XXXI.—*The Vegetable Individual, in its relation to Species.* By Dr. ALEXANDER BRAUN, Professor of Botany in the University of Berlin, &c.* Translated by CHAS. FRANCIS STONE, B.A.

[Concluded from vol. xvi. p. 354.]

WHILE thus, on the one hand, all the facts seem to unite in establishing the individual nature of the shoot, on comparing shoots in their qualitative relations, phænomena are brought to view which seem to contradict such a view of its individuality. The higher departments of the animal kingdom usually present as individuals, representatives of the specific type agreeing in all essential respects, though, perhaps, not perfectly identical. The fact of the separation of the sexes was all that modified this view; and here, indeed, the essence of the species does seem to be divided between two different individuals. Attempts have not been wanting to obviate this contradiction by the Platonic doctrine of the original unity of the sexes, by the assertion of Paracelsus†; that, in fact, the two together must be regarded as the one real individual—and such like.

This contradiction to the usual view of what constitutes the individual is shown in a far higher degree by *qualitative* comparisons of vegetable shoots, not merely of the same species, but also of the same stock. Thus we see, *e. g.* in *Equisetum arvense* (Field Horsetail), shoots totally different in aspect proceeding from the same root-stock; in early spring they are pale, discoloured, unbranched, terminating with a strobilaceous-like fructification; later, green and foliaceous ones appear, verticillately ramified. Investigations into subterranean vegetation show even other varieties of shoot-formation, viz. offsets dwindling down to a point, and club-shaped buds which, at a later period, drop off of themselves. The Colt's-foot (*Tussilago Farfara*) presents similar phænomena, in early spring putting forth leafless shoots, with asparagus-like scales terminating with yellow capitula, which in summer are followed by others bearing leaves. The flowers in the little capitula of the first present a third variety of shoots in their lateral branchlets. Even in common life we distinguish leaf-buds from flower-buds, on many trees. Let us consider this relation in the Cherry-tree, for example. On the same branch we find, on the one hand, buds which develop into branches bearing leaves, without producing flowers; on the other hand, some bearing only little squamate leaves on the shortened

* Reprinted from Silliman's American Journal for January 1856.

† "For this ye must know: man without woman is not a whole; only with woman is he a whole. That is as much as to say: both together make man, and neither alone."

axis, from whose axils the flowers rise and form a third kind of shoot.

On examining closer into the real origin of these differences, we find their ground to be a partition of the different steps of the metamorphosis (of the formations) among different shoots. True, there are many plants which go through the whole series of formations, from the inferior* and the foliaceous formations up to flower and fruit; but the cases are very numerous in which this does not take place, and in which the single shoot is not able to produce all the formations. Thus there are shoots which are only able to realize the lower steps, and never attain to flowers and fruit; while others overleap all the inferior degrees and commence immediately with the formation of flowers. Hence, on the one hand, we see the metamorphosis interrupted, a stoppage taking place at a determinate step; on the other, the metamorphosis attained by passing over the intermediate steps. Still more remarkable are the cases in which the retardation is not merely an interruption at a determinate step, but appears as a real retrogression in the metamorphosis, whereby an alternate rise and fall—an oscillation—usually takes place, which may at last pass over in victorious progress to the formation of flower and fruit; though in most instances it prevents the shoot in question from ever attaining its end. *Helleborus niger* is an example of the first case; for after many years of inferior- and foliaceous-leaf formation, at last it attains superior leaves and fruit by overleaping the formation of foliaceous-leaves which until then had prevented its further progress†. Many of our trees with true foliage present examples of the second case. Their branches commence with bud-scales (inferior-leaves), the succeeding foliaceous branch ends with a terminal bud (thus falling back to inferior-leaf formation), and in the next period of vegetation they rise again to foliaceous-leaf formation ‡,—as in

* On the terminology of the leaf-formations, see Wydler, Bot. Zeit. 1844, 36tes Stück, and A. Braun, Verjüngung, p. 66. (Hefrey's Transl. Ray Soc. 1853, p. 62.)

† Analogous cases occur in the branches in *Æsculus* and many Maples which attain to flowers. Among herbaceous plants *Anemone nemorosa* and *Asarum Europæum* also belong here, and especially remarkable is the Tulip, the plants of which, not yet ripe for flowering, annually develop one single foliaceous leaf, followed by a central bud hidden in the middle of the bulb and composed of several inferior-leaves. This bud preserves this position in bulbs deep in the ground, but in those nearer the surface it is, as it were, led out of the centre of the bulb, and sinks deeper into the earth, causing an indentation of the surrounding base of the preceding leaf in form like a spur, boring through the old bulb and penetrating vertically into the ground, and at the same time sinking itself into a deeper stratum with the spur;—an arrangement explained, but not with sufficient clearness, by Henry in Nov. Act. Nat. Cur. vol. xxi. p. 275. t. 16 & 17.

‡ In such librations, of course, the formation of the flower can only be

the Oak, Beech and Poplar. A similar oscillation between inferior-leaf formation and foliaceous-leaf formation, keeping pace with the change of season, is seen in the creeping main-shoot of *Adoxa*, and in the stock of *Hepatica nobilis*, creeping close to the soil, with its short internodes, and which in so far deserves its French name (*la fille avant la mère*) as its flowers, which unfold before the foliage, do not belong to the same individual as the foliage, but are produced laterally as a "daughter generation" from the axils of the inferior-leaves of the maternal stem*. A similar phenomenon, only in a higher degree (a rising and falling between foliaceous- and superior-leaf formation), is presented by those plants whose inflorescence ends in a foliaceous coma, as is remarkably the case in the Pine-Apple, and also in the New Holland species of *Melaleuca* and *Callistemon*, whose crowded, brush-like inflorescence (*i. e.* the region covered with superior-leaves and bearing the flowers in the axils of these) returns and forms foliaceous-leaves, and in the following year again attains an inflorescence.

While every leaf-formation may bring the progress of the metamorphosis on a single shoot to a consummation, it is conceivable that one shoot may be allowed to each step for itself alone. Thus, there are shoots which represent inferior-leaf formation alone; *e.g.* the root-stock of *Paris quadrifolia*, the tuberiferous branches of the rhizoma of the Potato†; and there

attained by particular branches, deviating in character from the rest,—the catkins which pass over leaf-formation advancing from the inferior-leaves immediately to the superior-leaves out of whose axils the flowers are emitted.

* The same obtains in *Galanthus nivalis*, in which every annual generation consists of one inferior leaf, one foliaceous-leaf with a vagina, and one without a vagina, which follow each other in simple alternation, in a distichous arrangement. The flower, as a branch, is emitted from the axil of the second foliaceous-leaf, while the direct continuation of the shoot returns again to inferior-leaf formation. In striking contrast to the extremely simple relations of this plant we find *Oxalis tetraphylla* and other species of that genus, in which the subterraneous main-stem also presents an alternation of inferior-leaf formation and foliaceous-leaf formation, advancing with the change of season, but conjoined with a rare abundance of leaves and a complicated phyllotaxis. The number of the inferior-leaves amounts to several hundreds; and transverse sections of the bulbs, which last through the winter and are formed by the close approximation of these leaves, form some of the prettiest specimens of phyllotaxis, showing 21-15 arrangement through easily computable 8-, 13- and 21-ranked oblique spirals. The number of the foliaceous-leaves is not so large; they develop in the summer, and form an 8- to 13-leaved rosette, out of which the axillary inflorescences issue, with their long peduncles.

