NECTARIES OF CERTAIN ARCTIC AND SUB-ARCTIC PLANTS WITH NOTES ON POLLINATION

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The nectaries, stamens, and pistils of the most common genera and species of seventeen Arctic and sub-Arctic families were studied from living material at Frobisher Bay, Resolute, Inuvik, and Tuktoyaktuk, N.W.T., and at Keno Hill, Dawson City, and Whitehorse, Y.T.

The study was initiated by the growing interest in the pollination of arctic plants, and importance of self-pollination, apomixis, and polyploidy in areas where weather conditions often reduce the numbers and activity of pollinating insects. There is a singular lack of detailed information on the position and type of nectaries and the mechanics of self- and cross-pollination in Nearctic plants.

The theory that nectaries in the primitive families usually occur on the outside whorl, and migrate to the base of the style in the most advanced, was evaluated in the seventeen arctic families, as well as the adaptations of the flower to facilitate either cross- or selfpollination.

An account of nectar and nectaries in the arctic flowers would be incomplete without reference to the type of insects involved in pollination in the areas where the field work was undertaken. Insects were collected from individual flowers in the relatively few species which were visited freely by them. Insect names were added to plant species' discussion, along with some data collected by others in a much more severe weather area further north, Ellef Ringnes Is., where the insects crawled rather than flew to their nectar food source, playing a part in the survival of the 49 species of flowering plants recorded there.

POLYGONACEAE

Two species of this family are circumpolar, and are very common in our Arctic, Oxyria digyna and Polygonum viviparum. The first is wind-pollinated, producing copious pollen from four stamens (rarely six), later trapped by the fimbriate red stigmas with branches 0.48–0.52 mm. No vestigial nectary was found. Pollen grains were found scattered all over the inflorescence in some specimens.

Polygonum viviparum has a well-developed nectary, and yielded 0.155 mg of sugar in the nectar per flower per day at Churchill, and 0.095 mg, with sugar concentrations of 18–31% at Lake Hazen (Hocking, 1968). Knuth (1909) lists a variety of insects visiting this species in Europe, although it is listed as apomictic (Fryxell, 1957). The flower spikes at Frobisher Bay had flowers at the tip and bulbils lower down, the bulbils seen to be germinating while still attached to the parent plant on July 4, 1976, an adaptation for quick establishment of new plants. There were well-filled trigonous achenes in the flowers examined there, although they are sometimes sterile. On the exposed shore of the Beaufort Sea at Tuktoyaktuk, July 12, 1965, there were large stands of dwarf *P. viviparum* which bore bulbils only, this species being increasingly viviparous as the climate deteriorates.

The hermaphroditic flowers examined had a greenish band on the petaloid calyx at the base of the filaments, changing to either purple or beige in the thickened glandular nectary ring immediately surrounding the ovary. Four stamens were attached to the perianth segments in the green band, and four were swollen at the base and embedded in the glandular tissue. The swellings fitted neatly into the three concave sides of the achene, stamens three and four compressed to fit together in one concavity (Plate 1, Figure 1).

The nectary was unique among all arctic species studied, perhaps closest to those in the Caryophyllaceae, but more primitive in the irregular disposition of the stamens.

Savile's statement that some species retain a pattern attractive to insects after becoming apomictic (1972) applies fully to *Polygonum viviparum*.

CARYOPHYLLACEAE

The Caryophyllaceae have six genera widely distributed in the arctic. Four of these, *Arenaria, Cerastium, Sagina,* and *Stellaria,* have small white flowers, each with a polysepalous calyx allowing it to open widely and expose the nectar to the visits of small flies. Two genera, *Lychnis* and *Silene,* have flowers of purplish shades and a gamosepalous calyx forming a tube concealing the nectar. In the Alps bees and syrphids with long probosces are known to visit them freely to suck nectar (Knuth, 1908), but in the eastern Canadian

Arctic they seem to attract few insects of any kind (Kevan, 1972b; Hocking, 1968).

Members of the first group, *Cerastium alpinum* and *Stellaria* longipes, were among the most visited flowers at Frobisher Bay in 1964. Savile (1972) pointed out that appreciable hybridization occurs between members of the four Arctic species of the *Stellaria* longipes complex. Flies probably play an active pollinating role in both *Cerastium* and *Stellaria*. I collected *Lasiops subrostratus* Zett., *Hylema* (Paregle) radicum (L.), (Muscidae), and Protophormia terrae-novae (R.-D.) (Calliphoridae) on Cerastium alpinum; Hylema sp., Spilogona (R.-D.) imitatrix (Mall.), (Muscidae), on Stellaria longipes; and Boloria polaris Bdv., (Nymphalidae) on Silene acaulis.

The nectaries of the Caryophyllaceae are associated with the base of the stamens. I examined *Cerastium alpinum*, *C. arcticum*, *Stellaria crassifolia*, *S. humifusa*, *S. longipes*, *Arenaria laricifolia*, *A. physodes*, and *A. peploides* in the field, and all had a yellow, or yellowish-green, nectary partially surrounding the base of every second stamen, the outer ones opposite the sepals (Plate 1, Figure 2). Sometimes, as in *A. peploides*, the nectary was wide enough to touch the adjacent stamen (the one opposite the petals), so there appeared to be nectariferous tissue between every stamen.

The flowers tend to be protandrous; the outer, nectary-bearing stamens elongate and dehisce before the stigmas are receptive, and before the inner whorl elongates, allowing a brief time for crossfertilization to take place. As they age, the stigmas curl outwards towards the anthers and the inner whorl of stamens mature, allowing for self-pollination.

In Lychnis and Silene the stamens are fused with the claws of the petals to form a short tube around the carpophore, or stalk, of the ovary. In L. affinis, this band was easily pulled off with forceps, the upper yellow swollen part of the nectariferous band being free from the carpophore and the lower green portion adhering loosely to it (Plate 1, Figures 5 & 6). Every stamen had contributed a nectary, rather than every second one, as in the polysepalous flowers examined.

Silene acaulis also had a continuous yellowish nectary band, but when a petal was pulled off, with its fused stamen, the individual part separated readily from the rest of the band (Plate 1, Figure 4).











This species has three kinds of flowers, one hermaphroditic, and two unisexual types, from the partial suppression of either stamens or carpels. All three types were found at Frobisher Bay, and the extent of the suppression noted. In pistillate flowers the ovary measured 2.5 mm in height, but fleshy vestigial stamens were present, measuring 0.6–1.3 mm, either completely lacking any signs of anthers, or rarely having them represented by a slight enlarging and roughening of the top of the filaments. The typical nectariferous band was present. In staminate flowers both whorls of stamens were well developed and there were vestigial ovaries, measuring 1.4–1.5 mm in height. The stigmas had papillae measuring only 0.06 mm, obviously not receptive, although ovules were seen in the ovary. Again the nectariferous band was well developed. The hermaphroditic flowers were strongly protandrous, starting off with the male stage, with long stamens, later becoming bisexual.

NYMPHAEACEAE

Nuphar and Ranunculus of the order Ranales share the primitive character of having nectaries if the form of pits in their petals, Nuphar on the under side of the petal next the sepals, and Ranunculus on the upper side next the stamens. The mechanism of pollination, however, differs markedly. In Nuphar a visiting insect lands on the wide platform formed by the fused stigmas of a multicarpellate ovary. The flowers are slightly protogynous, as the stigmas are fully mature when the stamens start to dehisce centripetally. The broad, flat stamens are first pressed against the ovary under the over-hanging stigma platform, but bend away from it as they mature, the anther curling slightly downwards, so that selffertilization would seem to be improbable. Nectar collects in the angle between the petals and sepals and the nectar-seeking insect

Plate 1, Figures 1-7. 1, Polygonum viviparum L. Achene, with two inner stamens and one outer shown; 2, Stellaria humifusa Rottb. Yellowish-green, horseshoeshaped nectary at base of stamens opposite sepals; 3 & 4, Silene acaulis L. var. exscapa (All.) DC.; 3, Longitudinal section through hermaphroditic flower in male stage. Yellowish nectaries fused to base of petals, forming a band around carpophore; 4, Single petal with inner nectary; 5 & 6, Lychnis affinis Fries; 5, Pistil with basal band around carpophore; 6, Segment of band removed to show free marginal nectariferous section, and lower section formerly adhering to ovary stipe; 7, Nuphar variegatum Engelm. Laminar stamen. 0, Ovary. STI, Stigma. AC, Achene. s, Stamen. CON, Connective. P, Petal. PS, Perianth Segment. N, Nectary. Line equals 2 mm.

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slips down an oblique slide some 14 mm long, over numerous powdery anthers, collecting pollen on his ventral surface (Plate 2, Figure 10).

Nuphar polysepalum Engelm. is widely distributed in Alaska and the Yukon, and sporadically along the lower MacKenzie River and as far east as the Anderson River (Hultén, 1968; Cody & Porsild, 1968). It was common on Shell and Hidden Lakes at Inuvik in 1965, and I found a large Caddis Fly, Agrypnia straminea Hagen (Phryganidae) on one flower. He was hairy on head, thorax, wing veins, and the tibia and tarsus. All parts of his body, even the smooth abdomen, were covered with the large, spiny pollen grains of this species. There was no doubt that this insect functioned as a pollinating agent (Plate 2, Figure 10).

Nuphar variegatum Engelm. is a more southern species, but occurs on the eastern flank of the Mackenzie Valley and in the Great Bear Lake corridor to the Alberta border (Cody & Porsild, 1968) as well as throughout Labrador to the tree line (Hultén, 1968). In both species the yellow sepals are large and the petals inconspicuous, about one-third as long as the sepals, but bearing nectar pits of very varied size near, or at, the tips. The pits may be as small as 1 mm and as wide as 3.5 mm, and secrete nectar copiously. (See Plate 2, Figures 8 & 9). No further collections could be made because of lack of a boat, but Phryganidae and Muscidae have been recorded on Nuphar luteum Sm. in Europe (Knuth, 1908), and could reasonably be expected to be pollinating agents in northern Canada.

Plate 2, Figures 8-17. 8-10, Nuphar polysepalum Engelm; 8 & 9, Under side of petal showing variation. Stamen as in N. variegatum; 10, Longitudinal section of flower with caddis fly, Agrypnia straminea Hagen (Phryganidae) on stigma, arrows show route to nectar. Outer stamens dehiscing, inner ones still appressed to style; 11 & 12, Ranunculus hyperboreus Rottb; 11, Petal with minute nectary pit; 12, Enlargement of nectary pit; 13, Ranunculus pedatifidus Sm. Petal with nectary pit; 14-16, Anemone patens (L.) ssp. multifida Pritzel (=Pulsatilla patens L.) Mill; 14, Normal stamen; 15, Stamen modified as nectary; 16, Flower showing outer stamens modified as nectary glands; 17, Delphinium glaucum L. Internal view of one of the two petals modified as nectaries. N, Nectary. NP, Nectary Pit. NS, Nectar Storage. S, Stamen. P, Petal. SE, Sepal. STI, Stigma. CF, Caddis Fly. Line equals 2 mm except in Figure 11 equals 1 mm, in Figure 17, 5 mm, and in Figures 10 & 16, equals 1 cm.

