WESTERN AUSTRALIAN HERBARIUM RESEARCH NOTES

No. 5, 1981: 71-79

NOTES ON THE BIOLOGY OF *PILOSTYLES* (RAFFLESIACEAE) IN WESTERN AUSTRALIA

By B. Dell* and A.H. Burbidge**

* School of Environmental and Life Sciences, Murdoch University, Murdoch, W.A. 6150

** Botany Department, University of Western Australia, Nedlands, W.A. 6009.

ABSTRACT

Pilostyles hamiltonii *is widely distributed throughout the south-west of Western Australia. This taxon has been recorded parasitizing the genera* Daviesia *(10 spp.),* Jacksonia *(2 spp.),* Oxylobium *(2 spp.) and* Gastrolobium *(1 sp.).* Pilostyles *is dioecious on* Daviesia *but monoecious on the other three host genera. Flowers break through the bark of all host species in summer (January) and probably are wasp pollinated. Fruits of the parasite remain on the plant for up to 8 months. It is suggested that speciation of* Pilostyles *may have occurred in Western Australia and that taxonomy of the group warrants further attention.*

INTRODUCTION

Pilostyles (Rafflesiaceae) is a small-flowered genus of stem parasites with a restricted range of host plants in the Mimosoideae, Caesalpinoideae and Papilionoideae. The genus is widespread, occurring in Iran, East Africa, Western Australia and the Americas where it can be found from California through the tropics to Chile (Kuijt, 1969). The single Australian species, *P. hamiltonii*, was described by Gardner (1948) from material collected near Mundaring Weir, some 30 km from Perth. The only other published information on this species are some notes by Smith (1951) and a brief report by Kenneally and Pirkopf (1979).

METHODS

During 1975-1979, field surveys were undertaken throughout south-western Australia to determine the distribution of *Pilostyles*. Infected plants could be recognized from some distance due to the darker appearance of the host plants. As well, infected plants, especially *Daviesia*, often had delayed and greatly reduced flowering. Wherever *Pilostyles* was found, records were made of host species and habitat, distribution of parasite on host and type of sexual expression in the parasite. If sufficient plants

were present, the sex ratio was determined. Incidental observations were also made on the general biology of the parasite. Voucher specimens are deposited in the Western Australian Herbarium (PERTH).

One site was selected for more detailed study (Fig. *). This was in *Eucalyptus marginata* (Jarrah) forest near Kalamunda, in the Darling Range, approximately 20 km east of Perth. Within this area, on an open, northerly facing slope, an area of understorey dominated by *Daviesia angulata* was divided into 1470 metre-square quadrats. Each square metre was scored for the number of individuals of *Daviesia* present. Where *Pilostyles* was found, its sex was determined, and the species of host plant was noted. This site was visited at least once per month for 15 months, so that observations could be made on the life cycle of *Pilostyles*. An adjacent area which had been burnt in the spring prior to the period when detailed observations began was used to note the effect of fire on *Pilostyles*.

RESULTS

Host Species

The type collection of *Pilostyles hamiltonii* includes two host species, *Daviesia pectinata* and *D. angulata*. (This species has been confused with *D. polyphylla* by many workers - Personal communication, Dr. M.D. Crisp, Herbarium, Canberra Botanic Gardens.) Smith (1951) extended the list of known hosts to four with the addition of *D. incrassata* and *D. rhombifolia*. The current range of host species is detailed in Table 1. All host species belong to the Papilionoideae Tribe Podalyrieae. Most species (10) belong to the genus *Daviesia*, with two species each of *Jacksonia* and *Oxylobium* and one species of *Gastrolobium* being parasitised by *Pilostyles*.

Table 1. Host genera and species infected by *Pilostyles* in Western Australia. The flowering time of the parasite (Jan. - April) varies little with host species even though the hosts' flowering months vary considerably.