† In case (as sometimes occurs) the tuber does not pass through this formation and advance to foliaceous-leaf formation. The tuber is the thickened apex of the inferior-leaf shoot. Cf. the figure by Turpin, *Mém. du Mus. d'Hist. Nat.* t. 19. pl. 2.

are some which are endowed with the foliaceous-leaf formation only, as the primary axis of many species of *Veronica*, the sterile leafy branches of several *Euphorbia*, as well as the leafy branches of those woody growths which have no bud-scales and no terminal inflorescence (e. g. *Rhamnus Frangula*). Cases of pure superior-leaved shoots may be seen in the peduncles of *Veronica Chamædrys*, *officinalis*, &c., in the (always lateral) spike-bearing scapes of *Plantago*, and the racemes of *Convallaria majalis*, which shoot out of the axil of the highest lower-leaf as branches. Even the leaf-formation belonging to the flower can be divided among different shoots, and thus the flowers may be produced piecemeal, so to say; as is the case in all diœcious plants, where the two most essential formations of the flower (the stamens and pistils) are found, not in the same flower, but in two separate ones. Even the less essential parts of the flower, the sepals and the petals, may occur separated from the other particular shootlets; as may be seen in the neutral flowers in the coma of the spike of *Muscari comosum* and in the ray-flowers of the cyme of *Viburnum Opulus*. The destitution of the shoot may be carried so far as to cause it to produce but one single leaf, or one single formation (whether from the sphere of the plant-stock, or from that of the leaves); in which case the individual represents only one single organ; as, for instance, in the branches which form the axis of the inflorescence in *Vicia monantha* and other Leguminosæ with racemes reduced to one flower, bearing one single superior-leaf, from whose axil the flower proceeds. The male flower of *Euphorbia* is a peduncle whose flower consists of one single stamen*. Must we, now, still regard as individuals, these

* The genuine cases will be of rare occurrence if we look at the cases which belong here rigorously, that is, if we take into account the dwarfed foliaceous formations which may possibly exist, suppressed or scarcely discernible. The male flower of *Euphorbia* itself properly belongs here only in appearance, as two small scales (inferior-leaves) occur, more or less developed, at the base of the peduncle. The small involucre of the male flower proceeds to develop itself out of one of these scales. (Cf. Wydler, *Linnaea*, 1843, p. 409.) Another example of a one-leaved shoot (though a spurious one) is presented in the Californian *Pinus monophyllos* (Fremont), whose lateral branchlets bear a fascicle of needle-shaped leaves reduced to one single needle: but this, as well as the pair of such leaves of our ordinary Pines, is preceded by a vagina composed of several bud-scales. Perhaps another deception is played upon us in this case, for the perfectly round form of this needle excites the suspicion that it may be composed of two which have grown together through their whole length. The seed-bearing fruit-scales of the cone of *Abietinae*, which are placed in the axils of the scales, also appear to be one-leaved shoots; but the series of changes which these scales present in cones of *Pinus Larix* which have completed their growth, proves that these fruit-scales are composed of two concrete leaves. The spurious axis of the Grape is a concatenation of alternating

shoots, so partially endowed, and the last-named so destitute? Certainly. For if the individual can fall short, though ever so little, of the perfect realization of the specific idea, then there are no limits to its imperfection and destitution; for, after all, the realization of this vegetable Idea by the different members of the vegetable kingdom is precisely similar to the realization of the species by its single individuals. To be sure, our idea of a plant implies that it shall manifest its life in a series of successive formations, that it shall put forth its leaves, flowers and fruit by successive steps; and yet there are plants which produce no leaves and no fruit (the Cryptogamia); again, there are others which hasten on to form flower and fruit with various intermissions of the regular steps, as is especially the case with the ugly parasites destitute of that green foliage which elsewhere is so characteristic a product of the vegetable world*. One of these (the *Hydnora*†, which preys upon the root of the South African *Euphorbia*) seems entirely devoid of all the foliage which is usually formed before the flower. Hence, therefore, in general we cannot necessarily regard individuals as perfect representatives of the specific idea, and hence, too, we cannot regard them as representations invariably identical in their realizations. Individuals appear rather as living attempts, by which the Idea is more or less attained, and is thus realized with various modifications. From this point of view even the differences in indi-

one- and two-leaved leaf-shoots, if we do not count the one or two little dwarfed superior-leaves, which in most cases are perceptible on the apex of the single shoot which finally forms a cirrus. *Ophioglossum* presents a genuine case of a one-leaved shoot. The spike of this plant is a single fertile leaf, standing in the axil of the sterile one, and hence belonging to a lateral axis, of which however nothing is perceptible but this leaf. (Cf. Schnitzlein, *Icon. fam. nat.* Heft ii. t. 32.) The utriculus of *Carex* is the solitary leaf of an axis which in its normal condition develops no farther, and out of which, as the axillary formation of the utriculus, the female flower is emitted. And the so-called neutral flower of *Panicum*, and the allied Grasses, is a shootlet which develops nothing but one leaf (the bract of the flower).

* *Orobanche*, *Lathræa*, *Monotropa*, *Cynomorium*, all of which agree in the inferior-leaf formation passing immediately into superior-leaf formation, and thus the formation of foliaceous-leaves is omitted. In the celebrated *Rafflesia* the immense flower is preceded by bud-scales only, which must be considered as the inferior-leaf formation. The same occurs in *Frostia*, which preys upon the branches of arborescent *Leguminosæ*, and which resembles a mere flower so much, that one might doubt whether it is merely a monstrous papilionaceous flower or a real parasite. (Cf. Endlicher, *Gen. Plant.* p. 76; and Guillemain, *Nouv. Ann. des Sc. Nat.* ii. t. 1; and as to parasites in general, Unger, *Annalen d. Wiener Museums*, part 2.)

† E. Meyer, *Nov. Act. Acad. L. C. Nat. Cur.* xvi. 2. p. 771. t. 58 & 59, and R. Brown, *On the female flower and fruit of Rafflesia and Hydnora*, 1844, pl. 6-9.

viduals, as pointed out by the doctrine of shoots, within the limits of vegetable species, will no longer surprise us; on the contrary, it will open to us a deeper insight into that independence presented to us even in the life of nature, in the realization of the internal problems of the creation.

But here, too, as is so variously the case in nature, the regulative law is admirably united to the free configuration; for what gives a peculiar interest to the differences among shoots in the same species is the regular reciprocal relation among the shoots, as they reciprocally complete each other by their very one-sidedness, and thus form a higher whole. In this respect the qualitative difference of shoots bears a certain relation to their origin, that is, to the order of ramification to which they belong. And as the formation of shoots, as was shown, is a process of propagation, we see here, in the history of the development of the species, propagation taking the place of individual development. A second individual takes up the thread of reproduction which the preceding one was unable to carry any farther. Thus, what we are accustomed to see elsewhere attained in the individual, is here reached by the generation in a more or less strictly determined cycle;—in other words, where the single shoot is incapable, a determinate succession of shoot-series arises to bring the internal problem of its existence to a consummation,—to complete the metamorphosis into flower and fruit. This remarkable phænomenon,—which is a very frequent one in the vegetable kingdom, and is one of the essential characteristics of many of the most important families of plants, *e. g.* the Grasses, *Symanthereæ*, *Labiatifloræ*, *Crucifera*, *Leguminosæ*, &c.,—is the same as that which in the animal kingdom (in whose lower orders it reappears) was, we cannot say discovered, but brought to a clearer comprehension not long since by the Norwegian naturalist Sars*, completed and confirmed by Von Siebold's investigations into the history of the development of *Medusa aurita* †, and soon after substantiated in its universality by the Dane, Steenstrup, under the name of "alternation of generation," or propagation and development by alternate series of generations ‡. Single cases of alternation of generation had been already carefully observed §; but they were too much in opposition to the

* In Wiegmann's Archiv, 1844, where the observations published in the author's earlier works, on the adolescent states of *Medusa*, are completed and concluded.

† Beiträge zur Naturgesch. der wirbellosen Thiere. Danzig, 1839.

‡ Ueber d. Generationswechsel, übersetzt von Lorenzen, Copenhagen, 1842.

