited, is held to be a primitive feature, as the phyton-theory indicates; from the facts of seedling-organization in the two great classes, it is argued that that of Monocotyledons is the most primitive.

Finally, Adventitious Leaves are treated of; these mostly arise as a result either of mutilation or other abnormal modes of stimulation.

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INDEX.

ADLARD AND SON, IMPR., LONDON AND DORKING.

ERRATUM.

P. 61, line 14, *for* apothecium *read* apophysis.

Plate 1

PLATE I.

Figs.

1. *Tricholoma grammopodium.* An inverted stipeless "cap" arising from the centre of the upper surface of the pileus. (Massee photo.) p. 28.

2. *Tricholoma sordida.* An inverted stiped "cap" on the upper surface of the pileus; it has been detached from the ground and carried up. pp. 20 & 27.

3, 4. *Armillaria mellea.* Fig. 3.—A fasciated specimen. Fig. 4.—A normal specimen. pp. 17, 18.

5. *Tricholoma sordida.* Formation of an alveolar hymenium on the upper surface of the pileus by invagination from the lower surface. p. 28.

PLATE I

Plate 2

PLATE II.

FIGS.

1, 2. *Lentinus lepideus.* Fig. 1.—A much-branched "fruit" caused by growing in the dark towards a weak light. p^1, rudimentary pileus; s^2, secondary stipes springing from its margin; s^3, tertiary stipe. Fig. 2.—A forked individual growing under similar conditions. (After Buller.) p. 16.

3. *Agaricus Aueri.* Multiple dichotomy of a "fruit" grown in the dark, each branch bearing a minute cap at its tip. (After De Seynes.) pp. 16 & 17.

4. *Polyporus squamosus.* Multiple forking of a "fruit" grown in the dark. (After Buller.) p. 17.

5. *Lentinus holumbrinus.* Five stalked "fruits" growing from the top of the pileus. (After De Seynes.) p. 18.

6. *Lentinus lepideus.* Elongation of the stipe caused by growth in the dark; no cap has been formed. (After Buller.) p. 20.

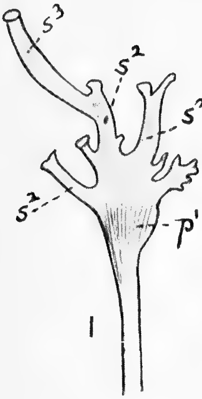
7. *Aleuria vesiculosa* (*Peziza*). Proliferation of two "cups" and a rudiment of a third within the normal one (longitudinal section). (After Morot.) p. 19.

8. *Lactarius torminosus.* A normally orientated stiped "cap" springing from the centre of an inverted stipeless "cap." (After Morot.) p. 21.

9. *Agaricus nanus.* Adventitious formation of tiny stiped "fruits" near the base of the primary stipe. (After De Seynes.) p. 23.

10. *Coprinus stercorarius.* Four generations (1–4) of "fructifications" formed as the result of excising the pileus at every stage of growth. Adventitious mycelium formed at regions of excision. (After Brefeld.) p. 23.

11, 12. *Tubaria furfuracea.* Fig. 11.—An agaric showing a morchelloid hymenium on the upper surface of the pileus. (G. S. Saunders.) p. 25. Fig. 12.—Another example of the same. (After W. G. Smith.) p. 25.



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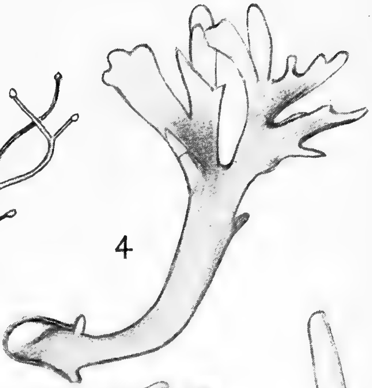

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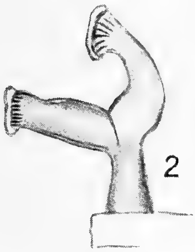

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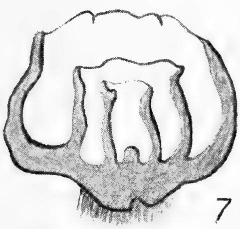

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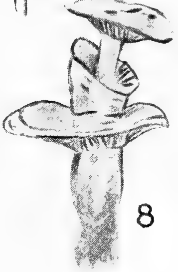

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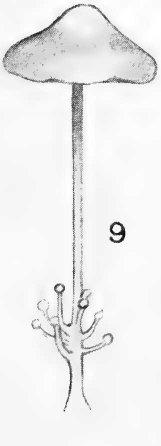

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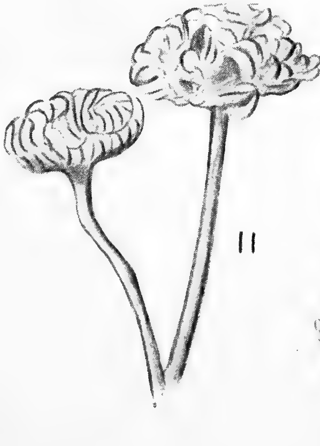

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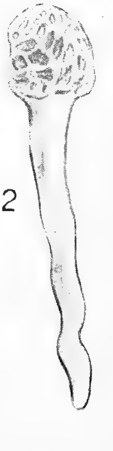

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Plate 3

PLATE III.

Figs.

1\. *Schistostega* (Moss). A dichotomously-branched stem of a male plant. (After Hagen.) p. 41.

2\. *Andreæa nivalis* var. (Moss). A leaf showing unequal dichotomy. (After Györrfy.) p. 48.

3, 4. *Hypnum serpens* (Moss). Fig. 3.—A protonema-thread springing from the cut end of a piece of the seta. (After Pringsheim.) p. 53. Fig. 4.—A protonema-thread arising from the single layer of the middle cortex of the seta. (After Pringsheim.) p. 53.

5\. *Molendoa Hornschuchiana* (Moss). An endorhizoid (*r*) growing from the foot of the seta through the tissues of the gametophyte. (After Györrfy.) p. 54.

6\. *Bryum pendulum* (Moss). "Podosyncarpy"; one half of the double capsule fully developed, the other half (*x*) abortive. (After Györrfy.) p. 58.