RANUNCULACEAE

Some genera of the northern Ranunculaceae produce no nectar, *Thalictrum* and non-plumose Anemones. The large-flowered *Anemone narcissiflora*, common on Keno Hill, Y.T., was dry, but with abundant pollen to attract pollen-eating insects. Most genera of this family are nectar producing and show unusual variation in nectary types, from simple circular pits at the base of petals in *Ranunculus hyperboreus*, to elaborately modified petals in *Aconitum* and *Delphinium*.

Ranunculus acris, apomictic in Spitzbergen (Polunin, 1959) but principally cross-pollinated according to Fryxell (1957), is now introduced as far north as Fort Smith in the N.W.T. (personal communication, W. J. Cody). This species, and *R. abortivus,* which occurs in the Mackenzie Mts. (Cody & Porsild, 1968) and in the Yukon (Hultén, 1968), have nectary pits at the base of each petal, covered by an upward-directed fleshy scale. *Ranunculus pedatifidus* has a crescent-shaped depression, with a slight infolding of the petal tissue above it at the two sides, suitable for storing minute quantities of nectar (Plate 2, Figure 13). *Ranunculus nivalis* has a pit 0.8 mm wide with a thickened petal ridge beneath it. *Ranunculus hyperboreus* has a minute pit surrounded by a circular ridge on petals as small as 0.3 mm. It is below the size likely to attract insects, and is listed by Fryxell (1957) as possibly apomictic (Plate 2, Figures 11 & 12).

The stamens in *Ranunculus* move away from the pistils as they mature, and the anthers dehisce laterally, allowing pollen to fall on both petals and filaments, to be picked up easily by short-tongued insects seeking pollen or nectar. Hocking (1968) found no nectar in *R. hyperboreus*, and although I saw no nectar on *R. nivalis* in the field there appeared to be dried nectar at the base of petals on some herbarium specimens.

Pulsatilla is recognized as a genus separate from *Anemone* by some authors, based on its possession of long plumose styles. Yuzapchuk, in the Flora of the U.S.S.R. (V. L. Komorov, ed., Vol. VII, 1937) lists 26 Asiatic and European species of *Pulsatilla*, 24 of which have the outer stamens adapted as nectaries. Only one of these, *P. patens* (L.) Mill., (*=Anemone patens* L.) reaches Canada It was in bloom July 12, 1965, at Tuktoyaktuk, N.W.T., and the outermost 12–14 stamens were reduced from the normal 7–13 mm length, with cream-coloured anthers, to amber-coloured stalked nectaries 2 mm (or slightly more) in length (Plate 2, Figures 14–16). The large flowers, attractive to bees, are protogynous at first, stigmas projecting well beyond the longest stamens, so that crosspollination at an early stage would seem likely.

The side of a small stream at Keno Hill, Y.T., yielded Aconitum delphinifolium, in the flowers of which the two petals were modified to two independent, long-stalked nectaries. The stalk had a channel some 9 mm long, followed the curve of the upper hooded sepal and ended in a purplish receptacle for nectar, open at the distal end like a trough, and closed at the proximal end within and near the tip of the hood (Plate 3, Figures 18-21). The closed dilated end has fleshy walls which secrete the nectar. The two lateral sepals were marked with dark veins acting as nectar guides, and an opening 7 mm wide was left for the entrance of insects between the hood and the two lower boat-shaped sepals. Bombus frigidus Sm. and Bombus polaris Curt. were seen to enter the opening readily, and passed over the stamens in an upside-down position, in order to insert the proboscis down the stalk channel to the nectar receptacle. The protandrous stamens, as in Delphinium, completely hid the immature pistils until the pollen was discharged, making cross-pollination obligate.

Dawson City, Y.T., was my source of *Delphinium glaucum*. In this blue flower the two petals were less completely modified than in the above, and fitted neatly into the spur of the upper sepal. Each had an open inner side which fitted together to form a channel posterior to the stamens (Plate 2, Figure 17) and into which a *Bombus* could push its head, extending its proboscis to reach the nectar secreted by the thickened petal wall within the spur. The nectary ended in a solid tip 4 mm long. Both protandrous genera, *Aconitum* and *Delphinium* are confined to areas in which bumblebees occur, as they require insects with long probosces to reach the nectar and accomplish cross-pollination.

CRUCIFERAE

A very limited number of arctic Cruciferae have flowers large enough to attract insects in spite of the fact they are borne in corymbs or racemes. *Parrya nudicaulis, Cardamine pratensis, Arabis alpina,* and *Erysimum pallasii* are among the largest, and the

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first three are probably apomictic. The sweet-scented *Erysimum* pallasii is self-fertilized. Many of the smaller ones, *Lesquerella* arctica, and at least six of our northern Drabas are capable of self-fertilization. Mulligan (1966; and Mulligan & Findlay, 1970) discovered that one of his experimental ones, *Draba oligosperma*, and also *Erysimum inconspicuum*, were apomictic. He adds that, given good weather, some out-crossing occurs in the Drabas and probably in other self-compatible Cruciferae.

In spite of the possible reduction or loss of functional significance of nectaries in arctic Cruciferae, nectaries are present in all species at the base of the short stamens. They contrast in colour from the staminal filament (ex. yellow filament and green nectaries in Draba nivalis) and vary in shape and size from species to species. Cochlearia officinalis has a very small wart-like nectary on either side of the short stamens (Plate 3, Figures 24-25), the Drabas have somewhat larger warts, Parrya arctica has nectaries like flat triangles, and Arabis alpina (Plate 3, Figures 22 & 23), a single conspicuous green flap beneath the short stamens connected laterally to a nectariferous ridge at the base of the long stamen next to it. Cardamine pratensis has a single horseshoe-shaped nectary around each short stamen, open on the side next the ovary (Plate 3, Figure 26), Ervsimum cheiranthoides the same type, but open on the outside. The long stamens, too, may have nectaries between their bases, a triangular one in C. pratensis (Plate 3, Figure 26), a flat vestigial one in E. cheiranthoides, or they may be missing entirely,

Plate 3, Figures 18-27. 18-21, Aconitum delphinifolium DC.; 18, Section through flower, stamens hiding immature carpels; 19, Carpel; 20, Stamen; 21, Petal modified as nectary; 22 & 23, Arabis alpina L.; 22, Saccate lateral sepals modified to store nectar; 23, Ear-like nectary at base of short stamen, vestigial nectary at base of long stamen; 24 & 25, Cochlearia officinalis L.; 24, Median view showing stamens closely appressed to ovary; 25, Lateral view showing small wart-like nectaries at each side of short stamen; 26, Cardamine pratensis L. (Apomictic in Arctic, not necessarily obligate, Fryxell, 1957). Anthers discharged, ovary elongating. Horseshoeshaped nectary outside short stamens, conical nectary glands between long stamens; 27, Parnassia palustris L. Staminode with short stalk, broadening into a thicker green band, the nectary, and then a blade with nine to many capitate filaments. MP, Modified Petal. SR, Storage Receptacle. Hse, Hooded Sepal, N, Nectary. vN, Vestigial Nectary. s, Stamen. STA, Staminode. YK, Yellow Knob. NT, Nectariferous Tissue. SS, Short Stamen. LS, Long Stamen. CAR, Carpel. O, Ovary. Line in Figure 18 equals 1 cm; in Figure 27, 1 mm; in Figures 19-26, 2 mm.

as in the Drabas. The numerous variations in nectaries of the Cruciferae of Europe are well illustrated by Hegi (1958).

The cruciform shape of the corollas in the family does not attract insects for basking, lacking the warmth found in sunshine within the cup-shaped forms of *Dryas* or *Stellaria*. As well, many bloom very early in the season when weather conditions preclude much insect activity. It is probable that many are self-pollinated in the Arctic. Few insect visitors to the white-flowered Cruciferae were noted by Kevan (1972) at Lake Hazen, or by me at Frobisher Bay.

Although the flowers of Cruciferae in general are slightly protogynous, the anthers of the young flowers may be above the stigma and capable of dropping pollen on it as they dehisce, or if below it, usually elongate and brush against the stigmas at maturity, producing self-pollination. Mulligan and Findlay (1970) noted the stigma of *Draba* was receptive some five and a half hours before the long stamens grew to its level, and discharged their pollen. The short stamens elongate later, giving still another chance for selfing.

SAXIFRAGACEAE

The genus *Saxifraga* is represented by 14 species in the Arctic Archipelago (Porsild, 1964), some reaching the northern limit of land. My studies have been primarily on the variation in position of the ovary, from superior to partly or wholly inferior, and the changes in the relative position and type of the nectary, with some observations on the movement of stamens.

The records in the floras on the position of the ovary vary greatly, partly due, in protandrous species, to the gradual upward growth of the ovary as the stamens dehisce, and the stage at which it was described. For example, Hitchcock *et al.* (1961) noted that the ovary of *Saxifraga cernua* was one-quarter inferior at anthesis, less so at maturity; Hegi (1961) said it was one-third inferior, and Komorov (1939) that it was half inferior. My own observations agreed with Hitchcock. I made longitudinal sections of mature flowers of the species studied, noting the percentage of ovule-bearing tissue above and below the point of attachment of the stamens, finding some variation between populations.

In *Saxifraga* the nectary is either in the form of a band at the base of the ovary (with the nectar exposed in open-type flowers, and halfconcealed when the petals remain close to the stamens and ovary), or in the form of an epigynous disk on the top of inferior ovaries, where it is exposed and easily reached by short-tongued insects.

The nectary band in species with superior, or nearly superior, ovaries (ex. Saxifraga davurica, S. foliolosa, S. hirculus, and S. cernua) is not marked by any swelling, but merely by a change of colour or texture, the commonest being a change from a green or purplish ovary to a yellow-green nectary band, or sometimes from a purple ovary to a narrow green band, the nectary always with a shiny smooth surface. The colours of ovary and nectary may vary with the habitat, but the two can be distinguished easily in freshlypicked specimens.

