THE CONCEPT OF VESTIGIAL ORGANS AND THE VASCULAR CRYPTOGAMS

By Dr. T. S. MAHABALE

(Gujarat College, Ahmedabad)

THE body of a plant is a complex organization made up of parts working together towards the common goal of maintaining its life. Some of these parts are concerned with the vital functions of absorption, assimilation and reproduction and others are there merely to help these. A few others do not undergo full development and are in no way concerned with the vital physiological processes and as such are quite useless. Such imperfectly developed parts in the body of an organism, in no way concerned with vital functions, "bearing a plain stamp of inutility" are called the vestigial organs. They are known to occur in many plants and are inherited with the same regularity with which the vital ones are inherited. But being in no way concerned with the essential process in the plant-life they seldom undergo modifications as do the other parts such as leaf or stem in response to the external stimuli acting on them. In fact they behave in this respect, in a manner quite opposite to that of the latter. Whereas with the passage of time the essential organs get modified according to the conditions under which they live, these organs get arrested or degenerated. Despite this fact they preserve their original character, though in a reduced form, in a very remarkable manner, and in course of time become "the unperished symbols of great antiquity". Viewed in this light the body of a plant is a bundle of some useful and some useless parts.

The form of such antic parts is often very simple, and therefore, systematists find it easy to trace their homology. In doing so they safely disregard the physiologist's warning that they are quite useless or ignore the anatomist's conviction that they are too simple, and use them in phylogenetic speculations. The number of such useless parts in the body of a plant is generally very small, although in stray instances it is so large as to give an impression that the whole body of the organism is a museum of such relict parts, *e.g.*, that of King-crab, *Limulus* in animals or that of *Welwitzia* in plants in which practically every degenerate part has some past history to proclaim.

As pointed out by Darwin[1] (1888), according to the earlier theories of 'Genesis' such parts found no satisfactory explanation. They were supposed to be present in the body of an organism either "to complete the scheme of Nature" or to "keep up the relations of symmetry" which they often did not. But according to Darwin's theory of descent through variations and Natural selection, they afforded another line of positive evidence in support of his theory. Ernst Hækel[2] (1886), Darwin[3] (1888), Goebel[4] (1900), Bower,[5,6] (1901, 1935), Jeffrey[7] (1917), Sahni[8,9] (1923, 1925), Browne[10] (1927) and others have used these structures in support of their views on certain problems in plant morphology; but on the whole, attempts at presenting them in a connected

manner have been very few in botanical literature. The reasons for this are not far to seek. The examples of such wasteful heritage are far more numerous in animals than in plants. For example, in the body of man alone, anatomists have enumerated a few hundreds of such vestigial organs such as the rudimentary stalk of the pineal body in his brain, the nictitating membrane in the eye, seven useless muscles never called upon to move his ears, and a good many others in the neck to hold his head down, the embryonic tail of commensurable dimensions in the third week of conception, not to mention the vermiform appendage, wisdom teeth cut at later age, etc. A plant has no such array of useless parts. The fixity of life means a rigid discipline. It means no scope for ambulation, less scope for speciation, and hence for acquiring new organs to master the new haunts of life. Whatever organs it has, have to be used to the best possible advantage, and that too if possible for purposes more than one. A plant, therefore, can hardly be extravagant or over-exuberant in its expression of parts, much less in the expression of its useless parts. Secondly, by far the most important process in the life of the plant is the process of photosynthesis. The law of surface expansion is very important here. More the surface exposed, better it is for the plant ; and to do that effectively many plants develop a diffuse form quickly. In attaining it some of the developmental stages are simply passed over in ontogeny and others are deleted. In doing so, however, each one of the innumerable growing points of a plant repeats the story of the development of the embryonic shoot on a miniature scale, and to quote Sahni (1925, p. 204), "in both space and time". Generally there is a tendency to delete obsolete parts : and the parts that succeed show a serial homology. For example, the first embryonic leaf is generally simple in the sporelings of many ferns such as *Osmunda* or *Marsilia* but becomes compound later after having passed through a series of transitional forms (see Bower,[11] 1923, pp. 87 and 93). In the sporelings of *Botrychium virginianum* and *Helminthostachys zeylanica*, however, the cotyledon is compound and trifoliate *ab initio*. The seedlings of some other ferns also omit the bifoliate stage like *Botrychium* and *Helminthostachys*. But despite such examples of rapid development involving the deletion of parts one is surprised to find that the vestigial organs occur in almost all the groups of plants, *e.g.*, the auxiliary cells in some red algæ, the suffultory cells in some species of *Bulbochœte*, the spermatia in many rust fungi, the paraphyses in mosses, the amphigastria, perigynia and perianth in some liverworts, the annulus in equiseta, the ligule in lycopods and selaginella, the aphebieæ in certain ferns, the stigma

