

The Explosive Pollination Mechanism and Mating System of the Weedy *Hyptis suaveolens* (Lamiaceae)

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Abstract The flower of the perennial shrubby herb, *Hyptis suaveolens* (L.) Poit. is representative of an explosive pollination mechanism. The carinal structure formed by the middle lobe of corolla lower lip conceals the stamens and stigma and does not open following the natural anthesis. Upon anthesis, the carinal lobe is under tension which is later released by wind or bees. The violent explosion of the carinal lobe caused by wind results in self-pollination; by bees, it results in self- and cross-pollination. Foraging activity of some bees which collect pollen from the anthers and stigma on *H. suaveolens* may reduce the success of pollination.

The mating system involves both autogamy and allogamy. Both require explosion of carinal lobe for pollination. The flexibility of the mating system is considered a safeguard ensuring its ruderal nature for weediness.

Key words: Lamiaceae, *Hyptis*, carinal lobe explosion, pollination, wind, bees.

Explosive or parallel floral mechanisms causing pollination as a result of the violent movement of anthers/stamens and style alone or together with restraining petals are reported for some members of the Loranaceae (Goebel, 1920; Docters van Leeuwen, 1931, 1954; Vogel, 1954; Wiens and Tolken, 1979; Gilbert, 1981; Feehan, 1985), Urticaceae (Taylor, 1942), Ericaceae (Marie-Victorin, 1942), Leguminosae (Meeuse, 1961; see Mosquin, 1985), Fumariaceae, Musaceae (Proctor and Yeo, 1972), Onagraceae (Plitman et al. 1973), Rhizophoraceae (Davey, 1975), Cornaceae (Mosquin, 1985), Stylidiaceae, Acanthaceae (see Mosquin, 1985) and Marantaceae (Davis, 1987).

The ocimoid mints (Lamiaceae: Ocimoideae) include both explosive and non-explosive pollination mechanisms. The explosive mechanism exists in the genera *Hyptis* (Burkart, 1939; Harley, 1971, 1976; Brantjes and De Vos, 1981; Keller and Armbruster, 1989), *Aeollanthus* (Hedge, 1972), *Eriope* (Harley, 1971, 1976), *Marsipianthes*, *Peltodon*, *Raphiodon* and *Homalocheilos* (Harley, 1976). Some species of the genera *Plectranthus* and *Coleus* have non-explosive mechanisms (Scott-Elliot, 1891; Blake, 1971; Tanaka, 1972; Faegri and Van der Pijl, 1979).

Hyptis, a genus of 400 species occurs as an annual or perennial herb, half shrub or tree in the tropical regions of the World (Nowicke and Epling, 1969;

Hickey and King, 1988). Previous limited studies document the explosive nature of the pollination mechanism in *H. mutabilis*, *H. fasciculata* (Burkart, 1939), *H. pauliana* (Brantjes and De Vos, 1981) and *H. capitata* (Keller and Armbruster, 1989), and the non-explosive mechanism in *H. macrantha* (Harley, 1971) in the New World. *Hyptis suaveolens* is a native of the American tropics where it grows as an annual herb and flowers between October and April (Adams, 1972). In Asia, it occurs in the tropical and subtropical regions, where it grows as an herb and flowers throughout the year in Taiwan (Anonymous, 1978). It is a perennial shrubby herb and flowers from September to December in India. The need for a comprehensively detailed knowledge of the explosive pollination mechanism in relation to the mating system of *H. suaveolens* growing as a widespread weed in India is the occasion for the present study.

Materials and Methods

Hyptis suaveolens (L.) Poit. is a ruderal, herbaceous species common in rough pastures and gravelly waste places in Visakhapatnam (17°42'N and 82°18'E), Andhra Pradesh, India. A population of about 700 plants near the Indira Gandhi Zoological Park was chosen for field observations

and experiments in September–December 1984 and 1985. Observations were made at the flowering patch of *H. suaveolens* by recording all flower visitors between 0700 h, when the flowers began to open, and 1800 h, when it became dark, the flowers ceased to open, and foraging activity of insects stopped. Nectar sugar concentration was noted using an Abbe refractometer, and sugar analysis was done by paper chromatography (Harborne, 1973). Pollen production per anther, pollen viability, stigma receptivity and the mating system were determined as in my previous studies (Aluri, 1988, 1989; Aluri and Subba Reddi, 1989). A hair hygrometer was used for recording relative humidity and a celsius thermometer for temperature. An anemometer was used for noting wind speed. Flower visitors (listed in Table 4) were caught after they visited. Dorsal and ventral sides of these specimens were washed separately in lactophenol stained with aniline blue and washings were observed under a microscope for pollen grains of *H. suaveolens*. The behavior of each flower visitor in relation to flower tripping or untripping associated with pollination was carefully observed. Seed fecundity was calculated as percentage of seeding in relation to the pollinated flowers.