At Frobisher Bay, no free nectar was noted in *Saxifraga rivularis*, a species with about a one-third inferior ovary, and no distinctive nectary band was seen, although there was a slightly yellower colour at the base. It seemed as though this small species with inconspicuous flowers would not be attractive to insects and was self-pollinated.

The nectaries of *Saxifraga* species with partly inferior ovaries, such as *S. aizoides, S. hieracifolia,* and *S. nivalis* are conspicuous as more or less swollen bands, usually of a more yellow colour than the ovary.

Saxifraga oppositifolia, slightly protogynous (Savile, 1972), has a purplish ovary, slightly inferior at anthesis and almost superior in fruit, changing to a brilliant flame colour in its lowest 0.3-0.5 mm. The bright coloured tissue continued among the bases of the filaments and was secreting abundant nectar in all plants examined from Stefansson I., Baillie Hamilton I., and Resolute between July 7 and 14, under weather conditions precluding insect flight (Plate 4, Figure 31). Normally, the flower is bell-shaped with petals 6-9 mm long, and has concealed nectar most readily obtained by insects with long probosces, but a second form, with mauve rather than magenta petals and a more open flower, was present at Resolute, and noted by Savile (1964) on Ellef Ringnes. By its form it was suited to visits from smaller insects. Kevan (pers. comm.) found that over-wintered Calliphoridae, the Blow Flies, went immediately to S. oppositifolia as soon as they became active at Lake Hazen, no doubt effecting cross-pollination. Savile found 30 males of a Chironomid, Lymnophyes sp., on this saxifrage on Ellef Ringnes in 1960, and McAlpine collected the Muscid Spilogona obsoleta (Mall.) on the same species and island two years later (McAlpine, 1965b) indicating possible











pollination activity within individual flowers by small flies, whose movement from flower to flower was restricted by weather. There are no Apidae on Ellef Ringnes, and probably none at Resolute (no specimens of bumblebees from there are in the D.A.O. insect collection). Kevan (1972) found autogamous seed production in S. oppositifolia at Lake Hazen was less than 10%. Savile (1964) credited Bombus polaris and B. hyperboreus with active pollination there and thought the bees responsible for the many genetic forms of colour and petal shape on S. oppositifolia at Lake Hazen.

There were few remains of 1975 capsules at Resolute in 1976, indicating little successful pollination in the previous year. Other species of *Saxifraga*, with uncrowded flowers and relatively exposed nectar, no doubt can be pollinated by flies. McAlpine (1965b) found the Muscid *Spilogona sanctipauli* (Mall.) strongly attracted to *Saxifraga caespitosa*, on Ellef Ringnes Is., but self-pollination is possible in the later stages.

Staminal Movements. Notes were made in the field on the staminal movements in *Saxifraga caespitosa*, *S. rivularis*, and *S. oppositifolia* (Plate 4, Figure 31). At first the position of the stamens was upright and close to the petals. Then the stamens elongated slightly and bent

Plate 4, Figures 28-34. 28, The male stage of Parnassia flower, with successive positions of stamens: Sa, immature; Sb, filament elongated, mature anther over undeveloped stigma; Sc, anther discharged and stamen moved outwards; Sd, anther deciduous; DA, dehisced anther; 29, Parnassia kotzebuei Cham. Petal with opposite staminode. Blade with four to six capitate filaments; 30, Saxifraga davurica Willd. (Keno Hill, Y.T.). Carpels, usually three, occasionally two. Both numbers can occur on the same plant. Nectary a non-swollen glistening yellowish or reddish-purple band on pale green ovary; 31, Saxifraga oppositifolia L. Nectariferous tissue of bright flame colour, or pale in form with mauve flowers. Stamen no. I dehisced and returned to original position; stamen no. 2, in early position by corolla; stamen no. 3, moving towards centre of flower; stamen no. 4, dehiscing by stigma; 32, Saxifraga aizoides L. Nectary a conspicuous yellowish swollen, somewhat lobed band on greenish ovary. Lobing due to pressure of staminal filaments; 33, Saxifraga caespitosa L. Nectary a broad yellow epigynous disc, the nectariferous tissue extending among the bases of the filaments. In S. aizoon the nectary differs in remaining within the staminal ring; 34, Dryas integrifolia M. Vahl. Nectariferous tissue lining shallow receptacle cup. 0, Ovary. 01, Half-inferior Ovary. 02, Inferior Ovary. STI, Stigma. s, Stamen (developmental stages: a, b, c, d). DA, Dehisced Anther. STA, Staminode. NT, Nectariferous Tissue. YK, Yellow Knob. NRC, Nectariferous Receptacle Cup. P, Petal. SE, Sepal. CL, Calyx Lobe. Line in Figure 29 equals 1 mm; in Figures 28, 30-33, 2 mm; in Figure 34, 3 mm.

towards the stigma, dehiscing as they reached the centre of the flower. The spent stamens moved back towards the corolla. Usually several stamens were in motion at once, one having reached and often touched the stigma, another bending towards it, and several dehisced and undehisced stamens pressing against the corolla. Variations in this pattern were frequent. One flower of S. oppositifolia from Baillie Hamilton I. had all stamens bending towards the stigma, and all dehisced; another had the two styles bending towards the petals and touching a dehiscing anther there; still another had the two long styles crossing and bending towards the stamens. In one flower, from Stefansson I., the stigmas were 2 mm higher than the anthers, even though two anthers had dehisced, and chances for self-pollination seemed nil. In most flowers the anthers reached the same height as the stigmas before dehiscence. Knuth (1908) remarks, "Failing insect visits, self-pollination frequently takes place in S. oppositifolia".

PARNASSIACEAE

Parnassia. This genus occurs on the mainland in Canada except for a single record, of Parnassia kotzebuei, on the southern coast of Baffin Island (Porsild, 1964). I found P. kotzebuei and P. palustris (both markedly protandrous) on the bank of a small stream at Keno Hill, Y.T., the former almost finished flowering and the latter at its peak. In this genus only the five stamens alternating with the petals produce pollen, the other five opposite the petals having been modified into scale-like staminodia. Each staminodium has a short basal stalk, either whitish or transparent in colour, followed above by a slightly thickened greenish band, the nectary, then a broadened blade terminated by capitate filaments (Plate 3, Figure 27). The two species can be distinguished readily by the form of the staminodium, that of P. kotzebuei measuring from 0.4-0.6 mm wide, and bearing four to six filaments (Plate 4, Figure 29), that of P. palustris measuring 1.8-2.5 mm wide, with nine to many filaments (Plate 3, Figure 27). The capitate knobs at the ends of the filaments in the former were slightly tinged with yellow, those of the latter were a bright transparent gold colour, very attractive to insects. The stamens move to a position over the sessile immature stigma one by one, and dehisce upwardly, so that any insect climbing over the staminodium to reach the nectar would automatically touch the anther which had reached the centre of the flower and become dusted with its pollen (Plate 4, Figure 28). The successive ripening of anthers allows more time for cross-pollination, should poor weather prevent insect flight on certain days.

ROSACEAE

The genera *Dryas* and *Potentilla* are found in every latitude of land above the Arctic Circle in Canada. *Dryas integrifolia* depends largely upon visits from flies for seed production (Kevan, 1972b), but *Potentilla* sp. may be apomictic (Fryxell, 1957). Davis and Heywood (1963) noted that both reduced and unreduced embryo sacs may occur side by side in the same population of *Potentilla*, and occasionally it may reproduce sexually. *Rubus chamaemorus*, widespread in the low arctic, is one of the few dioecious dicot species in the north, and must depend entirely upon insect pollination for seed set.

All three genera have perigynous flowers with shallow cup-shaped receptacles lined, between the stamens and carpels, with shining, often yellow or flame coloured, nectariferous tissue. The nectar can be reached easily by small or short-tongued insects, although *Dryas* and *Potentilla* are also visited by northern bumblebees (Milliron, 1973), (Plate 4, Figure 34).

Among unusually small flowers of *Dryas integrifolia* at Frobisher Bay there were a few purely staminate ones. However, they contained dark-coloured vestigial pistils 0.5 mm long. The staminate flowers of *Rubus chamaemorus* contained no vestigial pistils, but the pistillate flowers had vestigial stamens 1.4–1.8 mm compared with the functional ones on the staminate flower, which measured 5.0–7.0 mm.

Although *Potentilla* may not require insect visits for seed production, abundant nectar was found at the base of the stamens in *P. anserina* when picked on the banks of the Klondike River near Dawson City, and in fresh specimens of *P. hyparctica* from Melville I. Hocking (1968) noted *Potentilla* sp. at Lake Hazen produced 123 gm total sugar per hectare, with a maximum sugar concentration of 80%.

The stamens of both *Dryas* and *Potentilla* tend to move outwards towards the petals as they dehisce, and the anthers to turn laterally so that pollen may fall on petals, staminal filaments, and, as the

inner stamens dehisce, on stigmas as well. Pollen was noted scattered on styles, filaments, petals and sepals in *P. anserina*. Self-pollination could take place in an older flower of *Dryas*, or pollen contact on the stigma may stimulate seed formation in an apomictic *Potentilla*. Faegri and van der Pijl (1966) note that many apomicts need pollination to start the development of seed, even if fertilization does not seem to occur, possibly through the production of hormones and auxins.

Dryas integrifolia was one of the most insect-visited flowers at Frobisher Bay, partly for basking (Kevan, 1973), and partly for pollen and nectar. McAlpine (1965a) made careful notes on insect visitors to Dryas at Lake Hazen, and Mosquin and Martin at Melville I. (1967), to which I add the species I collected from individual flowers at Frobisher Bay: *Rhamphomyia* sp. (Empidae), *Amauronematus* sp. (Tenthredinidae), *Peleteria aenea* Staeg. (Tachinidae), *Eupogonomyia groenlandica* Lundback, *Hydrophora alaskensis* Mall., *Hylema* (*Paregle*) radicum (L.), Lasiops subrostratus (Zett.), Limosia sp., Spilogona imatatrix (Hall), Spilogona sactipauli (Mall.), (Muscidae).

The Potentillas were visited by bumblebees, *Potentilla hyparctica* by *Bombus hyperboreus* Schon. at Frosbisher Bay, and *P. palustris* by *Bombus frigidus* Sm., *B. jonellus* (Kby.) and *B. sylvicola* Kby., at Inuvik. McAlpine (1965a) recorded Syrphidae feeding on the pollen grains of *P. chamissonis*, and Calliphoridae on its nectar at Lake Hazen.