§ Bonnet's industrious observations, the first that were made, of the alternating mode of reproduction of *Aphis*, published in his 'Traité de

usual mode of reproduction to be understood in their true meaning. It was attempted to reconcile them with the customary mode by an unnatural interpretation, which regarded them as subversive exceptions to the general rule; while on the contrary almost all later works* bring to light a multitude of unexpected facts which take their places naturally under the law of alternation of generation as now known, and substantiate the pertinent words of Goethe with which Steenstrup opens his Memoir: "Nature keeps on her course, and what seems an exception is in rule." It was Sars, however, who first gave the answer to the riddle, the key to the newly opened domain, when he said of the course of development of *Medusa*, that here "it was not the individual, but the generation, which underwent the metamorphosis†." This was the true point of view; for Steenstrup dwelt too exclusively on the physiological side, the functional relations, of the alternating generations. Steenstrup, in fact,

'Insectologie' in 1745, though made in 1740, belong here. Also Chamisso's correct observations of alternation of generation in *Salpæ*, described in his Memoir, *De Animalibus quibusdam e classe Vermium Linnæana*, Fasc. 1, 1819. Fragments in regard to the alternation of generation of *Trematoda* were known (but as such they did seem very enigmatical) by Bojanus's Beschreibung d. königsgelben Würmer (the "nurses" of *Trematoda* according to Steenstrup) aus welchen Cercarien (the larvæ of the final generation) herauskommen (Isis, 1818), and by von Bauer's important work on *Cercariæ* and the related *Bucephalus* (Beiträge zur Kenntniss d. niederen Thiere, Act. Nat. Cur. vol. xiii. 1827).

* Of the later works, by which the field of alternation of generation has been extended, I will adduce in particular: Sars, *Fauna litoralis Norvegiæ*, 1846, in which the sections especially important in relation to alternation of generation are those on *Syncoryna*, *Podocoryna*, *Perigonimus*, *Cytais*, as well as on *Agalmopsis*, *Diphyes*, and *Salpa*.—Van Beneden, *Recherches sur l'Embryogénie des Tubulaires* (1814); *Mém. sur les Campanulaires de la côte d'Ostende* (1845, in the *Mém. de l'Acad. Roy. de Bruxelles*, t. xvii.); *Recherches sur l'Anat., la Physiol. et le Dével. des Bryozoaires* (*Mém. de l'Acad. Roy. de Br.* t. xviii.).—Dujardin, *Sur le Dével. des Méduses et des Polypes hydriques* (*Ann. des Sc. Nat.* Nov. 1845).—Krohn, *Bemerkungen über die Geschlechtsverhältnisse d. Sertularinen* (in *Müller's Archiv*, 1843, p. 174); *Ueber d. Fortpfl. u. Entw. der Biploren* (*Froriep's neue Notizen*, No. 868, 1846).—Busch, *Beob. über Anat. u. Entw. d. Infusorien* (*Arch. f. Naturgesch.* xv. p. 92). How great an importance must be attributed to the discovery of alternation of generation in dispelling the darkness which until then settled on the history of the life and development of *Entozoa*, may be seen in particular in Siebold's pregnant communications in R. Wagner's *Handwörterbuch d. Physiologie*, p. 640 (Article: Parasiten).

† Sars, *l. c.* p. 29. This assertion, of course, must not be understood as if the particular generation did not come in for its part of a metamorphosis. Sars' view is most beautifully corroborated by a comparison with plants; as in plants the metamorphosis of the individual itself is connected with the formation which leads to the completion of new parts, which in their turn have their own subordinate metamorphosis.

considered that the significance of alternation of generation consisted in its being an organic nursing of the brood connected with particular generations, for which reason he termed the individuals of *these* generations "nurses;"—a mode of viewing the subject, which, with all Steenstrup's pregnant elaboration of his idea, and with all the analogies he pointed out between it and the well-known phenomena of nursing the brood by particular individuals among bees, wasps, ants and termites, does not seize the *essential* point of the phenomenon of alternation of generations*. R. Leuckart† conceives alternation of generation from a more comprehensive physiological point of view, in connexion with the totality of all the other phenomena of the formation of different individuals, whether it occurs in a different or in the same generation; regarding all these phenomena from the point of view of a division, not merely of the generic task, but of the vital task in general, among certain individuals; considering it as a polymorphism determined by a division of labour. But even this view must lead to the morphological one; for the division of labour is determined by the organic development, while this itself obtains its peculiar character from the determinate step of the metamorphosis at which the development ceases;—and this is just what is so unmistakable in the phenomena of alternation of generation in plants. Hence as a typical phenomenon of development, as a metamorphosis of generation, alternation of generation (as well as the metamorphosis of the individual) presents analogies with the graduated series in the animal and vegetable kingdoms, and the organic scale of the creation, in general;—a point to which

* Steenstrup's explanation is most correct in regard to the history of the development of *Distoma*, whose nurses and grand-nurses are at last utricles entirely filled with the brood, and forming mere receptacles of the brood. Its application is less happy to those cases where the transition from the preparatory generations to the final generation takes place through *external* shoot- or bud-formation, as in *Sertulariæ*, *Campanulariæ*, and *Corynæ*, whose nurses forming the polype-stem can continue to live even after the concluding generations, comparable to the flower in plants, separate or wither off. Hence the vital activity of the preparatory generations is not exhausted in the production of the brood. Steenstrup's view, accordingly, would only be correct if non-sexual brood-production (by internal or external shoot-formation or by division) and alternation of generation were *correlative* conditions of each other. But this is not the case, as reproduction by shoots takes place without any alternation of generation in a great number of animals (*Ascidia*, *Bryozoa*, *Madrepora*), and by division as well (*Astræa*, *Annulata*, *Infusoria*). These cases are comparable to the occurrence of *unessential* branches in plants; while alternation of generation represents the succession of *essential* shoots.

† Ueber d. Polymorphismus d. Indiv. od. d. Ersch. der Arbeitstheilung in d. Natur. Ein Beitrag z. Lehre v. Generationsw. (1851).

Carus* called attention, and Reichert, his predecessor, as well.

The difficulties which the qualitative differences of shoots of one and the same species seem to present to our conception of shoots as individuals, will be entirely obviated if we can demonstrate that a partial outfit and equipment of individuals, perfectly analogous to those found among plants, are likewise found in the animal kingdom, where in most cases there is less doubt as to what is an individual,—if we can show that in both kingdoms, and in a similar manner, a polymorphism of individuals occurs which depends upon a division of the steps of development and of the vital problem of the species among individual members, whether of the same generation (divisions of generation), or of different generations cyclically succeeding each other (alternation of generation).

Let us first compare the phenomena of alternation of generation (or, as it should be called, *cyclical succession of generations*) in both kingdoms†. As is the case in the alternation

* Zur näheren Kenntniss. d. Generationsw. (1849); and, Einige Worte üb. Metam. u. Generationsw. (von Siebold u. Kölliker, Zeitschr. f. wiss. Zool. iii. 1851, p. 359).