PLATE III

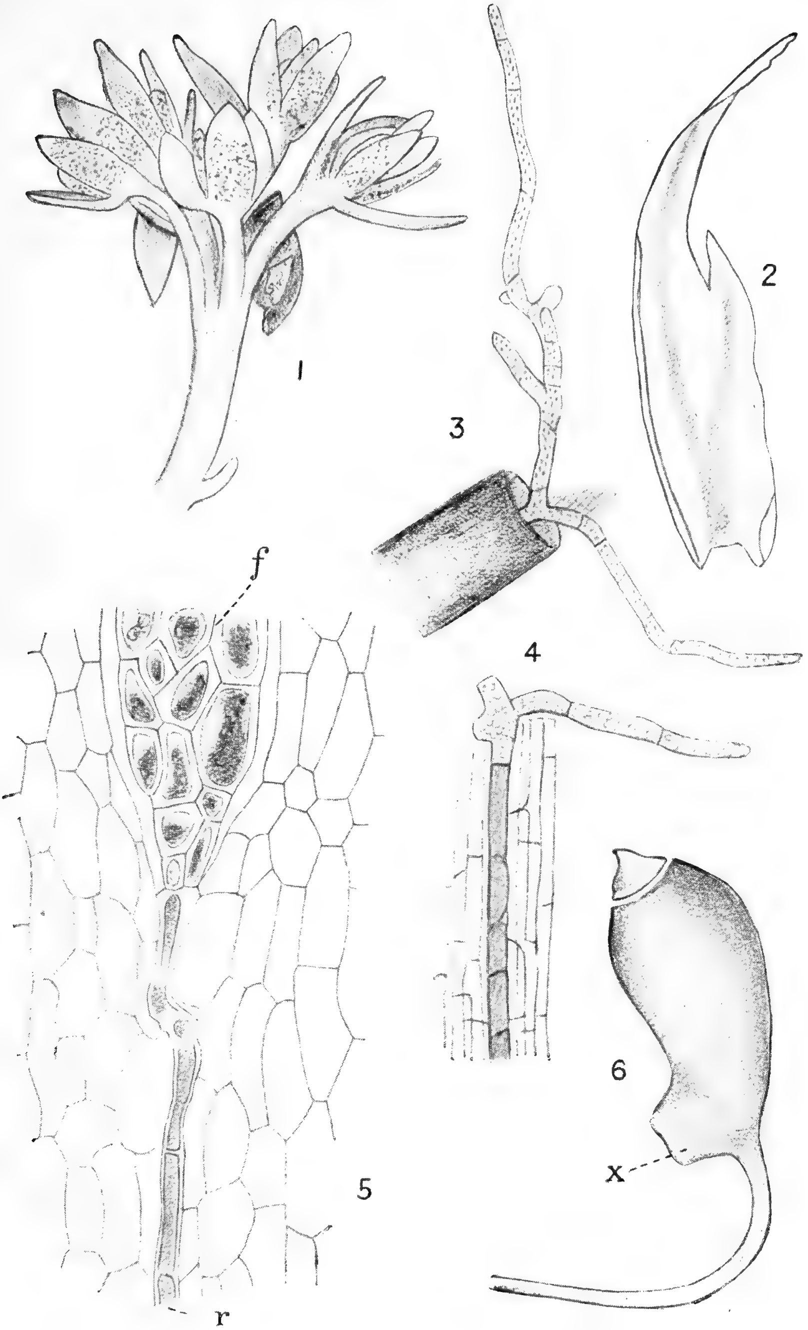


Plate 4

PLATE IV.

FIG.

1. *Ptilium crista-castrensis* (Moss). A shoot showing sympodial growth due to a lateral branch continuing the terminal growth of the main shoot after its apex has been excised at *v*. (After Schoenau.) p. 42.
2. *Blyttia Lyellii* (Liverwort). A portion of the thallus-wing with adventitious shoots of various ages springing from the surface. (After Goebel.) p. 43.
3. *Lunularia vulgaris* (Liverwort). *a,* a portion of the thallus with adventitious shoots springing from the cut edge of the apical end; *b,* shoots sprouting from the stalk of the inflorescence; *c,* a shoot sprouting from the lower side of the disc. (After Vöchting.) pp. 44 & 46.
4. *Mnium undulatum* (Moss). A plant, laid horizontally on the moist ground, giving rise to vertical lateral branches. (After Schoenau.) p. 42.
5. *Orthotrichum Lyellii* (Moss). A protonema changing into a rhizoid (*r*). (After Schimper, in part.) p. 50.
6. *Preissia quadrata* (Liverwort). *a,* a fasciated archegoniophore; *b,* normal archegoniophore. (After Coker.) p. 54.
7. *Buxbaumia viridis* (Moss). A double capsule with two distinct setæ springing from a single "vaginula." (After Györrfy.) p. 59.
8. *Bryum argenteum* (Moss). A double capsule caused by an insect-bite at the apex during the young stage. (After Mönkemeyer.) p. 59.
9. *Marchantia polymorpha* (Liverwort). Three rhizoids growing one within the other; the innermost tertiary one is in a young stage. (After Kny.) p. 50.

PLATE IV

Plate 5

PLATE V.

Figs.

1, 2. *Hedera Helix* (Ivy). Fig. 1.—A shoot bearing both forked and fasciated roots. Fig. 2.—A fasciated root (enlarged from fig. 1). (Original.) p. 68.

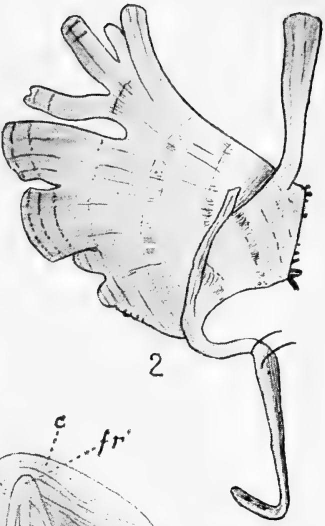
3 (*a* & *b*). *Phaseolus vulgaris* (Kidney Bean). Fasciated lateral roots (fr^1) induced by excision of the radicle. *pl*, plumule; *c*, cotyledons; *hyp*, hypocotyl. (Original.) p. 70.

4. *Vanilla planifolia*. Lateral roots arising from, and growing in the same direction as, the main aërial root as a result of the removal of its apex. (After Goebel.) p. 67.

5. *Selaginella Kraussiana*. Adventitious roots growing from the cut end of a leafy stem. (After Bruchmann.) p. 75.

