Fragments of the Flower Biology of Westralian Plants.

BY

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DURING the past twelve years I have paid special attention to the floral biology of just a few of the multitude of species constituting the flora of Western Australia. It is proposed in the present paper to state briefly the conclusions reached, and incidentally record a few isolated scraps of information that otherwise might not see the light. It seems most convenient to group the facts under the heads of pollination agents, commencing with

ORNITHOPHILOUS FLOWERS.

These are placed first because I have come to look upon birds as the most important agents of pollination in this country. Many flowers which at first struck me as entomophilous have on further investigation appeared to be specially adapted for birds. Observations of the habits of honey-eating birds have led me to think it possible (indeed even probable) that adaptation of the flower to their requirements is the price of the plant species' life. Not so much because of the advantages of ornithophily; but rather because of the disadvantages of any other course. Honey-eaters are aggressive, and if a flower's store of nectar is not readily available they rip open the blossom to secure it. Nectar need not be particularly copious to attract birds; and I have seen the corollas of several cultivated plants badly damaged by them. It is of interest that species of *Erica* and *Arbutus* suffer severely. My observations lead me to conclude that in order to escape the attentions of birds a flower must be nectarless or nearly so, or so situate on the plant as to be practically inaccessible to birds. I do not wish to argue that ornithophily is not directly advantageous; but simply to state that I have not seen unequivocal evidence of its positive advantages, though I have seen much of the negative. To state the matter in another way, the impression left is: given a species with varying forms of flower, one extreme form being best adapted to insects and another to birds, the latter will survive, because the birds will so injure the former that few will secure pollination. The one point that has struck me as possibly of direct advantage is the relative simplicity of structure adequate to secure pollination when birds are the

pollinators. Calyx and corolla may be absent from the open flower, or, if present, reduced to mere scales. In such cases the stamens are numerous; but when simplicity is attained by reduction of the perigone to scarcely more than a funnel-shaped tube the stamens are few. In most cases the style is slender, often quite filamentous (but usually very rigid), and the stigma a mere point. This reduction of parts is doubtless an advantage in an arid country such as this; but still my present impression is that the aggressiveness of birds has had more to do with the survival of so many ornithophilous plants, or is responsible for the prevalence of ornithophily, in this Southern Land. What has struck me more than anything else as the outstanding characteristic of bird-pollinated blossoms is the rigidity of the parts. The anthers are often almost woody, and, disregarding versatility, are usually only moved from their normal position with some difficulty because of the rigidity of the stamens. The style, if fleshy, is sufficiently thick to be rigid, and if slender is sufficiently woody to be springy or stiff.

In dealing more particularly with instances of bird pollination that have come under my notice it will be most convenient to classify the facts according to types of floral structure, proceeding from the simple to the complex. There is, right at the outset, a difficulty in judging; but I think the brilliant orange flower of *Nuytsia floribunda*, R. Br., is the least specialized on my list. It is practically tubeless as the petals with the attached stamens spread rather widely from their bases, so that the nectar is well exposed. The simple erect subulate style is crowned by a minute apicular stigma, which appears to be ripe at anthesis simultaneously with the anthers. The only trace of dichogamy I have noticed is that sometimes a few of the anthers do not dehisce on the day the flower opens. I have repeatedly watched hive-bees visiting the flowers; but though they often brush against the anthers I have never seen one touch the stigma. On just a few occasions I have seen a bird (honey-eater) visit the flowers. My observations and the structure of the flower incline me strongly to the opinion that birds are the 'official' pollinators, if that convenient and expressive term may be permitted me. My experience has made me desire a word to describe that visitor which seems specially connected with a flower. Others may be efficient pollinators; but one appears to be *the one* for whom the blossom is 'intended'. The parts of the *Nuytsia* blossom are rather rigid, which points to a vigorous pollinator. The flowers are borne in immense trusses; and, when a bird alights on a truss to sip the proffered nectar, it is highly probable that wholesale pollination takes place.

The flowers of *Loranthus linophyllus*, Fenzl., are slightly more specialized. Petal bases and epipetalous stamens are suberect, a short but definite tube is formed by the connivent bases of the petals, and the blossom is definitely proterandrous. I have many times seen birds (*Zosterops gouldi*, B'parte, and other honey-eaters) sipping nectar from the blossoms of this

plant, which is plentiful about York as a parasite upon *Acacia acuminata*, Benth. The flower is over-large for any insect—it is about an inch in length—but in dipping into it for nectar a bird can scarcely fail to receive pollen on some part of its head, or to leave some on a stigma. The inflorescence is a pendulous tangled tassel of petals, stamens, and styles. The flower parts are rigid; the style, though filamentous, is remarkably tough and springy, and seems well adapted for scraping pollen from feathers. It is worthy of note that this species is doubly ornithophilous: its seeds are distributed by birds, which devour the sticky-fleshed berries, and wipe the naked seeds off their bills on to convenient twigs. The plant flowers in December, and fruits ripen about March.

