

FERTILISATION OF FLOWERS BY INSECTS¹
XVI.

Alpine Species of *Gentiana* adapted to *Lepidoptera*.

GENTIANA BAVARICA (Fig. 106-108), *G. verna* (Fig. 109-111), *G. nivalis* (Fig. 112-114), of which I have examined living specimens in the Alps, and *G. imbricata*, *æstiva*, *pumila*, and *utriculosa*, of which I have examined only dried specimens,² agree so completely in the structure of their flowers, and in their contrivances for cross-fertilisation by insects, that they all obviously belong to the same section of the genus *Gentiana*, and are adapted to the same group of visiting insects. They all possess a long narrow corolla (Fig. 106),³ which contains in its lowermost portion the honey, secreted, as in our

dilated into a circular disc (cf. Fig. 106, 109, 112), and bordered at its margins with hair-like papillæ (Fig. 108). In all of them small openings are visible in the fully-opened flower between the margin of the stigma and the inclosing corolla (Fig. 109); but as soon as the corolla begins twisting (Fig. 110), these openings are concealed. In all of them the anthers surround the stigma, thus placing their pollen on the way to the honey (a, Fig. 106, 110, 114). They can all, therefore, be fertilised only by such insects as have a proboscis sufficiently long to reach the base of the corolla, and at the same time either sufficiently slender to enter through the small openings (*Lepidoptera*), or sufficiently strong forcibly to enlarge the entrance of the flower (*humble-bees*). Such an enlargement, indeed, would be possible by the expansion of the same folds between the petals (cf. Fig. 106, 107, 109, 110, 112), by which the flower is enabled to twist, and to close, as soon as colder weather frightens away its natural fertilisers.

Now, looking about to discover what *Lepidoptera* and *humble-bees* might be the natural fertilisers of the present

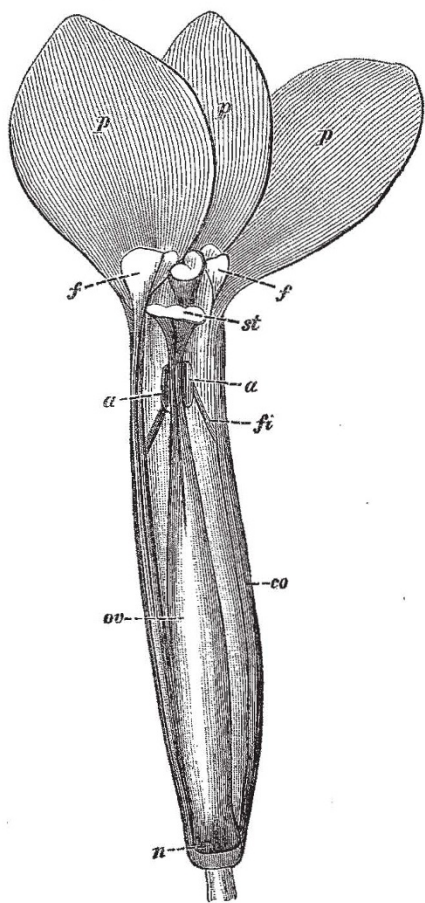


FIG. 106.

FIGS 106-108.—*Gentiana bavarica*. FIG. 106.—Lateral view of a flower which begins twisting and closing, the calyx and the anterior portion of the corolla having been removed (3½ : 1). FIG. 107.—The same flower viewed from above (3½ : 1). The margin of the circular stigma is already covered by the revolving corolla. FIG. 108.—The stigma seen from above (7 : 1).⁴

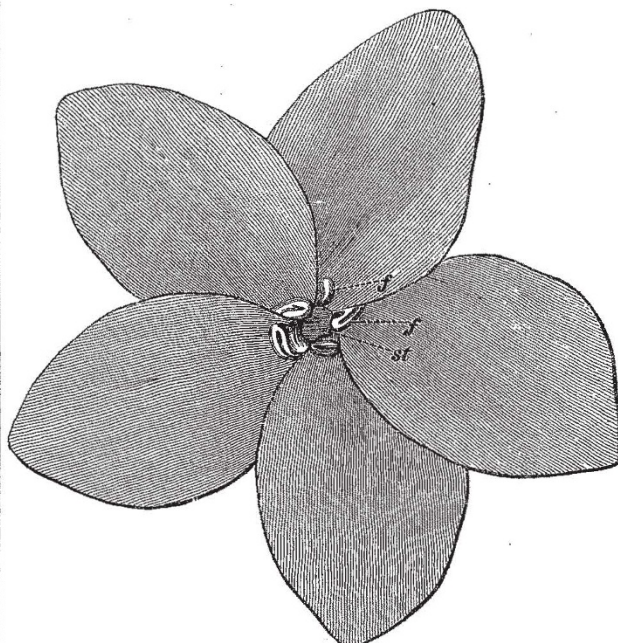


FIG. 107.