PLATE V


1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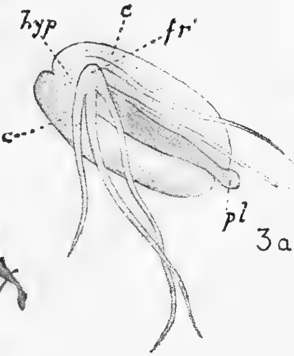

3a


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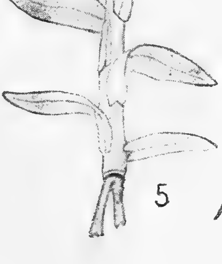
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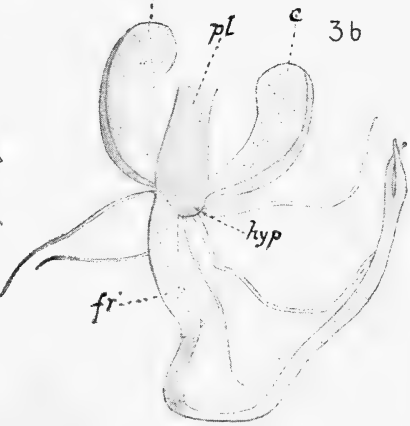


3b

Plate 6

PLATE VI.

Fig.

1 (*a* & *b*). *Cheiranthus Cheiri* (Wall-flower). Fasciated stems showing the commencement of winding growth. p. 88.

2. *Asparagus plumosus.* A fasciated shoot in which winding growth is absent. p. 85.

PLATE VI

Plate 7

PLATE VII.

FIG.

1. *Asparagus officinalis* (Garden Asparagus). A fasciated stem showing winding growth. (Massee photo.) p. 88.
2. *Pinus Pinea* (Stone Pine). A proliferated short-shoot, the two needles of which occupy a lateral position. *ls*, portion of long-shoot. (Saxton photo.) p. 102.
3. *Allium Cepa* (Onion). Axillary branches, in the form of bulblets, surrounding the parent bulb. p. 112.

PLATE VII

1

2

3

Plate 8

PLATE VIII.

Fig.

1. *Selaginella inæqualifolia.* Shoots bearing both normal and proliferated rhizophores (*rh*). p. 106.

Plate 9

PLATE IX.

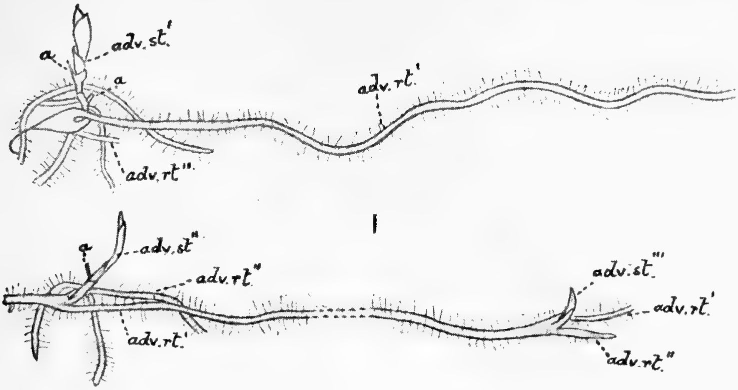
Figs.

1, 2. *Listera cordata* (Lesser Twayblade). Fig. 1.—Adventitious shoots (*adv. st.*) growing from a root. *adv. rt.*, adventitious roots from the shoot. (After Brundin.) pp. 127–128. Fig. 2.—Longitudinal section of tip of root, showing an adventitious shoot (*adv. st.*) growing out. *Adv. rt.*, an adventitious root from the shoot; *l*, the first leaves; *rc*, the root-cap. (After Brundin.) pp. 127–128.

3. *Drosera rotundifolia* (Sundew). Adventitious plants sprouting from the upper surface of a leaf. (After Nitschke.) p. 132.

4. *Eremostachys laciniata* (Desert-Rod). Twin-seedlings united at the primary node; the two cotyledons of each are fused together (1 + 2). (Original.) p. 94.

5. *Ulmus campestris* (English Elm). Adventitious shoots growing on a root. (After Duhamel.) p. 127.


a
adv.st'
a
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a
adv.st''
adv.rt''
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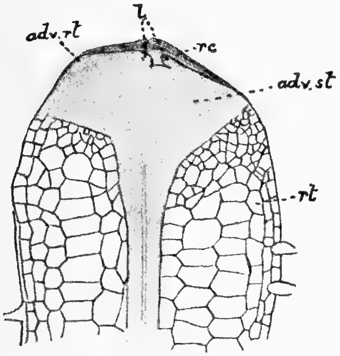
adv.rt''

1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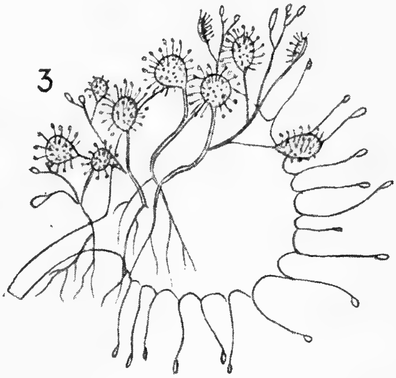
2



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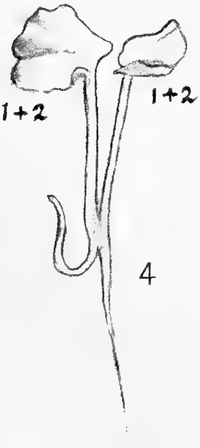
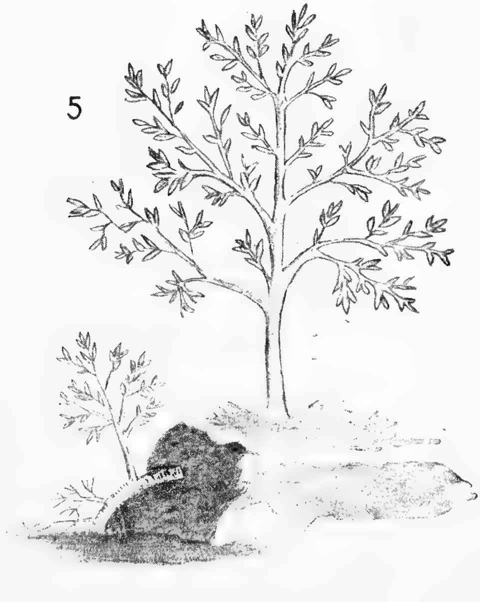

1+2
1+2

4



5

Plate 10

PLATE X.