FABACEAE

The nectar-secreting tissue of the two commonest arctic genera, *Oxytropis* and *Astragalus*, as well as *Lathyrus*, from Great Whale River on the Hudson Bay, were examined under a dissecting microscope. These genera have no obvious nectar glands, unlike some of the Phaseoleae which have collar-shaped nectaries (Waddle & Lersten, 1973), but the thickened membranous base of the nine fused filaments, and the top of the receptacle are lined with shiny secretory tissue (Plate 5, Figures 35 & 37). The tenth stamen is free from the membrane, leaving a slit through which a bee can push his proboscis to reach the nectar. The monadelphous genus *Lupinus*, common along the Mackenzie River above the Arctic Circle, has all

ten stamens fused, and no slit left for the entrance of a proboscis. It produces pollen only, no nectar.

Insect pollination of our arctic legumes must be confined to Bombus, or insects heavy enough to depress the keel and free the stigma and stamens. In order to estimate the chances of stamens and stigma coming in contact mechanically, I depressed the keels of Oxytropis podocarpa and O. maydelliana with forceps and the stigma and stamens sprang instantly into sight. In O. podocarpa, one anther was touching the stigma, the others slightly behind the receptive part. Although the tissue around the stipe of the ovary was shiny and glandular, there was no free nectar apparent. In O. maydelliana the stigma projected beyond the anthers in some cases; in others the anthers, with a peculiar fuzzy appearance, completely surrounded it. The basal chamber was very wet with nectar, and even the glabrous base of the ovary was damp, although probably not in itself secretory. Laboratory examination of the anthers showed them to be full of germinating pollen grains. The germ tubes reached a maximum length of 72 microns, sufficient to penetrate the stigma next to the anther. The germination of pollen in situ in O. maydelliana was first spotted in 1964 at Frobisher Bay, and further seen in fresh material brought in from Hooper I., N.W.T., in 1975 and finally noticed again at Frobisher Bay in 1976. My first reaction in 1964 was that some freak of weather had caused the pollen to germinate abnormally, but it seems that at least one strain of O. maydelliana has an adaptation to secure self-pollination, necessitated by the few insect visitors it receives. D.B.O. Savile remarked (personal communication) that it is far more abundant at many arctic sites than most legumes, indicating a successful selfing mechanism. In Frobisher Bay I saw only one visitor to its flower, Bombus sylvicola Kby., compared to dozens from both B. sylvicola and B. polaris Curt. to the fragrant, purple Astragalus alpinus growing beside it. Mosquin and Martin (1967) noticed on Melville I. the same difference between Oxytropis arctica and A. alpinus, the latter apparently being unusually attractive to bees.

According to Fryxell, perennial legumes of the low latitudes are normally self-incompatible (1957). Clapham, Tutin, and Warburg (1962) state Astragalus alpinus is usually cross-pollinated by bees, as well as Oxytropis. At Frobisher Bay in 1964 both Oxytropis maydelliana and A. alpinus freely produced well-filled pods, indi-



cating that the former (without insect visitors) must have been selfcompatible.

ONAGRACEAE

One genus only is listed for the Arctic Achipelago, *Epilobium* (Porsild, 1964). Two large and showy species are common, the territorial flower of the Yukon, *E. angustifolium*, which barely reaches the eastern islands, and *E. latifolium*, which extends to the northern limit of land at latitude 83° on Ellesmere I.

Epilobium angustifolium is a classical example of protandry, and cross-pollination by insects must be the usual method of fertilization. In the young flowers the style is curved downwards, the stigma lobes closed, while the stamens are upright in the process of dehiscing. The visiting bee must land on the anthers first when the flowers are in this condition and it normally proceeds upwards on the raceme, visiting still younger flowers, so pollination may not occur until it flies to another inflorescence. In older flowers the style straightens and elongates beyond the anthers, the stigma lobes open, and the bee lands on the stigma first, depositing pollen gathered previously from younger flowers. I examined an inflorescence on

Plate 5, Figures 35-47. Note: The tenth, or free, stamen in Fabaceae removed before drawings made. 35, Astragalus alpinus L. Lower half of ovary and staminal tube. Shiny nectariferous tissue at base of split tube formed by nine fused filaments; 36 & 37, Lathyrus maritimus (L.) Bigel. (Great Whale River); 36, Lateral view, showing proximity of anthers to the stigma; 37, Ventral view of staminal tube with basal nectariferous tissue. Anthers deciduous; 38, Epilobium angustifolium L. (Markedly protandrous). Nectary a green epigynous disc on purple inferior ovary. Style markedly curved in staminate stage, elongated and straight in the pistillate stage shown in drawing; 39, Epilobium latifolium L. (Slightly protandrous). Semi-diagrammatic drawing showing protective enlarged bases of four of the stamens, and fleshy, curved glabrous style and stigma. Epigynous nectary hidden inside filaments; 40 & 41, Pyrola grandiflora Rad.; 40, Pistil, with 5-lobed ovary, no nectary; 41, Stigma seen from above, with five sticky cones above collar; 42 & 43, Arctostaphylos alpina (L.) Spreng.; 42, Nectary a slightly lobed band at base of shiny green ovary. Stigma larger than in A. uva-ursi; 43, Stamen with enlarged pubescent base fitting in between scallops of nectary; 44 & 45, Arctostaphylos uva-ursi (L.) Spreng.; 44, Nectary a torulose band; 45, Stamen anther with long appendages decorated with transparent peg-like thickenings; 46 & 47, Andromeda polifolia L.; 46, Nectary a torulose band at base of lobed ovary; 47, Stamen. o, Ovary. STY, Style. STI, Stigma. COL, Stigmatic Collar. C, Stigmatic Cone. S, Stamen. F, Filament. A, Anther. AP, Anther Appendage. ST, split Staminal Tube. N, Nectary. NT, Nectariferous Tissue. Line equals 2 mm, except 3mm in Figure 36.

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the banks of the Klondike River, Y.T., and found the lowest four flowers had elongated styles, with open lobes, anthers fading; the next three had shorter styles, and stigmas closed, with anthers actively discharging pollen. Above that, the raceme bore flowerbuds only. The succession of changes in the flower is illustrated well by von Marilaun (1895).

There is a green, fleshy, slightly concave nectary on the upper end of the purplish, inferior ovary, which produces nectar with a high concentration of sugar, 77% (Hocking, 1968). The nectar is protected from rain by the bending of the broadened bases of the filaments over the nectary to form a covering cone. Above the cone, which continues for some 1.6–4 mm, the style has hairs up to 0.5 mm, acting as a deterrent both to raindrops and to insects too small to be useful for pollination (Plate 5, Figure 38).

Bee visitors were numerous and of eight different species, as follows: Bombus frigidus Sm., B. jonellus Kby., B. lucorum (L.), B. mixtus Cr., and B. sylvicola Kby., collected at Inuvik from individual flowers; B. bifarius nearcticus Handl., B. frigidus, B. mixtus and B. pleuralis Nyl., collected as above, at Dawson City, Y.T., B. frigidus, B. occidentalis Grm., and B. sylvicola, collected at Keno Hill, Y.T., at 914 metres altitude. As well, Syrphidae were common visitors to Epilobium angustifolium at Inuvik: Eristalis bardus (Say), Helophilus groenlandicus (O. Fab.), and H. obscurus Lw. Homoptera and Hemiptera were recovered from the inflorescence by sweeping, but they were probably getting sap from the flower tissue and not greatly involved in carrying pollen. The hairs were minute on those collected and little or no pollen was present on their bodies.

Epilobium latifolium is not markedly protandrous. The style remains curved and lower than the anthers even in older flowers, and lacks the hairs seen in *E. angustifolium*. The nectary is similar, green and concave, protected by the enlarged flat bases of the filaments (Plate 5, Figure 39). Hocking (1968) found it capable of producing up to 3.5 mg of sugar per flower per day at Churchill, well above the other species he tested. At least six observers have seen bees visit this species and I saw one bee, unidentified, at Frosbisher Bay on Aug. 2, 1975, in exceptionally warm weather. I did not see any bees visit it during the cool summer of 1964, but saw three butterflies, *Colias* spp., the Syrphidae, *Helophilus borealis* Staeg., the Muscidae, *Egle.* sp., and *Lasiops subrostratus* Zett., a

Swales — Nectaries

Heliomisidae, *Neoleria prominens* (Beck), and innumerable *Pro-tophormia terrae-novae* (R-D) of the Calliphoridae. The last were crawling over the flowers and were covered with pollen, so were probably active pollinating agents. The pollen grains of *Epilobium* tend to stick together with viscin threads, so it is doubtful if they fall readily onto the stigmas below, to effect self-fertilization.

ERICACEAE

Porsild (1964) lists seven genera in the Canadian Arctic Archipelago, many species possessing urceolate corollas and drooping flowers particularly suited to pollination by bees. One with an open flower, *Kalmia*, has an explosive mechanism for liberating the pollen, which normally is triggered by the movements of a heavybodied insect probing for nectar. The anthers are held in hollows of the corolla by bowed filaments under tension, and at a touch they are released, and send a shower of pollen onto the visiting insect.

Most of the Ericaceae are autogamous, according to Fryxell (1957) (although some *Vaccinium* species are known to be obligate out-crossers), but the distribution of the family in the arctic seems to reflect the local bee population. *Cassiope tetragona* is an exception, being distributed in most of the Queen Elizabeth Islands. Kevan (1972) found it to set seed well under insect excluders, but other ericaceous species seem to disappear in the islands where bees are absent or rare.

The flowers of all species studied, except *Pyrola grandiflora*, were found to have the attraction to insects of actively secreting nectaries. The anthers of a number had appendages which act as trip hammers when touched, shaking pollen over the visitors (Plate 5, Figures 43–47). Many specimens of the sweet-scented *P. grandiflora* were examined in the field at Frobisher Bay without finding a trace of nectar or nectaries, although Clapham *et al.* (1962) say nectar in *Pyrola* is secreted by the base of the petal. The stigma was unique, composed of five wet glistening cones (Plate 5, Figures 40–47). The fluid present seemed more than necessary to ensure pollen grains sticking to it, and was a possible attractant. The whole of the short, fleshy, yellowish-green style of *Cassiope hypnoides* was sticky to the touch and frequently bore holes made by insect larvae, perhaps the oviposition sites of a moth (Plate 6, Figure 48). It was not clear what advantage, if any, such a style had for the plant. There are devices,

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such as hairs on the filaments (Andromeda, Ledum, Kalmia) (Plates 5 & 6) or tangled hairs within the corolla (Arctostaphylos, Andromeda) to prevent small non-pollinating insects from reaching the nectar.

