Note on the Structure and Affinities of *Parnassia palustris*, L.

By Alfred W. Bennett, M.A., B.Sc., F.L.S.

[Read November 19, 1868.]

The true position of *Parnassia* has been a source of much doubt and variety of opinion among botanists, having been placed by authors of acknowledged repute among Hypericaceæ, Droseraceæ, Saxifragaceæ, and constituting an order by itself, Parnassiaceæ. The chief advocates of its place among the Hypericaceæ were Don and Lindley. It is singular, however, that of the characters which Lindley gives in his 'Vegetable Kingdom' as those by which St. John's Worts may be recognized, viz. the axile placentation, and the polyadelphous stamens, together with the long style, the unequal-sided petals, and the opposite dotted leaves, not one applies to *Parnassia*, the affinity being founded entirely on the exalbuminous seed, and on a fancied analogy between the polyadelphous stamens of *Hypericum* and the glandular scales which constitute the nectary of *Parnassia*. With Droseraceæ, under which order the genus is placed by Babington and most of the older English botanists, the affinities of *Parnassia* consist mainly in the unilocular ovary, terminating in several stigmata, the parietal placentation, the extrorse anthers, and the marcescent petals. Bentham and Oliver unite Droseraceæ with Saxifragaceæ, an alliance not recognized by the older botanists. Without presuming to express an opinion opposed to that held by such high authorities, I may point out the following important differences in structure between *Saxifraga* and *Parnassia*:—In *Saxifraga* the capsule is bilocular, the styles never more than 2, the placentation axile, and the anthers introrse; in *Parnassia* the placentation is parietal (Dr. Hooker finds no signs of any deviation from this structure in any of the Himalayan species he has examined), the capsule is unilocular, the styles 3 to 5, and the anthers extrorse.

In transferring *Parnassia* to Saxifragaceæ, I cannot help doubting whether too much force has not been given to the perigynous character of the stamens, as, if that is insisted on as a material point, *Parnassia* must be entirely removed from *Drosera*, with which genus all botanists seem to agree it has very close relationship, and which has the stamens truly hypogynous, at least in our European species. Indeed a strict carrying out of this test would necessitate the division of *Drosera* itself into widely separated orders; for St.-Hilaire describes Brazilian

species of that genus as passing by every grade into a true attachment between the stamens and the calyx, and the same variability occurs also among Violaceæ.

On the difference in the structure of the seeds I do not lay so much stress, as, if their exalbuminous character is to be taken as an essential point, *Parnassia* must either be referred back to Hypericaceæ, with which it has no other affinities, or be hopelessly consigned to the solitary confinement of a separate order. The extrorse stamens are, however, connected with an important physiological function presently to be described. In his 'Genera of North-American Plants,' Prof. Asa Gray describes the anthers of *Parnassia* as introrse, and gives a drawing of *P. Caroliniana* as an illustration. I do not, however, find any other observer to agree with Prof. Gray's observation in this respect, except two American botanists, Dr. Torrey and Mr. Chapman, who have probably borrowed their descriptions from him; nor do any specimens which I have been able to examine of this species confirm any departure in this respect from the ordinary type of the genus.

Before pointing out what seem to me the affinities between *Parnassia* and some tropical genera with which it has not been generally associated, a few remarks may not be out of place on the physiological structure of our British species. The true morphological value of the remarkable glandular petaloid scales of *Parnassia* has been a subject of much discussion. The advocates of its affinity with *Hypericum* of course consider these scales to be modified polyadelphous stamens united together at the base. The fact, however, that notwithstanding the countless number of specimens examined by some German botanists, I can find no record of a single flower having ever been gathered in which the glands have reverted into pollen-bearing anthers, seems to me a strong argument against this hypothesis. In certain Himalayan species these scales seem entirely to lose their staminoid appearance, and to be simply bifid or trifid at the apex, or even almost entire. I am rather disposed, on the other hand, to consider them to be a modified inner row of petals, the glands having an unmistakeable function, as we shall presently see, connected with the distribution of the pollen. Dr. Buchenau (Botanische Zeitung, vol. xx. p. 307) goes so far as to view the glands as metamorphosed carpels!, having found a specimen in which they are rolled up in a carpellary fashion. The 4 stigmata

present an anomaly in the otherwise quinary arrangement of the parts of the flower. Foreign species, however, present a more symmetrical structure. The drawing of *Parnassia Kotzebui* in Hooker's 'Flora Boreali-americana' clearly indicates 5 stigmata; and Dr. Seemann, in his 'Botany of the Herald,' speaks of frequently gathering both that species and *P. palustris* with 5 stigmata. Prof. Röper also records, in the 'Botanische Zeitung' (vol. x. p. 187), his supreme delight, after inspecting more than a thousand flowers of *P. palustris*, in being at length rewarded by gathering one with 5 stigmata. Dr. Hooker, on the other hand, describes Himalayan species with only 3 stigmata. If, therefore, we are to take the number of stigmata in *Parnassia* as variable from 3 to 5, with 5 as the normal number, as shown by the reversion of *P. palustris*, it will assimilate the genus more closely to *Drosera*, while removing it still further from *Saxifraga*.