Ornithogalum lacteum (Chinkerinchee). Adventitious bulblets sprouting from the veins of the upper surface of the leaf. (Raffill photo.) p. 135.

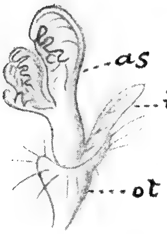
Plate 11

PLATE XI.

FIG.

1. *Sisymbrium Alliaria* (Garlic-Mustard). An ovular leaflet bearing an adventitious shoot. (After Celakovsky). *as,* adventitious shoot; *it,* inner integument; *ot,* outer integument. p. 138.
2. *Polystichum aculeatum* (Prickly Shield-fern). A sporophyte apogamously produced on a prothallus. (After Lang.) p. 140.
3. *Athyrium Filix-fœmina* var. *clarissima.* Prothalli sprouting from the sorus of a leaf (apospory). *anth,* antheridium; *arch,* archegonium; *pr,* prothallus; *pl,* pinnule. (After Bower.) p. 141.
4. *Scolopendrium vulgare* (Hart's-tongue). A rudimentary adventitious shoot growing out of an archegonium. *sp,* sporangium. (After Lang.) p. 140.
5. *Nephrodium pseudo-mas* var. *cristata.* Apogamous transition from prothallus to sporophyte, and subsequent aposporous transition to prothallus at apex and margins of leaf. *pr,* prothallus; *sph,* sporophyte. (From Bower, after Lang.) p. 145.

PLATE XI



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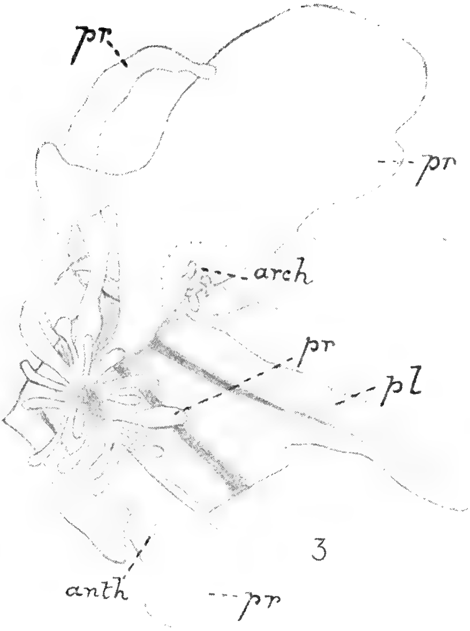

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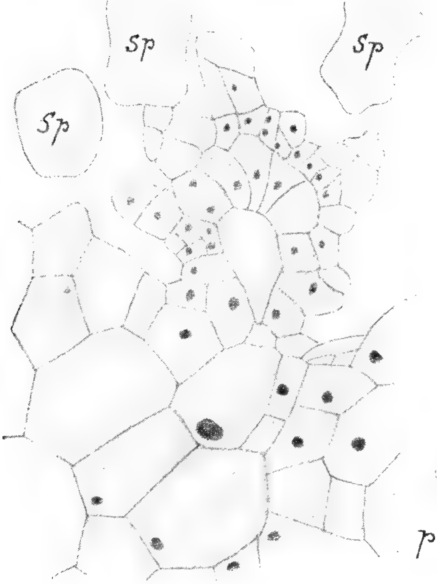

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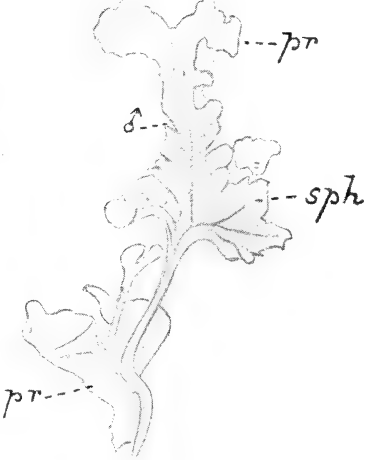


Plate 12

PLATE XII.

Plantago major (Great Plantain). Three spikes, showing many of the bracts developed as foliage-leaves. (J. Hutchinson photo.) p. 153.

PLATE XII

Plate 13

PLATE XIII.

FIGS.

1. *Lilium tigrinum* var. *Fortunei* (Tiger Lily). Transformation of a bulbil into a flower. 1 *a*, natural condition; 1 *b*, with the two outermost bulbil-scales removed, and the others laid open, showing the swollen bases of the perianth-leaves; 1 *c*, andrœcium, showing a petaloid stamen (*bst*) with a swollen base; 1 *d*, diagram of the flower. *bl*, bulbil-scales; *bp*, transition between bulbil-scales and perianth-leaves. (Miss M. Smith.) pp. 160–161, 163.

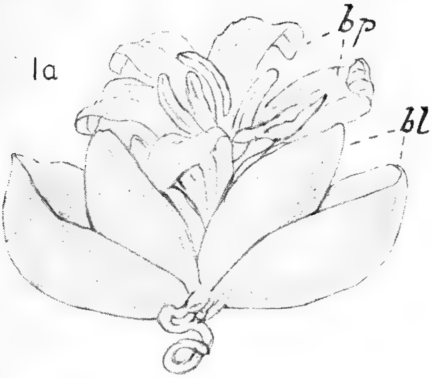
2. *Crocus*. 2 *a*, foliage-leaf bearing a stigma at its apex; 2 *b*, scale-leaf or bract bearing a stigma at its apex. (After Lutz.) p. 187.

3. *Marsilia hirsuta*. Two out of the four leaflets of a foliage-leaf changed into "fruits." (After Büsgen.) p. 185.

4, 5. *Gingko biloba* (Maidenhair Tree). Fig. 4.—Foliage-leaves (*a, b, c*) bearing anthers (*an*). (After Fujii.) p. 186. Fig. 5.—Foliage-leaf bearing an ovule (*ov*). (After Fujii.) p. 186.

6. *Picea nigra* (Black-leaved Spruce). A bract (*b*) of the female cone bearing ovules on the dorsal side. *ss*, seminiferous scale. (After Œrsted.) p. 189.