Closely similar in structure is the flower of *Xanthorrhoea Preissii*, Endl., the 'Black Boy' or 'Grass Tree'. The erect perigone scarcely extends beyond the general surface of the spike (the bract tips); the stamens spread, but not widely; and the style does not attain its full length till some days after anthesis. A glistening drop of nectar occupies the centre of each flower, the style leaning to one side. As I have frequently seen small birds clinging to the gigantic spike, and dipping their beaks into the flowers, I think they often, if not usually, act as pollinators, though the flowers are freely visited by many insects.

The delicate blossoms of *Acacia celastrifolia*, Benth., do not at first sight appear to be at all adapted for bird pollination, yet my observations have led me to regard birds as the official pollinators. The only visible part of the open blossom is a multitude of flimsy stamens so disposed as to form a fluffy ball. The flowers are borne in subsessile pairs on racemes about three inches long inserted in the axils of the phyllodes. The source of attraction is a gland on the upper edge of the phyllode, which secretes nectar at flowering time, and only then. *Zosterops gouldi* and *Glyciphila* spp. are frequent visitors, and in sipping nectar seldom, if ever, fail to brush against several flowers. Hive-bees visit the glands in swarms, but are too small to brush against the anthers. The raceme does not stand directly over the phyllode edge, but in a plane about 30° distant; so that, while birds are given thereby freer access to the nectar-gland, the visits of nectar-seeking insects are sacrificed. Bees gather pollen at times, and then probably act as pollinators. A more complete account of my observations will be found in the 'Journal of W. A. Natural History Society', No. vi.

Species of *Eucalyptus* come next on my list. Sepals and petals are discarded at anthesis in the form of a calyptra in this genus, and the open blossom is in some respects very simple in structure. A ring of numerous thread-like stamens surrounds the top of the ovary, which is surmounted by a slender terete style, whose apex only is stigmatic. A few figures recently obtained from a flower of *Eucalyptus macrocarpa*, Hook., will be much more effective than a long description in revealing the character of the flowers.

I estimated the number of stamens at fourteen hundred. Their bases occupied a band round the ovary top $2\frac{1}{2}$ mm. wide, while their anther-bearing tops spread to a width of about 25 mm. The middle circumference of the stamen ring taken over the anthers was 140 mm. The stigma was less than a millimetre in diameter! The area of the pollen-bearing surface was therefore over three thousand times the area of the surface adapted for receiving pollen. In this estimate I have included the spaces between the anthers; but even if that inclusion be disallowed the ratio would still be enormously disproportionate. What could be more eloquent of the low degree of specialization of this flower? I have no positive knowledge that birds are the chosen agents of pollination in this particular species, but I feel no doubt whatever that such is the case. While the above is perhaps an extreme case in all species of *Eucalyptus* the area of the pollen-bearing surface is enormously out of proportion to the area of the stigma, which is always minute. This points, I think, to a pollinator of comparatively large size. The top of the ovary secretes nectar, often very copiously, so that it falls in drops from the flowers. Birds seeking this nectar would certainly be liberally dusted with pollen, and could scarcely fail to bring some of their pollen-bearing feathers into contact with the stigma. I have many times seen small parakeets busy on the flowers of *E. redunca*, Schau., and *E. accedens*, W. V. Fitz. Once I observed *Zosterops gouldi* sipping nectar from the flowers of *E. loxophleba*, Benth. The only species I have observed at all closely is *E. calophylla*, R. Br. Its flowers are freely visited by insects seeking the very copious nectar or pollen. Various honey-eating birds are also frequent visitors. The latter appear to be efficient pollinators; but the insects seem useless: I have never seen one brush against a stigma, though I have watched long and carefully. I have found Eucalypts troublesome to observe, and I regard my present knowledge of their flower biology as very incomplete. Yet what I have so far seen has impressed upon me the belief that birds are the chief pollinators of the genus. The small size of some of the flowers at first led me to regard them as entomophilous, but I am now satisfied that birds could and would take nectar from the smallest, and in so doing would almost certainly effect pollination.

The flowers of *Beaufortia sparsa*, R. Br., show some degree of special structural adaptation to bird pollinators. Sepals and petals are much reduced: bud and ovary protection seem their only functions. The stamens, bright scarlet in colour, are collected into five slender bundles about an inch in length, only their tips being free; the anthers are minute; and the slender style, somewhat longer than the stamens, is tipped by an almost microscopic stigma. I often saw small honey-eating birds busily sipping nectar from the flowers, during visits to Albany in 1909 and 1910. The anthers freely rubbed against cheeks, foreheads, and throats; and I concluded that the birds were very efficient pollinators. This type of floral

structure—the reduction of the perigone and marked development of the androeceum—reaches its culminating point in the flower of *Calothamnus sanguineus*, Labill. The two upper stamen bundles are united into a broad half-tube, gradually becoming an almost flat band towards its apex, where it breaks into a fringe of short filaments. This structure is inclined towards the ground, so that the anthers are in a plane below that of the floral axis, though the bundles are inserted above it. The anthers are thus caused to press against the head of any bird taking nectar. The remaining two bundles are reduced each to a single filament, shorter and with smaller anthers than the others. At first sight these reduced bundles seem useless; but I have observed that their anthers brush the bird's cheek. Now the stigma usually rubs the bird's head; but it is easily displaced and it may sometimes rub the cheek. If so, the value of the reduced lateral bundles is obvious. My observations are insufficient to show whether this more highly specialized plant is more successful in securing pollination than *Beaufortia sparsa*. Both species fruit very freely.