It is probable that some cross-pollination takes place in the arctic in flowers so well adapted to it, and known to have bee and other flower visitors. On the other hand, self-pollination would be physically easy when the stigma is above the level of the anthers in nodding or pendulous flowers such as *Andromeda*, *Arctostaphylos*, and *Cassiope*. The pollen would simply fall by gravity to the stigma on a windy day. In the umbellate flowers of *Ledum* the stigma is below the level of the anthers, but the flower is upright and pollen would be shaken down onto the stigma with wind movement (Plate 6, Figure 52).

Nectaries. The species with superior ovaries bear a shiny nectariferous band at the base of each ovary, varying from 0.3–1.0 mm in depth, and swollen between the bases of the filaments, often giving it a scalloped or torulose appearance (Plate 5, Figures 42, 44 & 46; Plate 6, Figures 48–53). The band is readily seen because it is always of a slightly different shade from the ovary, usually a darker green. In *Vaccinium* spp., with inferior ovaries, the nectary occurs as a thin, shiny, fleshy epigynous disc, its thickness evident in a longitudinal section of the flower (Plate 6, Figures 54 & 55).

Plate 6, Figures 48-57. 48 & 49, Cassiope hypnoides (L.) Don; 48, Slightly scalloped nectary at base of 5-lobed ovary; 49, Stamen (1.5 mm) with long appendages, decorated with sharp peg-like projections; 50 & 51, Kalmia polifolia Wang; 50, Nectary band green; 51, Stamen with flat filament; 52, Ledum groenlandicum Oeder. Nectary of indefinite swellings at base of ovary. At right, details of ovary wall; 53, Phyllodoce coerulea (L.) Bab. Nectary a green glabrous scalloped band at base of greenish-yellow ovary with glandular hairs. Note: Although the Vaccinium species illustrated had eight stamens each, most were removed to prevent cluttering of drawings. 54, Vaccinium uliginosum L. Longitudinal section of flower. Nectary an epigynous disc; 55, Vaccinium vitis-idaea L. Longitudinal section of flower. Nectary an epigynous disc; 56, Armeria maritima (Miller) Willd. Nectary a vellowish swelling at base of staminal filament fused to petal; 57, Polemonium pulcherrimum Hook. Corolla opened to show 4 of the 5 lobes, and 3 of the 5 stamens. Nectary a dark-green cup-like rim at base of a light green ovary. O, Ovary (superior). 10, Inferior Ovary. ow, Ovary Wall, greatly enlarged. STY, Style. STI, Stigma. II, Insect Injury. S, Stamen. F, Filament. A, Anther. AP, Anther Appendage. CO, Corolla. P, Petal. CA, Calyx. N, Nectary. Line equals 2 mm.

PLUMBAGINACEAE

Armeria maritima (Mill.) Willd. ssp. labradorica (Wallr.) Hult. is a widely distributed species along the coasts, rarely inland. Although the European race has both "cob" and papillate stigmas and is self-incompatible, the North American race, presumably derived from it, has only papillate stigmas and is self-compatible (Baker, 1959). All Frobisher Bay plants examined had papillate stigmas, but retained the texture and colour of the dimorphic race attractive to insects.

There was a swollen yellowish nectary below the point at which the stamen was attached to each of the five petals. Nectar collected in the space between the petals and ovary, 7 mm below the tip of the flower, protected from rain and the invasion of small, non-pollinating insects by long hairs on the lower part of the style branches (Plate 6, Figure 56). As the flowers were slightly protandrous, insect visitors would become powdered with pollen before the five stigma branches opened, leading to possible cross-pollination. In older flowers the stigmas diverged, and the anthers were seen to bend inwards at right angles to the filament, so that a foraging insect would touch both stigma and anthers on the same visit, making self-pollination possible in this self-compatible race.

POLEMONIACEAE

The pleasant-scented *Polemonium acutiflorum* and the mephitic *P. pulcherrimum* are common in the Yukon and continue into Alaska, *P. acutiflorum* to well above the Arctic Circle, and *P. pulcherrimum* mainly south of it, as far as the mountain ranges of California.

The two species were studied at Dawson City, Y.T., June 23–28, 1969. Both had blue to purple campanulate corollas, with darker, purple veins converging towards the base, acting as insect guidelines to the nectary, a dark green cup-like rim at the bottom of the lightergreen ovary, thicker in *Polemonium acutiflorum* than in *P. pulcherrimum*. The stamens were attached to the corolla 2–4 mm from the base, in a tangle of white hairs 0.54–0.59 mm long, outgrowths of both the filaments and the corolla. Insects were further attracted to the nectary by the whitish throat in *P. acutiflorum* and the striking yellow one in *P. pulcherrimum* (Plate 6, Figure 57). Ekstam reported *Polemonium caeruleum* L. to be protogynous to homogamous in Novaya Zemlya (Knuth, 1909), but in the early flowering stage of both the Dawson species, the anthers dehisced while the stigma lobes were still closed, making them protandrous, and suited to cross-pollination. The stigmas were usually on a higher level than the anthers, occasionally opposite, so in the next, homogamous, stage, self-pollination might take place, particularly if the flower became horizontal, or drooped as it aged, more frequent in *P. acutiflorum*.

A strong proboscis would be needed to penetrate the tangle of hairs above the nectary and Knuth (1909) records bees and flies visiting the European species. I made no observations on their insect visitors, due to lack of time, but *Bombus* spp. were common along the Yukon River.

The corollas of *Polemonium acutiflorum* at Dawson City were thickly covered with short-stalked yellow glands 0.139–0.163 mm in diameter. The flowers at Keno Hill had only occasional yellow glands, and they were missing in Lac Laberge specimens. Kluane Lake plants had flat white hairs on the margins and backs of the petals. *Polemonium pulcherrimum* had very few, or no, glands on the corolla. It would be interesting to know if these clones would be consistent in the production of glands and hairs under varying conditions, and whether they had any effect on insect visits. They were not described in the floras listed.

BORAGINACEAE

Mertensia maritima, of gravel beaches, is the only species of the Boraginaceae found commonly in the Arctic. Other genera are known in the western sub-arctic mainland, of which I collected Myosotis alpestris at Whitehorse and Amsinckia menziesii at Dawson City in the Yukon. Mertensia maritima was studied at Frobisher Bay, from Ikaluit Beach.

There is much uniformity in the size of flowers, the type of nectary, and the position of anthers and stigmas in the northern Boraginaceae. The introrse stamens are attached to the corolla near the top of the tube by very short filaments, 0.5 mm in *Myosotis* to 1.2 mm in *Mertensia*, and intermediate in *Amsinckia*. The filaments tend to bend away from the corolla in the later stages, bringing the top or the bottom of the anther opposite the stigma, and close to it.



The corolla tube is not more than 2-3 mm wide, the limb expanded to a varying degree in the three species, but the throat is further narrowed in *Myosotis* by scales. Under this condition one side of the proboscis of a bee would touch the anther, the other the stigma, when inserted into the flower.

The style ends in an elongated pyramid-shaped gynobase in *Amsinckia* (Plate 7, Figure 59), with four membraneous wings radiating to the outside of the ovary in *Mertensia*, in both species allowing for lateral attachment of the nucules in the concavities between the "rays". The style of *Myosotis* widens only slightly between the nucules, which are attached basally (Plate 7, Figure 60). Beneath the ovary in all three genera is a somewhat irregular, fleshy, nectary ring, yellowish in *Mertensia* and *Myosotis* and a darker green than the nucules in *Amsinckia*.

The nectaries in these small flowers secrete scanty nectar and are visited very little by insects, although Knuth (1909) records bees, Lepidoptera and Syrphids visiting *Myosotis* in Europe. The close proximity of the anthers and stigmas in the later stages of the flower suggests that self-pollination is usual in these species in the Arctic.

Plate 7, Figures 58-67. 58 & 59, Amsinckia menziesii (Lehm.) Nels. & Macbr. (Dawson City); 58, Nucules and nectary from above. Nectary a dark green fleshy disc; 59, Pyramid-shaped gynobase, the nucules removed from the concavities; 60, Myosotis alpestris R. W. Schmidt. Nectary an irregular ring beneath nucules, enlarg ing slightly between them; 61, Penstemon procerus Dougl. Nectary a soft yellow disc at base of green ovary. Upper pair of stamens attached to corolla above lower stamens. Staminode opposite anthers of lower stamens, attached to corolla above both pairs of fertile stamens, with club-shaped enlarged tip, pubescent on one side; 62-64, Rhinanthus crista-galli L. (Great Whale River); 62, Pistil showing nectary and basal corolla "frill"; 63, Enlargement of corolla frill and nectary gland; 64, Pair of anthers (normally apposed and attached by connective at the proximal end) pulled apart to show dehisced pollen sacs; 65-67 & 68 (Plate 8), Pedicularis, General note: The dotted lines outline the upper lip, or galea, and show the position of the anthers of the stamens opposite the point the proboscis of the visiting insect enters to release the pollen sprinkling mechanism; 65, Pedicularis arctica R.Br. Pistil showing asymmetric nectary at base of ovary; 66, Pedicularis hirsuta L. Pistil with well-developed asymmetric nectary, and filaments markedly coiled for increasing tension; 67, Pedicularis labradorica Wirsing. Pistil with small asymmetric nectary. N, Nectary. NU, Nucule, GB, Gynobase, O, Ovary, STY, Style, S, Stamen, STA, Staminode, A, Anther, co, Corolla. Line equals 2 mm, except 1 mm in Figure 60.

SCROPHULARIACEAE

The Scrophulariaceae are particularly well represented in the arctic by the genus *Pedicularis*, with 16 species in Alaska (Hultén, 1968) and 8 in the arctic islands (Porsild, 1964). Other less common (sub-arctic) genera I have collected include *Castilleja*, *Lagotis*, and *Penstemon* in the Yukon, and *Rhinanthus* in Labrador. The long, tubular, and usually bilabiate corollas of the arctic and sub-arctic species are particularly adapted for pollination by *Bombus* spp. and the larger Syrphidae, such as *Helophilus borealis*.

The nectar of these genera is concealed, secreted by nectaries of varied form at the base of the ovary, either as asymmetrical discs, or single glands (Plate 7, Figures 61–63 and Plate 8, Figure 68). *Rhinanthus* has a cone-shaped fleshy gland on the side of the ovary below the terminal curve of the style. Nectar seems to be copiously produced and dries on the delicate base of the corolla so that a frill of tissue, strengthened by the sugar deposits, is left when the corolla is pulled off by hand. This frill was evident at the base of the capsules in herbarium specimens, collected in fruit, in which the corolla had dropped off naturally (Plate 7, Figures 62 & 63).