PLATE XIII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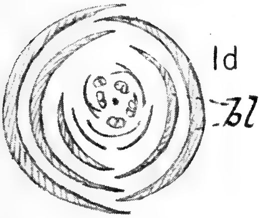
2a


2b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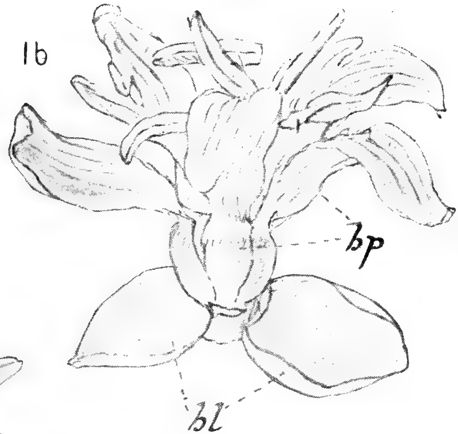
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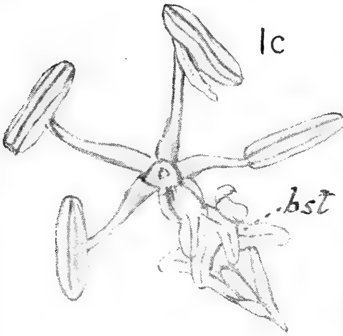
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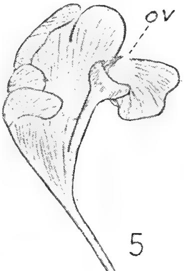
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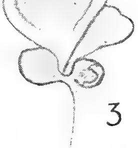
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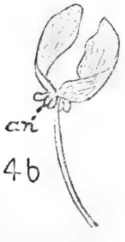
4a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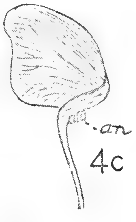
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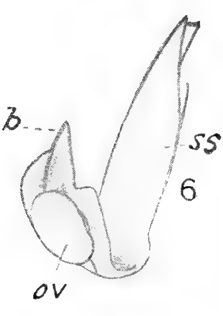
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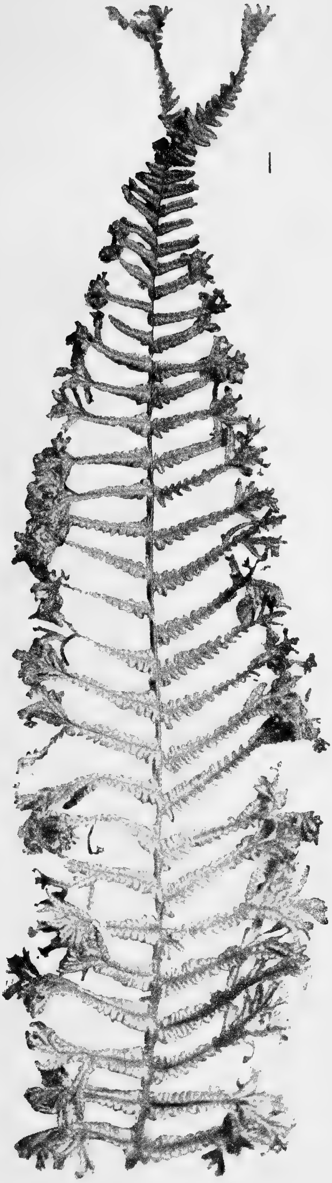
Plate 14

PLATE XIV.

Fig.

1. *Nephrodium Filix-mas* (Male Fern). A forked frond showing both terminal and lateral cresting. pp. 168, 171.
2. *Pinus Thunbergii.* Terminal portion of a shoot, showing the recurved fleshy leaves in the upper part. (Mingay photo.) p. 192.

PLATE XIV



1

2

Plate 15

PLATE XV.

FIGS.

1. *Trifolium repens* (Dutch Clover). A plant with numerous leaves producing four leaflets. (L. A. Boodle photo.) p. 170.

2, 3. *Brassica oleracea* (Cabbage). Fig. 2.—An ascidium (pitcher) growing from the upper surface of the leaf. p. 196. Fig. 3.—A "hypoascidium," representing an entire leaf. p. 198.

PLATE XV


1


2


3

Plate 16

PLATE XVI.

Figs.

1. *Cochlearia Armoracia* (Horse-radish). A laciniate leaf. (J. Hutchinson photo.) p. 163.

2, 3. *Thuja occidentalis* (Arbor-vitæ). Fig. 2.—A twig showing the adult foliage. (Mingay photo.) p. 176. Fig. 3.—A twig showing the juvenile foliage (“*Retinospora ericoides*”). (Mingay photo.) p. 176.

4. *Pinus monophylla*. A short-shoot showing the reappearance of the normally-suppressed second needle. pp. 156, 222–223.

PLATE XVI


2


1


3


4

Plate 17

PLATE XVII.

Fig.

1. *Codiæum variegatum* ("Croton"). Leaf with a long-stalked ascidial outgrowth from its lower surface. (Original.) p. 198.
2. *Brassica oleracea* (Cabbage). Two "pitchers," one sessile and the other long-stalked, springing from the upper surface of a leaf. *ls*, lower surface; *us*, upper surface. (Original.) p. 196.
3. *Richardia Elliottiana* (Yellow Arum Lily). A foliage-leaf partially transformed into a bract (spathe), and closely approximated to the normal spathe. (G. S. Saunders.) p. 184.
4. *Ficus benghalensis* (species of Fig). A leaf having a basal pocket on its lower side, constituting a "hypo-ascidium." *ls*, lower side; *us*, upper side. (Original.) pp. 198–199.
5. *Pelargonium zonale* ("Geranium"). A pitcher-shaped leaf ("epiascidium") bearing a small secondary "pitcher" on its lower surface. (Original.) p. 199.