The bright red tubular flowers of *Astroloma divaricatum*, Sond., are less than half an inch long, and the tube is only about one-eighth of an inch wide. The floral mechanism closely resembles that of *Erica* spp. I at first thought the flower entomophilous; but though I have kept an eye on the plants for many years I have not observed insect visits. On the other hand, I have often seen small birds on the shrubs at flowering time, and on one occasion my brothers saw a bird 'suck honey from a flower'. If this species is indeed ornithophilous, other species of *Astroloma* are probably so also. My observations of bird visits to *Arbutus* and *Erica* flowers are of interest in this connexion. I have not seen *Astroloma* flowers damaged by birds. Quite recently I saw a small bird thrusting its beak into the flowers of *Habrothamnus* sp. in a Perth garden. These flowers are comparable in size and shape with *Astroloma* blossoms, and were not damaged. I could not make out whether pollination took place.

The plant's close relationship with *Anigozanthus*, and the size of its tubular red blossoms, lead me to think that *Blancoa canescens*, Lindl., is probably pollinated by birds. The flowers of most species of *Anigozanthus* are tubes split open on their lower sides. In the species best known to me, *A. humilis*, Lindl. (flower orange and red), *A. bicolor*, Endl., and *A. Manglesii*, D. Don (flowers rich green with scarlet base, in both species), the perigone might well be likened to a ribbon fastened round the ovary at one end and having the other free and practically flat. Just below the flat end six linear anthers are set in an orderly row on very short filaments. The style is very slender, longer than the perigone, with somewhat swollen apex and apical stigma. I have never had the good fortune to see the flowers visited. My brothers, however, have repeatedly

seen the flowers of *A. bicolor* visited by small birds (*Glyciphila*?), and some years ago friends in South Perth told me they had seen small birds assiduously taking nectar from the flowers of *A. Manglesii*. I have spoken of the flower of *Calothamnus sanguineus* as the culminant of one type of floral structure. It is worthy of note that an almost identical arrangement (mechanically and in appearance) is reached by the flowers of *Anigozanthus*, which I think may be regarded as the culminant of the tubular perigone type of structure. Further development would require an alteration of plan.

Four papilionaceous plants I believe to be ornithophilous: *Templetonia retusa*, R. Br. (red flowers with yellow eye), *Crotalaria Cunninghami*, R. Br. (green flowers), *Clanthus Dampieri*, A. Cunn. (red flowers with black eye), and *Kennedya nigricans*, Lindl. (black flowers with yellow eye). I have only actually seen birds at work on the flowers of the first named; but the size and rigidity of all seems too great for insects. Structure and mechanism call for no special comment.

I come now to my last type, I think the most specialized of all. In this the style apex before the maturity of the stigma acts as pollen presenter. The perigone does little more than protect the essential organs in the bud. In some of the less specialized cases it assists perhaps in attracting pollinators. In many cases its base forms a useful nectar container. The anthers discharge their loads of pollen on to the style top before the flower opens, and are withered shells in the open flower, which consists essentially of a slender filament or rod bearing first pollen, and, later, a microscopic stigma. Surely that is simplicity *in excelsis*, and speaks eloquently of triumph over dry and trying conditions, because the simplicity is clearly not primitive but developed. The only plants I know in this class belong to the Natural Order *Proteaceae*. The multitude of individual forms is bewildering. Almost every variation occurs from the simple solitary flower through all degrees of aggregation to the compact spike or even a capitulum. I have notes concerning but few forms.

Adenanthos cuneata, Labill., has simple flowers solitary in the axils. They are dull red and seem small for the attentions of birds; yet I often saw birds—*Zosterops gouldi* chiefly—dipping their beaks into the flowers when in Albany a few years ago. The protruding style end rubbed the bird's head, and pollination seemed inevitable. This plant is interesting in that while the flowers are small and inconspicuous, the subtending leaves are of a crimson hue, and the branch tips bearing them, especially when seen against the light, resemble racemes of flowers. The behaviour of the birds, however, did not suggest that they were attracted by the bright colour. The flowers of species of *Grevillea* are closely similar in structure to those of *Adenanthos*, but they are aggregated in loose racemes, and perhaps render some mutual aid in the way of attraction.