† These remarks on alternation of generation in plants, do not depend, as one might perhaps be disposed to think, upon a zoological doctrine fancifully applied to plants. But I recognized the phenomenon as the same, and I treated of it in my papers, if not under the same name, still in the same meaning, before my attention was called to the occurrence of this phenomenon in the animal kingdom by Steenstrup's work. As soon as the doctrine of the shoot as the vegetable individual was assumed in all its consequences, a determinate succession of generations emitted one from the other necessarily appeared to be the ground of the flower's first making its appearance in many plants in a determinate degree of ramification, and of the occurrence of a determinate succession of steps in the series of axes up to this goal, caused by a peculiar partition of the leaf-formations. Hereby the essential shoot-succession, which is the one which represents alternation of generation, was accurately distinguished from the unessential one. Twenty years ago, or more, C. Schimper distinguished between essential and unessential shoots, denominating the first (in a wider sense of the word) "Ableger" [off-sets], the latter "Ausleger" [out-sets]. In the 'Versammlung d. Naturforscher' in Mayence in the autumn of 1842, I made a communication on this subject, and at the same time in particular I called attention to the frequent importance of the characteristics involved in these relations when applied to improving the differentiation and grouping of species. Of this communication a report appeared in the 'Flora' for 1842, p. 962, though, indeed, somewhat distorted by inaccuracies. Wydler treated the same subject in the 'Bot. Zeit.' 1844, St. 37, under the heading "Achsenzahl der Gewächse," and gives a compendium of examples, in which, however, much appears which needs qualification. As Wydler informs us, Aug. de St. Hilaire is said to have turned his attention to ascertaining the number of essential axes in plants; however, I find nothing in the place referred to in the 'Leçons de Botanique' but the distinction between determinate and indeterminate growth, which has been known since

of generation of animals, a twofold reproduction appears in plants: sexual and non-sexual. Disregarding for the present the various relations of alternation of generation among the Cryptogamia, we find sexual reproduction (in animals by fertilized ova,—in plants by fertilized seeds) always vested in the generation which concludes the cycle of generations. That the consideration of this generation as the concluding one is not arbitrary, is shown by comparing it with the usual course of the metamorphosis; for the concluding generation is invested with the concluding formations of the metamorphosis (flower and fruit), in the same way in fact as in the animal the complete development of the organs of generation occurs at the summit of the individual metamorphosis. The preceding (preparatory) generations, which Steenstrup calls “nurses,” on the contrary invariably produce their brood by non-sexual reproduction: in the animal kingdom this takes place, now through germ-granules which develop in the interior of the body (as the nurses of *Distoma*), now by a process of division in the posterior part of the body (the nurse of the *Medusæ*, the *Tape-worm*), or finally by external, persistent or deciduous, shoot-formations (*Corynæ*, *Campanulariæ*, *Sertulariæ*, &c.). Among Phanerogamia the last is the only kind occurring subservient to alternations of generation.

In animals, as in plants, the number of the generations in which the cycle of alternation of generation is completed, is for the most part a determinate one. *Medusæ*, *Salpæ*, *Corynæ*, and *Tubulariæ* conclude this cycle in the second generation: according to Steenstrup's showing, *Distoma pacificum* has a trimembral alternation of generation, and the family stock of *Pennatula* seems also to be formed by a trimembral succession of shoots. *Campanularia* has a quadrimembral cycle, in which however the two first generations are of the same character. Among *Sertulariæ*, cycles of still more numerous members appear to occur: eight to ten generations form the annual cycle of generation of

Joachim Jung's time, and was brought forward especially by Røeper and applied by him to classifying inflorescences. It is exemplified, in that place, by creeping stems, upright root-stocks, and by bulbs; and the section on indeterminate stems is unluckily exemplified by wrong cases, viz. *Scirpus palustris*, *Primula officinalis*, and *Menyanthes*, to which indeterminate main-shoots are falsely ascribed.—Steenstrup also lays down an alternation of generation in plants, in the concluding remarks in his work quoted above, as well as in his later book, ‘Ueber das Vorkommen des Hermaphroditismus in der Natur’ (On the Phenomenon of Hermaphroditism in Nature), though in an entirely different manner from mine as here given; for he compares the single leaves of the plant with the individual in animals,—a mode of viewing the subject in regard to which I have already expressed my opinion in the Introduction.

Aphides, though, excepting the last one, they are all similar and not even determinate as to number.

To these examples from the animal kingdom much more numerous ones from the vegetable kingdom might be added, though I will only adduce a few of them here. Most *Labiatifloræ*, *Synanthereæ*, *Grasses*, *Polygalæ*, *Primulacæ*, the *Dictamnus*, *Iris*, *Galanthus nivalis*, &c., have a bimembral alternation of generation in different ways, according to the partition of the formations. In *Paris*, for example, the first generation takes the lowest grade: it presents a subterranean inferior-leaf shoot (rhizoma), which never leaves the darkness of the earth, only reaching the world of light, towards which all plants strive, in its posterity, viz. in the quadrifoliate and unifloral lateral shoots which it sends up. The first generation of *Viola odorata* and allied species forms foliage proper; still, the main axis tarries close to the earth, and the second generations (the lateral flowers) scarcely rise above the foliage. In *Lysimachia nummularia* the main-shoot, a rooting leaf-stem, creeps along the surface of the ground, growing indefinitely, and terminating only in the (essential) lateral branches by its golden-yellow flowers. The main-shoot rises perpendicularly, forms foliage proper, and passes on to superior-leaf formation in many species of *Veronica*, e. g. *V. acinifolia*, producing its flowers as a second generation out of the axils of the leaves. The same holds good in regard to *Orobanche ramosa*, which fixes itself and preys upon the root of Hemp, though its main-shoot has no green leaves. A very remarkable bimembral alternation of generation is shown by *Adoxa*, now so famous, its name to the contrary notwithstanding*. The main-shoot creeps along the ground, oscillating with the seasons between leaf and inferior-leaf formation,—at every return of the latter stretching out like a runner and boring into the earth. Flowers and fruit, frustrated by the invariable retrogression of the main-shoot, are produced by the aspiring perpendicular branches, after a pair of small leaves on the scape, and several insignificant superior leaves, out of whose axils the lateral flowers are emitted as unessential shoots of the third degree. *Hepatica* presents a similar division of the formations among the two generations of shoots; but the main-shoot, rejuvenated from year to year and alternating between inferior-leaf and leaf formation, is short and upright. The branches with their single flowers, forming the second generation, arise in the axils of the scale-like inferior-leaves. A bimembral succession of shoots occurs in *Convallaria Polygonatum*, the genus *Aloe*, all species of *Plantago*,

* E. g. *Adoxa moschatellina*, which derives its name from *δόξα* (fame). The relations of growth in this plant have been correctly described by Wydler, Bot. Zeit. 1844, p. 657.

Veronica officinalis, *Chamædrys*, &c., *Viola sylvatica*, *Lysimachia thyrsifolia*, *Alyssum saxatile*, and some other *Cruciferae*, *Echeveria coccinea*, all the species of *Melilotus*, *Medicago*, *Galega*, in *Pisum*, and many other leguminous plants, and in *Succisa pratensis*, *Anacyclus*, *Pyrethrum*, *Polygonum*, *Bistorta*, &c. A familiar example occurs in *Secale*: its spiciferous culm forms the shoot of the first degree, the lateral spikelets which compose the spike itself are those of the second*, and the florets in the axils of the superior leaves (paleæ) of these spikelets are the shoots of the third degree, *i. e.* the third generation of the cycle. A quadrimembral succession of shoots occurs in *Trifolium montanum*, *Hedysarum coronarium*, and in several of the New Holland phyllodineous *Acaciæ*. Several species of *Carex*, *e. g.* *C. maxima* and *leptostachys*, have a trimembral succession of shoots up to the male flower and a five-membral one up to the female.

If we were to reckon the similar generations which are reared one above the other until the tree gains strength enough to perfect its flowers, in many trees without terminal buds, as in the Willow, or the Lime†, we might find a number of generations equal or even much superior to that presented by *Aphis*.

Besides the generation *essential* to itself, and by which it gives existence to the next grade in the cycle, every generation may have still another unessential reproduction, which only extends the same grade. As above we distinguished between essential and unessential shoots, so here accordingly we must distinguish an essential succession of generations,—the true alternation of generation,—and an unessential one. Very often both occur in the same species of plants. A fine example of this is shown in *Lysimachia nummularia*, from whose creeping and rooting leaf-axis are emitted not only peduncles, but here and there a new creeping leaf-axis exactly repeating the original one (except as to the two early-lost cotyledons): and from the undetermined leaf-bearing main-axis of *Tropæolum minus* are emitted in regular alternation three lateral flowers at a time, and then again one (unessential) leaf-shoot. In *Cardamine amara* the first generation (the stem bearing foliaceous and superior leaves) is repeated in a twofold manner, by lateral branches from the cauline leaves, and by creepers from axils of the root-leaves. Similar relations obtain in *Mentha* and a large number of other plants. This same phænomenon is repeated in the animal kingdom. The polype-like nurses of the *Medusa* increase as such (according to Sars and Von Siebold) by lateral buds and runners. *Syncorynæ*

* *Secale*, in fact, has no terminal spicule; neither has *Triticum monococcum*, while the other cultivated species of *Triticum* have.