in the flowers of *Welwitzia*, the papillæ representing a stamen or a pistil in flowers of angiosperms, the suppressed flowers in the spikelets of grasses, etc. These will suffice to show that the formation of vestigial organs is a phenomenon of very wide occurrence throughout the rubric of the plant kingdom. The present paper, however, deals with the vestigial organs of the vascular cryptogams mainly, as these plants constitute a compact and archaic group possessing some striking examples of such organs.

SOME CHARACTERISTICS OF THE VESTIGIAL ORGANS

From what has been said above, it will be seen that the two important features of the vestigial organs are the simplicity of their structure and uselessness. The former is often quite obvious, but the latter is not easy to prove in many cases. Theoretically it is easy to conceive of some organs as useful and others as useless; but even then it is necessary to remember that those organs that are supposed to be useless now, are believed to have been useful in some remote past in the ancestors of plants which possess them to-day. In other words, their present vestigial state only indicates the negative extreme to which they have been driven from a state of usefulness through the operation of time and environment: and, therefore, it should always be possible to find several intergradations between these two extremes at any time in the history of the plant kingdom. And so it is. There are thoroughly vestigial organs, dwindling organs, arrested or aborted organs, atrofied organs, conservative yet simple organs, rudimentary organs, nascent organs, ephemeral organs, a long series of more or less useless organs. In each one of these the emphasis is not only on their simple character but also on their doubtful utility; and to reach a level of uselessness from one of utility, there must have been a long process, involving in the majority of cases millions and millions of years, if not billions. At any rate a consideration of the element of time in the history of these organs is of paramount importance as it is undoubtedly so in the case of those structures with which a palæobotanist deals. When this fact is realized much of the controversy over the relative importance of these organs in morphological discussions loses its sting; as in one's eagerness to prove that a particular organ is vestigial in such and such a group, one is likely to emphasise either its simplicity or its inutility or its antiquity. But such a unilateral emphasis on any one of these features is likely to lead to erroneous conclusions. What matters most in their consideration is probably the relative level of vestigiation shown by the organ concerned at any particular stage in the history of the plant both in the cycles of ontogeny as well as phylogeny. Thus an organ may develop only in embryological condition and may become vestigial in adult state. Some other organs may persist in adult condition but only in an arrested or atrophied form. Still others may remain nascent for all the time to come under normal conditions but under certain abnormal conditions may resume their original form. A few others may adapt themselves to some secondary function and look quite odd, e.g., a root-like organ serving as a

stem, e.g., protocorm of *Lycopodium*, or a stem-like organ serving as a root, e.g., the rhizophore of *Selaginella*. From the phylogenetic point of view also, these must be carefully considered, as their occurrence is sometimes confined to the limits of individual plant, sometimes to those of a class. When they occur in two allied groups, we get good examples of recapitulation. Their testimony in phylogeny, therefore, has to be taken with a certain amount of scepticism, as the same organ may appear repeatedly in different periods in the past history of the same group; or it may occur polyphyletically in different groups at the same or different periods; and having lost its function, it may be reduced to the same level of vestige through a series of similar changes. The recognition of this fact is of great importance in dealing with them as many of our present-day series of plants are reduction series. And hence Goebel (1900, p. 61) warns :

"Arrested organs may be such as generally in the existing species (or in its one sex) never reached complete development; it is only our synthetic necessity which forces us always to the assumption of reduction-series, of which, however, many can only claim to be fictions, imparting æsthetic pleasure of bringing a series of facts into connection with one another."