Host genus	Host species	Host flowering months
Daviesia	*angulata* Benth. ex Lindl.	May
	colletioides Meisn.	July-August
	incrassata Sm.	Aug.-Nov.
	nudiflora Meisn.	June-Sept.
	pectinata Lindl.	June-Nov.
	pedunculata Benth. ex Lindl.	Aug.-Dec.
	polyphylla Benth. ex Lindl.	Aug.-Nov.
	preissii Meisn.	Dec.-Feb.
	quadrilatera Benth.	June-Sept.
	rhombifolia Meisn.	July-Aug.
Jacksonia	*floribunda* Endl.	Nov.-March
	spinosa (Labill.) R.Br.	Sept.-March
Oxylobium	*atropurpurea* Turcz.	Sept.-Nov.
	linearifolium (Don) Domin	Aug.-Dec.
Gastrolobium	*velutinum*	Aug.-Feb.

Distribution

Except for an outlier at Peak Eleanora, (host: *Oxylobium linearifolium*) *Pilostyles* is confined to south-west Western Australia (Fig. 1).

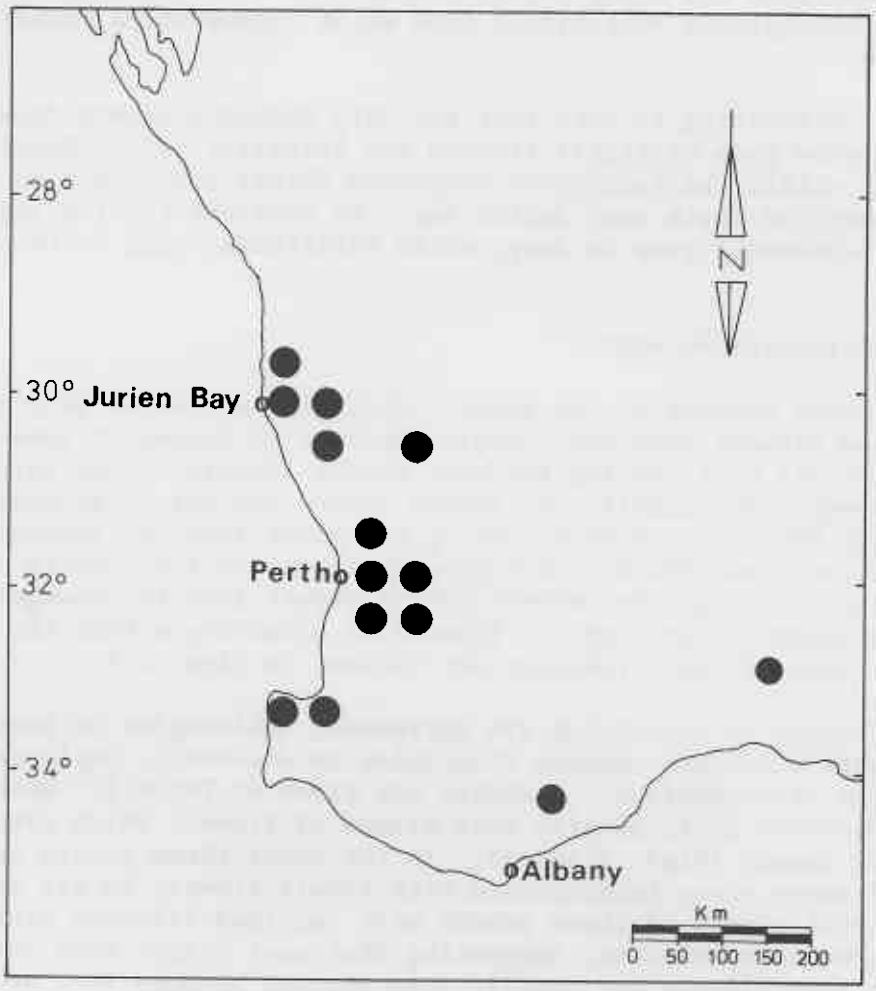

Fig. 1. Distribution of *Pilostyles hamiltonii* in Western Australia. Each dot shows the presence of the species in a 50 km square, based on the Australian Map Grid (50 km).

