Fruit-dispersal in *Adenostemma viscosum*¹.

A Biological Study.

BY

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With Plate XXIII.

IN the flower-like inflorescence of the Compositae, as is well known, the usual protective function of the calyx is performed by the involucre. This being so, the calyx proper is either very much reduced (in a few instances entirely suppressed), or else it becomes a highly modified 'pappus,' which appears to be, in a great number of cases, specially adapted to facilitate fruit dispersal. The pappus may assume a variety of forms, such as the well-known parachute mechanisms of many species, the hooked bristles of *Bidens*, etc., etc. But amongst this aggressive and dominant family, the genus *Adenostemma* appears to be unique in one particular, i. e. the possession of a sticky, glandular pappus².

It has been noted by more than one writer, that this peculiarity aids the plant in the dispersal of its fruits. Trimen states that the achenes of *Adenostemma* adhere to surrounding objects by their very viscid stalked glands (pappus)³; while Hildebrand points out that in its sticky pappus the plant possesses an excellent means of fruit-distribution by the agency of animals. Fritz Müller sent him some seeds of *Adenostemma*, which unfortunately did not germinate, and so, said he, 'it was impossible to study this interesting example any further⁴.' As the whole mechanism of dispersal in this plant forms a good example of co-ordinated adaptation, it may perhaps be worth describing in some detail.

¹ See the abstract of a paper read by the author before Section K of the British Association. B. A. Report, Southport, 1903, p. 859.

² The generic name, indeed, has reference to this fact—*ἀδής*, a gland, and *στέμμα*, a crown: see Forster, *Characteres Generum Plantarum*, London, 1776, p. 90.

³ Trimen, *a Handbook to the Flora of Ceylon*, London, 1895, vol. iii, p. 13.

⁴ Hildebrand, *Ueber die Verbreitungsmittel der Compositenfrüchte*, *Bot. Zeitung*, 1872, vol. xxx, p. 12.

My own attention was first called to this method of fruit-dispersal in *Adenostemma viscosum*, Forst., during a visit to the Malay Peninsula¹ in the year 1899, by finding one day a few of its fruits firmly gummed to my legs, by means of some short, sticky processes. The latter are in reality the glandular setae (generally three in number) which in this plant represent the pappus. These setae, or stalked glands, are situated on a projecting ring of tissue (the calyx ring), which crowns the inferior ovary (Fig. 4). At the base of each seta is a swelling, which is visible only during the flowering stage (*p.* Fig. 4).

As in the capitula of many other Compositae, the torus, during the ripening of the fruits, assumes a more convex shape, while the involucre bracts, which are at first erect, become spreading, and finally completely reflexed (Figs. 1–3). Meanwhile, all the corollas of the capitulum, as well as the styles, are detached at their bases, and fall off *en masse* (Fig. 2). The pappus now begins (usually, in the cases observed, before the actual throwing off of the corollas) to excrete an exceedingly viscid, clear liquid, which forms a large drop surrounding the tip of each seta. In this condition the pappus setae bear a marked resemblance to the leaf ‘tentacles’ of a *Drosera*. At the same time the setae gradually move from a vertical into a horizontal position; and, during this process, the swellings at their bases (which, as will be seen later, are really pulvini) disappear. The tiny fruits are now fully exposed, and are ready to attach themselves to any passing animal (Fig. 3)².

Under a low power of the microscope, the pappus bristles have the appearance shown in Fig. 4, each being crowned by a number of capitate secretory hairs, set so closely together as to form a continuous gland. The capitate hairs (Fig. 5), which are of a type not uncommon in the Compositae³, extend further down the seta on its exterior than they do on the side next to the corolla. Similar glandular hairs, but longer and narrower than those of the pappus, are found on many other parts of the plant, e. g., the lower part of the corolla, and the pericarp wall (Fig. 4), also on the peduncles, leaves, &c.

The secretion of the pappus-hairs is exceedingly sticky, and may retain (to a large extent) its adhesive power even after the fruits have been kept in a dry condition for some years. Water appears to have no effect on this secretion, though it readily dissolves in ether and some other solvents. It

¹ This species is widely spread throughout the tropics of both the Old and New Worlds, though the remaining four or five species of the genus are confined to the latter.