The most remarkable feature, however, in the physiology of *Parnassia* is the phenomena attending its fecundation, which I had an opportunity of observing somewhat closely during a stay last summer in Argyleshire. The fullest and most accurate description of these phenomena hitherto published I find in Vaucher's 'Histoire physiologique des Plantes d'Europe,' from which I translate as follows:—"The physiological phenomena which *Parnassia* presents belong chiefly to its fecundation. When the flower is fully open, the filaments, at first very short, suddenly lengthen, and place the anthers on the top of the ovary, so that all the glandular globules, and especially the scale which bears them, and which is covered with little drops of honey, can dissolve the pollen with which they are sprinkled. This operation accomplished, the anther falls and disconnects itself, and the filament resumes its original place. Each of the anthers successively executes the same movement; but those which succeed each other are alternate, and not contiguous, so that the march of the phenomenon is never interrupted. The anthers are extrorse and somewhat lateral; the pollen consequently cannot fall on the stigma, but falls on the nectaries, which are, as it were, smeared with it, and only the emanation from which can, I think, fertilize the stigmata. It would be difficult, at least, to assign any other function than that of the absorption of the pollen to this nectary, so remarkable and so constant in all the species of the genus. What confirms my conjecture is, that the stigmata are entirely invisible while the anthers are discharging their pollen, and that

they only begin to display themselves and to expose their papillose tongues at the moment when the emission is accomplished" (vol. i. p. 324). The successive lengthening of the filaments was observed so long ago as by Sir James Edward Smith; and the manner in which this takes place is very remarkable. The increase, to the extent of at least three or four times their original length, must be accomplished in an incredibly short space of time; the adhesion to the ovary is so strong during the whole of this time that they cannot be bent back without breaking them; but as soon as the pollen is discharged, they retire to a horizontal position between the petals, and the anther falls. My own observation does not, however, confirm Vaucher's statement that the lengthening takes place alternately; I have frequently noticed contiguous stamens to follow each other. It will be observed that the movement of the stamens in *Parnassia* presents but little resemblance to the "approach of the stamens to the pistil in pairs," which is described as taking place in certain species of *Saxifraga*; nor does it appear in this latter genus to be accompanied by the simultaneous lengthening of the filament, which serves an important physiological function. Together with this elongation of the filament, and previously to the discharge of the pollen, a singular contraction of the anther takes place; and I have no hesitation in concluding that the arrangement above described is one of the most remarkable provisions of nature yet observed for insuring cross-fertilization; for not only does the anther place itself, at the time of the ripening of the pollen, with its back on the very apex of the pistil, so as completely to close the approach to the ovary, but, as if to make assurance doubly sure, the stigmata are not developed until the whole of the anthers have successively performed this movement and discharged their pollen. The object of the glandular nectaries is now clearly seen, and is not, as Vaucher imagined, the return of the pollen to its own stigma, but to enable insects to carry it away to other flowers in which the stigmata are already expanded. I spent a considerable portion of one of those rainy mornings which in Scotland bring forth such countless clouds of insects, in keeping watch over a field as thickly studded with *Parnassia* as an English hedge-bank with primroses, and scarcely noticed a single flower in which several insects were not regaling themselves on the nectariferous glands—belonging to several species, but mostly a long-legged dipterous fellow, whose long thighs, straddling

right across the centre of the flower, could not fail to carry the pollen right on to the expanded stigmata of some other more fully developed flower. Those plants which were in a sufficiently advanced state invariably had the ovary loaded with seeds. It will be understood, from the above description, why I am disposed to lay considerable stress on the extrorse anthers of *Parnassia* as contrasted with the introrse organs of *Saxifraga*.

