

XXXI. *On Prolification in Flowers, and especially on that kind termed Axillary Prolification.* By MAXWELL T. MASTERS, Esq., F.L.S., Lecturer on Botany at St. George's Hospital.

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IN a paper which is inserted in the last Part of the 'Transactions,' I had the honour of laying before the Society the results of my inquiries into the subject of median proliferation. I propose now to treat especially of axillary proliferation in flowers. My materials have been derived from the same sources that are mentioned in my previous paper; and from them I have drawn up a list of genera in which this deviation from the ordinary rule has been observed. The list is, I believe, comprehensive enough to afford a sufficient basis for the opinions and remarks which follow, although I have no doubt many additions might be made to it by a more thorough search through the periodical botanical publications (especially those in the German language) than I have been enabled to make. Anything like a statistical record, showing the frequency with which this form of proliferation has been observed in certain genera and species as compared with others, would be very difficult, if not impossible, to draw up. The approximate estimates which I have formed are, I believe, sufficiently correct for the purposes of this paper.

Among the many points of interest presented by the subject, the following are particularly treated of in this memoir,—viz., the nature, number, and position of the adventitious buds, the genera in which the change is most frequently to be met with, and the inferences to be derived therefrom, the changes that occur in the flowers so affected, conjointly with the proliferation, &c. There are also certain flowers whose construction is such as to render them particularly interesting at all times, and yet more so when the subjects of any deviation which illustrates their normal mode of formation; these are, of course, not overlooked in this paper. Other flowers, that have been erroneously said to be the subjects of this malformation, also demand notice at our hands. A comparison of the two forms of proliferation, axillary and median, leads to such interesting results that I have devoted some space to it. This affords me the opportunity of showing how the morphology of certain of the large families of plants may be elucidated by cases of proliferation; and at the same time it enables me to insert certain particulars relating to median proliferation, which have presented themselves to me since the publication of my paper on that subject.

Axillary proliferation is the term applied to those cases wherein one or more adventitious buds spring from the axils of one or more of the parts of the flower. Engelmann makes use of the word "ecblastesis" to denote the same condition. Both terms are open to the objection that they do not clearly enable us to distinguish proliferation occurring within the flower from a similar state originating outside the flower, within the bracts of the inflorescence. This latter condition, called by Moquin-Tandon lateral

proliferation, is as truly axillary as that to which the name is restricted. In consequence of certain peculiarities in the structure of some flowers, to be hereafter alluded to, it is not in all cases easy to decide whether the new growth springs from the interior of the flower, or from the inflorescence beneath the flower.

The accessory bud presents itself as a leaf-bud, a branch, a flower-bud, or a miniature inflorescence; it may be sessile, but is far more frequently stalked, and in more than half the number of cases is a flower-bud or an inflorescence. There may be one or more of these buds; if two only, then they are usually placed directly opposite one to the other, on the opposite sides of the flower.

It will be seen, from the appended list, that the orders and genera in which this description of adventitious growth occurs most frequently are the following:—*Cruciferae*, especially the genus *Brassica*; *Caryophyllaceae*, e.g., *Dianthus*; *Resedaceae*; *Leguminosae*, e.g., *Melilotus*, *Trifolium*, &c.; *Rosaceae*, e.g., *Rosa*, *Potentilla*, &c.; *Umbelliferae*, and *Campanulaceae*. For the most part, these are groups also peculiarly liable to central proliferation.

All the parts of the flower may be thus affected; but, as might have been anticipated from the foliaceous nature of the sepals, the new bud usually arises from within the axil of one of those organs. Next in frequency to the calyx, the pistil is subjected to this change—the carpels, however, in such a case being disunited and leaf-like. The petals rank next, and lastly the stamens; these latter, indeed, are usually, but not invariably, absent in these instances, the new growth even occupying their position. Hence it may well be that, when such is the case, there is no real axillary proliferation, but rather the substitution of a bud for a stamen. Generally, however, the position of the accessory bud is such that it may properly be referred to the axil of an undeveloped stamen.

The largest number of instances of this malformation, not merely generically, but also individually, occurs in plants the members of whose floral whorls are not united one to the other: thus, it is far more common in polypetalous flowers than in gamopetalous ones. In the proliferated flowers belonging to the latter group, the sepals, if not actually uncombined, are only united for a short distance. The same relationship, but in a much less degree, exists in the case of median proliferation, as that aberration is likewise most commonly met with in polypetalous flowers. Another feature of interest is the rarity with which axillary proliferation is met with in irregular gamopetalous flowers. It may be that the irregular and comparatively excessive growth in some parts of these flowers, as compared with others, may operate in checking any luxuriant tendency in other directions.