² Hoffmann figures (in Engler and Prantl's *Pflanzenfamilien*, Teil IV, Abt. 5, p. 132, Fig. 77, o) a fruiting capitulum of *A. viscosum* with the involucre not reflexed. This figure was probably taken from an immature capitulum, as in all cases, I believe, the involucre is finally reflexed.

³ See Hanstein, Ueber die Organe des Harz- und Schleimabsonderung in den Laubknospen, Bot. Zeit., 1868, vol. xxvi, pp. 734 et seq., also Haberlandt, Physiologische Pflanzenanatomie, 2nd ed., Leipzig, 1896, p. 433.

stains a deep red with alcannin, and with osmic acid takes on a faint brown colour, though it is not blackened as an oil would be. In fact, it behaves generally like a body akin to resins, though, as seen above, it does not quickly harden, as an ordinary resin should. Possibly the secretion may be more or less allied to caoutchouc, or to the supposed caoutchouc-like substance which has received the name of 'Viscin¹.'

The pappus-setae are formed at a very early stage in the development of the flower. Each contains a single vascular bundle²; and, as the fruit matures, the walls of the cells surrounding this bundle become indurated and thickened, except in the region of the glandular hairs, and in the swollen base of the seta.

The structure of this basal swelling is interesting. It is composed, for the most part, of large, thin-walled cells (with no inter-cellular spaces), elongated in a direction at right-angles to the axis of the seta itself (Fig. 6). After the gland-stalks have assumed their final horizontal position, sections taken through the base of a seta show that these large cells have collapsed, their walls being much crumpled. This, together with the internal structure of the swelling, and the fact, observed in the field, that the swelling itself disappears during the movement of the gland-stalks, furnish, I think, sufficient proof that the dilated bases of the setae constitute the mechanism of movement. The base of each pappus-seta is in fact a pulvinus, composed largely of thin-walled motor cells, which probably act by losing water during the drying and ripening of the fruit.

The horizontal position assumed by the pappus-setae is probably advantageous in that it provides the fruit with a more extended (and therefore more secure) base of attachment.

In view of the fact that the feathery pappus of many Compositae executes similar movements, I examined some of our British species, with the result that, in a number of instances, a mechanism resembling that described above was found. In the cases examined, instead of the downward movement of the hairs being due, as stated by Haberlandt³ (apparently for Compositae generally), to an unequal thickening of the walls at the bases of the hairs themselves, it was effected by means of a continuous annular pulvinus, on the edge of which the pappus hairs were borne (Figs. 7-9).

I have since found that two other authors (Talieff⁴ and Hirsch⁵) have

¹ Cf. Parkin, Observations on Latex and its functions, Ann. of Bot., 1900, vol. xiv, p. 203.

² The Composite pappus rarely contains vascular tissue. Hoffmann, loc. cit., p. 97, states that only in some four genera (amongst which he does not mention *Adenostemma*) have even traces of vascular bundles been found in the pappus.

³ Haberlandt, loc. cit., p. 465.

⁴ Talieff, Ueber das hygroskopische Gewebe des Compositen-Pappus—abstract by Rothert: Bot. Centralblatt, 1895, vol. lxiii, p. 320.

⁵ Hirsch, Ueber den Bewegungsmechanismus des Compositen-Pappus. Dissertation, Würzburg Berlin, 1901.

fully described this hygroscopic tissue in the Compositae, so that my results merely confirm their more extended observations. Hirsch¹ states that though in the majority of cases movement is effected by a pulvinus ('Polstergewebe'), yet in a few instances it is brought about by special motor cells in the basal parts of the hairs themselves.

Two kinds of hairs are found on the corolla; glandular capitate hairs, which occur only on the lower part, and long filamentous hairs, which are confined to the upper region, just below the corolla-lobes (Fig. 4). This second type of hair is not found elsewhere on the plant. In the bud, the florets are so close to each other, that the growth of these long filamentous hairs, during their development, results in those of one corolla being entangled with those of all the adjacent corollas. A dense felt of interwoven hairs is thus formed, which effectually ties together all the corollas of one capitulum (Figs. 1 and 2). The falling of the corollas *en masse*, which is the result of their being bound together in this manner, is probably of considerable importance; for if they fell separately, there would be a risk of some corollas being caught by the secretion of the pappus, and so impeding the action of the latter in respect to passing animals.