Keeping this precaution in mind we shall now make a brief survey of the vestigial organs of the vascular cryptogams.

A SURVEY OF THE VESTIGIAL ORGANS OF THE
VASCULAR CRYPTOGAMS

For the sake of convenience these organs will be discussed as under :—

(1) *Embryonic organs* which become vestigial in later stages;
(2) *Rudimentary organs* which never attain full growth under normal conditions of life but under exceptional conditions reveal their true nature;
(3) *Arrested* or *atrophied organs* which persist in a simple form in adult configuration; and
(4) Internal organs reduced to vestigial state; the *vestigial tissues.*

(1) *Embryonic organs.*—The true nature of the embryonic organs is often difficult to decide as they are ephemeral and as such represent only decadent stages in the early development of a plant. Secondly, whenever an embryonic organ is said to be vestigial, it is with reference to a particular cycle of ontogeny. It may or may not be vestigial in the life-cycle of another plant belonging to the same or another group. Three embryonic organs have been recognized as such. They are : (*i*) Foot, (*ii*) Suspensor and (*iii*) Protocorm.

(*i*) *Foot.*—It is well known that the root is a secondary organ of absorption of a leafy sporophyte, the primary organ of absorption being foot. The main function of the foot is to absorb food material from the tissues of the gametophyte till the young sporophyte developing on it is able to absorb food material for itself from the soil with the help of the root, when present. It is generally formed from the hypobasal half of the two-celled embryo and takes a position diametri-

tally opposite to that of the leaf in the quadrant stage. This possibly suggests that the leaf and foot have opposite polarities like those of root and stem. And, therefore, what root is to the adult sporophyte, the foot is to the young plant. But in further development of the plant as the root and shoot assume greater proportions, the foot dwindles and is left as a small vestige completely lost in the adult stage.

That foot is an organ of considerable importance was known long since, as it happens to be the only absorbing organ of the non-leafy sporogonia of the mosses and liverworts. In the Anthocerotes also it becomes an organ of great physiological significance. In the sporophyte of this group, *Notothylas* excepted, there is a basal meristem which gives rise to a series of tetrads of spores from below. These ripen acropetally and are dispersed by the hygroscopic movements of the columella and elaters through the valves of the sporogonium. On account of the basal meristem the sporophyte has an infinite capacity for growth : and to nourish such a growing sporophyte the foot becomes very massive and a permanent structure in the morphology of the sporophyte. The foot, therefore, in this group is no longer an ephemeral organ as in the majority of liverworts but an organ of considerable utility throughout the life of the sporophyte. In the great majority of ferns also, the foot is only an embryonic organ but in the embryos of *Marattia douglassi, Kaulfussia œsculifolia* and *Equisetum debile* it is a massive organ which persists much longer than it does in other plants of these groups. It was in consideration of such facts in the embryogeny of the Anthocerotes and the Eusporangiatæ that Campbell[12] (1911, p. 211) stated, now more than thirty-five years back : "Indeed so marked are the resemblances in the early stage of development that they make the inference almost irresistible that the Ophioglossaceæ must have descended from some simpler forms whose sporophyte bore a strong resemblance to *Anthoceros*." As a matter of fact the embryo of *Anthoceros* bears such a close resemblance to the embryo of *O. moluccanum* or to the adult plant of *O. simplex* that one is tempted to call *Anthoceros* almost a pro-*Ophioglossum*. The significance of Campbell's inference, however, became apparent only after the discovery of the Psilophytales from the Rhynian cherts by Kidston and Lang[13] (1917-1921) and after the discovery of the gametophytes of the Psilotaceæ by Holloway[14] (1917) and Lawson[15] (1917) in 1917. In the embryogeny of the Psilotaceæ, there is no root, the whole of the lower part of the embryo being considered to be foot. Curiously enough this foot of the Psilotaceæ bears a close resemblance to the foot of *Anthoceros* and is as much prominent in the embryo of *Tmesipteris* as it is in *Anthoceros*. Nay, at a certain stage in the embryogeny, the whole of the embryo of *Tmesipteris* is considered to be all foot by Holloway (1917). In the early life of the plant, therefore, the foot is a very useful organ in *Psilotum, Tmesipteris* and *Anthoceros*. This was a striking confirmation of the earlier idea that even in the early vascular plants the foot must have been a very useful organ and not only vestigial as in the later vascular plants.