The parasite occurs as far north as Eneabba, is widespread throughout the Darling Range and occurs in the Stirling Range. It is expected that future discoveries will extend this range particularly along the south coast from Albany to Esperance. The range of habitats for *Pilostyles* includes the low heath vegetation of the Northern Sandplains, the understorey of the *Eucalyptus wandoo* and *E. marginata* forests, and the dense Myrtaceae, Proteaceae and Leguminosae scrub on the slopes of Bluff Knoll, in the Stirling Ranges. The parasite is apparently absent from the sandy soils of the Swan Coastal Plain near Perth even though two of the host species commonly occur. Elsewhere, probably with the exception of the *D. angulata* and *D. polyphylla* host group, only a small part of the hosts' range is occupied by the parasite. For example, *Jacksonia floribunda* is widely distributed through the Irwin and Darling botanical districts but parasitised plants have only been found in the Irwin district. Six of the 14 known host

species are infected on the sandplains or lateritic slopes of the Irwin district between the Moore River and Eneabba. Although species of *Daviesia* occur in the Stirling Range, no parasitized plants have been found there.

Some of the *Daviesia* hosts, particularly *D. angulata*, occupy disturbed sites, and plants bearing *Pilostyles* can often be found in old gravel pits, beneath powerlines and along forest tracks. Most of the *Daviesia* hosts have large underground root-stocks from which regeneration occurs after disturbance.

It is interesting to note that the only *Daviesia* plants found infected with *Pilostyles* grew on highly leached and lateritic soils characteristic of large areas within the *Eucalyptus marginata* forest and dissected duricrust plateaux north of Perth near Jurien Bay. By contrast the two infected species of *Jacksonia* grew in deep, white Pleistocene sand north of Perth.

Flower Distribution on Hosts

Like other species in the genus, *Pilostyles hamiltoni* is a stem parasite and flowers were only rarely observed on leaves in some *Daviesia* species. In all host species the most recent flowers of the parasite are borne on woody stems usually one growth season old but occasionally older. Consequently there is a progression up the plant from the remnants of past season's flowers and fruits, indicated by the scale-like bracts and ruptured bark, through the current year's growth into the younger stems where development of next year's flowers is occurring within the bark of the host. Some of these features are evident in Figs. 2-7.

The flowers of *Pilostyles* are unisexual. *Pilostyles* on *Daviesia* is almost always dioecious whereas *Pilostyles* on *Jacksonia*, *Oxylobium* and *Gastrolobium* is monoecious. Examples are given as Table 2. Hence, the stems of *Daviesia* hosts usually bear arrays of flowers which are either all male or all female (Figs. 3 and 4). In the other three genera (e.g. Fig. 7) the male flowers occur interspersed with female flowers on all branches. Though only 68 plants of these genera were recorded infected with *Pilostyles* this pattern was consistent, suggesting that most plants were infected only once. The male flowers are usually less obvious because they are short-lived and may abscise before the stigmatic surface of the female flowers hardens following pollination. Also, the male flowers are usually outnumbered two to three times by female flowers on these plants.

In the field, as previously mentioned, hosts may be sympatric. For example, in the Darling Range, *D. angulata*, *D. preissii* and *D. pectinata* grow together, each bearing dioecious parasites. Likewise, *Oxylobium* and *Gastrolobium*, with monoecious parasites, are sympatric in the Stirling Range. However, in the Irwin district where sand overlies laterite, mixed populations occur, with dioecious *Pilostyles* on *D. polyphylla* and *D. quadrilatera* together with the monoecious condition of the parasite on *Jacksonia*.

Occasionally male and female flowers were encourntered on the same *Daviesia* host (e.g. *D. angulata* - Table 2). Out of a total of 112 plants scored in a gravel pit near Kalamunda, six were monoecious. Unlike the flower distribution of *Pilostyles* on the other host genera, male and female flowers were not mixed at random. Two conditions were found. Firstly, half of the stems of the host arising from the rootstock bore seasonal arrays of male *Pilostyles* flowers whereas the other stems bore female flowers. As all stems were of the same age, this suggests that the host was infected

Fig. 2. Shoot of *Daviesia pectinata* infected with *Pilostyles* showing female flowers (x 0.3). Figs. 3 and 4. Stems of *Daviesia angulata* infected with *Pilostyles*; (3) with receptive female flowers, (4) with male flowers showing two (arrowed) at anthesis (x 1.5).

Table 2. Distribution of the unisexual flowers of *Pilostyles*. The number of host plants counted bearing male and/or female flowers of *Pilostyles* is shown.