Results

1. Plant Habit, Flower Morphology and Explosive Pollination

The perennial *Hyptis suaveolens* is a shrubby herb. It begins vegetative growth from a perennating root stock and seed after heavy local rains in September. About three weeks later, flowering is initiated and continues until December. Particular patches may reseed themselves and persist for several years. An individual plant usually reaches a height of 150 cm. The inflorescence is a verticillate cyme. Each cyme contains a 20 mm long puberulent peduncle with 3 or 4 flowers anthesing over 2–4 days.

The odorless flowers are small and flag-shaped. The five-toothed puberulent calyx is 8 mm deep and 3 mm wide at the opening. The corolla is tubular, 5 mm deep and 1 mm wide at the opening, with five lobes on the end of the tube. Two lobes point upwards, (two sideways), and the lower lobe with saccate carina is in the median plane below the adjacent petals. The entire corolla is blue except for a dark brown color line inside the upper petal lobes. The corolla tube has 6–8% sugary nectar as sucrose equivalents which averaged $0.9\ \mu\text{l}$ (Range $0.59\text{--}1.21\ \mu\text{l}$) per flower. Nectar sugars are glucose, fruc-

tose and sucrose. The nectar is produced for nearly 30 minutes between anther dehiscence and anthesis by a ring-shaped disk around the upperside of the ovary base. The corolla base closely surrounds the nectary and ovary. The four hairy stamens, in two pairs, are inserted on the distal part of the corolla tube. The short filaments (2 mm) of the upper pair are attached to the lower lip and those of lower pair (3 mm) to the upper lip. The 1 mm long single-celled anthers are introrse and firmly attached to the ends of the filaments. Dehiscence of each anther is longitudinal. Pollen grains averaged 630 (Range 590–670 per anther). They are loose, powdery, oblong and 3–6 colpae with a smooth surface. Grain dimensions are equatorial axis $38.25\ \mu\text{m}$ and polar axis $48.5\ \mu\text{m}$. The syncarpous ovary is bicarpellary with each carpel having one locule. A constriction appears on each carpel in the antero-posterior line in the initial stage of ovary development. Growth of the constriction is retarded in later development, and the carpels are not combined into a tetralocular ovary. The 6 mm long style with a shortly bifid stigma springs up between the carpels from the base of the ovary and is inserted 1 mm below the upper pair between the didynamous stamens. The stamens and style are hidden in the concave carinal lower lobe, which is closed by two closely appressed lateral membranous folds. The two adjacent lateral petal lobes partly close the carinal lobe at the base.

Mature flower buds begin to open each day shortly after dawn (7:00 h) and continue to open until dusk (19:00 h) with a peak at 9:00–13:00 h. The peak period of anthesis seems to correlate with relatively

Table 1. Rate of anthesis as a function of time in *H. suaveolens*.

Time (h)	Anthesis % of daily total	Relative humidity (%)	Air temperature (°C)
6:00	0	86	27
7:00	11	86	27
9:00	22	86	29
11:00	36	74	31
13:00	19	73	32
15:00	7	78	30
17:00	3	81	29
19:00	2	81	29
20:00	0	82	28

Quantified from ten tagged flowering stalks of individual plants.

lower relative humidity and higher air temperature (Table 1). Anthers dehisce fully while still in bud, 30 minutes prior to anthesis and do not release their pollen. Unfolding of the saccate lower lobe with stamens and style does not accompany with the opening of the other four petal lobes (Fig. 1A) but is

under increasingly powerful tension with a gradual elongation of stamen filaments and a very slight downward movement of the lower lobes (Fig. 1B-right). The margins of the saccate lobe and long-fimbriate, and these processes appear to interlock to keep the anthers from bursting out prematurely. A



Fig. 1. *Hyptis suaveolens*:

- A, Flower-opening with unfolded saccate lower lobe concealing with stamens and pistil.
- B, Right-Saccate lower lobe under tension for tripping. Left-Tripped saccate lower lobe and exposed stamens and stigma.
- C, *Amegilla* sp. tripping and foraging on the flower.
- D, *Megachile* sp. tripping and foraging for nectar.
- E, *Apis indica* tripping and foraging on the flower.
- F, *Pithitis binghami* tripping the flower with proboscis.

Table 2. Flower tripping by wind speed in *H. suaveolens*.