In the examples mentioned above the foot is a useful organ for a long time in the life of the plant. Quite an opposite of this is seen in the endoscopic embryos of *Selaginella* and *Lycopodium*. In these plants the foot becomes vestigial at a very early stage in the embryogeny. In *Selaginella* the embryo being endosporic, it is nourished by the parent-plant. The gametophyte becomes consequently reduced and the food material is stored in the lower part of gametophyte in the form of a frothy mass. The suspensor pushes the embryo in this region, and the foot, therefore, is reduced to a vestigial state soon. Between these two extreme cases (1) where the foot is an extremely useful and persistent organ and (2) where it is a mere decadent useless stage, in the great majority of the vascular cryptogams, it is an ephemeral organ which becomes vestigial in adult condition.

The other embryonic organ which becomes vestigial in adult state is suspensor. Its main function is to change the direction of the growing embryo in such a manner as to push it in those regions where the food material is stored. It is a matter of common knowledge that this organ occurred repeatedly in different groups of plants in the history of the plant kingdom, e.g., in the Lycopodiales, Filicales, Coniferales, Gnetales and in angiosperms. Its phyletic history shows that it is not of constant occurrence even within the limits of a genus, much less in larger groups such as classes or phyla. For example, it occurs in *Botrychium, Helminthostachys, Danea,* and *Angiopteris*; but it is not of quite constant occurrence in the first and the last genera mentioned above. Once Miss Lyon[16] (1915) was so much impressed by this structure that she actually proposed a new genus "*Sceptridium*" in the Ophioglossaceæ to include such species of *Botrychium* as have suspensor. It occurs in almost all the species of *Selaginella*, but it is said to be absent in *S. pumila* found in Cape Colony, South Africa (see Duthie,[17] 1926). Obviously then in suspensor we are having a decadent structure not of constant occurrence in phylogeny. According to La Motte[18] (1937) in *Isoetes* also it shows a great variability of direction.

As a rule the development of such decadent parts is very rapid in ontogeny and they disappear also very rapidly in the life-cycle : because, the parts that serve no useful purpose in the economy of a plant are last to appear and first to disappear, e.g., the corolla in Cruciferæ or the calyx in Compositæ. Very often these organs show precocious development and on that account look very conspicuous in comparison to the surrounding parts at certain stages in embryogeny. Thus the suspensor of *Angiopteris* is the largest part of the two-celled embryo, and so is the foot in the early embryos of *Tmesipteris, Marsilia, Equisetum,* etc.

The third embryonic organ of the vascular cryptogams which becomes vestigial later is the protocorm. The students of cryptogamic botany are familiar with the classical theory of protocorm as the forerunner of the vascular sporophyte enunciated by Treub[19] (1884-1838). This organ develops as a massive structure in lycopods, having all the characteristics of a

shoot. It closely resembles the adult plant of *Phylloglossum* with its tuber and annual cluster of leaves as in some orchids such as *Habinaria diphylla*. To this embryonic tuber-bearing protophylls Treub has given the name "protocorm". He considered it to be an organ of great antiquity. But his claim was freely contested by Goebel[20] (1904) and Bower[21] (1908) who looked upon it as an organ of perennation having only physiological significance. Holloway[22] (1917-1920), however, in his researches on the prothalli of the New Zealand species of the genus *Lycopodium* found that this organ though of great use to the plant in perennation, is capable of dividing dichotomously and can bear bulbils as are found on the sporophyte of *Lycopodium*. And, therefore, he came to the conclusion that it is not an organ of mere physiological importance but also of phylogenetic significance.