As in the case of median proliferation, plants having an indefinite inflorescence are more liable to be affected with ecblastesis than those having a definite one. The degree of branching of the inflorescence may be noticed, as this deformity is far more common in branched inflorescences than in those where there is either a solitary flower or a spicate inflorescence. More than two-thirds of the entire number of genera cited as the subjects of this malformation have a branched inflorescence of some form or other; and about two-thirds of the cases occur in genera having indefinite inflorescences. If individual instances could be accurately computed, the proportion would be even higher.

Fully three-fourths of the entire number of genera recorded as occasionally the subjects of this irregularity possess in their usual state some peculiarity of the thalamus; for instance, in about a third of the whole number of genera, the thalamus is more or less prolonged between some or other of the floral whorls, e. g., *Caryophyllaceæ*, *Potentilla*, *Anemone*, *Dictamnus*, *Umbelliferae*, &c. About one-fourth of the genera have numerous stamens or numerous carpels, or both, springing naturally from the thalamus. In others (about one-sixth) the thalamus is enlarged into a disk, or else presents one or more glandular swellings, e. g., *Reseda*, *Nymphæa*, *Cruciferae*. In the last-named family, as has been already remarked, proliferation is very common. It would be interesting to ascertain precisely what part of an inflorescence is most liable to this affection; but as information on this point is but rarely given in the records of these cases, I can only give the results of my own observations, which go to show that, in a many-flowered inflorescence, those flowers at the outside, or at the lower portion, seem to be more frequently the subjects of this change than those situated elsewhere. This may probably be accounted for by the fact that the malformation is met with most generally in plants with an indefinite form of inflorescence, and therefore the lowermost or outermost flowers are most fully developed; the upper flowers being in a less advanced condition, the change is more likely to be overlooked in them; or it may be that, from the unusual luxuriance in the lower flowers, the upper ones may be either present in their ordinary condition, or may be (as indeed frequently happens) stunted in the size and proportion of their several parts.

Various changes in the form or arrangement of the several floral whorls accompany this malformation; some of these affect the particular organ or organs implicated, and these only, while in other cases some other parts of the flower likewise undergo modification. The changes most commonly met with are such as may be classed under Goethe's theory of retrograde metamorphosis: for instance, if a supplementary bud be developed in the axil of a sepal, that sepal is likely to be more than ordinarily leaf-like in appearance. The dislocation of the affected sepal from its fellows is a very frequent occurrence; in cases of this kind the detached sepal is placed below the others, thus approximating, in position as well as in function, to the bracts. In some of the instances of proliferous pears, on which I shall have occasion to comment, the sepals are described as sharing in the succulent character of the fruit.

The petals, under such circumstances, often exist in the guise of sepals or of small leaves; and instances are recorded wherein the place of the calyx and corolla was supplied by a succession of overlapping green scales, from the axils of which the new buds arose. Such instances seem to afford an extreme degree of a more common change, viz., the diminished size and contracted appearance of the sepals and petals when affected with axillary proliferation. They have also a close relationship to such developments as we see in the Wheat-ear Carnation, in certain species of the genus *Mesa* and others, wherein the calyx is repeated over and again, to the partial or complete suppression of the other parts of the flower. All these cases may be in part explained by the operation of the principle of compensation.

When the androecium is affected, the stamen either remains unaltered, or is present

in a more or less petal-like condition ; but it far more frequently happens that the stamen is entirely suppressed, the adventitious bud supplying its place ; thus was it in the *Dianthus*, a figure of which accompanies this paper (Pl. LIV. fig. 1)*.

The pistil, too, is necessarily subjected to very grave alterations when affected with this malformation. It is separated into its constituent carpels ; and these assume a leaf-like aspect, and are in the great majority of instances destitute of ovules. Indeed, virescence or chloranthly is very intimately connected with this aberration, as might have been anticipated ; for if the parts of the flower assume more or less of the condition of stem-leaves or bracts, it is quite natural to expect that they will partake likewise of the attributes of leaves, even at the expense of their own peculiar functions.

It occasionally happens that an adventitious bud arises from the axil of a monocarpellary pistil. This takes place sometimes in *Leguminosæ*, and seems to have been more frequently met with in *Trifolium repens* than in other plants. The species named is, as is well known, particularly subject to a reversion of the outer whorls of the flower to leaves, and even to a leaf-like condition of the pistil. There are on record instances wherein a leaf-bud has been placed in the axil of a more or less leaf-like carpel ; while at other times a second imperfect carpel has been met with in the axil of the first †. I have myself seen numerous imperfectly developed cases of this kind.

It may be asked whether such cases are not more properly referable to central proliferation—whether the axis is not in such flowers terminated by two, rather than by one carpel ? It is, however, generally admitted by morphologists that the solitary carpel of *Leguminosæ* is not terminal, but is the sole existing member of a whorl of carpels, all the other members of which are suppressed as a general rule, though exceptional instances of the presence of two and even of five carpels have been described ‡.