Wind speed (m/sec.)	Flowers tripped	
	Number	Percentage
0.2	0	0
0.4	0	0
0.8	8	40
1.2	14	70
1.7	20	100

Flowers observed = 20.

slight disturbance to the carinal lobe by flower-visitors or wind speed above 0.8 m/sec. (Table 2) cause it burst violently releasing the pollen-liberating stamens and the receptive stigma. An average of 47 (Range = 30–88) pollen grains remains in the anther following explosive pollen release. After the explosion, the saccate lobe bends backward (Fig. 1B-left). The filaments and the two side petal lobes serve as an alighting place for flower visitors. The stamens are straight, and the stigma is bent very slightly downwards without further growth. The stigma is receptive in the bud stage about 30 minutes before dehiscence of the anthers and ceases receptivity about 90 minutes after anthesis. Pollen grain viability lasts for 19 hours after anther dehiscence. The calyx persists and shelters the ovary. The corolla, stamens and pistil drop off immediately after the loss of stigma receptivity.

2. Mating System

Results of the breeding systems provided in Table 3 indicate that *H. suaveolens* was both self- and cross-compatible and was not apomictic. Fruiting by autogamy in closed conditions by bagging shows that the flowers were pollinated automatically by the

wind activated explosion. Although fruit-set was 100%, seed set and fecundity rate was related to the amount of pollen deposited on stigma during auto-pollination. In natural conditions, it is not always expected because wind speed varies through time of day which ranged between 0.2 to 1.7 m/sec. Strong winds caused the wind-activated carinal explosion as well as flower drop. Fruiting within and between individual plants after hand-pollination was a reflection of the ability to reproduce through cross-pollination. Natural-fruitlet was a product of both wind and insect-mediated pollination. There were no differences for the fruiting, seeding and fecundity ratios between hand cross-pollinated and open-pollinated flowers. But there were significant differences in such parameters (Chisquare test used) exist between hand cross-pollinated and self-pollinated flowers. Such differences in fruit, seed and fecundity rates reveal that there are handicaps for the success of pollination by both wind and insects.

3. Flower-visitor Activity, Flower Tripping and Pollination

Flower-visitors are day-active, visited *H. suaveolens* flowers shortly after the initiation of anthesis, and continued until night fall. The regular foraging activity of bees gradually rose to a peak at 1000–1200 h and declined thereafter, ceasing at 1800 h. Occasional foraging visits of butterflies were mainly confined to the period between 0900–1100 h. Bees probed the flower after landing on the filaments and/or lateral petal lobes and rubbing the stamens and stigma with their ventral side (Fig. 1C–E). Except for the small *Trigona*, *Ceratina* and *Pithitis*, bees were not disturbed by the violent explosion of the carinal-lobe when probing the flower. Consequently, small bees first moved around the flower and touched the carinal-lobe with their pro-

Table 3. Results of breeding systems for *H. suaveolens*.

Test	Treatment	# Flowers pollinated	# Flowers fruited	Fruiting (%)	Seeding (%)	Fecundity (%)
Apomixis	Emasculated, bagged	30	0	0	0	0
Automatic self-pollination	Untreated, bagged	35	35	100	92	92
Effectiveness of self-pollination	Self-pollinated by hand within individual plant, bagged	40	34	85	82	70
Effectiveness of cross-pollination	Cross-pollinated by hand, bagged	40	30	75	68	51
Open-pollinated	Untreated, not bagged	500	394	79	69	54

Table 4. Flower visitors, their forage type and pollen grains of *H. suaveolens* deposited on their bodies.

Insect species	Forage type		# Pollen grains deposited		
	Nectar	Pollen	Range	Average	Standard deviation
HYMENOPTERA					
<i>Apis indica</i>	+	+	34–121	58	22.32
<i>Trigona</i> sp.	—	+	59–95	70	10.80
<i>Xylocopa latipes</i>	+	—	27–152	71	26.54
<i>Pseudapis oxybeloides</i>	—	+	73–278	230	83.24
<i>Ceratina</i> sp.	+	+	72–103	90	11.21
<i>Amegilla</i> sp.	+	+	77–643	233	236.95
<i>Thyreus histrio</i>	+	—	7–45	23	12.17
<i>Pithitis binghami</i>	+	+	22–83	65	24.96
<i>Megachile</i> sp.	+	—	27–111	70	37.35
LEPIDOPTERA					
Butterflies	+	—	0–23	5	8.20

Pollen is deposited only on ventral side; # specimens examined for each species = 10.

boscides (Fig. 1F). These behaviors caused the explosion. After the explosion, they foraged on the flower. *Ceratina* and *Pithitis* first foraged for nectar and then collected pollen remaining in the anthers, on the filaments and pistil. *Trigona* foraged for pollen only. There was little or no pollen in the anthers or on the stigma after the bees have left the flowers. Butterflies probed the untripped flowers laterally, landing on the adjacent flower calyces, and the tripped flowers frontally as bees did. A separate analysis of ventral and dorsal sides of each bee and butterfly species indicated that pollen is deposited on the ventral side only. *Amegilla* and *Pseudapis* picked up pollen grains nearly thrice the amount that was deposited on the ventral side of the other bee species. The butterflies probing frontally (Table 4), picked up pollen grains from tripped flowers only. They picked up no pollen by frontal probing when they visited the flowers that received too many visits by pollen collectors. A single foraging visit of any bee species caused the tripping of the carinal lobe of the flower. Butterflies did not trip the flowers.