Host	Locality	Number of host plants bearing		
		male parasite flowers	female parasite flowers	both male and female flowers
Daviesia angulata	Kalamunda (forest plot)	38	38	0
Daviesia angulata	Kalamunda (gravel pit)	51	55	6
Daviesia pectinata	Kalamunda	6	3	0
Jacksonia floribunda	Cataby-Eneabba	0	0	31
Oxylobium atropurpurea	Stirling Range	0	0	23
Gastrolobium velutinum	Stirling Range	0	0	14

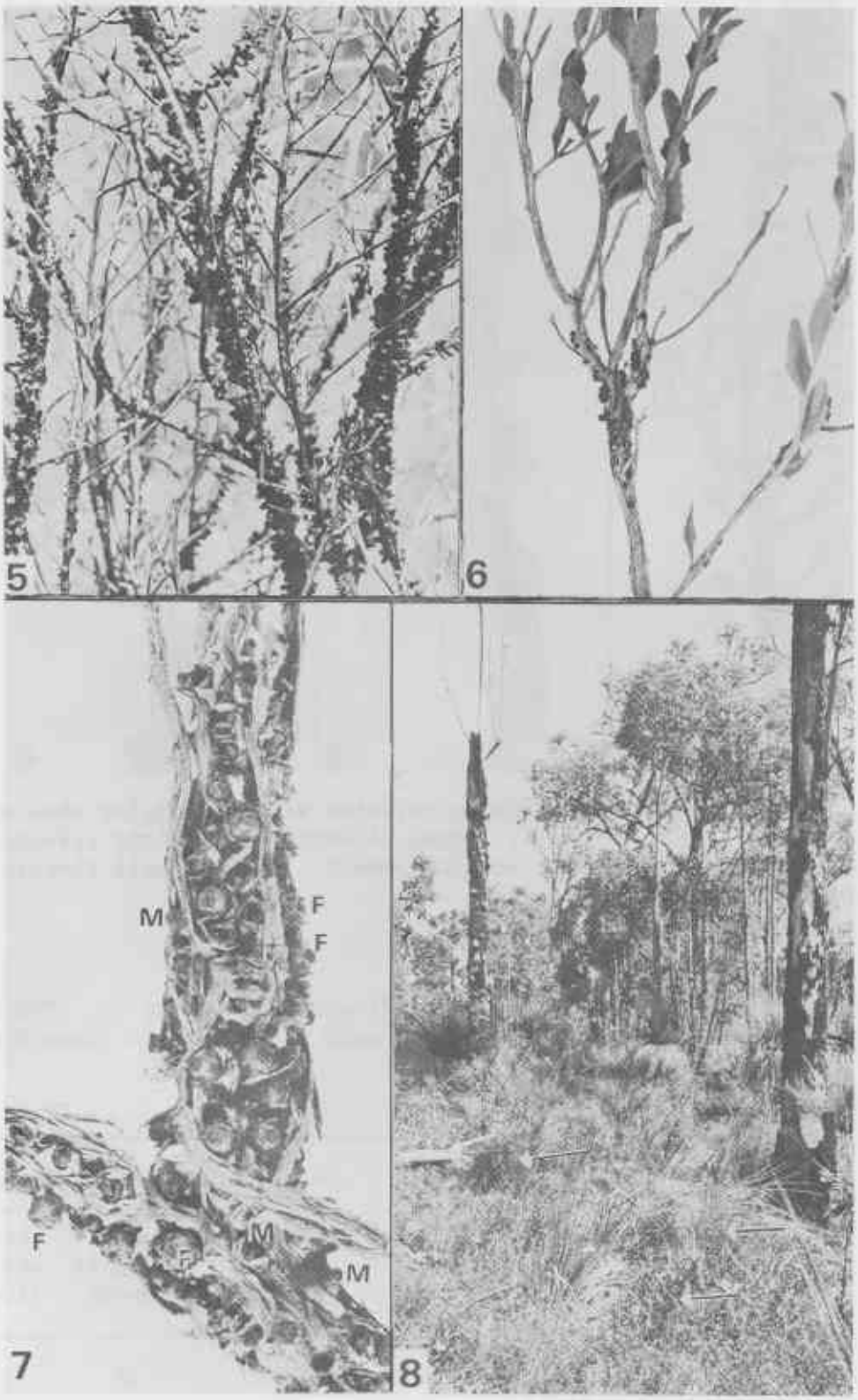

Fig. 5. Heavy infestation of *Pilostyles* (female) on *Daviesia angulata*.
Figs. 6 and 7. Infected stems of *Jacksonia floribunda*; (6) general view of small shoot, (7) details of flowers of *Pilostyles* (x 1.5) pushing through the thick bark. Young fruits (F) and dehydrated male flowers (M) are indicated.
Fig. 8. Overcut jarrah forest near Kalamunda showing understorey with infected *Daviesia* plants (arrowed) where data for Table 4 was obtained.

twice simultaneously by *Pilostyles*. Secondly, most of the branches of the host were colonized by a *Pilostyles* plant producing flowers of one sex. However, several younger branches arising from the root stock bore parasite flowers of the opposite sex. Possibly a second invasion by *Pilostyles* had occurred in a fairly mature host.

Darling Range Study Site

(a) Distributions within site

Daviesia was a prominent component of the understorey (Fig. 8). The plot contained 650 individuals of *D. angulata* and 70 of *D. pectinata*. *Pilostyles* was found infecting 76 (12%) of *D. angulata* bushes, and 9 (13%) of *D. pectinata*. Of the 76 of *D. angulata*, exactly half (38) were infected with male *Pilostyles*, and half with female.

Each metre quadrat contained from zero to four individuals of *D. angulata* (Table 3). The plants were shown to occur in clumps rather than randomly, with respect to the metre square plots, by comparing the observed distribution with that expected from a Poisson distribution. The departure from the latter was highly significant ($\chi^2 = 40.17$, d.f. = 3, $p < 0.001$).

It was expected that the distribution of *Pilostyles* would be clumped both around female individuals and within host groups. However, the highest percentage of parasitization (Table 3) occurred in quadrats containing only one individual of *D. angulata*, whilst all quadrats which contained either three or four individuals of *Daviesia* contained no *Pilostyles*.

(b) Response to fire