The coral red blossoms of *G. bipinnatifida*, R. Br., and the brilliant scarlet ones of *G. Wilsoni*, A. Cunn., are almost certainly bird-pollinated: their styles project too far from the perigone for insect pollinators to be efficient. The inflorescence of *Hakaea myrtoides*, Meissn., is highly specialized. I have, indeed, felt some inclination to set it down as higher than the forms next to be considered; but, as each branch bears many inflorescences simulating a raceme, I have decided it is inferior to those forms whose branches bear one terminal inflorescence. It is a diffuse subshrub. The last few inches of each branch bears in every axil an umbel of from three to six tiny blossoms of ruddy purple hue. The perigone is but one millimetre across and four millimetres high, yet the style is twelve millimetres in length. The posterior side of each floweret, which faces the umbellar axis, is split to the base where the tiny disc (about 0.12 c.mm.) protrudes. The secretion of nectar is out of all proportion to the disc's size: I have found drops measuring at least 60 c.mm. resting between five flowers. I do not think rain could have contributed: the drops were quite sweet, and drops of water carefully placed in the centres of umbels always quickly disappeared, finding their way down the stem. The nectar would certainly attract birds; and the flower seems ill adapted for insect pollinators. The bird which could sip a nectar-drop without brushing at least one of the erect (or slightly incurved) styles surrounding it would be skilful indeed.

Grevillea eriostachya, Lindl., will serve well as a connecting link with the most highly specialized inflorescences. Its yellowish flowers are borne in dense secund racemes terminating the branches. Though the flowers are packed very closely together, the stigmas all face one way—towards the apex of the stem—so probably each flower would need individual attention from a pollinator. A bushman recently remarked to me that though the flowers secrete nectar very freely—boys are fond of sucking the flower spikes and call the shrub 'honeysuckle'—bees very rarely visit them. Doubtless birds are the official pollinators.

The inflorescence of *Banksia* spp. is a large somewhat cone-like spike, singularly beautiful in appearance, and often brightly coloured. The flowers are so densely crowded together as to form almost a solid mass from which the hard tough styles project. I have many times seen small honey-eaters taking nectar from the flowers of *B. attenuata*, R. Br., *B. prionotes*, Lindl., and *B. Menziesii*, R. Br., and cannot doubt that they act as pollinators. The bird usually perches on the top of a spike and bends down to take nectar, probably brushing many styles which point upwards in the process.

The highest degree of specialization is found, I think, in those species of *Dryandra* whose inflorescences strikingly resemble, superficially, those of Compositae. Many times and often have I seen birds thrust their

beaks into the thistle-like heads of *D. floribunda*, R. Br., and *D. carduacea*, Lindl.

ENTOMOPHILOUS FLOWERS

now claim some attention. Though Lepidoptera are numerous here, I do not yet know for certain even one species of plant chiefly pollinated by either butterfly or moth: indeed I have observed extremely few visits of these insects to any flowers. On the rare occasions when I have seen a butterfly visit a flower it has seemed useless as a pollinator. The flower of *Stackhousia Brunonis*, Benth., seems to be specially adapted for moths. The corolla is a longish tube, and at night it exhales a most delightful, Narcissus-like perfume (Mr. C. R. P. Andrews first called my attention to this fact). The flower is yellow or tawny in colour, and does not seem particularly visible at night.

Indigenous Hymenoptera visit many flowers; but only in one case have I definitely connected one with a flower as official pollinator. The Orchid *Caladenia Barbarossae*, Reichb., is visited by a large black wasp, whose name I have not yet ascertained. The labellum of this Orchid is so arranged that when the wasp alights on the lamina it swings forwards towards the centre of the flower. This movement brings the wasp's back forcibly into contact with the stigma, whose secretion renders a circular patch of the wasp's back sticky. When the insect seeks to leave the flower, one edge of the sticky patch comes in contact with one or more of the disc-like pollinia peeping from the anther just above the stigma. Even momentary contact serves to attach the edge, and the whole disc is withdrawn from the anther as the wasp's egress continues. When withdrawal is complete the pollinium falls upon and exactly fits the sticky patch on the wasp's back. Obviously the next flower visited will receive upon its stigma a liberal supply of pollen. A full account of my observations will be found in 'Journal W. A. Nat. Hist. Soc.', No. iv (Nov. 1907). At that time I had not determined what is the attraction of the flower. Subsequent investigation has, I think, revealed it. The central labellar appendage, which the wasp seizes with its mandibles, seems to be a true gland, secreting nectar so slowly that crystallization takes place practically simultaneously. In one instance I found the crystals aggregated into tiny globular masses much resembling raspberries as I viewed them against the purple skin of the gland. The crystals appear to be sucrose. An amorphous sticky substance (glucose?) is also present. My investigations are at present very far from complete; but I have reason to believe that the peg-like calli of all species of *Caladenia* and allied genera secrete similarly. I have never yet found them gnawed by insects (excepting cases where a large portion of the labellum has been damaged—evidently not by a pollinator): I believe they are simply 'licked'. The genus *Drakaea* is highly interesting.

As it is closely allied to *Caladenia Barbarossae*, and is, I believe, pollinated by Hymenoptera, I will include a brief account of it here. Near York *D. ciliata*, Reichb., is plentiful. It grows round the edges of shelving granite outcrops where the soil is almost swampy during winter. It flowers in November, when the soil is very dry and warm, its fleshy scape dying from below upwards as flowering proceeds. *D. elastica*, Lindl., and its near ally *D. Glyptodon*, R. D. Fitz., occur sparingly on sand. Both flower in September. I have not observed the process of pollination in any of these species; but after careful and prolonged study of the flowers I have formed an idea of the mode of operation of the flower parts. The labellum, which in all three species is strongly suggestive of some weird insect perched upon the blossom, is thinly clothed with shaggy hairs, and is attached by a loose but tough hinge. In none of these species is there any trace of irritability in any part of the flower. The basal calli bear crystalline nectar. My conclusion is that when an insect settles on a labellum it is allowed a meal in peace; but when it seeks to leave, its legs being somewhat entangled by the shaggy hairs, it is temporarily attached to the labellum, and so is constrained to fly in an arc which quickly brings it into forcible contact with the stigma, where it soon manages to free itself; but not without removing pollen or pollinating the stigma. In the case of *D. ciliata* I actually induced a small hymenopt to perform part of the operation; but it was evidently not the proper pollinator.