group, I was surprised at the fact that of all the 162 species of *Lepidoptera* which I had observed visiting flowers in the Alps, *Macroglossa stellatarum* alone has a proboscis sufficiently long (25-28 mm.) to reach the honey in all the species of *Gentiana* in question, and that of the Alpine *humble-bees*, even those provided with the longest proboscis of all, *Bombus hortorum* (18-21 mm.) and *B. opulentus*, Gerst. (22 mm.), are incapable of reaching the honey in all the above-named species, except by thrusting the whole of their head into the narrow corolla-tube. Moreover, direct observation seems to prove that *humble-bees* insert at the most their proboscis into these flowers, but never their whole head. For instance, in the Albula Pass, July 28, 1876, I saw a *humble-bee* flying about for a long time in search of flowers; at length it hastily visited *Gentiana verna*, but having only once thrust its proboscis into a flower, it flew away out of my sight. Likewise near Pontresina, August 4, 1876, I saw *Gentiana nivalis* visited by *Bombus mendax*, Gerst. ♀, but, after having hastily tried one or two flowers in the same



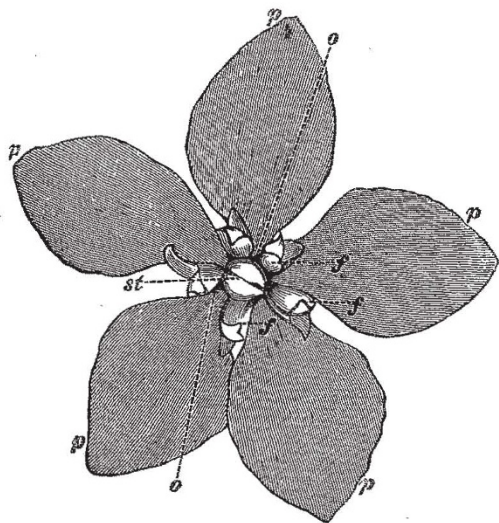
FIG. 108.

two first groups, by an annular swelling at the base of the pistil⁵ (n, Fig. 106, 111, 113). They all have the entrance to the corolla-tube closed by the bi-lobed stigma being

¹ Continued from p. 379.
² For specimens of *G. pumila*, *æstiva*, *prostrata*, *Fralichii*, and *purpurea*, I am indebted to Prof. Ascherson of Berlin.
³ Only in *G. æstiva* the corolla-tube seems to be considerably wider than in the other species.
⁴ The following explanation of the lettering applies to all the figures:— a = anthers, co = corolla, f = filaments, n = nectary, o = openings conducting to the honey, ov = ovary, p = petals, s = sepals, st = stigma, f = folds of the corolla by which its twisting is made possible.
⁵ I found the length of the corolla-tube, from the nectary to the stigma, in the species in question as follows: *G. æstiva*, 26-28 mm.; *G. verna* and var. *brachyphylla*, 23; *G. bavarica*, 20-22; *G. utriculosa*, 18-22; *G. pumila*, 16-18; *G. imbricata*, 15; *G. nivalis*, 13-16 mm.