Again, the adventitious bud or carpel is placed, not laterally to the primary one, or opposite to it, on the same level, but slightly higher up—in fact, in the axil of the primary carpellary leaf. Griffith figures and describes § an instance of the kind in a species of *Melilotus*. The stalk of the ovary is mentioned as having a sheathing base, bearing in its axil a prolongation of the axis of inflorescence, in the form of a short spike with hairy bracts and imperfect flowers, the latter having a well-formed calyx and rudimentary petals and stamens. Griffith infers, from this specimen, that the legume is not to be considered as a terminal leaf.

I have, in my paper on median proliferation, adduced reasons for discarding the term “proliferation of the fruit ;” and the instances now to be commented on supply additional force to those reasons. A very frequent malformation in pears is one wherein a second pear proceeds from the centre of the first, and even a third from the centre of

* This *Dianthus* has the more interest from its similarity to the one described by Goethe, *Metam. der Pflanzen*. cap. 16. sect. 105 ; but in that instance median proliferation also existed. For my specimens I am indebted to Mr. T. Moore, F.L.S.

† Linnæa, vol. xv. p. 266. c. ic. Caspary, *Schriften d. Physik.-Oek. Gesell. zu Königsberg*, Bd. ii. p. 5, tab. 3. fig. 39, &c.

‡ Lindley, *Veg. King*. p. 545 ; also Clarke on the Position of Carpels, *Linn. Soc.*, December, 1850.

§ *Notulæ*, vol. i. *Dicot.* p. 126. *Atlas*, pl. xliii.

the second *. Pears are occasionally also observed arising either from the axils of the sepals of the primary pear or from the axil of leaves originating on the outer surface of the fruits—using the term fruit in its popular sense. These cases afford strong confirmation of the view, that the outer portion of the so-called fruit in these plants is rather to be considered as an expansion and hollowing-out of the flower-stalk, than as formed from the calyx-tube. It is noteworthy that the true carpels and seeds are frequently entirely absent in these cases †. M. Trécul has described and figured an instance in a species of *Prismatocarpus*, in which a second flower proceeded from the axil of a bract attached to the side of the fruit of the first flower ‡. I have in my previous paper alluded to the occasional presence of leaves on the calyx-tube, so-called, of the Rose, Pear, and Apple, to which I may now add, on that of *Cratægus tanacetifolia*.

The unripe fruits of some species of *Lecythis* were stated by Von Martius, at the Meeting of the German Naturalists at Carlsruhe, to produce buds when placed in the earth. The fruit of these plants is probably of the same nature as that of the *Pomaceæ*.

The fruits of *Opuntia Salmiana* and *O. fragilis* § have been observed to form small fruit-like branches around their summits. M. Napoléon Doumet describes the fruit as ripening as usual, but as being destitute of seeds in the interior; after a little while, the fruit begins to wither, and then a circle of small buds, like those of the stem, may be seen at the top of the fruit, each bud springing from the axil of a little tuft of wool and spines found on the fruit. These little buds elongate into long shoots, produce flowers the following year, which flowers exhibit the same peculiarity. Gasparini and Tenore are said to have recorded the same fact as long since as 1832. The specimen from which my figure was taken produced its fruits in the Royal Gardens at Kew, and is now preserved in the museum of that establishment (Pl. LIV. fig. 2). The adventitious growth in these cases appears to arise from the tufts of spines, which, it has been suggested, are the homologues of the sepals. There can be little doubt that the outer and lower portion of the fruit of *Opuntia* and its allies is a dilatation of the flower-stalk. This is borne out by the fruits of *Pereskia*, which bear leaves on their surface arranged spirally.

The fruits of *Pereskia Bleo* are mentioned as producing buds from their summits, in the same way as the *Opuntia* just cited. *P. Bleo* is said, by M. Delavaud ||, to present this anomaly as a constant occurrence. On the summit of the primary fruit, arising apparently from the axils of the sepals, or of small leafy bracts in that situation, are a series of fruit-like branches, which, in their turn, are surmounted by others, even to the fourth generation. I have not seen an instance of this myself; but a figure is given in the work below cited. Tenore also has recorded “the transformation of the fruits of *Nymphæa alba* and *N. Lotus* into true tubercles, after the seeds had returned to the condition of elementary mucilage ¶.” I have not seen the paper wherein this extra-

* Cf. Moq.-Tandon, p. 384; also Lindl. Elements of Botany, p. 65, fig. 130; “Theor. Hort.” Gard. Chron. 1851, p. 67; Irmish, Flora, 1858, &c.

† Caspary, Bull. Soc. Bot. Fr. vol. vi. 1859; also Payer in vol. i. 1854.