The petaloid calyx of *Thomasia montana*, Steud., simulates the corolla of a *Solanum*. It is usually of a delicate bluish pink hue, though sometimes clear rose. The petals are tiny black scales and seem functionless. The stamen bases are connate, forming a shallow cup (this structure is peculiar to the species) on whose rim the horny anthers are almost sessile. These anthers stand close together and form a black cone from whose apex the slender style protrudes. The stamen cup contains thick nectar, to obtain which an insect must probe between anther tips and style. That done a further obstruction is met: the staminodes, which alternate with the fertile stamens, lean inwards and form a tangle round the style. Altogether a deal of poking is necessary before nectar is secured. This disturbs the anthers and dry, dusty pollen is shaken from their terminal pores. I have never seen an insect seek nectar, but I have seen small black indigenous bees gathering pollen from the flowers. They perched inverted (the flowers are pendulous) upon the anther cones, and agitating the anthers with their legs caused pollen to fall out. I concluded that they would effect pollination whilst so engaged. They are very active creatures, frequently flitting from shrub to shrub. True xenogamy is probably the rule when they act as pollinators. The flowers are, however, fertile with pollen from others of the same shrub. Some years ago I observed that a solitary shrub,

miles away from any congener, produced a few fruits from its wealth of blossom.

The rosy calyces of *Guichenotia Sarotes*, Benth., both in shape and colour are reminiscent of advanced inflorescence-buds of *Bougainvillea Sanderiana* of horticulture. The floral structure is essentially similar to that of *Thomasia montana*; but nectar and staminodes are both wanting. The anthers form a cone round the pistil, which is an object of most exquisite beauty. This beauty, however, is only revealed by a lens. The pale green ovary is sparsely clothed with glistening starry hairs, amongst which are dotted plump ovoid trichomes filled with purple sap. The style is so densely and delicately clothed with starry hairs that it appears to be surrounded by a halo. Description, I fear, fails utterly to convey anything like an adequate idea of the beauty. The purple trichomes are, I presume, either gnawed or sucked by visiting insects. Either action would doubtless cause sufficient agitation of the anthers to shake out pollen. I have not seen the flowers visited by any insect. The close relationship of the species with *Thomasia* induces me to make some mention of it here.

I now come to one of the choicest gems of the Westralian flora—*Leschenaultia biloba*, Lindl. It seems almost sacrilege to attempt a description, yet one, confessedly inadequate, must be offered. The flower suggests to me a bright blue ten-rayed satin star, crinkled and curved most elegantly. While celestial blue is the rule the shade of colour of the petals varies from almost pure white (*very rare*) to deepest ultramarine. Sometimes the bright blue blossom possesses a pure white 'eye', which at times occupies nearly one-third of the limb. The corolla is actually, though not obviously, two-lipped, and the 'eye' is always limited to the anterior lip of three petals. The anthers shed their pollen into the indusial pouch, then a gaping mouth, some time before anthesis. In the open flower the stamens are simply shrivelled shreds. The style is a thick column of tissue with a broadly expanded, slightly dorsiventrally flattened apex. The structure of the expanded part is remarkable. On its anterior edge there is a furry-looking whitish line, which indicates the closed mouth of the pollen-containing indusium. On the opposite side of the style top there is a broad slightly curved line of short fleshy hairs. The central space is occupied by a glistening, sticky, oval patch—the stigma. The edge of the indusium stands about one millimetre distant from the corolla tube. An insect entering the flower would first brush against the fringe of fleshy hairs and the stigma almost simultaneously; it would then brush against the edge of the indusium, and thus cause the pouch to open, and allow pollen to fall out, or at least expose it, so that some might be removed. I have spent much time in watching the plants; but only twice have I seen flowers visited. Once a small indigenous 'bee' entered a flower just as I have described; but the pouch was empty, so I did not see the complete operation. The