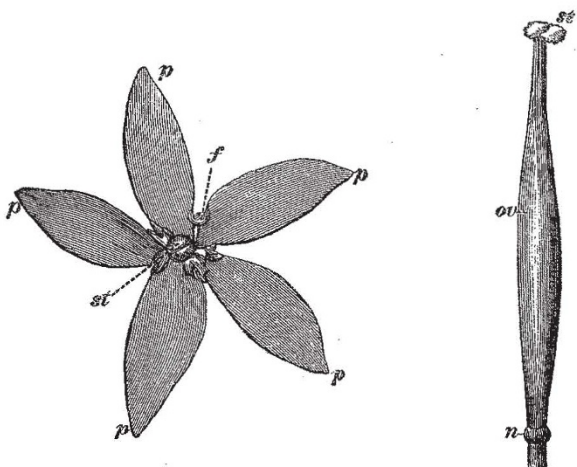
manner, it passed over to *Trifolium nivale*, which it then sucked perseveringly. If from these observations we may infer that the forcible enlargement of the narrow corolla-tube of the species of *Gentiana* in question is too inconvenient for the humble bees, then the only insects capable of gaining the honey in all the species of the present group and capable of regularly visiting and cross-fertilising them, are *Macroglossa stellatarum*, and perhaps some other Sphingidæ not yet observed by myself in the

is exclusively adapted to Lepidoptera, we ought to embrace this opinion with due precaution; for all visits of Lepidoptera, hitherto directly observed by the comparison of the length of their proboscis with the length of the corolla-tube, prove to have been only fruitless attempts. On *G. nivalis* (corolla-tube 13-16 mm.), near Pontresina, August 4, 1876, I observed *Cænonymphea satyrion*, Esp. (proboscis, 7 mm.), and *Hesperia serratulæ*, Rbr. (10-11 mm.); on *G. verna* (corolla-tube, 23 mm.) in the Albula Pass, July 28, 1876, I found *Melitæa aurinia*, var. *Merope*, Prunn. (7 mm.), *Argynnis pales*, S. V. (9-10 mm.), and *Erebia lappona*, Esp. (8-9 mm.); on *G. bavarica* (20-22 mm.), Kerner¹ observed *Agrotis cuprea* (12 mm.), I myself, upon the Piz Umbrail, July 15, 1875, saw *Erebia lappona*, Esp. (8-9 mm.); in the Albula Pass, July 27, 1876, *E. lappona* and *Melitæa asteria* (5-6 mm.); in the Val del Fain, August 5, 1876, *Melitæa aurinia*, var. *Merope*, Prunn. (7 mm.), all easily inserting their proboscis into the corolla-tubes, but all apparently without any advantage to themselves, though, by their repeated fruitless attempts, some cross-fertilisation of the flowers may have been effected. No direct observation



FIGS. 109-111.—*Gentiana verna* (3/4: 1). FIG. 109.—Flower, completely opened, seen from above. FIG. 110.—Upper portion of the same flower, bisected longitudinally, showing the pistil and the anthers. FIG. 111.—Lowermost portion of the same flower, showing the nectary.

Alps. The smallest of the species in question, *G. nivalis* (13-16 mm.), *G. imbricata* (15 mm.), and *G. pumila* (16-18 mm.), may also be fertilised by some moths¹ and by many butterflies² which will all easily insert their slender proboscis into one of the small openings at the base of the corolla-tube, then, withdrawing it smeared with pollen, will leave some pollen-grains on the margin of the stigmatic disc, and, when inserting the proboscis into another flower, will effect its cross-fertilisation by stripping off some of the pollen-grains from the hair-like papillæ at the margin of



FIGS. 112-114.—*Gentiana nivalis* (3/4: 1). FIG. 112.—Flower seen from above. FIG. 113.—Pistil. FIG. 114.—Upper portion of the flower bisected longitudinally, showing one of the anthers (a) in contact with the margins of the stigma.

of the true natural fertilisers of the species of *Gentiana* belonging to our fourth group has yet been made.

In former articles I have shown that frequently, of different species of the same genus, those possessing the most conspicuous flowers are adapted to cross-fertilisation by insects, whilst other species of the same genus, possessing less conspicuous flowers, have recourse to self-fertilisation, in case the visits of insects are wanting. This statement is also confirmed by the species of *Gentiana* in question. For in *G. verna* and *bavarica*, differing from *nivalis* not only by the considerably larger size of the separate flowers, but also by a number of flowers which stand close together, thus being easily seen from a great distance, the possibility of self-fertilisation is excluded by the position of the stigma and the anthers (as shown by Fig. 106 and 110); whereas in *Gentiana nivalis*, whose flowers are much smaller and more distant one from another, one or some of the anthers commonly come into contact with the margin of the stigma (as shown by Fig. 114), and effect self-fertilisation in case cross-fertilisation by insects is wanting.

¹ Kerner, "Schutzmittel der Blüten gegen unberufene Gäste." (Wien 1876).