PLATE XVII

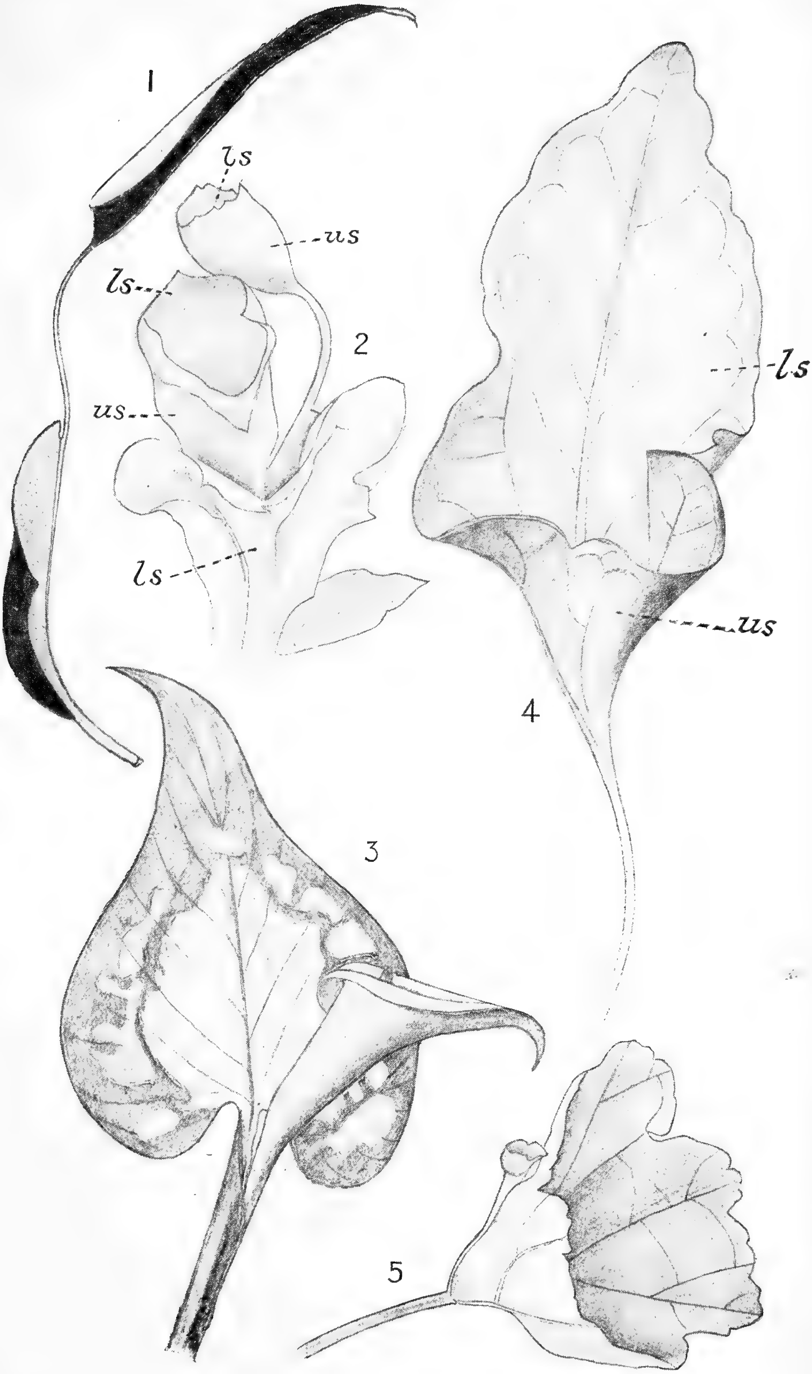


Plate 18

PLATE XVIII.

Saxifraga ligulata. Leaves showing formation of basal pockets and of laminar outgrowths from the midrib. (Smith photo.) pp. 199, 201.

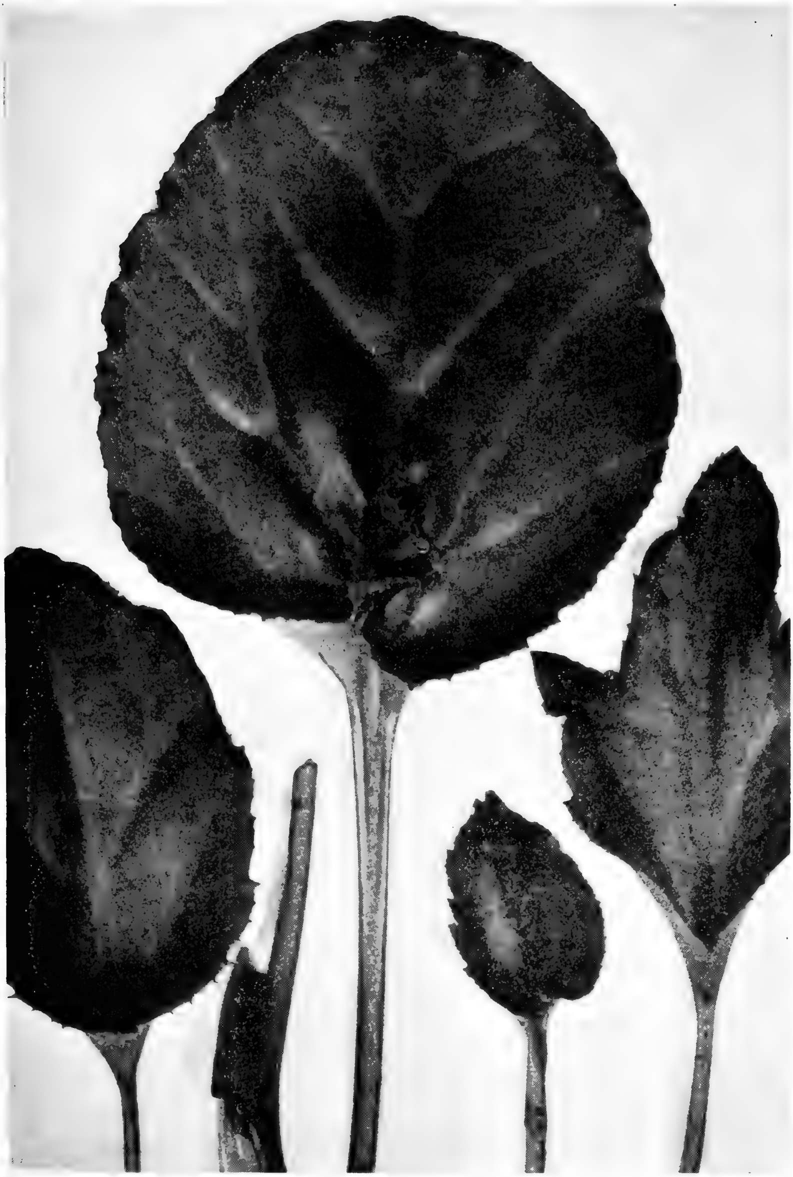


Plate 19

PLATE XIX.

Fig.