† I have described the Grape in reference to this subject in another place (Verjüngung, p. 49) [Henfrey's Transl. *op. cit.* p. 46].

are spadix-polypi, which represent trees by their formation of unessential branches, emitting finally from every branch and from the middle stock a whorl of individuals of the second (and last) degree. *Campanulariæ* and *Sertulariæ* put forth runners from the bases of the main-individual, which again shoot up and become new main-stems, or new stems emerge out of them; and perhaps the ramifications of *Bucephalus* (which according to Steenstrup's supposition is the larva of *Aspidogaster conchila*), as represented by Baer in Nov. Act. Acad. Nat. Cur. xiii. 2, belong here.

In our qualitative comparison of shoots, it was shown how the shoot may be limited to a few leaves, or even to a single one; in like manner the animal individual, in the division of rôle which occurs in alternation of generation, may become the representative of one single organ, of one single function. Thus the females of *Coryne squamata* are hardly anything more than egg-stocks, and the males than sperm-stocks*. The members of the *Tape-worm*, which are so many individuals of the final generation, hardly represent anything more than hermaphrodite sexual apparatus. As an analogous example in the vegetable kingdom perhaps the *Willow*† may be compared to the *Coryne*; here too the shoots of the last degree are nothing but naked unisexual apparatus of reproduction. In *Potamogeton*‡, on the contrary, they are hermaphrodite, as in the *Tape-worm*. The construction of many of the lower animals, which when considered as individual animals seem to be the strangest monsters, becomes more intelligible as soon as they are regarded from this point of view,—as soon as we make up our minds to regard the supposed individuals as a family stock, and its parts (formerly held to be mere organs, and which, physiologically considered, are really nothing more) as individuals. In particular this is true of *Physophora*, *Stephanomia* and *Agalmopsis*.

In many cases we find alternation of generation connected with division of generation, that is, the appearance of heterogeneous individuals in one and the same generation. Just as is the case in animal and vegetable forms without alternation of generation, so, where it is connected with alternation of generation, division of generation relates principally to the sexual functions; and a glance at the animal kingdom shows us relations of alternation of generation complicated by division per-

* Hence Rathke regards the male individuals as mere testicles. Cf. Wieg. Archiv, 1844, p. 155, and Steenstrup, Hermaphr. tab. 1. f. 17-20.

† The two stamens in the *Willow*, and the floriferous bud as well, are preceded by only two very small bracts, which grow together and form a little scale.

‡ The flowers of *Potamogeton* are branches which bear only stamens and carpels.

factly similar to those which occur in the vegetable kingdom. In animals which go through an alternation of generation, the individuals of the preparatory generations are non-sexual; still they may nevertheless have a determinate importance in relation to the completion of the race which is to form their posterity. When in fact the final generation does not consist of hermaphrodite individuals, as obtains, for instance, in the Tape-worm, various alternations are conceivable: the final individuals of both sexes can be nourished by the same nurse, and hence the sexual division will first take place in the second, or generally speaking, in the last generation; or, different nurses may nourish the two sexes, so that a division of generation will occur even at the degree of nurse-formation. If in the last case the nurses are not single ones, but even then form *per se* a family stock, then on the same stock we may either have male-bearing and female-bearing nurses together, or these two kinds of nurses may be divided among different stocks, according as the division of generation occurs in a determinate later generation, or is present already in the first. Although as yet the observations of these relations by no means form an unbroken chain*, still this much is certain, that in animals, in the same way as in plants, both monœcious and diœcious forms occur; and hence there are families partly bisexual, partly unisexual. *Corynæ*, *Tubulariæ*, *Campanulariæ*, and probably all *Sertulariæ* (hence, doubtless, the greater part of *Hydroids*), also *Veretillum*, *Cynomorium*, according to Steenstrup, Krohn, and other observers, are diœcious, whether they form small simple stocks, as *Coryne squamata*, or small ramified trees, as *Syncorynæ*, *Campanulariæ*†, &c. On the other hand, the *Siphonophora*, according to Milne-Edwards's description of *Stephanomia*‡ (and judging from Sars' description of *Agalmopsis*), are monœcious family stocks; *Hydræ* are also monœcious§. To enter any further into these relations as they occur in the lower animals would lead us too far from our subject; but it may be in place to give some details as to

* Thus, *e. g.*, as far as I know, it remains to be shown whether the single nurses of *Medusæ* produce *Medusæ* of both sexes, or, as is most probable, only those of the same sex. In *Aphis* also this point still needs to be more accurately determined.

† Steenstrup, *Hermaphr.* pp. 66, 67, 72.

‡ *Ann. des Sc. Nat.* 1841, p. 217. pl. 7-10.

§ The later investigations into the *Siphonophora* by Huxley, *Edin. Phil. Journ.* 1852, Kölliker, *Zeitschr. f. wiss. Zool.* 1852, and Leuckart, *Zool. Untersuch.* Heft 1, 1853, corroborate the monœcious relations of these wonderful creatures as regards most of their genera, *e. g.* *Agalma*, *Agalmopsis*, *Stephanomia* (*Apolemia*), *Physophora*, and the other closely related genera. Busch's researches into the group of *Diphyidiæ* have proved them to be diœcious, and the same obtains in the related genus *Epibulia*. (Later note.)

the manifold relations under which sexual division of generation occurs in plants.

Diœcious relations may occur without alternation of generation when, in fact, the flower has a terminal inflorescence and no branches, or only unessential ones,—when, therefore, as it is usually expressed, it is “uniaxial,” as *e. g.* in *Rubus Chæmæmorus*, *Lychnis*, and *Viscum*. Much more frequently, however, division of the sexes occurs in plants which at the same time have a cyclical succession of shoots (alternation of generation),—a succession which each of the two heterogeneous stocks passes through independently, and not always *pari passu*. This is a circumstance which must not be neglected in considering the differences of *habitus* in male and female flowers. Thus, in *Mercurialis* the female plant bears flowers even on the second axis; in the male plant, however,—if I do not misunderstand the inflorescence (a spike composed of small glomerules),—this first occurs on the third. In *Carex dioica*, *vice versâ*, the male plant flowers in the second line and the female in the third*. In other diœcious plants, on the other hand, the male and female flowers appear in the corresponding generation: *e. g.* in the second, *Stratiotes*, *Empetrum*, and *Taxus*; in the third, *Salix*, *Populus*, *Myrica*, *Cannabis*; in the fourth, *Phœnix*. In Hemp, the extremely heterogeneous appearance of the inflorescence of the male and female plants does not depend upon a division of the flowers of the two sexes among different axes, but upon the production of numerous unessential peduncles in the male inflorescence†.

Monœcism necessarily presupposes a succession of shoots (alternation of generation); in the simplest case at least for one of the two sexes, as both cannot be united in the same terminal flower; but, *vice versâ*, both may easily appear in determinate (equal or unequal) degrees of ramification. The most important circumstance to be considered in monœcious relations, consists in both the sexes (*i. e.* the shoots which bear them) occurring either subordinately or coordinately‡, for one either arises out of

* The second axis, which is a complete dwarf or a mere bristly spine, bears the so-called ‘urceolus,’ in the axil of which the female flower is placed, as the third member of the succession of generations.

† The female flowers are placed at the sides of the primary branches as branches of the second degree. In the same place where one single flower occurs in the female plant, a furcately ramified inflorescence is found in the male, produced by branching out of the two bracts of the original flower.