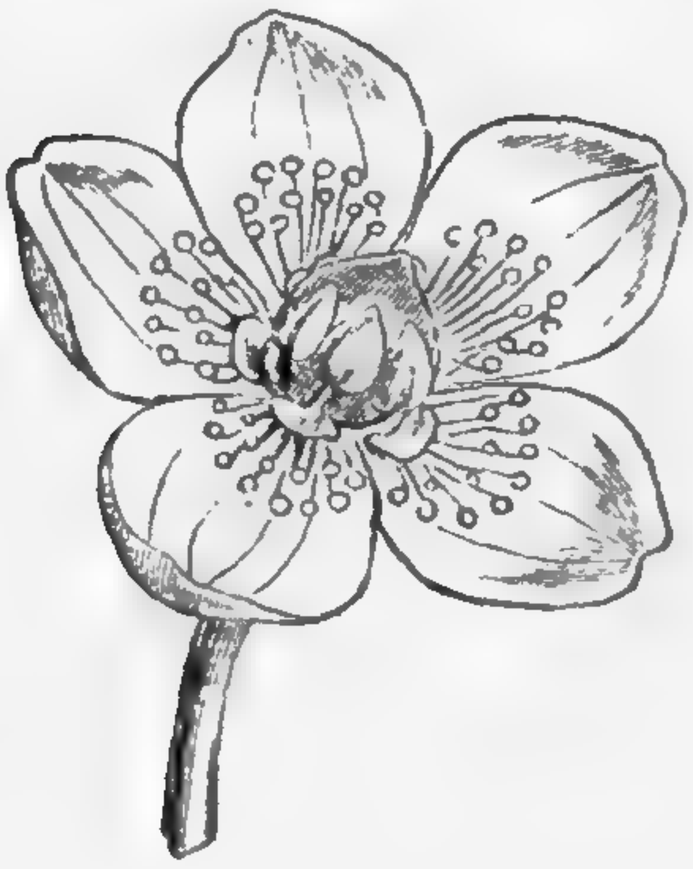
While investigating the affinities of *Parnassia*, I was struck with the resemblance, in more than one point, between this genus and two others not generally associated with it, principally located in Tropical America, *Sauvagesia* and *Lavradia*, which have also been referred by botanists to a number of different orders, having been variously placed under Cistineæ, Violaceæ, Frankeniaceæ, Elatineæ, Droseraceæ, or, to cut the Gordian knot, have been erected into an order by themselves. The most general view of their correct position may probably be taken to be that adopted by Bentham and Hooker in the 'Genera Plantarum,' where they are ranged under Violaceæ. Here, again, I may be permitted simply to point out the discrepancies which separate them from the typical genera of that order; and in this, as well as in tracing their relationship to *Parnassia*, I am chiefly indebted to the admirable monograph of the two genera contained in St.-Hilaire's 'Histoire des Plantes les plus remarquables du Brésil et du Paraguay.' In *Viola*, then, the corolla is irregular, there is but a single row of petals or stamens, the anthers are turned inwards, frequently united into a ring or tube, and with the connective extended considerably beyond the anther-cells, and the dehiscence of the capsule is loculicidal. In *Sauvagesia*, on the other hand, the corolla is regular, there is a single or double row of inner petals or staminodia, the anthers are turned outwards, entirely distinct, and with the connective not prolonged, and the dehiscence of the capsule is septicidal. The so-called "staminodia" of these genera, which I cannot but look upon as the analogues of the glandular scales of *Parnassia*, are very remarkable. In *Lavradia* they present a single row of petaloid organs, united together into a tube completely enclosing the pistil and the stamens, which are furnished with very short filaments, and closely resemble those of *Parnassia* at an early stage, having the same extrorse dehiscence. In *Sauvagesia*, instead of one, there are two rows of these additional organs; and, what is very remarkable, the exterior has a staminoid, and the interior row a

petaloid appearance. The exterior row are described by St.-Hilaire as varying in form in the different species, but always thread-shaped at the base, and thickened upwards to the shape of a club, a nail, or a spade; the inner row consists of 5 distinct petaloid scales, surrounding the generative organs, but not united, as in *Lavradia*, into a tube. Taking these two rows of organs unitedly as constituting the nectary, it would be difficult to consider both the inner and outer row metamorphosed stamens, the inner row appearing never to present an approach to a staminoid form, and the outer row being frequently partially or entirely aborted; and this would seem to confirm the view that the scales of *Parnassia* should be regarded in the light rather of petals than of stamens. I can find no record of any observation of phenomena connected with the stamens of *Sauvagesia* similar to those I have described in *Parnassia*, or identifying, as I should expect would be the case, the functions of the extrorse anthers and nectary of *Sauvagesia* with those of our English genus. In all the species of *Lavradia*, however, the inner corolla is described as purple or rose-coloured, as if for the purpose of attracting insects, while the exterior corolla is generally white.

The most conspicuous structural differences between *Parnassia* and *Sauvagesia* are the 3–5 stigmata and exstipulate leaves of the former, contrasted with the single style and stigma and the remarkable laciniated or fimbriated stipules of the latter genus, together with the difference in their general habit. It will be interesting, therefore, to trace what aberrant forms exist connecting the two. In Hooker and Thomson's 'Præcursores ad floram Indicam' (Journal of the Linnean Society, vol. ii. p. 55), I find that Himalayan *Parnassiæ* are described as "styles 3 or 1," while in *P. tenella*, on which species they remark (p. 79) that, "though it is decidedly the most abnormal species of the genus yet discovered, it is somewhat singular that it does not throw any light on the affinities of the genus," we have the "fimbriated stipules" so characteristic of *Sauvagesia* and *Lavradia*, and the curious scutiform staminodia irresistibly remind one of those of several species of *Sauvagesia*. In *Sauvagesia tenella*, on the other hand, the smallest species of the genus, the slender habit and distant alternate sessile spathulate leaves, together with the partial or entire abortion of the outer row of staminodia, show a marked approach to some of the species of *Parnassia* with foliose scapes, while the stipules, described by St.-Hilaire as very small,

are either deciduous or entirely absent in the specimens preserved in the Kew Herbarium.

