sophical Transactions for 1857; but many other papers of the same thorough and original character proceeded from his pen. Amongst them will be remembered the following:—"On the Olfactory Apparatus in the Bullidæ" (1852); "On the Nervous Systems of *Ommastrephes todarus*" (1852); "On the Anatomy and Physiology of the Dibranchiate Cephalopoda" (1861); "On the Structure and Homologies of the Renal Organ in the Nudibranchiate Mollusca" (1863); "On the Anatomy of *Doridopsis*" (1865); "On the Anatomy and Physiology of the Tunicata" (1867).

For some years previous to his death Mr. Hancock had devoted much attention to the fish of the Carboniferous period, and in conjunction firstly with Mr. T. Atthey, whose fine collection afforded ample material for the purpose, and subsequently with Mr. Howse, published a series of fifteen papers on these coal-measure fossils.

The promised Monograph of the British Tunicata, preparations for which had made some progress even before the death of Mr. Alder, had occupied much of his time; and though probably still unfinished, it may be hoped that the results of his investigations are so far complete in themselves, that the work, as far as it has gone, may be saved to science. A supplement to the Monograph of Nudibranchiate Mollusca had been a matter long on his mind, but one that he had never been able to devote himself to realising, beyond the collection of materials.

Allusion has been made to Mr. Alder, Mr. Atthey, and Mr. Howse, as having been associated with Mr. Hancock in certain of his papers; to these must be added the names of Dr. Embleton and the Rev. A. M. Norman as occasional colleagues.

On the establishment of the Natural History Society of Northumberland, Durham, and Newcastle-upon-Tyne in 1829, Mr. Hancock became an active supporter, and was one of the original staff of honorary curators; and on the formation of the Tyneside Naturalists' Field Club in 1846, he was one of its principal and most influential promoters. When the new College of Physical Science in Newcastle was instituted, his name, almost as a matter of course, was placed on the provisional committee; and it was only when this body had completed its labours and gave place to a permanent board, that he was permitted, on the ground of ill-health, to retire from active service in connection with the institution. He was a Fellow of the Linnean Society, a corresponding-member of the Zoological Society of London, an honorary member of the Imperial Botanico-Zoological Society of Vienna, and perhaps of some other similar bodies; but honours of this sort, though valued in their way, were thrust upon him rather than sought. Though living a retired life, no man more highly prized social intercourse. His kindly helping hand was held out to every young naturalist: Such were always welcome at his house; and when appealed to by them, as was often the case, he made their difficulties his own till he could help to solve them.

It is yet too soon to attempt to shake oneself free from a sense of his presence, or to essay to weigh in judicial balance the value of his contributions to human knowledge: considerations of this sort are overwhelmed in the sense of irreparable loss to science.

H. B. B.

FERTILISATION OF FLOWERS BY INSECTS*

IV.

On the two forms of flower of Viola tricolor, and on their different mode of fertilisation.

VIOLA tricolor presents a further example of the same kind of dimorphism as that described in the last article in the case of *Lysimachia*, *Euphrasia*, and *Rhinanthus*.

* Continued from vol. viii. p. 435.

One of its two forms, illustrated by Fig. 15 in natural size, is more conspicuous than the other (Fig. 16), not only by its larger size, but also by the more striking colour of its petals. When the flower has just opened, its two upper petals are light violet, or, in rarer cases, nearly white; but they gradually become a deep violet, or even dark blue. Far more striking is, ordinarily, the change of colour in the two lateral petals and the lower one, which, immediately after the opening of the flower, are nearly white, while in a fully-developed state they are always violet. The petals of the small-flowered form of *Viola tricolor*, illustrated in natural size by Fig. 16, are, on the contrary, uniform in colour and nearly white during the whole time of flowering. The attractiveness for insects of the two kinds must therefore be very different, whereas those particular marks round the opening of the flower which serve as a guide to insects in search of the honey, the "Saftmal" of Sprengel, are nearly the same in the two varieties. That part of the lower petal immediately before the entrance of the flower (*y*, Fig. 21, 22) is in both dark yellow, and the lower petal is also marked by black streaks converging towards the same entrance. There is only this difference between the two forms as to their guide-mark (*Saftmal*), that in the large-flowered form seven black streaks on the lower petal, and three on each of the lateral ones point towards the entrance of the flower; whereas in the small-flowered form there are but five black streaks in the lower petal, and none at all on the lateral ones.*

Although these two forms have been generally known, at least since the time of Linnæus, all botanists who have published observations on the fertilisation of *Viola tricolor* have apparently turned their attention exclusively to the large-flowered form (Fig. 15), whose beautiful adaptations to cross-fertilisation by insects, have been, therefore, very accurately described; while the peculiarities in structure and fertilisation of the small-flowered form have not even been mentioned. If, in this case, we clearly see that even scientific inquirers have been far more attracted by the larger violet flowers than by the smaller whitish ones, we need not wonder that insects are influenced in like manner, and that from this cause smaller and less conspicuous flowers are so frequently quite overlooked by insects, that they would rapidly become extinct, unless slight modifications of structure and development enabled them to produce seeds by self-fertilisation.