Following the fire, both species of *Daviesia* had regenerated from extensive rootstocks. In some of these, *Pilostyles* was evident in one and a half year old shoots, suggesting that *Pilostyles* had survived the fire within the root-stock and grew up within the regenerating *Daviesia* stems. Rapid reappearance of *Pilostyles* in stems regenerating after fire was also observed in other host species in the northern sandplains.

(c) Life Cycle

During December, swellings appear on the woody stems of the previous year's growth of the host. These swellings enlarge until flower buds emerge in January. Flower initiation and emergence in the parasite are apparently unrelated to flower initiation in the host (Table 1). Male and female flowers emerge concurrently, the buds opening towards the end of February.

Table 3. Occurrence of *Pilostyles* on *Daviesia angulata* near Kalamunda. For details see text.

Number of host plants in each quadrat	0	1	2	3	4
Number of quadrats	998	326	117	26	3
Number of plants parasitized		62	14	0	0
% plants parasitized		19.6	5.9	0	0

However, male flowers which are short-lived are only present until early April, while many young female flowers can still be found in late April. Both male and female flowers of *Pilostyles* on *Daviesia* are burgundy in colour. This contrasts with the orange flowers of *Pilostyles* found on *Jacksonia* and the orange-red flowers of *Pilostyles* on *Oxylobium* and *Gastrolobium*.

The most probable pollen vector is a small, unidentified, native wasp, which has been observed visiting flowers of both male and female plants of *Pilostyles*. For example, during a one-and-half hour period in a population near Kalamunda, wasps were observed visiting male flowers on two host plants (over 14 separate visits to flowers), and female flowers on five host plants (over 13 separate visits to flowers).

When visiting the flowers, the wasps land in the middle of the flower, on top of the central column. The insects then probe between the column and the perianth in search of nectar. Both male and female flowers have nectaries near the point of attachment of the perianth. Foraging at the nectaries necessitates that the same part of the insect touches either the anthers or stigmatic surface. The morphology of the wasps is such as to facilitate pollen transport, and the observed behaviour should lead to pollen transfer from male to female plants. It is therefore suggested that these wasps are the pollinators of *Pilostyles*.