flower contains a fair-sized drop of nectar at the base of the corolla tube, yet hive-bees always pass the flowers and visit those of other plants, though they contain less nectar. I was puzzled by this strange behaviour till recently when I saw a hive-bee visit several flowers. Her head was blocked by the sturdy style, and I do not think her tongue reached the nectar-drop about 7 mm. distant. So far as I could see the pouch did not open. I discovered by accident not long ago that the flowers so blue by day appear brilliantly white in the moonlight. This appears to be due to the structure of the cuticle of the petals, making them excellent reflectors of light—so excellent, indeed, that the flowers appear brighter than many pure white blossoms. This fact suggests night-flying insects as pollinators. I have not yet been able to make any definite observations in this direction. I cannot think that Lepidoptera would prove efficient pollinators. The pollen is somewhat moist or waxy, and does not readily fall from the pouch, which, moreover, is broad-mouthed and seems intended for the back of a pollinator. This species is a very erratic fruiter. I have made some attempt to discover the reason. The plants commonly occur in groups or colonies. Careful digging reveals that the rhizome spreads widely underground and sends up aerial shoots at intervals. What seem to be several separate plants growing near together are often in reality simply branches of the same plant. I have found that the flowers are infertile with pollen from other flowers of the same plant. I have observed that when two distinct individuals grow in close proximity, both usually fruit freely; groups, on the contrary, seldom produce many fruits. This seems to show that the pollinator does not as a rule travel far between visits. In all other genera of Goodeniaceae known to me, viz. *Goodenia*, *Scaevola*, *Dampiera*, and *Brunonia*, the indusium surrounds the style apex, which pushes the pollen before it as it grows; and the stigma is not mature till the style tip has extended beyond the indusium and all pollen has gone.

Species of *Stylidium*, Sw., bear flowers in some respects more highly specialized than those of Goodeniaceae. Stamens and style are closely welded together into a highly irritable column, which in the 'set' position leans upon the much reduced fifth petal ('labellum') with its apex below the plane of the corolla limb. The labellum is morphologically anterior, but torsion of the corolla tube carries it to the side or back of the flower. The column is bowed forwards a little just as it emerges from the corolla, so that it almost occludes the entrance. Slight *pressure* (a mere touch is not enough) against this bowed part causes the column to move with great rapidity till it leans over on the opposite side of the flower. It soon returns to its former position, but does not regain irritability till after a short rest there. I have seen various hymenopter visit the flowers and apparently obtain nectar *without* causing the column to act. Once I saw a largish 'bee' visit several flowers on a raceme in rapid succession, working from

below upwards. Not a single column flew over, though all were in the irritable condition! The back of this bee appeared to be pollen-dusted. I think the anthers or stigmas (according to the stage of flowering) usually strike the back of a visitor when the column reacts to gentle pressure. In some species the under-surface of the visitor may be struck. Anthers ripen first, and are pushed aside by the growing style tip just before the stigmas mature. The motion of the column is too rapid for the eye to follow.

A pollination mechanism recalling that I have described for species of Proteaceae is found in *Verticordia pennigera*, Endl., and *V. densiflora*, Lindl., and probably other species, but I have not specially observed them. The style is an erect column with an apical stigma. Just below the stigma is a ring of hairs; and on to this ring the anthers discharge their pollen-grains, floating in a sticky fluid just before the flower opens. The stamens are not functionless in the open blossom; they partially close the floral orifice and so make the nectar less readily accessible. The flowers are visited by hymenopts, which are, I believe, efficient pollinators.

The flowers of *Actinodium Cunninghamii*, Schau., which are borne in heads strongly suggestive of 'double' *Bellis perennis capitula*, follow a closely similar plan to that of *Verticordia*, and are, I believe, also pollinated by Hymenoptera.

The mechanical structure of the flowers of Compositae scarcely differs essentially from the above-named. I have seen the flowers of *Helichrysum Lawrencella*, F. Muell., visited by small hymenopts which seem to pollinate effectively.

Marianthus lineatus, F. Muell., depends chiefly for pollination upon a small dipteran, as I have shown at some length in 'Journal N. H. & S. Society of W. A.', vol. iii, No. 1. The plant blooms during the hottest months of the year—January and February. Its elegant blossoms, cream-coloured with purple longitudinal stripes, are borne in great profusion. In the bud, neglecting the pistil, the flower, even to a fairly late stage, is actinomorphic: sepals, petals, and stamens are regularly spaced in their respective whorls, and in each whorl the units are not perceptibly dissimilar in any respect. When the blossom opens, though their claws are still almost equally spaced round the sporophylls, the limbs of the lateral and anterior petals are bent back, so that the complete corolla forms a half-bell only at the back of the flower. The stamens now differ in length and are so arranged that their anthers form a compact little cushion facing the petals. About four days after the flower opens the small stigma will be found occupying the place of the anther cushion, the stamens having spread widely away from their first position. Nectar is not secreted; but the tiny teat-like trichomes, which thickly stud the petal bases, contain a sugary juice. My observations and experiments point to the conclusion

that the flies obtain the juice by squeezing or sucking it through the cell-walls without injuring them.

A genus of small terrestrial Orchids, *Pterostylis*, has received considerable attention from me. As I have given a fairly full account of my observations in 'Annals of Botany', vol. xxiii, p. 265, the briefest mention is sufficient here. T. F. Cheeseman in 'Trans. N. Z. Inst.', vol. v, was, I believe, the first to give an account of the mechanism of the flower. R. D. Fitzgerald also describes it in his great work, 'Australian Orchids'. My own observations and conclusions were, however, made and reached independently before having read the account given by either of those authors. Further observations and experiments have tended to confirm my conclusion that the flowers are pollinated by gnat-like Diptera.