Penstemon gormanii and P. procerus had small soft nectary discs of rather indefinite shape, differing in colour from the ovary, and wet with nectar in the latter species, when picked at Whitehorse, Y.T. (Plate 7, Figure 61). Pedicularis had firm asymmetrical discs, thicker on the side below the curvature of the style, and usually of a different shade from the ovary, and easily distinguished. The nectary of Pedicularis flammea was smaller than that of the other species studied, and may be functionless in this species, found to be autogamous, and stated to be nectarless, by MacInnes (1972). Macior (1970) noted that P. lanceolata in Colorado was nectarless.

Pollination in *Pedicularis* has been studied experimentally through the artificial exclusion of insects by MacInnes (1972) and Kevan (1972b) in the Canadian Arctic, by Sprague (1962) in California, and by Macior (1970, 1973, 1975) in California, Colorado, and Washington. Sprague said the flowers of *P. crenulata* were limitedly self-compatible, and autogamy occurred rarely. Macior found the California species had obligate dependence on insects for fruit production and that no species in Colorado were self-pollinating, including *P. sudetica*. Our northern species seem to have evolved towards autogamy. Mosquin and Martin (1967) saw no

bees visiting *P. arctica* and *P. sudetica* in Melville I., and thought they must be autogamous there, although Savile saw bees visiting *P. arctica* on Somerset Island, a bit further south (1959).

MacInnes (1972) found *Pedicularis lapponica* totally dependent on insects, *P. labradorica* and *P. sudetica* only partially dependent and *P. flammea* wholly independent of insects for seed production. Kevan (1972b) found *P. capitata* and *P. arctica* dependent on insects, although 7% of the plants of the latter were able to produce capsules under an insect excluder. *Pedicularis hirsuta* and *P. lanata* are structurally well suited to selfing, and have produced seeds vigorously in Spitzbergen where there are no bees (Knuth, 1909). The genus is usually homogamous.

Correlation between exsertion of stigma outside of corolla and insect pollination. A correlation of possible significance was noted between the exsertion of the style in *Pedicularis* and the experimental results on the need of different species for insects. The style was conspicuous outside the corolla of *P. capitata*, slightly less conspicuous in *P. sudetica* and with a short exsertion in *P. labradorica*. All these are dependent or partially dependent on insects, the most completely dependent being *P. capitata*, with the longest exsertion. The style is enclosed in the galea in *P. flammea* and *P. hirsuta*, known to be mainly autogamous. *Pedicularis lanata*, known to be self-pollinated in Spitzbergen (Knuth, 1909), usually has the style within the hood, but occasionally the stigma projects slightly on the lower older flowers of the spike.

Mechanics of pollination in *Pedicularis* and *Rhinanthus*. The "sprinkling apparatus" of the sub-family Rhinanthoideae, to which these two genera belong, is well known (von Marilaun, 1895). The lower lip of the bilabiate corolla serves as a landing platform for the bee. Of interest is the fact that the heads of *Bombus polaris* and *B. sylvicola*, known pollinators of *Pedicularis* (MacInnes, 1972) measure 1.0–1.3 mm more from side to side than in depth (measured in personally collected specimens), and that the lower lip of most of our arctic *Pedicularis* species is oblique (noted in *P. arctica, P. hirsuta*, and *P. lapponica*), lower on the left side than on the right so that the bee is tilted on its landing platform and its head automatically enters the very narrow slit of the galea by its narrower

dimension. The pressure of the bee on the lip and galea distends the slit laterally. The lower end of the galea has papillae on its margin, hazardous to the sensitive proboscis, so the bee inserts it at the top end where its head will brush against the stigma, depositing on it any pollen grains it may have collected from other flowers.

The four stamens are arranged in pairs, the anthers pressing tightly against one another to form potential pouches. When the pollen sacs dehisce, they discharge the pollen into the pouch, where it is held by the tension of curved staminal filaments in *Pedicularis* (Plate 7, Figures 65–67; Plate 8, Figure 68) or stiff flat filaments in *Rhinanthus* (Plate 7, Figures 62–64). At the touch of the bee's proboscis the tension is released in *Pedicularis*, the anthers spring apart, and a shower of pollen falls on the bee's head and the anterior part of its thorax.

I tested the mechanism by sticking a dissecting needle into the top of the galeal slit in freshly picked *Pedicularis arctica*, *P. hirsuta*, and *P. flammea*. In all three species the touch of the needle triggered an instant shower of pollen, which scattered over the inside of the galea.

Self-pollination with aging of the flower. As the flower of *Pedicularis* ages it tends to move to a horizontal or lower position, so that released pollen may fall by gravity onto stigmas now below the anthers and autogamy may take place. If the sprinkling mechanism is not released by the touch of an insect, the pollen will fall eventually as the pairs of anthers become flaccid and no longer press firmly against one another.

No explosive mechanism in *Penstemon. Penstemon*, a protandrous genus, belongs to a different sub-family, the Antirrhinoideae, in which the anthers discharge their pollen gradually. The mouth of the narrow, dark blue corolla of *P. procerus* is only 2–3 mm wide, and the bee's proboscis is guided to the purple anthers over a glabrous palate between two patches of white hairs on the lower lip. The base of the ovary was wet with nectar from a soft yellowish nectary when the plant was picked at Whitehorse, Y.T. The blue corolla of *P. gormanii*, with a reddish-purple tinge, measured 2.8 cm long by 1.8 cm wide, but the throat was protected from the entrance of small non-pollinating insects by copious long white hairs. *Bombus* spp. were the effective pollinators, aided by purple lines on a whitish corolla background, leading to the narrow pale green nectary at the base of a darker green ovary.

The hairy staminode, a modified fifth stamen, was below the stigma and the long pair of stamens in both species of *Penstemon* at Whitehorse. However, examination of herbarium material showed that in *P. gormanii* the staminode elongated even beyond the corolla in age. It is possible it had some function in carrying pollen grains past the stigma to pollinate a flower lacking insect visitors.

CAMPANULACEAE

Campanula is the only genus of the Campanulaceae to reach the arctic, and the pollination mechanism and nectaries of three arctic and two sub-arctic species were studied. All had bell-shaped flowers, *C. rotundifolia, C. lasiocarpa,* and *C. uniflora* with shallow-lobed corollas, *C. scouleri* deeper lobes, and *C. aurita* with lobes four-fifths of its length. The structure influences the type and size of insects able to enter. The size of the corolla mouth varied from 0.6–1 mm in *C. uniflora,* up to 2 cm in large specimens of *C. rotun-difolia* and *C. lasiocarpa* giving ample room for large Hymenoptera (Plate 8).

In all species the nectary is in the form of a fleshy yellow epigynous disc at the base of the style. It is covered by the triangular bases of the five stamens, firmly held together by marginal interlocking hairs, requiring a stout proboscis to penetrate. The style is glabrous in the lower part, but densely pubescent for a substantial part of the upper end. In the young stages the stigma lobes are tightly closed, and surrounded by the anthers which form a tube. The flower is strongly protandrous and the anthers discharge introrsely onto the hairy part of the style. Once the anthers are empty the style elongates carrying its load of pollen upward, and the stamens shrivel to the bottom of the corolla. Then the stigma lobes open and become receptive. Any bee entering the bell at this stage must brush against the stigma, and, as it probes for nectar, would have its coat powdered with pollen. The method is an ingenious one for ensuring cross-pollination, but should insects fail to visit, selfpollination is possible in the last stages of the flower, when the stylar branches curl backwards and touch the hairy pollen-dusted style.

In Campanula aurita, which I collected at Dawson City in the Yukon, the corolla lobes curled backwards so that short-tongued







insects could reach the bottom of the bell, and if strong enough, could penetrate between the staminal bases to the nectar. The relative length of pubescent and glabrous parts of the style varied greatly between species, and could be used as an additional character to distinguish between them (Plate 8).

ASTERACEAE

The nectaries of the Asteraceae occur as small swellings at the base of the style which fit neatly within the narrow tube of the corolla. If the nectar is copious, it may rise in the tube so that shorter-tongued insects may reach it. However, long-tongued insects of the Hymenoptera, and members of the Lepidoptera are the usual successful nectar seekers in the Asteraceae. The genus *Achillea* is exceptional in having short corollas (2–3 mm long in *Achillea borealis* at Inuvik) so that flies are its main pollinators.

The length of the disc florets varies with latitude and habitat, but most arctic Asteraceae fall within the range of *Senecio congestus* and *S. lugens*, 5 mm at Inuvik, *Solidago multiradiata*, 6 mm, and *Arnica alpina*, 8 mm at Dawson City, all requiring long-tongued insects to reach the nectar. The width of the corolla at the base varied from 0.3–0.5 mm. A very narrow tube was noted in *Petasites palmatus* from Great Whale River, in which the tube of the ligulate flowers was only 0.25 mm wide. Butterflies are known to favor sucking nectar out of a narrow tube and are attracted to this family.

Plate 8, Figures 68-75. 68, Pedicularis lapponica L. Pistil with conspicuous asymmetric nectary at base of ovary; 69 & 70, Campanula rotundifolia L.; 69, Longitudinal section through the protandrous flower in pistillate stage. Anthers dehisced, stamens shrinking. Nectary epigynous; 70, Stamen with broad base and protective interlocking marginal hairs; 71-75, Diagrammatic drawings of five northern species of Campanula in pistillate phase. The lobing, and depth and width of corolla, indicate probable size and type of insects adapted for their pollination; 71, Campanula scouleri Hook (Alaska). Corolla length 10-15 mm, corolla mouth 8-12 mm. Stigmas frequently 2-lobed, sometimes 3-lobed; 72, Campanula aurita Greene (Dawson City). Corolla length 10-13 mm, corolla mouth 15 mm. Style often curved in older flowers; 73, Campanula rotundifolia L. (Frobisher Bay). Corolla length 15-30 mm, corolla mouth 15-20 mm; 74, Campanula uniflora L. (Frobisher Bay). Corolla length 5-15 mm, corolla mouth 6-10 mm; 75, Campanula lasiocarpa Cham. (Dawson City). Corolla length 15-32 mm, corolla mouth 10-24 mm. N, Nectary. O, Ovary. STY, Style. P.C.H., pollen-collecting hairs. s, Stamen. A, Anther. co, Corolla. cA, Calyx. Line equals 2 mm.