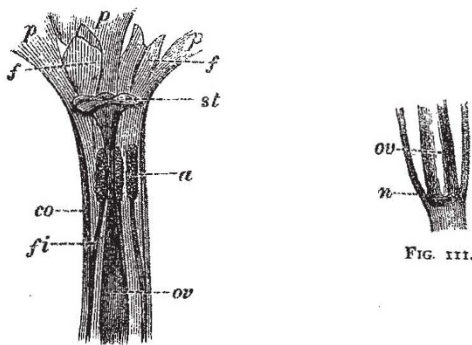


FIG. 110.

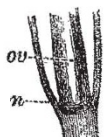


FIG. 111.

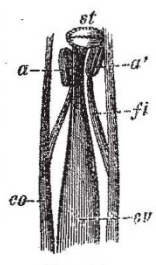


FIG. 114.

the stigmatic discs. Humble-bees, on the contrary, at all events, seem to be of very small or no importance as fertilisers of this group. If thus, by indirect inference, we are led to the conclusion that the present group

¹ *Plusia gamma*, 15-16 mm.; *P. interrogationis*, 15; *P. Hoehenwarti*, 13.
² *Argynnis adippe*, 13-14; *A. aglaia*, 15-18; *A. niobe*, var. *eris*, 13-16; *A. paphia*, 12-14; *Colias phicomone*, 13-14; *Erebia goante*, 11-14; *Hesperia sybanus*, 16; *Papilio machaon*, 18-20; *Pararge maera*, 13-14; *Parnassius apollo*, 12-13; *P. delius*, 11-16; *Pieris brassicae*, 15-16; *P. crataegi*, 15; *P. rufæ*, 14-18; *Vanessa cardui*, 15; and *V. urticae*, 14-15 mm.

The most striking peculiarity of our fourth group of *Gentiana* is the sensibility of their flowers to the influence of the weather, which is apparently connected with the sensibility of their natural fertilisers to the same influence. The following observation clearly shows that different species differ widely in this sensibility, even when growing in the same locality. On the Piz Umbrail, July 16, 1874, I had collected some plants of *Gentiana bavarica*, var. *imbricata*, and of *G. verna*, and put them in my sleeping-room in the Quarta Cantoniera, upon a plate filled with water. The next morning, at half-past four o'clock, I found the flowers of *G. bavarica* already opened, those of *G. verna* still closed. I placed the plate outside the window, where the intensity of light was at least as great, but the temperature much lower, and all the opened flowers began twisting. After they had closed, I brought them back into the room, and they opened again. Repeating this trial from half-past four to half-past six o'clock, I saw them two or three times closing and opening again. *Gentiana verna*, standing upon the same plate, during this time, had not yet opened a single flower.

From this observation, the further prosecution of which was prevented by my departure, it is obvious (1) that the opening of the flowers of these species of *Gentiana* is caused

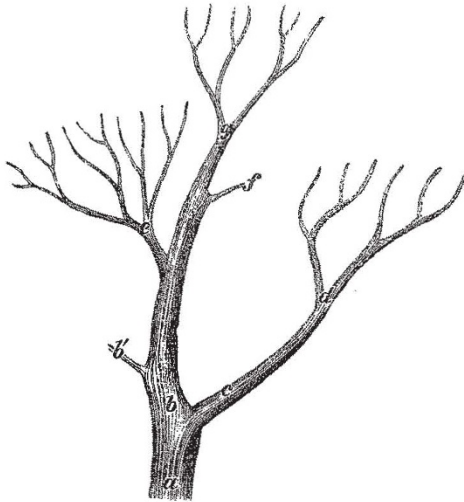


FIG. 115.—Pedigree of the species of *Gentiana* of Germany and Switzerland.

by heat, not by light; (2) that *G. verna* requires a higher temperature for opening than *G. bavarica*, var. *imbricata*. Possibly this is one of the causes which makes *G. verna* descend into sub-Alpine and low lands, whilst *G. bavarica* is confined to the Alpine region.

Comparing the present group with the foregoing ones, we need hardly doubt that it is most nearly allied to our second group, from which it differs only by the narrowness of the corolla, by the further development of the folds between the petals, and in connection with this by their greater sensibility, and by the lobes of the stigma being dilated. *Gentiana prostrata*, agreeing in every other respect with our fourth group, has as yet retained the two twisted stigma-branches, and therefore may be considered as a connecting species between the second group and the fourth, which is descended from it.