But the most unexpected confirmation of Treub's views came with the discovery of the Psilophytales by Kidston and Lang (1917). In the morphology of these of primitive land plants, there is a swollen portion at the base, and especially in *Hornea lignieri*, which bears a close resemblance to the protocorm of lycopods. This means that we are able to telescope the existence of the protocorm of modern lycopods in the Devonian plants, a period of not less than 300 millions of years. What is then the real significance of this organ? Was not Treub[23] (1890) right in regarding it as a vestigial structure of great antiquity? Probably he was. Because, it is quite possible that this structure might have arisen as an organ *sui generis* which might have had in some remote past adapted itself secondarily to its present function later, for which it was not very well suited. And hence in course of time it may have become partly vestigial and partly useful as Holloway[24] (1920, p. 233) thinks. Such examples of secondary adaptations of vestigial organs are quoted by Darwin[25] (1888) himself. For example, the styles in the flowers of some Compositæ though vestigial for their original purpose, secondarily help to brush aside the pollen. This is really a good example of successful secondary adaptation on the part of a vestigial organ, whereas protocorm and rhizophore suggest imperfect secondary adaptation. To my mind the same is probably the explanation of the axes of intermediate character such as Nathorstiana stem base, rhizomorph of *Isoetes*, Stigmarin axes, rhizophore of *Selaginella*, etc.

Another good example of successful adaptation on the part of a reduced structure is to be found in the hydathodes of *Equisetum*.[26] It is generally believed that the Calamites had leaves larger than those of the modern *Equisetum*. The former had stomata on the adaxial surface which became useless later; but subsequently they got associated with a vein and were transformed into hydathodes of epithem-type, and are functioning as such in many species of living *Equisetum·*

(2) *Rudimentary or Nascent Organs.*—Apart from the vestigial organs noticeable in embryogeny, a rudimentary organ may persist to a much later stage in a nascent form. Ordinarily it does not reveal its vestigial nature; but under the strain of some abnormal conditions it is brought out very clearly. Two such

examples at least are known. In some species of *Selaginella* there are small pads or protuberances in the axils of leaves in the place of rhizophores, e.g., in *S. rupestris*. These generally remain localised, but under the exceptional conditions they grow out into normal rhizophores and bear even leafy shoots. The other example is to be found in the annulus of *Equisetum*. In the majority of species of *Equisetum*, the annulus does not bear any sporangia ; but the annulus of *E. giganteum* and *E. præaletum* is normally sporangiferous. What is more interesting, some species such as *E. palustre*, or *E. arvense* show this condition occasionally.

Many of the abnormalities interpreted as reversion to the ancestral condition are probably due to the fact that the organs in question have been retained in course of evolution in a very reduced form. It is on this hypothesis that Bower (1901) considers the abortive sporangia found at the base of the strobilus in many species of *Lycopodium, Selaginella, Isoetes* and *Psilotum* to be vestigial.

(3) *Arrested or Atrophied Organs.*—These also persist in adult configuration and it is only the comparative or the developmental history that reveals their true character. In the adult leaflet of *Nephrolepis, Osmunda* and some other ferns there is a small auricle at the base of the leaflet. This little organ represents the third lobe of the embryonic pinna which is tri-foliate and acquires its elongated adult form by suppressing the basal lobes through a series of developmental changes. Similarly on the adaxial surface of the sporocarp of *Marsilia* there are two or more teeth present which represent arrested pinnæ and confirm the foliar nature of that organ. The common kidney-shaped indusium of *Nephrolepis, Nephrodium* and other genera is supposed to have been derived from the cup-shaped indusium split into two parts outer and inner as in some Davalloid ferns. The inner indusium does not develop. Only the outer one develops and forms the usual kidney-shaped type. But in some genera of the Davalloid ferns to which *Nephrolepis* belongs the inner indusium is seen in a rudimentary form, e.g., in *Hypolepis* (see Bower,[27,28] 1923, pp. 221-223 and 1928, p. 11). A similar vestigial indusium is also found in *Marsilia* and *Pilularia* which suggests their affinity with the Schizæceæ.