‡ Trécul, Ann. Sc. Nat. 2 sér. vol. xx. p. 339.

§ Bull. Soc. Bot. Fr. vol. i. p. 306, vol. v. p. 115.

|| Bull. Soc. Bot. Fr. 1858, p. 685.

¶ Atti della Reale Accademia delle Scienze di Napoli, t. iv. 1839, pp. 41–45.

ordinary phenomenon is described; but, in reference to it, I may cite the opinion of Prof. Alex. Braun, of Berlin, who states that he has read the memoir of Sig. Tenore with astonishment and incredulity: "His idea of the transformation of a ripe fruit, provided with seeds, seems quite inadmissible; and the application which he makes of it to *N. Lotus*, which has stolons like the Strawberry, is surely inexact: he may have confounded with *N. alba*, a different species which bore stolons, or he may have seen a chloranth of *N. alba*, with metamorphosis of the pistil into a foliar bud; but then the flower would not be normal, still less would the metamorphosis have been preceded by the formation of a ripe fruit" *.

Tetragonia expansa has been mentioned frequently as the subject of a similar adventitious development. M. Clos has, however, shown that there is no real proliferation in this plant, or, at least, no axillary proliferation, strictly speaking †.

The specimens that I have examined in Sir W. Hooker's herbarium differ in some measure from those described by M. Clos; and hence, as considerable interest is attached to this plant, I have deemed it advisable to speak of it here at some length.

Prof. Oliver has directed my attention to the earliest notice of this plant, and of its peculiar growth, in a catalogue of plants published by Pallas ‡. The eminent Russian naturalist has figured and described the plant under the name of *Demidovia tetragonoides*, and seems to have had juster notions of the structure of this flower than other more recent botanists. I shall extract such portions of his description as are necessary for the elucidation of the nature of the fruit, and of the adventitious growth attached to it; and intercalate the observations of other botanists, as well as the results of my own examination. Pallas correctly describes the flowers as being placed on short stalks, while other authors describe them as sessile. In truth, the length and thickness of the flower-stalk are subject to considerable variation in different specimens. M. Clos says that the flower-stalk becomes gradually blended with the base of the fruit; and this is usually, though by no means universally, the case. Moreover, in some allied species, particularly in *T. implexicoma*, the flowers are borne on long slender stalks, which do not pass by such insensible gradations into the base of the fruit. Pallas likewise mentions the fact that there are sometimes two flowers in the axil of one leaf, especially towards the upper part of the stem; and I have seen instances where there were three flowers in this situation. In such cases, it is the uppermost flower that is affected in the manner hereinafter mentioned. In speaking of the flower, Pallas thus proceeds:—"Receptaculum cartilagineum, inverse conicum, compressiusculum, coronatum spinis quatuor vel quinque patentibus, et versus pedunculum, ramentis duo oppositis, minimis, sub-barbatis, notatum." Omitting such portions of the description as are not relevant to our present purpose, we come to the following passage:—"E superioribus pericarpis (non omnibus), ad ramenta, prodeunt flores secundarii minores, &c." Here, then, we

* Bull. Soc. Bot. Fr. vol. v., and 'Ueber Polyembryonie und Keimung von *Cælobogyne*.' For a figure and description of indubitable axillary proliferation in the flower of a cultivated sp. of *Nymphaea*, see Gard. Chron. August 18, 1855.

† Bull. Soc. Bot. Fr. 1855.

‡ Pallas, Enum. Plant. Hort. Demidof., Appendix, Petrop. 1781, c. ic.

have the four or five horn-like processes referred to the receptacle of the flower, instead of to the calyx or to the calyx-tube, as is done by DeCandolle, Endlicher, and others. M. Clos considers them to be processes of the upper portion of the flower-stalk,—a view which he supports by citing the fact that the supplementary flower, with its bract, is occasionally found on the top of one of the horn-like processes; and I have myself seen a small leaf in that situation. The figure given by MM. Seringe and Heyland* shows the secondary flower as springing directly from the summit of one of the horn-like processes; and DeCandolle says, “*cornua calycina interdum flores accessarios gerunt*” †. Reverting to Pallas’s description, we find mention made of the ramenta, or small scales which are occasionally found on the fruits of this plant; and the supernumerary flowers are stated to take their origin from them (their axils?). The figures given by Pallas show that the adventitious growths have nothing to do with the true sepals.