Cephalotus follicularis, Labill., claims inclusion here on account of its intrinsic interest, though my knowledge of its flower biology is far from complete. The inflorescence is a narrow panicle of small starry white flowers. It is borne upon a remarkably long foot-stalk, which serves to elevate it well above the sedges and low shrubs closely surrounding the plant. The calyx is a shallow cup with limb divided into six triangular lobes. Each of the twelve stamens has a comparatively large gland, strongly suggestive of a miniature strawberry, at the back of the anther. When the flower opens the stamens are reclined, and their glands form two neat rows round the conical pistil, whose style tips are closely folded together. Soon a few (2, 3, or 4) of the outer row of stamens unbend and their anthers dehisce. The rest come into action on the following day. The stamens of the inner row behave similarly on the two succeeding days. Then the style tips spread out and the stigmas ripen. The anthers have usually lost all their 'moist' or waxy pollen before the styles diverge. The flowers exhale a faint perfume reminiscent of fine honey. There is no free nectar, but the inner surface of the calyx tube is studded with glistening papillae containing sugary sap. I have seen the flowers visited by hymenopter and by Diptera. All the visitors seemed equally efficient as pollinators. The inflorescence is clearly visible at a distance of 30 yards, appearing as a pale grey smudge upon the surrounding verdure. I made a rough estimate of its relative visibility by setting up near an inflorescence a raceme of small yellow flowers (*Comesperma* sp.) and one of scarlet *Beaufortia*, both trimmed to the size of the *Cephalotus* panicle. The last named was quite as visible or conspicuous as the yellow flowers, but somewhat less so than the scarlet to my eye. The flowering season was not over when I left the locality; but I found twenty-three panicles that had completed their course. Thirty-eight per cent. (261) of their flowers (696) had produced follicles.

Only one anemophilous plant—*Opercularia vaginata*, Labill. (N. O. Rubiaceae)—has received any attention from me. The slightest agitation

causes clouds of pollen to float lazily away from its dark green heads, if the plant is examined first thing on a still morning.

I have met with one rather remarkable instance of *autogamy* in the case of *Levenhookia pusilla*, R. Br. The plant is very tiny, often scarcely half an inch high. Its pretty pink blossoms are borne in a compact terminal panicle. The corolla measures about one millimetre across. The galeate labellum (fifth petal) closely embraces the erect gynostemium throughout the flower's lifetime unless disturbed. The anthers are mature at anthesis and dehisce within the labellum. A few days afterwards the stigmas are forced up between the anthers by growth of the style apex and receive pollen in the process. In due course fruit matures. That appears to be the usual process. Sometimes, I believe, the labellum is forced off the column by an insect. It seems scarcely possible for one to dip into the blossom without dislodging the labellum as it leaves. Once dislodged the labellum never again embraces the column; so that a flower once visited is dependent upon insect aid for pollination (unless it had been self-pollinated before the visit). I believe the process is exactly similar in *L. stipitata*, F. Muell. In both these species the labellum fits the column very closely, and is quite devoid of irritability. This is of special interest, because in 'Flora Australiensis', vol. iv, p. 34, Bentham states that in contrast with the irritable column of *Stylidium*, the labellum is irritable in *Levenhookia*. I have only seen the two species named above. In these loss or lack of irritability has made the labellum an excellent organ for autogamy. This has permitted reduction in size of flower and plant, and made possible the occupation of the arid situations where I have seen it growing.

Throughout this paper I have arranged my examples in inverse order of the *mechanical* complexity of their flowers. I have avoided phylogenetic considerations, which it seems to me could only have tended to obscurity and contention. From the mechanical view-point the flowers of the Proteaceae I have mentioned for simplicity and economy of tissue are a very close approach to perfection, if not, indeed, perfection itself. Yet it is a genus of Myrtaceae—*Eucalyptus*—that forms the dominant vegetation of this country. The perfection of its floral structure is certainly not the only factor governing the measure of a plant's success—often, perhaps, it is of little consequence. There are, however, considerations which suggest that the Proteaceae have over-specialized flowers, their mechanical perfection being a physiological fault, for the simple reason, I suppose, that their pollinators fail to behave in a mechanically perfect manner. Recently I estimated the number of flowers borne and seeds produced by two trees growing within sight of one another. One was a Jarrah (*Eucalyptus marginata*, Sm.) and the other *Banksia attenuata*, R. Br. In round numbers the former bore six hundred and seventy thousand (670,000) flowers and

produced one million seeds, while the latter's sixty-seven thousand flowers produced only four hundred seeds. This surely gives the Eucalypt an enormous advantage over the *Banksia*. It took only seventy-five inflorescences to produce the four hundred *Banksia* seeds, while the Eucalypt required eighty-four thousand to produce its million. The advantage seems not so great; but it must be understood that the *Banksia* inflorescence is enormous compared with that of the Eucalypt. I think these estimates, somewhat rough though they are, fairly represent the advantage in seed production that Eucalypts possess over Grevilleoid Proteaceae. Surely the immensely greater number of its seeds should favour variability in *Eucalyptus*, and even without variation should give it immensely greater power to seize new territory and increase its numbers.