The spore-producing parts of the Ophioglossaceæ were a very controversial topic since long; but the discovery of the early Devonian plants in which sterile and fertile parts have been associated together, called telome, threw a new light on these structures. At the distal ends of the little sporangiophores arranged in two rows in *Helmonthostachys* there are clusters of small leafy outgrowths. These little appendages were meaningless so far. But now with the help of our knowledge of the Devonian genera we interpret these as vestiges of leafy parts which were of commensurable dimensions in the ancestors of the Ophioglossaceæ. The affinity of the Ophioglossaceæ to the Cœnopteridinæ, though remote, is largely based on this fact.[29] The same is probably the interpretation of the ligule of lycopods, *Selaginella* and *Isoetes* and also of the buds sometimes noticeable in the seedlings of *Osmunda* and in *Botrychium*.[30]

(4) *Vestigial Tissues.*—The last category of the vestigial parts found in the vascular cryptogams are the internal organs reduced to a vestigial state, the so-called vestigial tissues. A large number of examples of these are known; but I do not propose to survey them all here. Only a few striking examples are cited below.

It is well known that the centripetal xylem is not seen in the stem of living *Equisetum* but it was quite a general condition of the whole stock in the anatomy of Protocalamites. Curiously enough this condition is seen in the traces of the reduced vegetative leaves of *E. maximum* and in the traces of the reproductive leaves of *E. palustre* and *E. hiemale*. The condition here is identical with that of the leaf-traces in Lycopodineæ.

Another good example is to be found in the leaf-trace of the living Cycadales and the Cycadofilicales. In the Cycadofilicales of the Palæozoic period the bundles of the stem were always characterized by the presence of centripetal or cryptogamic xylem. But this is conspicuously absent in the stem of the living Cycadales. However, there is a clear and universal presence of centripetal wood in the foliar fibro-vascular bundles of the living Cycadales.

Similar vestigial traces of xylem are also found in the teeth on the sporocarps of *Marsilia* and *Pilularia* and in the ochreola noticeable at the bases of branches of *Equisetum* species. In many species of *Equisetum* ochreola lack vascular traces; but Milde[31] (1867) has found them in the ochreola of *E. arvense, E. limosum* and *E. hiemale*. It is well known that the nodal structure of *E. variegatum* and allied species where remnants of siphonostele are noticeable has been interpreted to be vestigial by many competent authors. The cambium found in the stem of *Botrychium, E. maximum* and *Isoetes* is also of a similar nature.

All these examples are quite sufficient to show the widespread occurrence and the variety of structures called vestigial in the vascular cryptogams. In dealing with them, it is obvious that the concept when structures are being considered is qualitative; and it is quantitative when the functions are being considered. This distinction, however, is not well recognised in botanical literature; but to my mind it is of considerable theoretical importance as will be seen from what follows.

THE ORIGIN OF VESTIGIAL ORGANS: A RATIONALE

We shall now turn to some theoretical considerations. How can the origin of the vestigial organs be conceived? There is but little positive information to which we can turn in answer to this question. We have no doubt sufficient information at our disposal regarding the course of their development and degeneration also but that does not take us much further. It is possible, nay probable, that an organ having gone out of use for several generations thriving under the same set of environments for millions of years may have been atrophied and reduced to a state of a rudimentary structure in heredity. But how can disuse ever act on an organ never used and already reduced and reduce it still further to a state of vestige? The principle of economy of materials in an expanding form of the body

may perhaps be one of the reasons for this: but that does not solve the whole problem as there are cases on record where no such economy seems to have been effected, *e.g.,* in the production of a small papilla consisting of a few cells in a flower. The difficulty is genuine and has been well recognized by many investigators. Here is an example :

"After an organ has ceased being used, and has become in consequence much reduced, how can it be still further reduced in size until the merest vestige is left : and how can it be finally quite obliterated? It is scarcely possible that disuse can go on producing any further effect after the organ has been functionless. Some additional explanation is here requisite which I cannot give."[32]