Seringe and Heyland ‡ seem to consider the ramenta or scales to be calycine lobes, as they say, “*Des aisselles de quelques lobes du calice naissent, pendant la maturation, des fleurs bien conformées.*”

Misled by these assertions, Moquin-Tandon § and others have considered the plant to afford an instance of true axillary proliferation. It is evident, however, from what has been stated, that the calyx is not affected with proliferation, but that the supplemental bud arises either from the extremity of one of the horn-like processes of the flower-stalk or from the axil of a small bract attached to its side (Pl. LIV. fig. 3). There are a few flowers, however, in which the pedicel supporting the additional flower is united to the side of the primary fruit for a considerable distance; in these flowers, I have not been able to ascertain precisely whether the supernumerary flower-stalk arises from the base of the primary one, or is distinct from it, in the axil of the same bract. If it originates from the stalk of the primary fruit, it affords an instance of lateral proliferation, or proliferation affecting the inflorescence. I have only to add on this point, that the pedicel of the primary fruit is sometimes provided with two rather large-stalked leaves near its base—a circumstance which would lead us to expect that the supplementary flower takes its origin from the axil of one or other of them, and thus constitutes, as just remarked, a case of lateral proliferation (Pl. LIV. fig. 3, *b*).

Similar conclusions apply to the fruit of *Philadelphus*, in one species of which, *P. speciosus*, M. A. Gris has observed that the so-called calyx-tube was provided with two small bracts, from the axil of one of which proceeded a small flower-bud ||.

As to the nature of the adventitious growth itself, but little need be said beyond what has been already stated at the beginning of this paper,—the conditions presented being, with few exceptions, of such a nature, as not to demand special comment in this place, albeit some of them are curious as illustrations of morphological doctrines—such, for instance, as the occurrence of tubers in the axils of the sepals of the Potato, mentioned by Knight ¶. Here the leaf-bud shows itself in the form of a tuber; and the true nature of the latter organ is thereby elucidated.

* Bull. Bot. No. 1, p. 18. † Prodrusus, vol. iii. p. 452.

‡ Op. cit.

§ Terat. Veget. p. 373.

|| Bull. Soc. Bot. Fr. 1858, p. 331.

¶ Proc. Hort. Soc. vol. i. p. 39, fig. 2.

In the *Dianthus* (Pl. LIV. fig. 1), the adventitious growth occurred in the form of a circle of flower-stalks bearing alternate, strap-shaped, petal-like scales and one or two imperfect flower-buds, which were made up externally of leafy or petal-like scales, within which was a gamosepalous calyx enclosing rudimentary petals, stamens, and carpels. In other cases, the outer scales were like carpellary leaves destitute of ovules, their margins widely separated one from the other, and their summits surmounted each by a style nearly as long as the leaf itself.

A comparison of the two forms of proliferation, axillary and median, leads to some interesting results, and enables me to mention a few circumstances that have occurred to me since my former paper, on median proliferation, was published, or that were omitted or overlooked during its compilation. Axillary proliferation is a much less frequent malformation than the central form. If only the number of orders and genera be reckoned, the truth of this statement will be scarcely recognized; but if individual cases could be estimated, the difference in this respect between the two would be very much more obvious. This may perhaps be explained on the following grounds:—

It is now almost universally admitted that the flower is homologous with the branch; that, up to a certain time, the branch-bud or leaf-bud and the flower-bud do not essentially differ*. At a later stage, the difference between the two is manifested, not only in the altered form of the lateral organs in the flower-bud, but in the tendency to an arrest of growth in the length of the central axial portion. Now, in prolified flowers, the functions and to a considerable extent the appearance of a leaf-bud or of a branch are assumed, and with them the tendency to grow in length. Median proliferation, therefore, in this sense, is a further step in retrograde metamorphosis than is the axillary form. To grow in length, and to produce axillary buds, are alike attributes of the branch; but the former is much more frequently called into play than the latter; for the same reason, median proliferation is more common than the axillary form.

The frequency with which “apostasis,” or the separation of the floral whorls one from another, to a greater degree than usual, is met with in prolified flowers has been before alluded to.

In both forms, the adventitious growth is much more frequently a flower-bud or an inflorescence than a leaf-bud or a branch. How this is to be accounted for I can only conjecture. Perhaps it may be due to the position of the flowers on a portion of the stem of the plant especially devoted to the formation of flower-buds to the more or less complete exclusion of leaf-buds, *i. e.* the inflorescence. This is borne out by the comparative rarity with which proliferation has been observed in flowers that are solitary in the axils of the ordinary leaves of the plant. If the lists of genera be perused, it will be seen that nearly all the cases occur in genera where the inflorescence is distinctly separated from the other branches of the stem. In direct proportion, then, to the degree in which one region of the stem or branches of a plant is devoted to the formation of flower-buds to the exclusion of leaf-buds, is the frequency with which those flower-buds may become affected with floral proliferation.

* Linn. *Prolepsis Plant.* § vii.; Goethe, *op. cit.* §§ 103–106.