Summing up the above relations between the species of *Gentiana* of Germany and Switzerland, we obtain a pedigree like Fig. 115, in which the signification of the lettering is as follows:—

(a) Hypothetical ancestral form with fully open flowers, twisted stigma-branches, diverging stamens, and honey secreted at the base of the flower in the angle between the base of the pistil and the corolla. From this ancestral form we see two branches *b* and *c* descend; *b*

with the nectary confined to the base of the pistil, *c* with nectaries at the base of the corolla. From the branch *c* has developed the sub-genus *Entotricha* Frœlich (*d*), containing six species:—*G. campestris*, *germanica*, *amarilla*, *obtusifolia*, *tenella*, and *nana*, adapted both to Apidæ and to Lepidoptera. Of the branch *b* an original form, *G. lutea* (*b'*), has been preserved, accessible to insects of all orders, but from the same branch has descended the large sub-genus *Calanthe* Frœlich (*e*), containing eleven species:—*G. punctata*, *pannonica*, *purpurea*, *cruciata*, *asclepiadea*, *Pneumonanthæ*, *Frœlichii*, *frigida*, *acaulis*, *excisa*, and *ciliata*, all adapted to humblebees. One branch of this sub-genus (*e*), by narrowing the corolla, perfecting the folds between the petals, dilating the stigma-branches, and thus adapting the flowers to Lepidoptera, has further developed the sub-genus *Cyclostigma* (*g*), containing seven species:—*G. bavarica*, *verna*, *astiva*, *imbricata*, *pumila*, *utriculosa*, and *nivalis*. As a link between the ancestral sub-genus (*e*) and the derived subgenus *G.*, has been preserved *G. prostrata* (*f*).
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RECENTLY PROPOSED IMPROVEMENTS IN MUSICAL INTONATION

THE harshness of the present system of tuning has been a source of constant complaint since it was first introduced, about a century and a half ago. But of late years several more or less practical attempts have been made to overcome this defect without interfering with the quality of our musical tones. Instruments with fixed tones, as the organ, piano, and harmonium, lead voices, and the inalterable quality of vocal tone has therefore to be constantly kept in view. The instruments exhibited in the Loan Collection of Scientific Apparatus at South Kensington are enough to show both the objects aimed at and the nature of the mechanical appliances by which it is hoped they may be more or less reached. It is difficult to give an intelligible account of them within the compass of an article, but Dr. Stone's two lectures¹ and Mr. Bosanquet's more recent work² will supply details and figures.

On examining musical tones generally,³ we are led to the conclusion that the first requisite is to have a succession of notes forming perfect Octaves, Fifths, and major Thirds, that is, making numbers of vibrations which the air executes during the same length of time in the ratios 1 : 2, 2 : 3, and 4 : 5 respectively. An examination of prevailing systems of modulation, has shown⁴ that a strict fulfilment of this condition would require 117 notes to the Octave—a mechanical impossibility on any instrument with fixed tones. Such a scheme must, however, be made the basis of subsequent work. Moreover if combinations with what is called the harmonic Seventh or 6 : 7 be admitted, then we should require very nearly to double the above number of separate notes. It follows, therefore, that we must either restrict our desires of modulation (which is not likely to happen) or be content to use more or less imperfect intervals, and the question turns upon the degree of endurable imperfection. It must be remembered that these apparently innumerable delicacies of sound present no real difficulty to the singer or violinist when he once knows the theory on which they have to be produced, for they are all generated by extremely simple intervals. The difficulty, indeed, is to avoid them, especially in part music, and to put up with alterations, apparently arbitrary and certainly neither

¹ "Sound and Music," by Dr. W. H. Stone, in the series of Science Lectures at South Kensington, 1876, pp. 46. (Macmillan.)

² "An Elementary Treatise on Musical Intervals and Temperament, with an Account of the Enharmonic Harmonium Exhibited in the Loan Collection of Scientific Instruments, South Kensington, 1876; also of an Enharmonic Organ Exhibited to the Musical Association of London, May, 1875," pp. 94, 1876. (Macmillan.)

³ For reasons and details see Helmholtz's "Sensations of Tone."

⁴ See my translation of Helmholtz, pp. 669-672.