1. *Lonicera conjugalis* (species of Honeysuckle). Ascidium springing from the lower surface of the leaf and representing its greater part. 1 *a.*, front view. 1 *b.*, side view. *ls*, lower surface of leaf; *us*, upper surface. (Original.) p. 197.
2. *Phlox paniculata.* Naked midrib borne on lower surface of leaf. 2 *a.* front view. 2 *b.* side view. (Original.) p. 198.
3. Syncotyly. 3 *a.* *Eremostachys laciniata* (Desert-Rod). Normal seedling. 3 *b.* Abnormal seedling of the same. (Original.) 3 *c.* *Salvia amplexicaulis* (species of Sage). (Original.) 3 *d.* *Mercurialis annua* (Annual Dog's Mercury). (After De Vries.) 3 *e.* *Raphanus Raphanistrum* (Jointed Charlock.) Cotyledons united by both margins. (After De Vries.) pp. 214–215.
4. Schizocotyly. *Acer Pseudo-platanus* (Sycamore). Seedlings. 4 *a.* One of the cotyledons forked. 4 *b.* A further stage, in which three cotyledons are formed; of the three corresponding plumular leaves one is an ascidium, and is inserted lower on the axis than the other two. 4 *c.* Final stage, in which four cotyledons are formed. (All original.) p. 215.

PLATE XIX

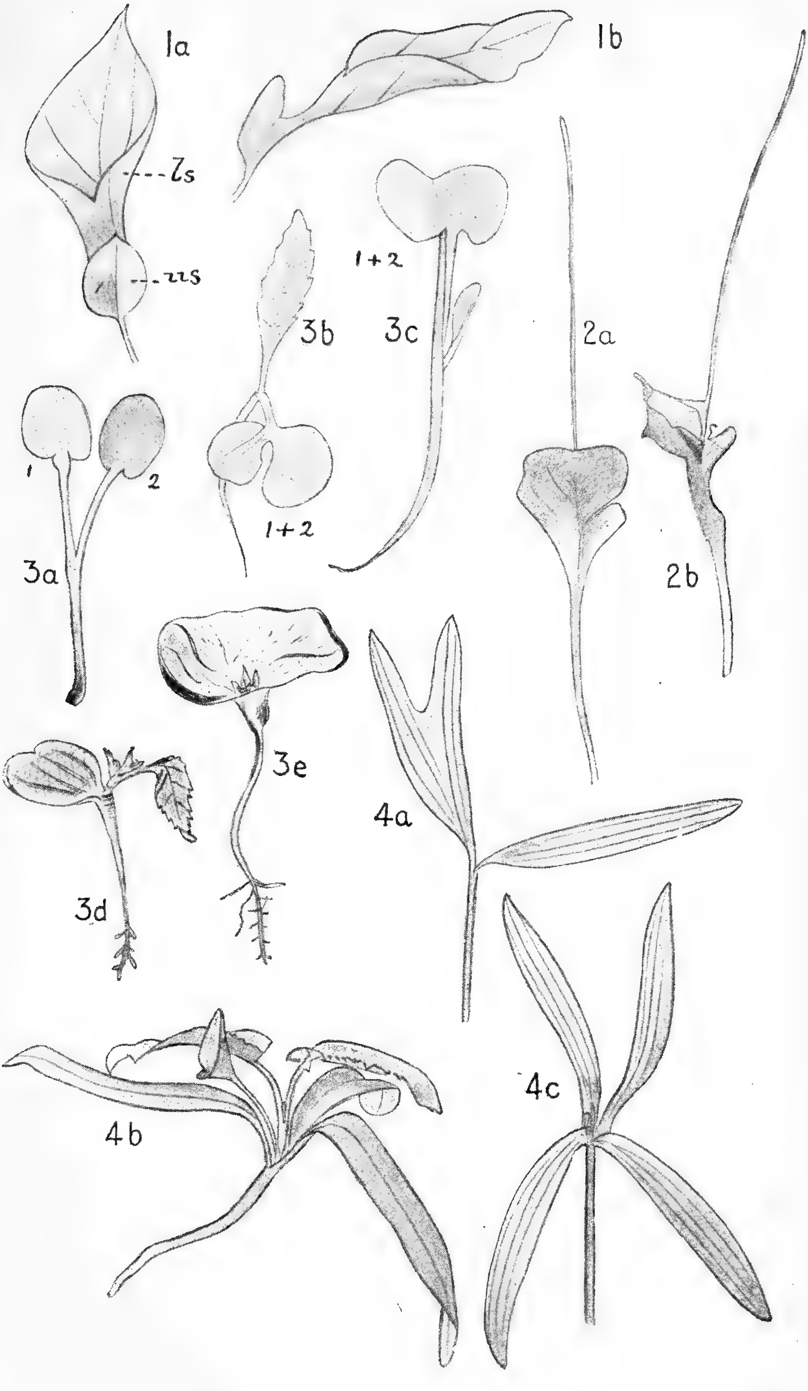


Plate 20

PLATE XX.

Lonicera thibetica (Tibetan Honeysuckle). Shoots showing incomplete changes from the normal opposite-decussate phyllotaxis to the shorter and scattered arrangement. pp. 216–218.

Plate 21

PLATE XXI.

Dianthus Caryophyllus var. (Carnation). Torsion of stem caused by reversion of opposite-decussate to spiral phyllotaxis, which is shown on the terminal bud (*b*). (Smith photo.) p. 219.