These lines come from an ardent investigator no less than Darwin himself. But we must remember that these lines were written by him in 1858 when he had not had any occasion to see much of the later development in the science of modern Biology. Too great a faith in orthogenetic continuity of species as Darwin had, can lead to no other conclusions than these. But with the recent advancement of the surging wave of mutation theory, the breaks in the life lines now appear to us to be more real than apparent. By some fruitful chance, by some strange reorganization of the chromatin matter, by some sudden change in temperature either hot or cold, by an unknown chemical or bacterial stimulus, by the action of some unseen and unknown radiations, the nucleus of a cell in a species undergoes gene-mutations which result in bringing out new forms with new morphological characters, howsoever small they may be; and some of these do persist in times to come. Some of these characters are stable and useful and help the organism in adapting itself to its environments and in mastering them better ; and others are equally useless for all that. A few others are of doubtful utility and get simplified and reduced to a rudimentary state in course of time. Some of these useless features get secondarily adapted to some purpose other than the original one for which they were meant and become partly vestigial and partly useful. Still others result in monstrosities and bring forth odd forms with strange characters. Many of these are quite unstable and are soon lost in heredity, but some do persist and become vestigial. How significant in this connection is T. H. Morgan's finding that quite a large number of mutations he was able to induce in *Drosophila* resulted in the atrophy of some parts and were both unstable and useless.[33] But some of the gene-mutations of doubtful use do persist in the body of an organism. May it not be that in the plants also some such mutations have given rise to changes which resulted in producing parts apparently useless, at any rate of doubtful utility. Natural selection having acted upon these and having found them useless may have reduced some of them to a rudimentary state and others to a state of vestige only. However, it is necessary to state here that I do not want to suggest that every vestigial organ owes its origin to gene-mutations, though I do feel that many of them may have arisen that way. Natural selection having acted upon

them and having found them to be of no direct use to the organism, may have reduced them to a vestigial condition. Truly vestigial organs, therefore, would be those that have arisen in heredity qualitatively as parts *de novo* on account of gene-mutations and have persisted in heredity notwithstanding the plain stamp of inutility they might have obtained later. Herein then perhaps lies the rationale of a problem left quite open by the unbiased mind of Sir Charles Darwin.

I take this opportunity to thank Professor J. J. Asana for his kindness in going through the manuscript and making me some useful suggestions.

1. Darwin, C., *The Origin of Species*, 1888, John Murray and Co. London 2. Hækel, Ernst, *Generelle Morphologie*, 1886, Berlin. 3. Darwin, *loc. cit*. ch. 14. 4. Goebel, K., *Organography of Plants*, 1900, Part 1. English Ed. 5. Bower, F. O., " Imperfect sporangia in certain pteridophytes. Are they vestigial?," *Ann. Bot.*, 1901, **15**, 225-267. 6. —, *Primitive Land Plants*, 1935. 7. Jeffrey, E. C., *The Anatomy of Woody Plants*, 1917. 8. Sahni, B., " On the theoretical significance of the so-called ' abnormalities ' in the sporangiophores of the Psilotaceæ, " *Journ. Ind. Bot. Soc.*, 1923, **3**, 185-191. 9. —, " The ontogeny of vascular plants and the theooy of recapitulation," *Op. cit*., 1925, **4**, 202-216. 10. Browne, I. M. P., " On a new theory of Calamarian cone," *Ann. Bot.*, 1927, **41**, 301-320. 11. Bower, F. O., *The Ferns*, 1923, Vol. 1, Cambridge. 12. Campbell, D. H., *The Eusporangiatæ*, 1911. 13. Kidston and Lang, W. H., " On Old Redsandstone plants showing structure from the Rhynie Chert bed, Aberdeenshire, Parts I-V," *Trans. Roy. Soc.*, Edinburgh, 1917-1921, **51-52**. 14. Holloway, J. E., " The prothallus and young plants of *Tmesipteris*," *Trans. Proc. N. Z. Inst.*, 1917, **15**, 1-44. 15. Lawson, A. A.,