Indeed, in *Viola tricolor*, as in those species hitherto considered, regular self-fertilisation in the small-flowered form is effected by such slight modifications of structure and development, that by far the larger number of the contrivances in the large and small-flowered forms are identical.

In both forms, honey is secreted by two long appendages (*n*) of the lower filaments (*f*), from which it ascends by adhesion into the uppermost part of the hollow spur (*sp*); the style (*st*), Fig. 22) is directed downwards on its base, slender and bent like a knee, while above it is straight and gradually thickened, but does not increase at all or only slightly in breadth, ending in a skull-like stigmatic knob (*k*), thick enough to completely stop the entrance of the flower. This knob is provided with a wide open moist stigmatic cavity (*st*) and is protected from above by two sets of hairs (*pr*, Figs. 21, 22, Sprengel's "Saftdecke") on the two lateral petals, which at the same time defend the entrance of the flower against rain, and prevent insects from entering into the flower in any other way than by the lower side of the skull-like knob. In both forms the five anthers open inwards, are narrowed towards their

* My description relates exclusively to those varieties of *Viola tricolor* which grow in the environs of Lippstadt. From Sprengel's, Bennett's, and other descriptions and illustrations, I am aware that in other localities somewhat different varieties are found. But I do not doubt that differences in the manner of fertilisation, identical or closely allied with those here to be described, will be found wherever a large-flowered and a small-flowered form of *Viola tricolor* co-exist.

end, and prolonged above into orange-coloured triangular appendages of their connectives (*c*, Figs. 21, 22), and lie so close together round the style, as to form a hollow cone containing the pollen, and overtopped only by the skull-like crest of the style. This position of the stigmatic knob rising out of the anther-cone but immediately below its summit, is secured by a remarkable contrivance, the skull-like knob being prevented from sliding into the anther-cone by two tufts of hairs, projecting like whiskers from its two cheek-like lateral surfaces. Thus a lifting up of the stigmatic knob, which must always be effected by insects seeking for honey or for pollen, and which is easily accomplished by them in consequence of the base of the style being slender and bent like a knee, will be more likely to tear off the filaments than to push the stigmatic knob into the anther-cone. Indeed, we find that by the swelling of the fertilised ovary the filaments are always torn off, whereas the anthers remain, enclosing like a hollow cone the narrow portion of the style, and the skull-like knob is never drawn between the anthers. If the anther-cone containing the pollen were densely closed all round, the pollen-grains would not fall out unless the anthers were separated from each other by lifting up the stigmatic knob; but there actually exists an opening on the lower side of the summit of the cone directed downwards, the appendages of the two lower anthers being cut out (*op*, Figs. 21, 22), by which nearly all the pollen may fall out spontaneously. When it has fallen out, a great part of the pollen is collected in the close hairy lining of the fore part of the spur.

Thus far the two forms of *Viola tricolor* are identical in structure; and the same, or nearly the same, insects may *a priori* be supposed and have really been observed, to visit the two forms. The distance between the closed entrance of the flower and the honey contained in the uppermost part of its spur being in both of the two forms 6-7 mm., an insect must be provided, in order to reach the honey, with a proboscis of at least that length, unless it be enabled by its small size to crawl with its whole body into the flower. A proboscis of 6-7 mm. length or larger is only to be met with among all our insects in Lepidoptera, Apidæ, and some few Diptera; insects sufficiently minute to be able to crawl into and out of the flowers, are to be found chiefly in the genera Thrips and Meligethes. It may therefore be supposed, *a priori*, that Lepidoptera, Apidæ, and Diptera provided with a proboscis of at least 6 mm. long, and very minute insects of the genera Thrips and Meligethes, will visit the two forms of *Viola tricolor* for honey, and that, besides, some other insects provided with shorter probosces will seek for their pollen. By direct observation this supposition has been thoroughly confirmed, as shown by the following list of visitors actually observed:—