From about May onward, the female flowers enlarge as fruit and seed maturation proceeds, until fruit-fall occurs in October-November. Each female flower contains about seventy ovules when on *Daviesia angulata* and *Jacksonia floribunda*, but over 100 when on *Oxylobium atropurpurea* or *Gastrolobium velutinum* (Table 4). Fruits are rarely found on the ground beneath female plants, but it is not known how dispersal is effected, or how parasitisation occurs.

Table 4. Ovule counts for *Pilostyles* on four hosts.

Host	Number and range of ovules/ovary (n = 5)
Daviesia angulata	69 (60-77)
Jacksonia floribunda	73 (65-84)
Oxylobium atropurpurea	122 (87-138)
Gastrolobium velutinum	102 (59-143)

DISCUSSION

Pilostyles hamiltonii is more widespread, and has a greater host range than was previously thought, yet its distribution in Western Australia remains an enigma. There are several disjunctions, even though some of the intervening areas have an abundance of some of the known host species. There appear to be considerable differences between some of these disjunct occurrences, as reflected in flower colour, host preferences and sexual expression. These differences may well deserve taxonomic recognition.

It is also unclear why *Pilostyles* should parasitise such a small proportion of the species in each genus which is utilized as a host, even though it is known to infect four different genera in Western Australia. Less than a fifth of the Western Australian species of *Daviesia* are known hosts of *Pilostyles*, and *Jacksonia*, *Oxylobium* and *Gastrolobium* each contain 20-40 species, yet only five species from these three genera are known hosts. Uninfected species are frequently found occurring sympatrically with infected ones. Considering the morphology and distribution as well, the most likely explanation is that three taxa of *Pilostyles* occur in Western Australia - one on *Daviesia*, one on *Jacksonia*, and one on *Oxylobium* and *Gastrolobium*. *Pilostyles* on *Oxylobium* and *Gastrolobium* is of restricted, disjunct occurrence on a relatively old land surface and hence may represent a relict distribution. *Pilostyles* on *Jacksonia* being marginal to the larger distributional area wherein *Daviesia* is a host, may be of recent origin. If such is the case, then the observed relationship between host range and parasite range is in accord with the distributional pattern. Clearly much more needs to be known, particularly concerning host/parasite relationships and control of sexual expression in the parasite and floral morphology of *Pilostyles*, before the evolutionary history of *Pilostyles* in Western Australia can be elucidated.

Further aspects of the biology of *Pilostyles* which require further investigation are the processes of seed dispersal and infection of a new host.

The scarcity of fruits on the ground beneath female plants suggests either that they are eaten, or that an effective dispersal mechanism exists, but nothing is known beyond this. Ants are likely dispersal agents, and have been reported dispersing seeds of several species in the jarrah forest (Majer 1978). Storage of seeds by ants might provide the germinating seed with an easy pathway to the host tissues via the root system. Although Kuijt (1969) claims that *Pilostyles* infects only stems, and not roots, our evidence suggests that root-stocks may be infected.

ACKNOWLEDGEMENTS

We wish to thank Dr. N.G. Marchant, Mr. K.F. Kenneally and Professor J.S. Pate for providing information on *Pilostyles*, and Dr. M.D. Crisp for identifying the *Daviesia* species. The work was carried out whilst A.B. was in receipt of a University of Western Australia Research Studentship.

REFERENCES

Gardner, C.A. (1948). Contributions florae Australiae Occidentalis XII. *Journal of the Royal Society of Western Australia* 32: 75-81.

Kenneally, K.F. and K.C. Pirkopf (1979). A disjunct occurrence of *Pilostyles* on two new host genera. *Western Australian Naturalist* 14: 135-136.

Kuijt, J. (1969). *The Biology of Parasitic Flowering Plants*. University of California Press, Berkeley, California.

Majer, J.D. (1978). Studies on invertebrates in relation to bauxite mining activities in the Darling Range - a review of the first eighteen months research. *Alcoa Environmental Research Bulletin* No. 3: 1-18.

Smith, G.G. (1951). New records of distribution of *Pilostyles hamiltonii*. *Western Australian Naturalist* 3: 21-24.