Flowers borne upon indefinite inflorescences are liable to be affected with either form of proliferation more frequently than those borne upon definite inflorescences. Proliferation in both varieties is also more frequently met with in branched inflorescences than in those in which the flowers are sessile; but the degree of branching seems less material, inasmuch as this malformation is more commonly recorded as occurring in racemes than in the more branched forms of inflorescence. From the similar arrest of growth in length in the case of the flower, to that which occurs in the stem in the case of definite inflorescence, it might have been expected that axillary proliferation would be more frequent in plants having a cymose inflorescence than in those whose inflorescence is indefinite; such, however, is not the case. The reason for this may be sought for in the lengthening of the floral axis, so common in proliferated flowers—a condition the reverse of that which happens in the case of definite inflorescence.

Median proliferation occurs frequently in double flowers; the axillary variety, on the other hand, is most common in flowers whose lateral organs have assumed more or less of the condition of leaves. The other coincident changes have either been already sufficiently alluded to, or do not present useful points of comparison, and may therefore be passed over.

The investigation of these two kinds of aberration from the usual floral arrangement brings to light many interesting facts bearing on the structural peculiarities of certain natural orders. On some of these I propose now to speak, premising, however, that the conclusions drawn from teratological researches, should be checked by the results of a keen scrutiny into the mode of origin and progressive growth of the various flowers, and by the analogies derived from a minute and cautious comparison of one natural form with another.

In the genus *Anemone*, the supernumerary bud has been often seen to spring from the axil of one of the leaves of the involucre, as it is generally called. If so, the proliferation must be classed as lateral, and not axillary. This view is borne out by the analogies presented by *Eranthis*, *Nigella*, and other genera. On the other hand, there are grounds for considering the so-called involucre as a calyx removed to a long distance from the corolla. *Hepatica*, and some species of *Hamadryas*, in which the petals show a tendency to become tubular, may be compared with *Anemone* in support of this latter notion.

The *Cruciferae* seem peculiarly liable to proliferation in one or other of its varieties. When median, it usually happens that the pistil is separated into two leaves,—never into four, as might be expected were the fruit made up normally of four carpels as has been suggested*. Another common change is one which is suggestive of the relationship between this order and *Capparidaceae*, inasmuch as the pistil is placed on the end of a lengthened thalamus or gynophore. When cruciferous flowers are affected with axillary proliferation from the region of the stamens, it almost always happens that the adventitious buds are placed on a level with the two short stamens. This may perhaps be cited in support of the hypothesis that there are normally in this family eight stamens, the two that are usually suppressed being represented in the proliferated flowers by the

* Cfr. Lindl. Veg. Kingd. 3rd ed. p. 355 a.

two adventitious buds. It may be here stated that there are usually (always?) two such buds, and two only, in this family. I have been disappointed in not having been able to discover anything in the cruciferous flowers I have examined that throws light upon the morphology of the hypogynous glands, so common in this family. Either these bodies have been unchanged in the prolified flowers, or they have been entirely absent.

The order *Caryophyllaceæ* is very liable to these malformations. This has been before alluded to, in speaking of the elongation of the thalamus, and the displacement of the members of the floral whorl.

Since the publication of my paper on median proliferation, I have been informed of the presence of that malformation in the flowers of a *Geranium*—a genus of an order in which such an occurrence was to have been expected, from the nature of the thalamus.

Proliflication among the *Umbelliferae* is interesting, from the fact that frequently the calyx is completely detached from the pistil, and is separated into its constituent leaves; at other times the structure of the calyx is less extensively interfered with. The pistil is frequently present in the guise of two disunited lance-shaped leaves. The most remarkable instance that has fallen under my notice is a specimen of *Daucus Carota*, gathered by myself in Switzerland in July 1858 (Pl. LIV. fig. 4). In this specimen the calyx was tubular, its limb divided into five small teeth. The carpels were leaf-like, disjoined, and unprovided with ovules; between them rose a central prolongation of the axis, which almost immediately divided into two branches, each terminated by a small umbel of perfect flowers, surrounded by minute bracts. The petals and stamens were little changed; but the calyx and the leafy carpels demand a more explicit description. The lower part of the carpellary leaves was inseparably united to the interior of the calyx-tube. This latter organ was traversed by ten ribs, apparently corresponding to the primary ridges of the normal fruit; these ribs were destitute of spines, and the bristly secondary ridges were entirely absent. Those portions of the carpels which were detached from the calyx had each three ribs, a central and two lateral ones, which appeared to be continuous with the ribs of the calyx below,—although in the case of the calyx there were ten, in the case of the carpels six ribs, three to each. This diversity in number is thus explained:—A circle of vascular tissue ran round the interior of the calyx-tube, at its junction with the limb, and at the point of insertion of the petals and stamens. This vascular circle seemed to be formed from the confluence of the ten ribs from below. Of the five ribs in each half of the calyx, the three central ones were joined together just at the point of confluence with the vascular circle, above which they formed but a single rib—that traversing the centre of the carpellary leaf; the two lateral ribs of each half of the calyx seemed to be continuous, above the vascular rim, with the lateral ribs of the carpel; these lateral ribs were connected on either side with the central one by short branches of communication. The disposition of the ten ribs may be thus represented:—