I have been struck by the number of instances I have seen in which several or many small flowers are gathered together into inflorescences resembling, and perhaps often behaving as, one large flower. Its prevalence suggests that there is some special advantage in such an inflorescence. It is seldom, I think, an economy of tissue or a reduction of transpiring surface. A study of the genus *Eucalyptus*, however, suggests an advantage of considerable importance. The large solitary flower is found, for example, in *E. macrocarpa*, and *E. loxophleba*, Benth., will serve for an instance of the anthoidal inflorescence of many small flowers. In the first-named species of 3,000 sq. mm. of flower surface adapted for the disposal or receipt of pollen only the central square millimetre is stigmatic, whereas the inflorescence of *E. loxophleba* presents 12 sq. mm. of stigmatic surface evenly distributed amongst 1,000 sq. mm. of anthers. As there is nothing in the structure of the flowers to compel a pollinator to brush a central stigma with a part of its body which has been pollen-dusted, it seems to me certain that a flower of the latter species has a far better chance of pollination than one of the former, and I think it is not unlikely that it also has a better chance of cross-pollination. I have no exact data; but my experience of the species has given me the impression that the flowers of *E. loxophleba* are far more fertile than those of *E. macrocarpa*. It is possible, however, that failure to fruit is not always due to failure to secure pollination. The solitary-flowered Eucalypts, I believe without exception, are few, well-marked, and restricted in range. The umbel-bearing species are numerous, usually very variable, and they often range over a wide area of territory. It seems possible that the form of inflorescence is contributory to these effects. *Banksia attenuata* has an inflorescence presenting many stigmas well distributed over a very large area, yet it is a very shy seeder. This tends to emphasize the fact that floral structure is but one factor in the production of seed. *Banksia*, however, differs from *Eucalyptus*: its pollen-bearing surface is not very much larger than its stigmatic surface, and its pollen easily rubs off.

THE ORIGIN OF HONEY-EATING.

Many times, early in the morning, in spring, when a certain Pear-tree is in blossom, I have seen small birds (*Zosterops gouldi*) sipping dewdrops from the leaves of the said tree, and, just occasionally, dipping into a blossom for a sip of sweetness. While in Albany some years ago I saw the same bird taking dewdrops from the foliage of *Adenanthos cuneata*, disdaining apparently the sweeter moisture of the flowers. After a shower a large drop of water remains at the eye of *Templetonia retusa* flowers. These observations seem to me strongly suggestive of the origin of honey-eating in birds. How profoundly what was perhaps an accident—the mistaking of a nectar-drop for a dewdrop—in the far distant past has modified the present face of nature!

VARIATION.

Three well-marked instances of variation have come under my notice. The labellum of *Caladenia dilata*, R. Br., is usually deeply fringed; but occasionally a flower occurs fringeless. In one locality, Mt. Bakewell, I have never yet found a single specimen with a fringed labellum; all are fringeless. I have seen no intermediates. The change is abrupt and striking. The inner rows of the involucral bracts of *Helichrysum Lawrencella*, F. Muell., are petaloid and usually bright pink. A solitary plant with pure white bracts is occasionally found. On the slopes of Mt. Bakewell white-bracted plants are common, and often form small communities. When such a community is bordered by a pink-bracted one, intermediates of various degrees occur. In this locality pure whites seem the most vigorous. I believe both the above species are frequently self-pollinated, though with insect aid. *Drosera macrantha*, Endl., is usually white flowered, but in one locality I have found pink-flowered plants fairly common, intermixed with the white ones. The pinkness varies in shade from the merest suggestion to pale rose. In the year 1913 thirty-two white-flowered plants produced 39 per cent. of fruits from their flowers, and 36 per cent. of the flowers of sixteen pink-flowered plants were fertile. Selecting several different sixteens from amongst the thirty-two, I found percentages varying between 33 and 48; so that the percentage for the pinks falls well within the limits of observational error. My conclusion is, therefore, that a pink tint to the petals had no selection value that year in the locality in question. In the years 1912 and 1914 I managed to examine a few plants of each variety, and on both occasions the white flowers showed a higher percentage of fertility; so possibly a pink tint is detrimental to these flowers. This raises the question of the value of colour as an attractive agent. All the definite evidence I have collected is negative. Under suitable conditions *Marianthus lineatus* blossoms develop their sweet odour quite strongly; and then they are powerfully

attractive to house-flies. Dried in fine sand the flowers retain their shape and colour perfectly, but they quite lose their attraction for house-flies. This points to the conclusion that their colour is without influence upon those insects. Whether it has any effect upon the indigenous pollinator I do not know. Flowers of every hue are visited by hive-bees apparently with perfect impartiality. Birds also seem quite indifferent to colour. Yearly for some considerable time I have observed cream-coloured flowers (*Dryandra carduacea*), yellow flowers (*Acacia celastrifolia*), and bright red flowers (*Calothamnus sanguineus*) blooming simultaneously in the same locality, so that they compete for the attentions of the same identical birds. Available time has never permitted a serviceable count of visits; but no obvious partiality is shown for either species, and all fruit freely.

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