Hooker² noticed that the corollas fall off in a mass in some species of *Adenostemma*, but attributed this to their adhering together by their viscid surface. In this I think he was mistaken, as the lower parts of the corollas, which alone could be reached by the secretion of the hairs, are invariably free from each other (Fig. 2). Other species of *Adenostemma* have similar filamentous hairs on their corollas³, which probably serve the same purpose.

In *Taraxacum officinale* and some other Composites, the corollas tend to fall, after withering, more or less in one mass. In these cases, however, the corollas merely adhere slightly to one another during drying, or at most are entangled by their ligulate tips.

Not only are the corollas bound together, but special arrangements exist, by means of which both they and the styles are cut off from the ripe fruits, and the latter are separated from the torus. In each case, during the ripening of the fruit, the walls of certain cells become thick and woody. This serves to give a special rigidity to these parts of the flower or fruit, while the adjacent parts, whose cell-walls remain thin and delicate, are easily ruptured. The direction of rupture is determined by the relative positions of the hard and soft tissues.

Thus in the corolla, a cylindrical mechanical layer is formed, by the thickening of the outer epidermis of the whole of its lower part. A few cells of the calyx-ring just below the corolla also become thickened. Abscission is then effected by the rupture of the thin-walled cells at the extreme base of the corolla (Fig. 10). Similarly the epidermis of the lower

¹ Hirsch, loc. cit., p. 38.

² W. J. Hooker, *Icones Plantarum*, 1840, vol. iii, tab. 239.

³ See figures in Martius and Eichler, *Flora Brasiliensis*, 1873-6, vol. vi, Part II, t. 51 and 52.

part of the style forms a cylinder of thickened cells. Separation in this case occurs by the breaking down of the thin-walled tissue at the base of the style (Fig. 10).

The fruits themselves are separated from the torus in a manner essentially similar to that described for the abscission of the corolla and style. Each fruit is attached to the base of a shallow pit in the torus, and is detached by the breaking down of fragile parenchymatous cells lying between the thick-walled epidermis of the lower part of the fruit, and a funnel-shaped layer of thickened cells of the torus (Fig. 11). Only those cells which form the rim of this 'funnel' are epidermal, the remaining cells being of a more deeply seated origin¹.

The vascular strand which supplies the ovary contains but few vessels, but is accompanied by numbers of short sclerotic cells (Fig. 11), which probably help to render the strand itself more brittle. In any case, the strand breaks across with great readiness.

In all these cases, the actual thickening of the cell-walls (including those of the sclerotic cells mentioned above) takes place only during the maturation of the fruit.

As we have seen, the process of fruit-dispersal in *Adenostemma* is facilitated by the abscission of certain parts of the flower, and later, of the fruit itself: and moreover, that this is aided by the topographical relations of hard and soft tissues. But such relations really do little more than determine the direction of rupture. The actual breaking down of the fragile tissues is probably due partly to their desiccation as the fruit ripens, and partly to the mechanical strains set up by such causes as the increasing convexity of the torus (Figs. 1-3).

The term 'absciss-layer,' which has sometimes been used in speaking of corollas², would appear to be, in cases such as that described above, somewhat of a misnomer. In those instances where (as in many *Onagraceae*) a definite meristematic layer is formed in connexion with the cutting off of parts of the flower, the term might be retained. But where separation of an organ depends more on the relative disposition of hard and soft tissues than on meristematic activity, some such term as 'absciss-mechanism' would seem preferable.

Although, as stated at the commencement of this paper, the genus *Adenostemma* appears to be unique in possessing a glandular pappus, yet certain other *Compositae* have glandular structures which aid, more or less effectively, the process of fruit-dispersal. Of these, the genus *Siegesbeckia*, which has glandular hairs on the involucre bracts, appears to be the most

¹ Not (at least in *Adenostemma*) merely epidermal, as stated by Kraus, Ueber den Bau trockner Pericarpien. Pringsheim's Jahrb. f. wiss. Bot., 1866, vol. v, pp. 123-4.