" The gametophyte generation of the Psilotaceæ," *Trans. Roy. Soc.*, Edinburgh, 1917, **52**, 93-113. 16. Lyon, H. L., " A new genus of Ophioglossaceæ' *Bot. Gaz.*, 1905, **4**, 455-458. 17. Duthie, A. V., " Studies in the Morphology of *Selaginella pumila*, Part III," *Trans. Roy. Soc. South Africa*, 1926, **11**, 275-295. 18. La Motte, C.. " Morphology and Orientatig of the embryo of *Isœtes*," *Ann., Bot.*, New Series, 1937, **1, 4**, 695-711. 19. Treub, M., " Etudes sur les Lycopodiacees," *Ann. Jard Bot. Buitenzorg*, 1884-1888, **4-5** and **7**. 20. Goebel, K., *Organography of Plants*, 1904 Part II. 21. Bower, F. O., *The Origin of a Land-flora*, 1908. 22. Holloway, J. E., " Studies in the New Zea.and species of the genus *Lycopodium*," *Trans. N. Z. Inst.*, 1917-1920, **48-52**. 23. Treub, M., *loc. cit*., 1890, Part VIII. Considerations theoretique, pp. 23-37. 24. Holloway, J. E., *op. cit*.. Part IV, " The structure of the prothallus in five species," *Trans N. Z Inst.*, 1920 **52**. 25. Darwin, C., *op. cit*., 1888, pp. 397-402. 26. Johnson, A. A., " Hydathodes in the genus *Equisetum*," *Bot. Gaz.*, 1937, **99**, 598-608. 27, 28 Bower, *The Ferns*. 1923, Part I and Part III, 1928. 29. See Bower, *op. cit*., 1935, pp. 361-365 and p.. 394-395. 30. See Lang, W. H., " On some deviations from the normal morphology of the shoot in *Osmunda regalis*,' *Mem. and Proc. Manchester Lit. and Phil. Soc.*, 1924, **68**, 53-67 and " Studies in the morphology und anatomy of the Ophioglossaceæ," *Ann. Bot.*, 1914, **27**, 203. 31. Milde, J., *Monographia Equisetorum, Nova Acta etc.*, 1867, **32**. 32. Darwin, *Origin of Species, op. cit*., 1888, p. 401. 33. Morgan, T. H., *The Theory of the Gene*, 1932, Chs. 18 and 19 and Ch. 6, p. 75 and pp. 72-94.

OBITUARY
ALEXANDER BOGOMOLETS
(1881-1946)

IN the death of ALEXANDER BOGOMOLETS the Soviet people have lost one of their best and most devoted scholars. He was born sixty-five years ago within the dreary walls of Kiev prison where his mother had been imprisoned for revolutionary activities by the Czarist regime. As a child he was marked for his exceptional abilities. After a brilliant high school career he joined the medical faculty in Odessa University in 1900, passed his final examination with honours in 1906, and was appointed Assistant Professor of Pathology. His researches on "Structure and functions of suprarenal glands both in the healthy and sick organisms" got him his doctorate in 1909. After one year's work in the physiological laboratory at Sorbonne he was appointed Professor of General Pathology in Saratov University which post he held till 1925 when he was elected Professor of Pathological Physiology at the Second Moscow University. On the death of Bogonov, Bogomolets succeeded him as the Head of the First Blood Transfusion Institute, Moscow.

Bogomolets' researches and contributions are varied and many. He established the lipoid nature of the secreta of cortex of suprarenal glands and originated the idea of iono-endocrinous regulation. He attached great import-

ance to the reticulo-endothelial system and its role on longevity and immunity. He showed that the disturbances in the functions of this system led to a number of ailments and to premature old age. By causing immunity in animals using elements of reticulo-endothelial system he obtained a serum which was used in the U.S.S.R. with particular success during the war in the treatment of wounds and fractures. Bogomolets and his school undertook intensive study of conditions which facilitate longevity in certain parts of U.S.S.R. and elaborated modes for preventing premature old age and prolongation of life.

His publications include important works in the sphere of immunity, anaphylaxis, allergy, pathology of blood circulation and mechanism of the action of blood transfusion. In 1929 he was elected member of Academy of Sciences, Ukranian S.S.R., of which he subsequently became President. In 1932 he was elected member of the Academy of Sciences of the U.S.S.R. He achieved the highest honours possible in the Soviet Union; twice he was elected deputy to Supreme Soviet of U.S.S.R., and was the Deputy Chairman of Supreme Soviet of Ukranian S.S.R. He was one of the recipients of the "First-class Stalin Prize".