With the exception of *Sauvagesia erecta*, which spreads into Mexico and the West Indies, and even into Madagascar and Java, these two genera are confined to South America and almost entirely to Brazil, while the less important allied genera of *Schuurmansia* and *Neckia*, presenting the same general features in their structure, belong to the Indian archipelago. Without, therefore, assuming a definite opinion that *Parnassia*, *Sauvagesia*, and *Lavradia* should be united into the same order, I would venture to suggest whether our pretty little English Grass of Parnassus, so foreign in many respects in its appearance, may not be looked on in some sort as a European and temperate representative of the tropical *Sauvagesiæ* and *Lavradiæ*.



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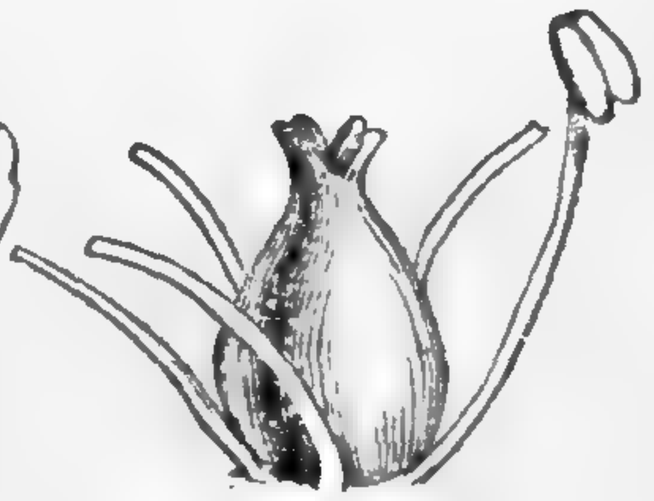

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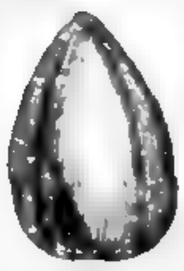

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1. Flower of *Parnassia palustris* at the time of opening.
2. Stamen commencing to discharge pollen.
3. Flower with all the stamens discharged.
4. Stamen retiring from pistil; stigmata developed.
5. Pistil at the time of opening of the flower.
6. Stamen discharging pollen (magnified).
7. Pistil after the stamens are discharged.

Note.—Since the above paper was written, some observations

on the same subject, by M. Gris, have been published in the 'Comptes Rendus' of the French Academy for Nov. 2nd, 1868. The conclusions at which M. Gris has arrived concur, on almost every point, with those to which I have been led, as far as the physiological structure of *Parnassia* is concerned. That botanist points out that, as long ago as 1793, Sprengel observed that the relative positions of the pistil and stamens in this genus necessitate the hypothesis of fertilization by insect agency. Linnæus, St.-Hilaire, and other botanists have presented different views of the structure of the flower; but a careful series of observations by M. Gris fully confirm in almost every respect the accuracy of Sprengel's description. The points to which M. Gris especially refers as having been lost sight of by most recent writers are, the completely extrorse character of the anthers at the period of their dehiscence, the non-maturity of the stigma until after the whole of the stamens have discharged their pollen, and the fact that the stamens never do "approach the pistil in pairs" (which has been urged as an analogy between *Parnassia* and *Saxifraga*), but that their remarkable elongation is accomplished in close contact with the ovary, which they do not quit till after the discharge of the pollen.

Notes on the Stamens of *Saxifragæ*.

By Mr. Duncan. Communicated by J. E. Baker.

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The two species to which the remarks which follow appiy are *Saxifraga cæspitosa* and *S. hypnoides*; and, without any modifications of importance, what is true of the stamens of any one of these is true also of the other.

Shortly after the expansion of a flower, the stamens, which are of two lengths and in two rows, lie back to the petals; and in this spreading position they continue until the pollen is almost ready for being shed. The contents of only one anther at any given time are ready for dispersal; and each mature stamen is brought at the right moment into that position which is most favourable for the contents of the anther being emptied on the stigma, by the timely bending inward of the filament. So soon as the pollen is discharged, the stamen slowly retires again, through the unbending of the filament, and takes up its old station close to the petals. Every stamen goes through the same per-