² Von Mohl, Ueber den Ablösungsprocess saftiger Pflanzenorgane, Bot. Zeitung, 1860, vol. xviii, p. 276, speaks of certain corollas as possessing an absciss-layer (Trennungsschicht), but he nowhere describes its structure.

interesting¹. Cases, also in the Compositae, in which the fruit itself becomes mucilaginous, are described by Darwin² and Hildebrand³; while a number of instances are given by various authors⁴, of plants of other natural orders whose fruits are said to be dispersed through the agency of animals, by means of glandular hairs situated on pericarp, calyx, bracts or other organs. But so far as I know, in none of these cases (except perhaps in *Siegesbeckia*) is the adaptation so complete as in the one which forms the subject of this paper.

In conclusion, I wish to thank Mr. Ridley, director of the Botanic Gardens, Singapore, and Mr. Macmillan, Curator of the Peradeniya Gardens, Ceylon, for kindly sending me a supply of both spirit material and ripe fruits of *Adenostemma*, that which I had myself collected having unfortunately been lost in transit.

¹ Hildebrand, loc. cit., pp. 12, 13, also Buchenau, Ueber Blütenentwicklung bei den Compositen, 1872, Bot. Zeit., vol. xxx, p. 366, with Taf. V, figs. 19-27.

² C. Darwin, Note on the Achenia of *Pumilio argyrolepis*, Gard. Chron., 1861, p. 4.

³ Hildebrand, Ueber die Verbreitungsmittel der Pflanzenfrüchte durch Haftorgane, Bot. Zeit., 1872, vol. xxx, p. 910.

⁴ See Kerner and Oliver, Natural History of Plants, London, 1894, vol. ii, pp. 869, 870; also Hildebrand, loc. cit. (two papers), and Die Verbreitungsmittel der Pflanzen, Leipzig, 1873, pp. 88 et seq.

EXPLANATION OF PLATE XXIII.

Illustrating Prof. Yapp's paper on Fruit-dispersal in *Adenostemma viscosum*.

All the figures except 7-9 refer to *Adenostemma viscosum*, Forst.

Fig. 1. A flowering capitulum cut vertically through the middle. × 3.

Fig. 2. A later stage. The involucre bracts are becoming reflexed, and the corollas, bound together by the hairs at their apices, are in the act of falling off in one mass. × 3.

Fig. 3. Fruiting stage. The involucre is completely reflexed, and the fruits (only 5 of which remain) fully exposed. The tip of each pappus-seta is surrounded by a drop of viscid secretion. × 3.

Fig. 4. Part of a single floret, showing the calyx-ring and two stalked glands, each with a pulvinus (*p*) at its base. Note the filamentous hairs on upper part of corolla, and the glandular hairs on the pericarp, pappus-setae and lower part of corolla. × 30.

Fig. 5. Three mature glandular hairs from a pappus-seta, as seen in a longitudinal section of the latter. Note the density of the cell-contents of both hairs and epidermis. × 360.

Fig. 6. Longitudinal section through the dilated base (pulvinus) of a pappus-seta, *m.c.* motor cells, *cor.* corolla. × 140.

Fig. 7. Fruit of *Hypochoeris radicata*, before expansion of pappus, *p.* annular pulvinus. × 2.

Fig. 8. Do. after expansion of pappus. Note the flattened pulvinus, *p.* × 2.

Fig. 9. *Tragopogon pratense*. Longitudinal section through the apex of the beak of a fruit, showing the annular pulvinus, *p.* *K.* pappus. × 90.

Fig. 10. Longitudinal section showing the absciss-mechanisms of the corolla and style in *Adenostemma*. N.B. The thick-walled cells are shaded. *cor.* corolla, *n.* nectary, *st.* style. Corolla ruptures at *a*, style at *b.b.* × 140.

Fig. 11. Longitudinal section to show absciss-mechanism of fruit; *ep.* thick-walled epidermis of base of fruit; *f.* funnel-shaped layer of mechanical cells connecting epidermis of torus with the vascular strand; *t.* thin-walled tissue which initiates the rupturing process. × 100.

R.H. Yapp del.

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