1	1	1		1	1	1	
3	2	3	2	3	3	2	3
1	1	1	1	1	1	1	1

The lower line of figures represents the calycine ribs, the middle row shows how each of these ribs is divided at the vascular rim, and the uppermost row shows their distribution

above the rim. From this it will be seen that six of the calycine ribs divide into three branches, one prolonged upwards as a lateral or median rib into the carpellary leaf, the other running horizontally to join with similar branches sent out from the neighbouring rib; the four intermediate calycine ribs divide into two branches only, which join the side branches of the first mentioned, but have no direct upward prolongation into the carpel. The ten ridges are placed opposite to the sepals and petals (Pl. LIV. fig. 5). The nature of the carpophore and of the placenta in *Umbelliferæ* are also illustrated by prolified flowers: thus, in some specimens described by Mr. Townsend*, the ovules were seen hanging from the margin of a leafy carpel. The carpophore, moreover, in place of being, as Dr. Lindley describes it, a forked placenta, which has become in process of development exterior to the carpels†, is in reality, as Mr. Townsend has suggested‡, “a continuation of the axis, serving at first to solder the parts together, and ultimately separating to suspend the freed mericarps.” That such a prolongation of the axis should in some cases bear flowers (as in my specimen) is only a further proof of the real nature of the organ.

It will also be obvious, from what has been before said as to the calyx in prolified flowers of this family, that there is in this group a real calyx-tube.

The proliferous flowers in *Rosaceæ* and *Pomaceæ* have already been alluded to as throwing light on the nature of the fruit of these plants, and on the share which the expanded flower-stalk takes in their production; and similar conclusions may be drawn as to the fruit of some other orders, wherein the ovary is said to be inferior, e. g. *Cactaceæ*, *Philadelphaceæ*, *Myrtaceæ*, *Tetragoniaceæ*, *Campanulaceæ*, and probably also of many other families not here alluded to. The conclusions tally well with the organogenic researches of Payer, Trécul, and others.

Furthermore, the accessory buds which are occasionally found on these fruits are rather to be referred to lateral than to axillary proliferation, strictly so called. They have been mentioned in this place inasmuch as they are usually recorded as cases of axillary proliferation, and are to be found under that head in the works treating on such matters. Other important changes affecting the characters of certain natural orders, such as the change from an adherent to a free ovary, from perigynous to hypogynous stamens, &c., have been already mentioned, and need no further comment in this place §.

* Bot. Gazette, vol. iii. p. 52.

† Veg. Kingd. p. 774.

‡ Loc. cit.

§ For figures and descriptions of flowers affected with proliferation, which are not specially referred to in these papers, the reader is referred to the oft-cited treatises of Moquin-Tandon and Engelmann, where numerous references are given; also to Dr. Lindley's 'Theory of Horticulture,' and to a memoir of Prof. C. O. Weber, in Verhandl. des Nat.-Hist. Vereins des Preuss. Rheinlandes und Westphalens, vol. vi. 1858, &c. &c.

List of Genera in which Axillary Prolifcation has been observed.