‡ Both these cases doubtless occur in the animal kingdom; the first probably in *Aleyonella*, where the stock is said to be composed partly of males and partly of females. As the stock is here formed by individuals continually shooting out of each other, one sex must shoot out of the

the other, or they both spring from a common mother-stem. In the first case, the female flower usually belongs to the earlier, the male to the later (subordinate) generation; the male flower-shoot springing from the female*, as e. g. in *Euphorbia*, *Ricinus* and *Poterium*, in which the female flower terminates the main axis, and the male occurs as a lateral shoot†. In *Buxus* the female flower occurs as the second, the male as the third axis; in many species of *Phyllanthus* (e. g. *Ph. niruri*), the female as the third, the male as the fourth; in *Xylophylla*, the female (on the margins of the spurious leaves) as the fourth, the male arising from the bracts of the female flower (as in *Phyllanthus*) as the fifth. In *Momordica*, *Ecbalium*, *Cephalanthera*, and some other *Cucurbitaceæ*, the female flower, placed in the axils of the foliaceous leaves of the main-stem, belongs to the third axis, and the male to the fourth; for the third axis, which here arises from the base of the peduncle of the female flower as main axis of the racemose male inflorescence, is a superior leaf-shoot. In the other cases,—in which the succession of shoots, in order to arrive at the two kinds of flowers, separates into two coordinate lines,—both kinds of flowers may appear either immediately in the first generation after this separation, or, since here again preparatory generations are intercalated, in a later one. Further, the number of the generations (axes) in the two lines arising from the division, may be either equal or unequal. A few examples may serve to explain the manifold cases which thus occur. In *Musa*, *Myriophyllum* and *Sagittaria*, the coordinate male and female flowers appear in the first generation after the separation, and in the whole as a second system of axes. Here the female flowers stand in the lower, the male in the upper part of the spicate or racemose inflorescence. The contrary holds true of *Cucurbita* and the monœcious *Bryonia*‡; for here

other. The second case occurs in *Agalmopsis* (according to Sars), where partly female (seminal vesicles) and partly male individuals grow out of the same main-stem.

* The opposite case seems to occur very rarely or not at all. A monstrosity, which for some reasons might be adduced here, is found in *Larix Europæa* and *Picea alba*, in which transitions of the amentaceous male flowers into female cones occur, where the fruit-scales are emitted from the axils of stamens which are often only slightly abnormal.

† As in all the examples adduced, the unessential aggrandizement of the inflorescence must be disregarded, which occurs in *Ricinus* and *Poterium* in the form of lateral female flowers emitted beneath the terminal female flower.

‡ *Bryonia* has apparently axillary racemes; but a more careful investigation shows that they do not spring immediately out of the axil of the foliaceous leaf, but (as secondary branches) out of the peduncle of a single flower standing directly in the axil of the leaf which exactly corresponds to the flower in *Cucurbita*.

the earlier flowers, which appear in the axils of the foliaceous leaves, are male; while the later ones, which appear on the further continuations of the stems, are female. *Arum** has below female, in the middle male, and above again female flowers, though these last are dwarfed and sterile. Likewise in the first generation after the separation, but in the whole as the third system of axes, we find both kinds of flowers in *Pachysandra* and *Acalypha*, and here again, as is usually the case in indeterminate spicate inflorescences of mixed sexes, the female flower is in the lower, the male in the upper part of the inflorescence. The same obtains in monœcious Palms with axillary spadices; though here the flowers appear in ramified spikes from the fourth system of axes. When the flowers make their appearance in the second generation after the division, they cannot easily be united in the same inflorescence, and special male and female inflorescences will arise. Thus, *e. g.*, in *Platanus*, *Liquidambar* and *Sparganium*, in which the female inflorescences occur on the lower part of the main-shoot, and the male in the upper; likewise in *Quercus* and *Fagus*, though here, *vice versâ*, the male inflorescences are the lower, and the female the upper. Finally, if the division of the succession of shoots is an unequal one in the separated lines of generation leading to the two kinds of flowers, *i. e.* if the number of essential axes is unequal, it is greater sometimes for one sex and sometimes for the other. In the Walnut (*Juglans*) it is the male flower which attains the higher degree of ramification; in *Xanthium*, and the species of *Carex* with separated male and female spikes, it is, on the contrary, the female flower†.

Other dimorphisms or even polymorphisms of the flowers, more or less independent of sex, occur when the sexes appear in the two different lines of generation; for even among flowers of the same sex, whether hermaphrodite, male, or female, differences often reveal themselves of a very striking character, which are generally coordinate according to fixed laws of division of generation. Thus, in all *Primulæ*, and in several *Labiata*, two kinds of hermaphrodite flowers occur, in a state of diœcious

* The inflorescence in *Arum* is terminal, as well as that in *Calla*.

† In species of *Carex* with terminal male and lateral female spikes, the male flower belongs to the first generation after the division, and the female to the third. In most of the species where the shootlet which bears the inflorescences is a continuation of the main axis of the plant, the male flowers represent in general the second generation and the female the fourth; in those species, on the other hand, which have a shortened main axis, which forms a mere rosette of leaves whence the shootlets bearing the inflorescences proceed as branches, the male flower is the third system of axes, and the female the fifth; as *e. g.* in *C. maxima*, *leptostachys* and *pilosa*.

separation; one with a large corolla and strongly developed stamens (*forma brevistyla*), the other with a small corolla and strongly developed pistils (*forma longistyla*). According to C. Schimper's observations* both forms occur at times in *Labiata* even on the same stock and in the same inflorescence, e. g. in *Dracocephalum Moldavicum*. Many species of *Viola* also produce two kinds of hermaphrodite flowers on the same stock; early ones of the usual form, and late ones without petals. In *Viola mirabilis* the first arise directly out of the main-stem (as branches of the first degree) and are mostly sterile, while the latter spring from the foliaceous branches (as branches of the second degree) and are fertile. In *Impatiens*, sterile flowers with perfect corollas and apetalous fertile ones occur in the same raceme. The cases in which normally formed above-ground and abnormally formed under-ground flowers appear, belong here; the latter have their corolla developed slightly or not at all, and are merely female, and, *par excellence*, fertile. If both kinds of flowers are fertile, the subterranean fruit differs from that borne above the soil; such cases are found especially in the family of *Leguminosæ*, e. g. in several species of *Lathyrus* and *Vicia*, in *Amphicarpæa*, and *Arachis*†; and also in the very remarkable Abyssinian Convolvulaceous plant, *Hygrocharis Abyssinica*‡. Among the most striking cases of dimorphous flower-formation are those described by Jussieu§ in *Gaudichaudia*, *Camarea*, and other *Malpighiaceæ*. Here, besides the flowers conjoined in racemes or in corymbs, and formed according to the common type of the family, other apetalous flowers occur, standing alone and hidden in the axils of the leaves. Besides the normally formed glandulose corolla, they have only one stamen and two carpels. In several cases the dimorphism of the flowers is confined to the formation of the fruit alone, as e. g. in some species of *Æthionema* (especially *Æ. heterocarpum*, Gay), which in the same raceme bear partly dehiscent silicles with two cells and several seeds, and partly one-celled and one-seeded indehiscent silicles. *Cerato-carpus*||, a North African genus of *Fumariaceæ*, bears in the lower part of the spike oval, ribbed, one-seeded nutlets, and in

* Communicated in the Versamml. d. Natur. zu Wiesb. in Sept. 1852.

† For details, *vide* Treviranus, Bot. Zeit. 1853, p. 393.

‡ Hochstetter, in Schimp. Iter Abyss. Nos. 572 & 1701. The same plant is called *Nephrophyllum Abyssinicum* by Richard, Tent. Flor. Abyss. and figured in pl. 76. The two kinds of flowers are emitted from the axils of the foliaceous leaves of the same creeping stem; those provided with corolla, stamens and pistil stand upright; the others without corolla and stamens bend down to the ground on their long peduncles.