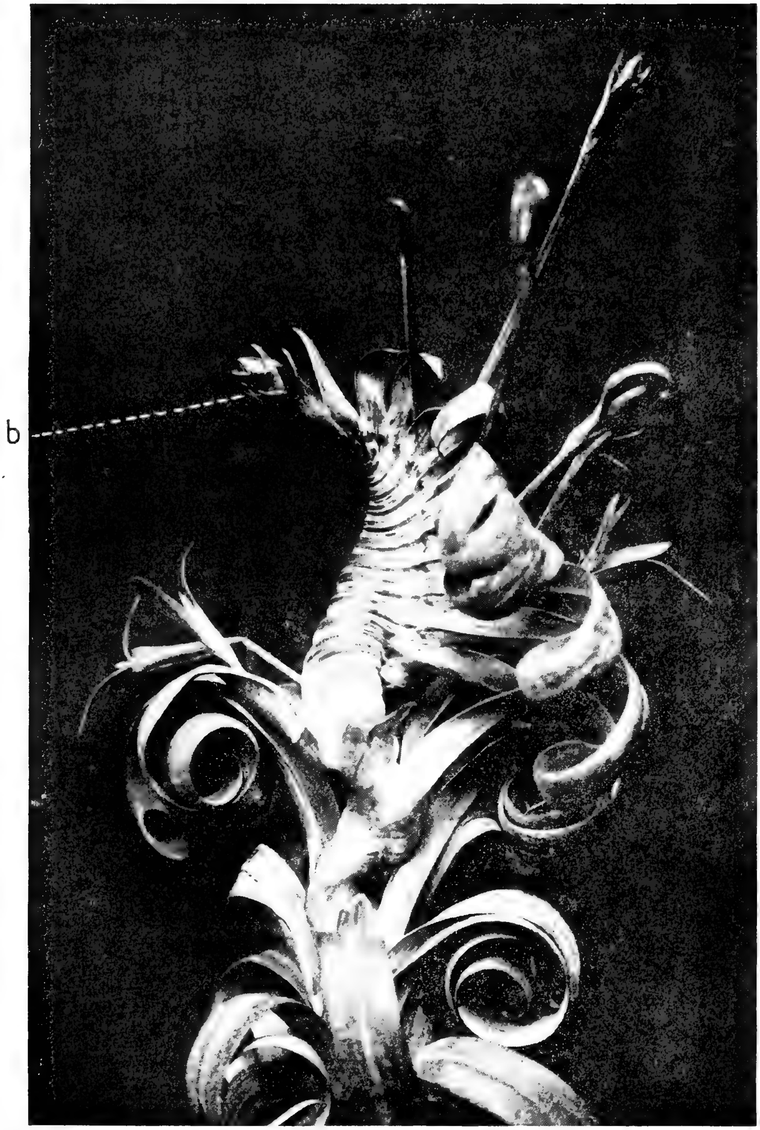
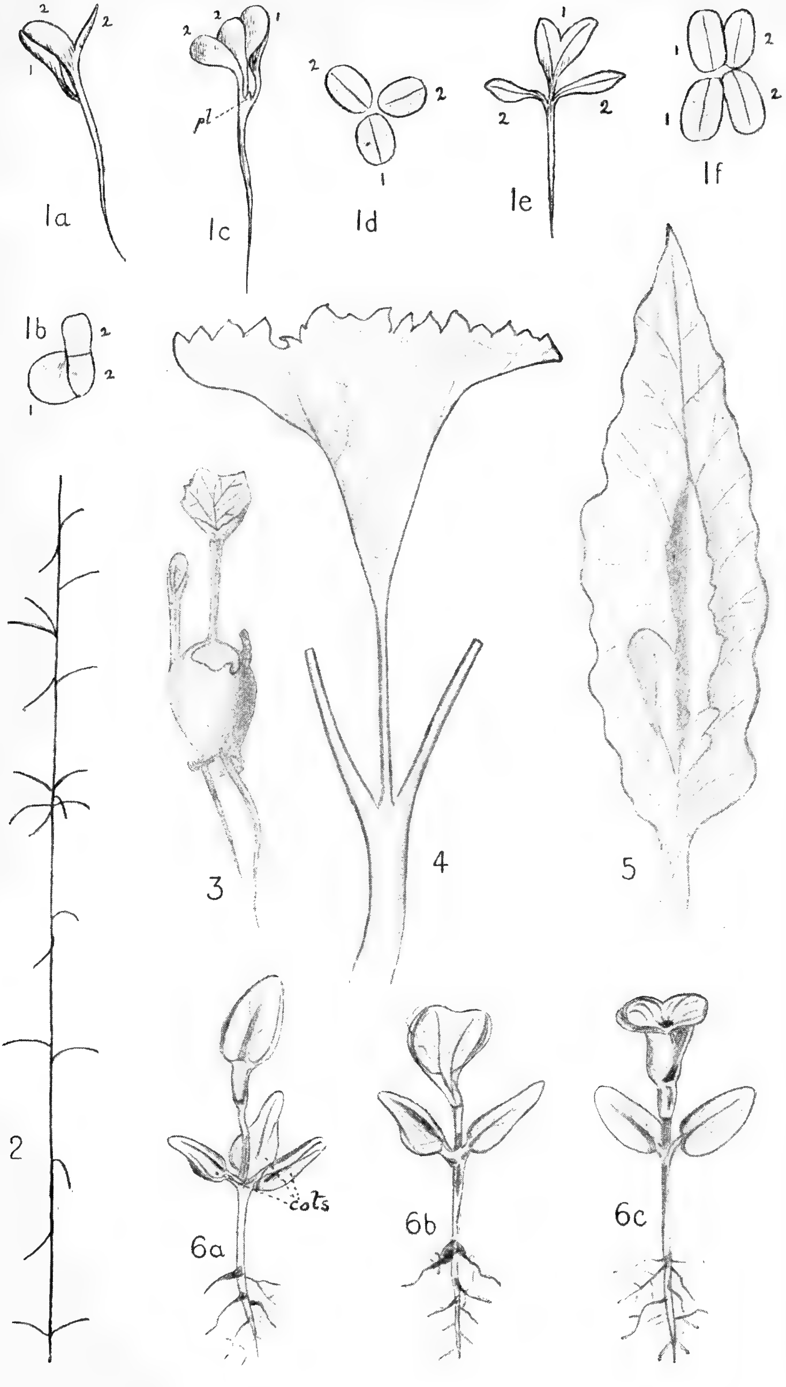

b

Plate 22

PLATE XXII.

Fig.

1. *Cheiranthus Cheiri* (Wallflower). Showing changes in the production of three to four cotyledons (see text for description). (Original.) pp. 215–216.
2. *Buddleia Hemsleyana.* Shoot showing incomplete change from the normal opposite-decussate phyllotaxis to the whorled and scattered arrangement (diagrammatic). (Original). pp. 217–218.
3. *Cyclamen persicum* (Sow-bread). Adventitious leaves on hypocotyl; apex of seedling excised. (After Goebel.) p. 244.
4. *Marrubium vulgare* (Horehound). Terminal double-leaf formed by union of leaves of uppermost pair. (Original.) p. 226.
5. *Phlox paniculata.* Laminar enations from upper surface. (Original.) p. 201.
6. *Antirrhinum majus* (Snapdragon). Three seedlings (*a*, *b*, and *c*) each showing a distinct form of terminal double-leaf. (After De Vries.) pp. 225–226.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1a
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1c
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1d
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1f
1b
2
2
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2
3
4
5
cots
6a
6b
6c

Plate 23

PLATE XXIII.

Buddleia Hemsleyana. Shoot showing terminal leaf with basal pocket. pp. 223–224.

Plate 24

PLATE XXIV.

Buddleia Hemsleyana. Terminal double-leaf due to union of leaves of the uppermost pair by their upper surfaces. On the left is the displaced terminal portion of the shoot. pp. 224–225.

Plate 25

PLATE XXV.

Buddleia Hemsleyana. Leaves of the uppermost pair united by the midribs of their lower surfaces. p. 225.

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