Order.	Genus.	Leaf-bud or Branch.	Flower-bud or Inflorescence.	From what organ.
Ranunculaceæ . . .	Clematis	Flower-bud	Sepals.
	Caltha	Ditto	Ditto.
	Aconitum	Ditto.
	Delphinium	Ditto	Ditto.
	Anemone	Ditto	Involute ?
Nymphæaceæ . . .	Nymphæa	Fruit ?
	Nymphæa	Flower-stalked . . .	Petal.
Cruciferae	*Brassica	Leaf-bud	Flower-bud	Sepals and petals †.
	Brassica	Ditto	Stamens.
	Brassica	Ditto	Ditto	Pistil.
	Cardamine	Ditto	Sepals.
	Cheiranthus	Ditto	Ditto.
	Erysimum	Ditto	Sepals and pistils.
	Lepidium	Ditto	Petals and stamens.
	Arabis	Ditto	Sepals.
	Diploaxis	Flower, inflorescence	Pistil, calyx and corolla.
	Cleome	Flower-bud	Sepals.
Capparidaceæ . . .	*Reseda	Ditto	Ditto.
Caryophyllaceæ . .	Arenaria	Branch	Ditto.
	Agrostemma	Leaf-bud	Ditto.
	*Lychnis	Ditto	Ditto.
	Stellaria	Ditto	Ditto.
	Silene	Ditto	Ditto.
	*Gypsophila	Ditto	Ditto	Sepals and stamens.
	*Dianthus	Ditto	Ditto	Sepals.
	Dianthus	Ditto	Inflorescence	Petals and stamens.
	Alcea	Flower-bud	Stamen.
	Citrus	Ditto	Ditto.
Malvaceæ	Dictamnus	Ditto	Pistil leafy.
Aurantaceæ	Tropæolum	Ditto	Petals.
Rutaceæ	Celastrus	Ditto	Ditto.
Tropæolaceæ . . .	Celastrus	Ditto	Ditto.
	*Melilotus	Inflorescence	Sepals and petals.
	Medicago	Flower-bud	Sepals.
	Coronilla	Ditto	Ditto.
	Trifolium	Ditto	Second carpel axillary to first . . .	Pistil.
Rosaceæ	Trifolium	Flower-bud	Sepals and petals.
	Pyrus	Fruit ?	Fruit ?
	Cerasus	Flower-bud	Petals and stamens.
	Potentilla	Ditto	Leafy carpels.
	Crataegus	Ditto	Petals.
	*Rosa	Ditto	Ditto	Sepals, petals, stamens and pistil.
Myrtaceæ	Lecythis	Ditto	Fruit ?
Tetragoniaceæ . . .	Tetragonia	Ditto	Ditto.
Cactaceæ	Opuntia	Fruit-like branch	Tufts of spines.
	Pereskia	Fruit-like branch	Sepals ?
Philadelphaceæ . .	Philadelphus	Ditto	Sepals ?
Umbelliferæ	*Athamanta	Ditto	Calyx.
	Daucus	Ditto	Calyx and pistil.
	Bupleurum	Ditto	Ditto ditto.
	Torilis	Ditto	Ditto ditto.
	Apium	Ditto	Ditto ditto.

† A mark * is attached to those genera that are the most frequently affected with axillary proliferation.

Order.	Genus.	Leaf-bud or Branch.	Flower-bud or Inflorescence.	From what organ.
Umbelliferæ . .	Pastinaca	Flower-bud	Calyx and pistil.
	Heracleum	Ditto	Ditto ditto.
	Angelica	Umbel	Ditto ditto.
Campanulaceæ .	*Campanula . .	Branch	Sepals.
	Prismatocarpus	Ditto	Fruit	Sepals, &c. ?
Gentianaceæ . .	Gentiana	Flower-bud	Sepals.
Convolvulaceæ .	*Convolvulus	Ditto	Outer calyx.
Solanaceæ	Solanum	Ditto	Sepals.
	Solanum	Tubers	Sepals and petals.
Scrophulariaceæ	Digitalis	Ditto	Petals, &c.
	Veronica	Raceme	Calyx.
Primulaceæ . . .	Anagallis . . .	Branch	Ditto	Petals.
Polygonaceæ . . .	Rumex	Ditto	Sepals.
Santalaceæ	Thesium	Leaf-bud	In place of stamens and pistils, both absent.
Euphorbiaceæ ? .	Euphorbia ? . .	Ditto	?	
Liliaceæ	Herreria	Ditto	Outer bracts ?
	Hyacinthus	Flower and raceme	Sepals.
	Convallaria	Flower-bud	Perianth.
	Leucoium	Ditto	Ditto.
Cyperaceæ	Carex	Inflorescence . . .	Ditto.
				Utricle.

Note.—The following genera must be added to the list of those occasionally affected with median proliferation (*vide* p. 368 *hujus voluminis*) :—

	Leafy.	Floral.
Ranunculaceæ	Clematis.
	Delphinium.
Cruciferae	Diplotaxis.
Geraniaceæ	Geranium.
Rosaceæ	Cerasus.
Compositæ	Carthamus.
Euphorbiaceæ	Euphorbia.
Liliaceæ	Leucoium.

EXPLANATION OF PLATE LIV.

Fig. 1. Flower of *Dianthus*, sp.? The calyx is removed; the petals are reflected to show the adventitious flower-buds, &c., occupying the situation of the stamens.

Fig. 2. *Opuntia Salmiana*, showing the accessory buds arising from the tops of the fruits.

Fig. 3. Flowers of *Tetragonia expansa*, showing the position and attachment of the secondary flowers.

a. Vertical section of a flower.

b. Flower with two bracts on the pedicel.

Fig. 4. Flower of *Daucus Carota*. Petals and stamens removed. Calyx without prickles. Carpels prolonged and developed in the form of leaves; between the two rises a flower-bearing axis, one branch of which alone is represented.

Fig. 5. *Daucus Carota*. Diagrammatic sketch of the interior of the calyx and carpels, showing the arrangement of the ribs and the prolonged axis, the upper part of which has been removed.