§ Adr. de Jussieu, Monographie des Malpighiacées (1843).

|| Durieu, Explor. scient. de l'Algérie, pl. 78. Endlicher, Gen. Plant., Suppl. iv. p. 32.

the upper part, lanceolate two-valved and two-seeded siliques. Polymorphism of flowers and fruit occurs in the most heterogeneous manner in the family of *Compositæ*; I will only refer to *Zinnia*, *Dinorphotoeca*, *Heterothecca*, *Thrincia*, *Geropogon*, *Crupina*; and especially to *Calendula*, where the hermaphrodite blossoms of the ray produce three different forms of fruit, so that, including the male flowers of the disk, the capitulum presents four different forms of flower-shoots (belonging to the same generation). As somewhat similar cases in the animal kingdom, the instances of dimorphous insects, of which there are several, might be adduced*.

A separation of the series of generations into several distinct lines occurs in fact not only as regards the flower, but also, though less frequently, even among the inferior formations of the plant; this is especially the case where a particular lateral line is allotted to the leaf as well as to the flower. The true Pines afford the best known example of this. Their fascicles of needle-shaped leaves are nothing but foliaceous branches of circumscribed growth †, which lie outside of the line which leads to the two kinds of flowers, while they are essential, as the leaf-formation appears on them alone ‡. Here the generation splits up into three kinds of essential and coordinate shoots: 1st, the small leaf-shoots, which, after some few inferior-leaves forming the vagina, bear two, three, or five foliaceous leaves; 2nd, the male flowers, or small shoots, which are provided with stamens only; 3rd, female inflorescence, shoots with superior-leaves (the integumentary scales of the strobile) in whose axils the fruit-scales of the cone are formed, belonging to a further system of axes. In the animal kingdom cases analogous to these occur in monœcious *Siphonophora*, especially in *Stephanomia* and *Agalmopsis*, where even more than three kinds of coordinate individuals are emitted from the main axis: in particular motory individuals (the so-called *Swimming-bells*), nurses, the proboscis-like formations or imbibing tubes, and as already mentioned, two kinds of sexual individuals.

The differences of shoots thus far considered depend princi-

* The first in several species of *Dyticus* (*D. marginalis*, *circumcinctus*, *Laponicus*, *Ræselii*, according to Erichson, Gen. *Dyticeorum*, 1832, p. 31); the last in *Aphis Quercus*, according to Bonnet.

† That the fascicles of leaves in *Pinus* are branches, is proved by the phenomenon of perescence, which is not unfrequent, especially in young Pines.

‡ The main-stem, as well as all the elongated branches essentially resembling the stem, bear only leaf-scales, which may be best compared to bud-scales, and ascribed to the inferior-leaf formation. It is only in early youth (in the first and second years) that the main-stem itself bears needle-shaped leaves.

pally upon this: one portion represents exclusively the vegetative formation, or a certain part thereof; the others represent the degrees of formation which belong exclusively or principally to the sphere of fructification. Hence, in regard to the division of functions, to one portion the functions of nutrition are allotted, to the others those of generation. For this reason the different kinds of shoots of such a partial character must unite in a determinate succession, and complete each other; and even those which we have designated as unessential are of importance in enriching, preserving, and increasing the plant-stock. Finally, we have still to consider those shoot-formations which properly do not belong either to the essential or the unessential succession of shoots, but rather to an *aberrant* formation; as they neither conduce to the perfection of any of the common steps of the metamorphosis, nor perform any essential physiological function in the plant, but at the best are only of some service as organs of defence, support, or adherence. These are the shoots which take the form of thorns, bristles, hooks and tendrils, which for the most part owe their peculiar abnormal character to an entire suppression of the leaf-formation, and a final induration of the point of vegetation: these seem to be the last, terminal or lateral members of the generation, abortive in every respect. Not unfrequently they form the last ramification of paniculate and dichotomous inflorescences, like terminal flowerless peduncles, as *e.g.* in *Teloxys* (*Chenopodium aristatum*, L.), *Acroglochin*, and in a very peculiar form, branching and complicated by aculeate or setiform leaf-formations, in *Pupalia*, *Desmochata*, *Digera* and *Cometes**; also in *Scleropus*, where they take the form of short, thick, cartilaginous stalks, with two converging leaf-apicules. Among the Grasses they are known under the form of bristles in *Setaria*. In many Rhamnaceous and Sapindaceous plants (*Helinus*, *Cardiospermum*) they appear as small cirrhi; not as the last sterile ramifications of the inflorescence, but on the contrary as the first, followed by other fertile peduncles. They often occur in the axils of foliaceous leaves; and wherever they make their appearance they naturally arrest the further succession of shoots, when they have neither of the two leaves at their origin, out of whose axil an additional shoot may be developed. This is the case in *Passiflora*, whose flower

* The plumose tails which form the "envelope" of *Cometes* are the last branches of the dichotomous inflorescence, accompanied by similar accessory (secondary and tertiary) branchlets. All these numerous sterile branchlets are elongated and beset with setiform leaflets arranged in spiral order ($\frac{2}{3}$), commencing with two similar anterior leaves. The direction of the phyllotaxis in all these branchlets follows the law of furcate inflorescence.

arises from the axil of a leaf situated at the side of the base of the tendril. The thorns of *Ononis*, *Elaeagnus* and *Maclura** present the same phenomenon. In other cases the succession of generation thus arrested by the aculeate shoot is restored by secondary formations; when, with the thorn, a second shoot follows out of the axil, which in some cases may form a leaf-shoot, and in others a flower-shoot. This happens in *Gleditschia*, in several *Acaciae* (e. g. *A. pulchella*), in *Prinsepia utilis*†, the Lemon, the Egyptian *Balanites*, *Duranta*, *Bougainvillea* and *Randia*, in which the secondary shoot arises close under the spine; while in *Celastrus pyracanthus*‡ and *Europæus*, as well as *Pisonia aculeata*§, the secondary shoot occurs above the thorn. In *Uncaria pilosa*|| and *Strychnos spinosa*, pairs of leaves with axillary thorns alternate with pairs which have peduncles in their axils.

Have even these phenomena of extreme alienation of the individual (as they occur in the thorns and hardened shoots of plants) analogous forms in the animal kingdom? Yes, I believe they have! I believe I may assert that in the animal kingdom itself there are individuals which occur as mere fixed claws, pincers, scourges, tactile and predial filaments, &c.—individuals which perform neither functions of nutrition nor of reproduction in the society to which they belong, but which probably merely assist in seizing the food, or lend a helping hand in defending the community. The cases which I have here in mind are of frequent occurrence among Bryozoa, and especially in the group of *Cellariae*. Individuals in the form of horns (which usually conclude the series of complete cell-inhabiting individuals) occur, e. g. in *Eucratea cornuta*¶ and *Cordierii*** ; in another form (reminding us of *Teloxyis*), as forked terminal spines, in *Vesicularia spinosa*††. Moveable individuals, representing mere weapons, in form like a bird's beak, a crab's claw, or a pincers, appear in *Acamarchis avicularia*‡‡ and *flustroides*§§, *Retepora cellulosa*, *Scrupocellaria scruposa*||| and many others. In the last-

* Here belongs also the curious hook of *Uncinia*, which is also visible, though less developed, in many species of *Carex*. The utriculus is a leaf at the base of this spine.

† Royle, Illustr. of the Bot. of Himal. pl. 38. fig. 1.

‡ Boissier, Voy. bot. en Espagne, t. 38.

§ Rheede, Hort. Malab. vii. t. 17.

|| Wallich, Plant. As. Rar. t. 170.

¶ Ellis, op. cit. pl. 21. f. 10 (*Cellaria cornuta*); M.-Edw., Ann. d. Sc. Nat. (1838) t. 8. f. 2 (*Crisidia cornuta*).