I. As visitors of the large-flowered form, there have been observed:—(a) Lepidoptera: (1) *Pieris rapæ* L.* (12), †—(b) Apidæ: (2) *Bombus muscorum* L.* (10-15); (3) *B. lapidarius* L. ♀ ‡ (12-14); (4) *B. sp.* §; (5) *Anthophora pilipes* F. || (19-21); (6) *Andrena albicans* K. ♂ (2-2½), in vain seeking for honey. ‡—(c) Diptera: (7) *Rhingia rostrata* L. § (11-12); (8) *Syrilla pipiens* L. (2-3), eating pollen. ‡—(d) Thysanoptera: (9) Thrips. ¶

II. As visitors of the small-flowered form, there have

* By W. E. Hart (NATURE, vol. viii. p. 121).

† The numbers enclosed between parentheses after the names of the insects indicate the length of their probosces in millimetres.

‡ By myself ("Befruchtung der Blumen durch Insecten," p. 145).

§ By Ch. Darwin, who writes me, May 30, 1873:—"Between twenty and thirty years ago I observed, for two or three years, large beds (of *V. tricolor*) in the flower-garden, and saw several times *Rhingia rostrata*, and a nearly black humble-bee visit and fertilise the flowers. I say fertilise, because I had watched the flowers for a long time previously, and saw no insect visit them; but two or three days after the above visits a multitude of flowers withered and set capsules."

|| By Delpino ("Ulteriori osservazioni," p. 62).

¶ By Sprengel ("Das entdeckte Geheimniss," p. 397), and Mr. A. W. Bennett (NATURE, vol. viii. p. 49).

been observed:—(a) Lepidoptera: (1) *Pieris rapæ* L.* (12), repeatedly; (2) *P. napi* L.* (11), repeatedly; (3) *Polyommatus Doritis* Hfn.*—(b) Apidæ: (4) *Apis mellifica* L. (6) ♀; † (5) *Bombus hortorum* L. ♀* (18-21), perseveringly visiting the flowers for honey, although every flower is drawn down by the weight of this large humble-bee; (6) *B. Rajellus* Fll. ♀* (10-13), the same individual visiting sometimes *V. tricolor*, sometimes *Lamium purpureum*; (7) *B. muscorum* L. (*agrorum* F.) ♀ (10-14), visiting, without distinction, now the flowers of *V. tricolor*, now the nearly equally large and equally coloured flowers of *Lithospermum arvense*, while omitting the smaller ones of *Capsella bursa-pastoris*, *Valerianella olitoria*, and *Myosotis versicolor*; (8) *Osmia rufa* L. ♂* (7-9), but once hastily visiting a flower for honey.—(c) Diptera: (9) *Rhingia rostrata* L.* (11-12), several specimens, repeatedly visiting flowers for honey.—(d) Coleoptera: (10) *Meligethes** crawling into the flowers.

Direct observation has thus shown that no essential difference exists between the fertilisers of the large and those of the small-flowered form. But it must appear a striking fact that not only an equal number of different species, but even one more species has been observed on the small than on the large-flowered form. All the visitors of the small-flowered form, with the exception of only one, having been observed by myself, I must add, as an explanation of this fact, that I have repeatedly watched at the most favourable weather, for several hours, a neglected field, in which, besides some other weeds, there grew an abundance of vigorous specimens of the small-flowered form of *Viola tricolor*; whereas I have never had an opportunity of watching the large-flowered form under favourable conditions. Therefore I have no doubt that, in spite of the incomplete observations hitherto made on this subject, the more conspicuous flowers are in this species also really far more frequently visited by insects than the less conspicuous ones. Otherwise the differences in structure and development of the two forms now to be described would be quite inexplicable. These differences are:—I. In the large-flowered form the stigmatic cavity lies somewhat more towards the top of the skull-like end of the style than in the small-flowered one (as shown by the comparison of Fig. 17 with Fig. 18, and of Fig. 19 with Fig. 20.)

(1) When the skull-like knob in the two forms is pressed against the lower petal, in the large-flowered form the opening of the stigmatic cavity is directed outwards, so that pollen-grains which have fallen out of the anther-cone spontaneously can never fall into the stigmatic cavity unless carried by insects; whereas in the small-flowered form the opening of the stigmatic cavity is directed inwards, so that pollen-grains falling out of the anther-cone spontaneously, fall directly into the stigmatic cavity.