In the Asteraceae pollen is pushed up to the mouth of the corolla and beyond by the growing style, after the five cohering anthers have discharged introrsely within the corolla. At this stage the stigma lobes are pressed against each other and are variously adapted by epidermal outgrowths to carry the pollen upward. In Solidago multiradiata the stigma lobes are marginally and internally beset with oblique upward-pointing papillae, longest at mid-point (0.06 mm), becoming shorter towards the narrow tip, down to as little as 0.036 mm. In Arnica alpina the inner surface of the stigma lobes was fairly smooth with rounded cells, the outer slightly rougher, with small oblique papillae. The enlarged tip had a tuft of one-celled hairs well suited for brushing the pollen from the corolla tube to the mouth. In Senecio lugens the inner and outer surfaces of the stigma lobes were covered with upward pointing, but closely appressed, papillae, and the blunt tips had a tuft of hairs from 0.072-0.096 mm long, adapted to carry pollen upwards (Plate 9, Figures 76-78).

The stigma lobes then diverge, the inner surfaces becoming receptive, and, as the flower ages further, they curl downwards until they are able to touch pollen sticking to their own style, or on a neighbouring floret, ensuring pollination in self-compatible flowers, should cross-pollination not have taken place through the agency of insects.

I collected insects on *Senecio congestus* and *S. lugens* at Inuvik, both species attractive to insects through copious pollen lying on the

Plate 9, Figures **76-82**. **76**, Arnica alpina (L.) Olin. Style pulled from ovary, leaving round epigynous nectary surrounding its base; **77**, Senecio lugens Richardson. Nectary a small ring-like epigynous swelling around base of style. The blunt tip of stigma branches with a tuft of upward and outward pointing papillae about 0.06 mm long; **78**, Solidago multiradiata Ait. Nectary a small epigynous swelling around base of style. Stigma branches sharp pointed, the surface with outer and inner upward-pointing papillae, longest 0.06 mm, becoming shorter, 0.036 mm, towards tip; **79**, Tofieldia pusilla (Michx.) Pers. Nectar exuded between incompletely fused partitions of tricarpellary ovary; **80**, Allium schoenoprasum L. Nectary three septicidal pits (0.47-0.54 mm wide, 0.3 mm deep) at base of ovary. Nectar secreted copiously; **81**, Lloydia serotina (L.) Reichenb. Nectary a dark yellow ridge of nectariferous tissue at base of each of the six whitish tepals; **82**, Zygadenus elegans Pursh. Nectary an obcordate gland. Present on all six tepals. N, Nectary. O, Ovary. STY, Style. STI, Stigma. F, Filament. A, Anther. PA, Pappus. PS, Perianth Segment. Line equals 2 mm.

disc flowers. Senecio lugens was visited by the syrphids Scaeva pyrastri (L.), Syrphus sp., and the apid, Bombus sylvicola Kby. Senecio congestus was visited by the syrphids Eristalis bardus (Say), Helophilus obscurus Lw., and Syrphus bigelowii Cn., and the apids, Bombus sylvicola Kby., B. frigidus Sm., B. jonellus (Kby.), B. mixtus Cr., and B. lucorum (L.). The bees are listed in order of proboscis length, and probably all but the workers of Bombus lucorum, with glossae only 2.85 mm, could reach the nectaries. All could gather pollen freely. One species of butterfly, Colias hecla L. (Pieridae) was seen sucking nectar from Senecio congestus.

LILIACEAE

Only one species of Liliaceae, *Tofieldia pusilla*, occurs in the Canadian Arctic Archipelago (Porsild, 1964), but it is widely distributed on the mainland across northern Canada, along with *Allium schoenoprasum* var. *sibiricum. Zygadenus elegans* occurs west of the Hudson Bay in the N.W.T., and *Lloydia serotina* west of the Mackenzie River (Cody & Porsild, 1968; Hultén, 1968). I found *Lloydia* on Keno Hill in the Yukon.

Nectar is secreted between the incompletely fused partitions of the syncarpous ovary in *Tofieldia* and by septicidal pits in *Allium*. *Tofieldia* is the most primitive type because of "the absence of septal glands, with epithelial lining of the intercarpellary spaces unlike those of higher sub-families" (Eames, 1964). I could see no slits or external canal openings by microscopic examination, but the three carpels pulled free from one another at the distal end of the ovary with a slight pressure from a dissecting needle, indicating a very fragile connation between them through which nectar could be exuded.

The greenish-white perianth segments and the stamens of *To-fieldia pusilla* were about the same height, 1.5 mm, the latter closely appressed to the shorter ovary. At Frobisher Bay the whole inflorescence was only 3.5 mm long, and the combination of small size and dull colour did not seem to attract insects to the flowers. The relative position of stigmas and anthers, and the fact the anthers dehisce introrsely, suggest self-fertilization takes place in this species (Plate 9, Figure 79).

Allium schoenoprasum had three septicidal pits at the base of the

ovary sutures, measuring 0.47–0.54 mm wide and 0.3 mm deep. Nectary is produced freely in these and collects between the ovary and the inner whorl of stamens. The shining mauve papery perianth, and the many flowers in a compact umbel, have a strong attraction for bees and other insects, important for seed-set, as Fryxell (1957) lists it as self-incompatible (Plate 9, Figure 80).

The perianth segments of Zygadenus elegans and Lloydia serotina open widely in sunshine, exposing the nectary at the base of each tepal. The former has a conspicuous obcordate nectary, about 3 mm wide by 2 mm deep, on a greenish background. The green is replaced by white towards the tip and margins of the tepal and the gland is raised above its surface 0.8 mm at its upper end (Plate 9, Figure 82).

In *Lloydia serotina* the nectary is a dark yellow horizontal ridge at the base of the tepal (Plate 9, Figure 81), and purplish veins on a whitish background serve as nectar guides for insect visitors. Both species are slightly protandrous and are pollinated by flies and short-tongued Hymenoptera. The position of the anthers, higher than the stigmas in *Zygadenus*, and about opposite in *Lloydia* would allow for self-pollination in the later stages.

NECTARIES IN ARCTIC AND SUB-ARCTIC SPECIES. SUMMARY

POLYGONACEAE: Swollen base of inner stamens embedded in nectariferous ring on petaloid sepals, Polygonum viviparum. NYMPHAEACEAE: Small to large irregularly-shaped pits on underside of petals, Nuphar. CARYOPHYLLACEAE: Swelling around base of outer row of stamens opposite sepals and occasionally at side of inner row, polysepalous Caryophyllaceae, Arenaria, Cerastium, Stellaria. Fused with base of petals, forming ring around carpophore, gamosepalous Caryophyllaceae, Lychnis, Silene. RANUNCU-LACEAE: Simple small pits, open or covered with a scale, upper side of petals, Ranunculus. Two greatly modified petals, Delphinium, Aconitum. CRUCIFERAE: Basal swellings on sides or partly surrounding short stamens, occasionally developed by long stamens. SAXIFRAGACEAE: Band of different colour and texture from ovary, Saxifraga cernua, S. davurica, S. foliolosa, S. hirculus. Band slightly swollen, S. aizoides, S. hieracifolia, S. nivalis, S. rivularis. Concave band between ovary and stamens, S. oppositifolia. Epigy-

nous disc, S. aizoon and S. caespitosa. PARNASSIACEAE: Thickened band on each staminode. ROSACEAE: Receptacle cup, tissue lining cup between stamens and carpels, Dryas, Potentilla, Rubus. FABACEAE: (Diadelphous). Nectariferous tissue lining base of membrane formed by nine stamens and top of receptacle, Astragalus, Lathyrus, Oxytropis. ONAGRACEAE: Fleshy epigynous disc. Epilobium angustifolium, E. latifolium. ERICACEAE: Swollen, often torulose band at the base of ovary, Andromeda, Arctostaphylos, Cassiope, Kalmia, Phyllodoce, Rhododendron, Epigynous disc, Vaccinium. PLUMBAGINACEAE: Swollen base of each stamen below fusion of stamen and petal, Armeria maritima. POLEMONIACEAE: Fleshy concave rim surrounding base of ovary, Polemonium acutiflorum, P. pulcherrimum. BORAGINACEAE: Flat cushion beneath gynobase, thicker between nucules, Amsinckia, Myosotis. SCRO-PHULARIACEAE: Asymmetrical swelling at base of ovary, Castilleja, Pedicularis. Single prominent curved gland at one side of base of ovary, Rhinanthus. CAMPANULACEAE: Epigynous disc, Campanula. ASTERACEAE: Very small swelling around base of style, Arnica, Senecio, Solidago. LILIACEAE: Base of tepals, Llovdia, Zvgadenus. Nectar secreted between carpels, exuding at septa, Tofieldia, or secreted in three septal pits, Allium.

PHYLOGENETIC TREND IN NECTARIES

Fahn (1967) considers the phylogenetic trend in nectaries to be acrocentripetal and he is supported by Radford *et al.* (1974) who state, "As evolutionary advancement occurs the nectaries migrate to the inner floral parts and in the pistil from the base of the ovary to the base of the style".

The above summary agrees in part with Fahn's theory but there are notable variations even within the same family. In Ranunculaceae there are perigonial nectaries in *Ranunculus* and *Aconitum* and staminodial in *Anemone patens;* in Liliaceae nectar is secreted by the ovary in *Tofieldia* and *Allium*, and by distinct nectaries on the tepals in *Lloydia* and *Zygadenus*. In a family such as the Ericaceae, which achieves epigyny in the genus *Vaccinium*, there is an inevitable upward movement of ovary nectaries. Generally speaking, the trend is towards the centre of the flower and upwards in the more highly evolved families.

POLLINATING INSECTS

Nectar may be reached readily by small, short-tongued insects in most open, polypetalous, polysepalous, actinomorphic arctic flowers. They are prevented from reaching the nectar in many of the larger gamopetalous flowers by devices such as copious hairs on the staminal filaments, or on the inside of the corolla itself, and by the hiding of the nectaries under enlarged filament bases. Zygomorphic flowers such as *Aconitum, Delphinium,* and the Faboideae, require heavy-bodied insects with strong probosces to penetrate to the nectar. They depend on bumblebees to such an extent that they disappear in northern areas where such insects are missing or rare.

CROSS-POLLINATION AND SELF-FERTILIZATION

A number of arctic and subarctic species are apomictic (Fryxell, 1957; Mulligan, 1966; Mulligan & Findlay, 1970; Mosquin & Hayley, 1966), and they as a rule do not require insect visits in order to set seed. Those cross-fertilized by necessity are the dioecious species (e.g., Rubus chamaemorus), or the protandrous species in which the anthers dehisce before the stigmas are receptive, (e.g., Campanula, Parnassia, Polemonium acutiflorum, P. pulcherrimum - last two at Dawson City). Protogyny seemed to be of short duration in the species studied, soon changing to homogamy in Anemone patens, Drvas integrifolia, and Draba species. Many arctic species are slightly protogynous, Lloydia serotina, Allium schoenoprasum, and the Carvophyllaceae, for example. The gap between the time of ripening of anthers and stigma allows a short period for cross-pollination. A large percentage of northern plants are homogamous, Ericaceae, Fabaceae, and Pedicularis among them, all with many species known to be self-fertile.