** Descrip. de l'Egypte, Polypes, t. 13. f. 3.

†† Van Beneden, Rech. sur les Bryozoaires, t. 4. f. c.

‡‡ Van Beneden, l. c. t. 6. f. 1-8 (*Cellularia avicularia*, Pall. *Crisia avicularia*, Lamx.).

§§ Ellis, op. cit. pl. 38. f. 7.

||| Van Beneden, l. c. t. 5. f. 8-16 (*Cellaria scruposa*, Auct.).

named *Cellariæ*, besides the claw-individuals, there are also scourge-individuals, which Van Beneden himself compared to the cirrhi in plants, and which even Leuckart* acknowledges to be individuals. Besides the 'Swimming-bells' evidently resembling *Medusæ*, the peculiar retractile predial filaments of the *Siphonophora* doubtless belong here also; they are remarkable for a purplish-red swelling on or under the apex, and they shoot out singly as branches from the stalk of the nutritive individual (imbibing-tubes), and themselves bear a series of similarly formed filaments as secondary branches. They are found with unimportant departures from this form, especially in *Physophora*†, *Diphyes*‡, and *Agalmopsis*. In the last-named genus, according to Sars§, they have even three modifications: the spadiceferous terminal piece ends in a long simple filament, or in a short two-parted one, or without any filament at all. In *Stephanomia*|| numerous filaments, called tentacles, arise out of the stalk of the nutritive animals (the so-called proboscis-formed organs) without such coloured swellings, which in the same manner may also be regarded merely as individuals with a very incomplete outfit of organs¶.

After having in the foregoing review regarded all lateral shoots which spring from the main axis of the plant as real individuals, however unimportant a fraction of the total specific character they may realize, it will hardly be deemed surprising if we finally apply this mode of view to the *branches of the root* and to *adventitious shoots*. It is only possible for the main-shoot to develop freely both the points of vegetation of the axis; yet

* Polymorphism. p. 17.

† Philippi, Müller's Archiv, 1843, taf. 5.

‡ Sars, Fauna lit. Norv. tab. 7.

§ *Ib.* tab. 5.

|| Milne-Edwards, Ann. d. Sc. Nat. 1841, pl. 7-10.

¶ Since Sars observed the separation of the Medusa-like sexual individuals in *Agalmopsis*, the view that *Siphonophora* are composite animal stocks has gained ground more and more among zoologists. But this mode of viewing the subject was for the first time carried out (after a fashion) consistently in Leuckart's latest work on strange animal forms (Zool. Unters., erstes Heft, Siphonophoren, 1853); and this idea had forced itself upon me as early as 1847, when I compared the description of *Diphyes* with *Agalmopsis*, in Sars' Fauna lit. Norv. In the above-named work, Leuckart extends the view which allows individual importance to the parts of the stock of *Siphonophora*, not only to the tentacles and predial filaments, but also to the covercles, which in most of the genera are placed close above the nutritive individual as protective envelopes; these formations, like all the other appendages of individual importance, being emitted from the stem as shootlets, and in the first stages of their formation, resembling the tentacles in particular. Accordingly the *Siphonophora* have not less than *eight* different forms under which the individual may appear on the whole stock. (Later note.) [I have omitted the enumeration of these forms.—Tr.]

even here the lower point remains undeveloped. On the contrary, the lateral shoots, thus far considered, have no lower point of vegetation; for their base is united to the maternal shoot, and hence they are mere developments of the upper point of vegetation. Opposed to these, there are, however, other shoots by which the lower point of vegetation is represented, and which on the other hand have no upper point of vegetation. Among these may be reckoned not only the root-branches which take their rise from the main root, but also all adventitious roots which spring from the stem at determinate or indeterminate places. I must, however, content myself with this general hint, as any attempt to particularize these relations could after all only show the deficiency of the investigations into this subject, and how desirable a more comprehensive work is on root-formation in the vegetable kingdom.

The few points which I have selected out of the inexhaustible field of shoot-formation in the vegetable kingdom may in the mean time suffice to show that the comparison of the vegetable shoot with the animal individual is not far-fetched or arbitrary, but is presented to us by Nature herself. The solution of the difficulties which this mode of conceiving the vegetable individual encounters in the lowest grades of the vegetable kingdom, I must defer to a later day. These difficulties are founded upon the less complete organization of the inferior plants, and at all events cannot invalidate the results gained in considering the higher organizations. We may therefore consider it settled, that although the individual has not exactly the same importance in the vegetable kingdom as in the animal, plants still realize their vital cycle in sections which are not only comparable to the animal individual, but are in fact its complete analogues. What distinguishes plants is the formation of family-stocks (a formation manifested in the highest vegetable representations, and here in the richest fullness),—as ancestral trees organically connected, variously disposed in their ramifications, and comprising numerous generations, rendered reciprocally complete through individuals variously endowed. And this leads us back again to the tree from which we set out; in which even our natural perceptions seemed to discern something more than one common individual, and whose high import scientific research must confirm. Just what at the outset appeared to be an obstacle to our allowing the single shoots of the tree their true significance,—now that we have compared them with alternation of generation in animals, at length proves to be the most conclusive demonstration of the correctness of our first conception. The conception of these so heterogeneous shoots as individuals of one and the same species has led us, in fact, to a more pro-

found and more pregnant conception of individuality, which will no longer seem paradoxical when we perceive it is confirmed even in the highest realms of life—in the sphere of the mental development of the individual. Or are the differences of human individuals in mental endowment and development less important than those which we have seen in the morphological and physiological endowment and development of shoots? Do we not meet with a similar reciprocal completion, a similar division of labour among the individuals of the family, of the state, and of nations, and cannot even the human individual become likewise a mere organ? Do we not see the development of the human race itself bound up with a succession, in which the later generations continue the edifice their predecessors began, like branches depending upon the earlier stocks and nourished by them;—in which generation is added to generation, and cycles to cycles; so that thus, by the ever-renewed labour of the individual, the problem of human life may be ceaselessly aspired to, and at last reach its final accomplishment?*

* The preceding pages were almost all printed when I was fortunately enabled to read Reichert's memoir (*Die monogene Fortpflanzung*, Dorpat, 1852), upon a subject closely allied to the one here discussed. His work is full of new views of the subject, elaborated with great acuteness. The vegetable individual itself is considered in detail, and the author is thus led to a mode of viewing this subject similar to the Schultz-Schultzenstein-ian doctrine of *anaphyta*—regarding not only the shoot, but even its single parts, the internodes, with their leaves, as series of individuals shooting out of each other, or intimately connected by continuable bud-formation. Since, however, it is implied in the idea of an individual, that it shall somehow be limited by, and distinguishable from (notwithstanding it is connected with), others, it seems to me that even from this point of view Reichert's idea can by no means be carried out. I will not deny that there are still other considerations in the nature of the shoot which it is difficult to reconcile with the idea of the simple individual, and I can only find the ground of this phenomenon in the fact, that the individual appears in its full import in the higher steps of the series of created beings, while in the lower it loses more and more its reality, if I may so say. I must reserve farther remarks on this subject until I treat of the individuality of the lower plants.

[We cannot but think, after all, that this view of Reichert's, &c., which our author rejects, is the legitimate conclusion, to which the very line of argument so completely and ably presented in the preceding pages, when fully carried out, naturally leads. It is merely a question of *degree* of individuality. As yet, perhaps, no sure middle ground has been secured between the two extreme views,—one of which regards all the vegetative offspring of a seed, however numerously multiplied, as philosophically the individual; while the other views the phyton, or in the simplest lower plants, the cell, as philosophically representing the individual,—real individuality being incompletely realized (and with various grades of incompleteness) in all vegetables, and in many animals. The mind is reluctant to accept either of these conclusions, and seeks—thus far in vain—for some stable intermediate view. Of the two extreme views, if forced to the choice, we should incline to prefer the latter.—Asa Gray.]