(2) In the large-flowered form the opening of the stigmatic cavity (*st*, Figs. 17, 19, 21) bears on its lower side, as discovered by Hildebrand, a labiate appendage (*l*, Figs. 17, 19, 21) provided with stigmatic papillæ, so that a proboscis inserted into the flower, when charged with pollen of a previously visited flower, rubs off this pollen on to the stigmatic lip (*l*), thus regularly effecting cross-fertilisation; whereas, when withdrawn out of the flower, charged with its pollen, the proboscis presses the lip (*l*) against the stigmatic opening (*st*), thus preventing self-fertilisation. This nice adaptation to those visitors provided with a long proboscis (Lepidoptera, Apidæ, Rhingia) is completely wanting in the small-flowered form (Figs. 18, 20, 22).

(3) In the large-flowered form there is a black wedge-shaped streak (*w*, Figs. 17, 19) on the front side of the style, to which Mr. A. W. Bennett first called atten-

* By myself (June 1873).

† By Sprengel (*loc. cit.*) and by myself (June 1873), perseveringly visiting the flowers for honey.

tion,* and which he has interpreted as a guide-mark for those visitors, which are diminutive enough to crawl entirely into the flower. This streak is also wanting in the small-flowered form (Figs. 18, 20).

(4) In the large-flowered form pollen-grains do not spontaneously fall out of the anther-cone before the flower has been fully developed for several days; whereas in the small-flowered form, in by far the majority of cases, a great number of pollen-grains fall spontaneously out of the anther-cone into the stigmatic cavity and there develop long pollen-tubes, even before the opening of the flower, in much rarer cases a short time after it has opened.

(5) When the visits of insects are prevented by a fine net, the flowers of the small-flowered form wither two or three

diminutive insects crawling into the flower may effect both self- and cross-fertilisation; fertilisation by insects is possible from the opening of the flower for twenty days or more; spontaneous self-fertilisation never takes place. On the contrary the less conspicuous flowers are

FIG. 15.—Front view of the more conspicuous flower of *Viola tricolor*, natural size. FIG. 16.—Front view of the less conspicuous flower. FIG. 17.—Pistil of Fig. 15, viewed on the under side, 12 times natural size. FIG. 18.—Pistil of Fig. 16. FIG. 19.—Lateral view of the pistil of Fig. 15. FIG. 20.—Lateral view of the pistil of Fig. 16.

The following explanation of the lettering applies to all the figures:—*a*, anthers; *a*¹, upper, *a*², lateral, *a*³, lower anther; *ap*¹, appendage of the upper sepal; *b*, beard, *i.e.* tuft of hairs on the lateral surface of the skull-like crest of the style; *c*, appendage of the connective; *f*, filaments; *k*, knob of the stigma; *l*, lip, labiated appendage of the stigmatic opening; *n*, nectary, *i.e.* honey-secreting appendage of the lower filaments; *op*, opening of the anther-cone; *ov*, ovary; *p*, petals; *p*¹, lower, *p*², lateral, *p*³, upper petal; *po*, pollen-collecting hairs; *pr*, protective hairs (Sprengel's "Saftdecke"); *s*, sepals; *s*¹, upper sepal (with the appendage *ap*¹); *s*², lateral sepal; *sp*, the uppermost part of the spur, containing the honey; *st*, stigmatic cavity; *str*, streaks converging towards the opening of the flower; *sty*, style; *w*, wedge-shaped streak of the style; *y*, yellow coloured part of the lower petal.

days after opening, everyone setting a vigorous seed-capsule; those of the large-flowered form remain in full freshness more than two or three weeks, at length withering without having set any seed-capsule; when fertilised they wither also after two or three days.

Summary.—The more conspicuous flowers of *Viola tricolor* are adapted to regular cross-fertilisation by Lepidoptera, Apidæ, and Rhingia; whereas self-fertilisation by these visitors is prevented. Pollen-eating flies and

FIG. 21.—Lateral view of Fig. 15 after the half of its sepals and petals having been removed, 7 times natural size.

adapted to regular self-fertilisation; although visited now and then by the same insects as the more conspicuous flowers, cross-fertilisation by these visitors is by no means secured; in most cases it is even prevented by the pollen having previously fallen into the stigmatic cavity; it

FIG. 22.—Lateral view of Fig. 16, but one lateral anther and the half of one lower anther have been removed and the pistil bisected longitudinally.

is possible only in those cases where the flower has opened before its pollen has filled the stigmatic cavity; and even in these rare instances the possibility of cross-fertilisation lasts but a few hours.

Lippstadt, October 1873

HERMANN MÜLLER

* In his interesting article on the Fertilisation of the Wild Pansy, NATURE, vol. viii. p. 49.