Some of the commonly found adaptations for selfing in mature flowers noted in arctic and sub-arctic species:

- 1. Flowers change in position from partly upright to drooping, allowing pollen to fall on stigma by gravity (*Pedicularis*).
- 2. Stigma branches move outwards towards the anthers (Caryophyllaceae and *Armeria maritima*) or curl downwards to touch pollen (Asteraceae, *Campanula* species).
- 3. Stamens elongate as the flower matures, becoming level with the stigmas (*Draba* species).

- 4. The stamens move towards the stigmas until contact is made (Saxifraga oppositifolia).
- 5. Stamens twist so that anthers scatter pollen on stigmas and filaments, or the flowers close in dull weather, making contact with stigmas or scattered pollen (*Potentilla* species).

As a result of flower stigma and stamen movements, selfcompatible species have additional chances for pollination in an area where insect activity may be very low.

The possibility of wind pollination in entomophilous arctic plants has not been considered, lacking data on the numbers and types of pollen grains in the air. Proctor and Yeo (1975) found it of some importance in Great Britain.

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The illustrations were drawn by C. C. Hsiung of the Lyman Entomological Museum at Macdonald College, based on my field sketches, augmented by microscopic examinations in the laboratory of the McGill University Herbarium.

ADDENDUM: RECORDS OF SCENTS OF ARCTIC FLOWERS, 1976

SALICACEAE: Salix arctica, scent of clover, Frobisher Bay, CARYOPHYLLACEAE: Cerastium alpinum, honey scent, Frobisher Bay; C. arcticum, mild sweet scent, Resolute. CRUCIFERAE: Parrya arctica, strong pleasing scent, Resolute. SAXIFRAGA-CEAE: Saxifraga cernua, no scent, Resolute. ROSACEAE: Dryas integrifolia, no scent, Frobisher Bay. FABACEAE: Astragalus alpinus, honey scent, Frobisher Bay; Oxytropis podocarpa, very strong pleasant scent, Frobisher Bay. ERICACEAE: Arctostaphylos alpina, no scent, Frobisher Bay; Cassiope tetragona, resinous scent, Frobisher Bay; Rhodendron lapponicum, slight spicy fragrance, Frobisher Bay. SCROPHULARIACEAE: Pedicularis arctica, light, pleasant scent, Norway I., off Banks Is.; Pedicularis flammea, no scent, Frobisher Bay; Pedicularis lanata, faint sweet scent, Devon I.

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LITERATURE

- ANDERSON, J. P. 1959. Flora of Alaska. 543 pp. Iowa State University Press.
 BAKER, H. G. 1959. The contribution of autecological and geneological studies to our knowledge of the past migrations of plants. Amer. Natur. 93: 255-272.
- CLAPHAM, A. R., T. G. TUTIN, & E. F. WARBURG. 1962. Flora of the British Isles, 2nd. ed. 1269 pp. University Press, Cambridge.
- CODY, W. J., & A. E. PORSILD. 1968. Checklist of vascular plants of the continental Northwest Territories, Canada. 102 pp. Plant Research Inst., Ottawa, Ont.
- DAVIS, P. H., & V. H. HEYWOOD. 1963. Principles of angiosperm taxonomy. 558 pp. Oliver and Boyd, Edinburgh and London.
- EAMES, ARTHUR J. 1947. Morphology of the angiosperms. 510 pp. McGraw-Hill Book Co.
- FAEGRI, K., & L. VAN DER PIJL. 1966. The principles of pollination ecology. 248 pp. Pergamon Press, N.Y.
- FAHN, A. 1967. Plant anatomy (trans. from the Hebrew). 534 pp. Pergamon Press, N.Y.
- FRYXELL, P. A. 1957. Mode of reproduction in higher plants. Bot. Rev. 23: 135-233.
- GILLETT, JOHN M. 1963. The gentians of Canada, Alaska and Greenland. Publ. 1180: 1-99. Res. Branch, Can. Dept. of Agric., Ottawa, Ont.
- HEGI, GUSTAV. 1958. Illustrierte Flora von Mitteleuropa, Band IV₁ (includes Cruciferae). 1961. Band IV₂ (includes Saxifragaceae).
- HITCHCOCK, C. LEO, ARTHUR CRONQUIST, MARION OWNBEY, & J. W. THOMPSON. 1955–1969. Vascular plants of the Pacific Northwest, Parts 1–5. Univ. of Washington Press, Seattle.
- HOCKING, B. 1968. Insect-flower associations in the high arctic, with special reference to nectar. Oikos, Vol. 19(2): 359-388.
- HULTÉN, ERIC. 1968. Flora of Alaska and neighbouring territories. 1008 pp. Stanford Univ. Press, Stanford, California.
- KEVAN, PETER G. 1972a. Floral colours in the high arctic with reference to insectflower relations and pollination. Canad. J. Bot. 50(11): 2289-2316.
- _____. 1972b. Insect pollination of high arctic flowers. J. Ecol. 60: 831-847.
- _____. 1973. Flowers, insects and pollination ecology in the Canadian high arctic. Polar Record 16: 667-674.
- ______. 1977. High Arctic insect-flower relations; the interrelationships of arthropods and flowers at Lake Hazen, Ellesmere Island, Northwest Territories, Canada. Ph.D. thesis, Dept. of Entomology, University of Alberta, Edmonton, Alberta, Canada.
- KNUTH, P. E. O. 1908–1909. Handbook of flower pollination, based on Hermann Müller's "The fertilization of flowers by insects". Vols. II and III. Clarendon Press, Oxford.
- KOMOROV, V. L. (editor). 1937 & 1939. Flora of the U.S.S.R. Vol. VII, 1937, (Ranunculaceae); Vol. IX, 1939, (Saxifragaceae). Translated from the Russian by the Israel Program for Scientific Translation, Jerusalem, 1970–71.
- MARILAUN, ANTON KERNER VON. 1895. The natural history of plants. Translated from the German by F. W. Oliver. Vol. II, 1–983.

- MACINNES, K. L. 1972. Reproduction in arctic populations of *Pedicularis* (Scrophulariaceae). Unpublished Ph.D. thesis, Dept. of Biology, University of Western Ontario.
- MACIOR, LAZARUS WALTER. 1970. The pollination ecology of *Pedicularis* in Colorado. Amer. J. Bot. 57: 716-728.
 - _____. 1973. The pollination ecology of *Pedicularis* in Colorado. Amer. J. Bot. **57:** 716-728.
- _____. 1975. The pollination ecology of *Pedicularis* in the Sierra Nevada Mountains of California. Abstract of paper given at meetings of Bot. Soc. of Am. at Oregon State University, Corvallis.
- MILLIRON, H. E. 1973. A monograph of the western hemisphere bumblebees (Hymenoptera) Apidae; Bombinae. Memoirs of the Ent. Soc. of Canada, Ottawa, No. 89: 1-237.
- MOSQUIN, T., & D. E. HAYLEY. 1966. Chromosome numbers of some Canadian arctic plants. Canad. J. Bot. 44: 1209-1218.
- MOSQUIN, T. 1966. Reproductive specialization as a factor in the evolution of the Canadian flora. *In:* The evolution of Canada's flora, edited by S. L. Taylor and R. A. Ludwig. 137 pp. Univ. of Toronto Press.
- MOSQUIN, THEODORE, & J. E. H. MARTIN. 1967. Observations on the pollination biology of plants on Melville Island, N.W.T., Canada. Can. Field Nat. 81: 201-205.
- MCALPINE, J. F. 1964. Arthropods of the bleakest barrenlands: composition and distribution of the arthropod fauna of the northwestern Queen Elizabeth Islands. Can. Ent. **96:** 127-129.
- MCALPINE, J. F. 1965a. Observations on anthophilous Diptera at Lake Hazen, Ellesmere Is. Can. Field Nat. 79: 247-252.
- MCALPINE, J. F. 1965b. Insects and related terrestrial invertebrates of Ellef Ringnes Is. Arctic 18: 73-102.
- MULLIGAN, G. A. 1964. Chromosome numbers of the family Cruciferae. Canad. J. Bot. 42: 1509–1519.
 - ____. 1966. Chromosome numbers of the family Cruciferae. Canad. J. Bot. 44: 309-319.

_____. & JUDY N. FINDLAY. 1970. Sexual reproduction and agamospermy in the genus *Draba*. Can. Jour. Bot. **48**: 269–270.

POLUNIN, N. 1959. Circumpolar arctic flora. 514 pp. Clarendon Press, Oxford. PORSILD, A. E. 1964. Illustrated flora of the Canadian Arctic Archipelago. Bull.

No. 146, Nat. Museum of Canada. PROCTOR, MICHAEL, & PETER YEO. 1975. The pollination of flowers. 418 pp.

Collins, St. James Place, London.

RADFORD, A. E., W. C. DICKISON, J. R. MASSEY, & C. RITCHIE BELL. 1974. Vascular plant systematics. 891 pp. Harper and Row publishers, New York.

SAVILE, D. B. O. 1959. The botany of Somerset Island, District of Franklin. Canad.J. Bot. 37: 959-1002.

_____. 1961. The botany of the north-western Queen Elizabeth Islands. Canad. J. Bot. **39:** 909–942.

____. 1964. General ecology of the vascular plants of the Hazen Camp area. Arctic 17: 237–258.

_____. 1972. Arctic adaptations of plants. Monograph No. 6, Res. Branch, Can. Dept. of Agric., Ottawa, Ont.

SPRAGUE, E. F. 1962. Pollination and evolution in *Pedicularis* (Scrophulariaceae). Aliso 5: 181-209.

SWALES, DOROTHY E. 1966. Species of insects and mites collected at Frobisher Bay, Baffin Is., 1964, and Inuvik, N.W.T., 1965, with brief ecological and geographical notes. The Annals of the Entomological Society of Quebec 11: 189-199.

WADDLE, ROBERTA M., & NELS R. LERSTEN. 1973. Morphology of discoid floral nectaries in Leguminosae, especially the tribe Phaseoleae (Papilionoideae). Phytomorphology 23: 152-161.

WILLIS, J. R. Rev. ed. by A. K. Airy Shaw 1973. Flowering plants and ferns. 245 pp. University Press, Cambridge.

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Swales, D E. 1979. "NECTARIES OF CERTAIN ARCTIC AND SUB-ARCTIC PLANTS WITH NOTES ON POLLINATION." *Rhodora* 81, 363–407.

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