Discussion

Many members of the Lamiaceae, being self-compatible, exhibit protandry, which is highly prevalent in the sub-family Ocimoideae. The group is characterised by anthers and stigma enclosed by a carina formed by the lower lip of the flag-shaped flowers adapted for sternotribic pollination (Vogel, 1954; Van der Pijl, 1972). The genus *Hyptis* for its species

thus far known is unique in this regard. The carina formed by the middle lobe of the lower lip does not open upon anthesis but is under tension which is released in an explosive way by a gentle disturbance. The carina then flips backward and downward, causing the anthers eject pollen onto the stigma resulting in self-pollination. The stigma is receptive after elongation of the style and protrusion beyond the anthers in *H. pauliana* (Brantjes and De Vos, 1981) and by opening of the bilobed stigma in *H. capitata* (Keller and Armbruster, 1989) after the explosion of the carinal lobe and after the stamens bend down into the same lobe. The last condition also occurs in *H. mutabilis* (Burkart, 1939) and in *Eriope crassipes* (Harley, 1971). In *H. suaveolens*, however, the shortly bifid stigma is receptive before the anthers dehisce, and stigma receptivity remains until before the corolla wilts or drops. In addition, the style does not elongate after the carinal lobe has exploded, and the stamens do not bend down but remain straight, as in *Aeollanthus njassae* (Hedge, 1972). Such a condition might favor pollen reaching the receptive stigma when the forager trips the flower.

Foragers reported on *Hyptis* flowers include bees, wasps, butterflies and hummingbirds. *Bombus brevivillus* triggers the floral explosive mechanism sternotribically in *H. paradisi*, *Exomalopsis auropilosa* in *H. subrosea*, and *Centris tarsata* in *H. irwinii* in Brazil (Harley, 1974). Brantjes and De Vos (1981) treat the flower of *H. pauliana* as ornithophilous and possibly pollinated by a hummingbird in Brazil. The floral mechanism in *H. capitata* grow-

ing in Panama is visited by bees, wasps and butterflies and is tripped only by a wasp, *Omicron flavonigrum*, which collects nectar nototribically. It is very unusual to have nototribic pollen deposition in flag-shaped blossoms (Keller and Armbruster, 1989). The floral explosive mechanism in *H. suaveolens* in India is tripped by a slight disturbance. The wind-caused explosion results in fruiting and seeding in untreated flowers covered with porous bags. The complete success of pollination in fruiting as a result of wind-activated explosion in this treatment is due to wind pressure inside the bags developed by the influx of wind through pores on the bags. It means that wind could cause 100% self-pollination in natural conditions only when the wind-speed is above 0.8 m/sec. and upto certain limit. The seed output and fecundity is, however, subjected to the amount of pollen deposited on the stigma. Since the flowers are delicate, strong winds cause carinal-explosion followed by flower drop. The strong winds therefore have negative effects in that they indirectly limit the natural fecundity and also reduce the foraging activity of insects.

Foraging bees cause the carinal-lobe, to reflex and release the stamens and stigma. Deposition of pollen is always on the ventral side of the bee's body. The foraging behavior of the small *Trigona*, *Ceratina* and *Pithitis* suggests that they are disturbed by the explosive mechanism. Consequently, from past experience, they first touch the carinal lobe with their proboscides to make sure it is exploded. they then probe the flower for nectar or pollen. Although they trip the explosive mechanism as a result of which pollen is deposited on the stigma, their pollen collecting behavior leaves little or no pollen on the stigma after they have left the flower. They are therefore not ordinarily pollinators, can be treated as mere visitors for exploiting the floral resource. The medium-sized *Amegilla*, *Apis* and *Pseudapis* pollinate ordinarily but also collect pollen as small bees do. The medium sized *Megachile*, the large-sized *Xylocopa* and *Thyreus* trip the explosive mechanism and collect nectar only. Their habitual movement between flowers of the same or different conspecific plants increases the chances for cross-pollination and can be major pollinators. The dual behaviors of nectar foraging butterflies seem to exploit both tripped and untripped flowers. This behavior and their infrequent visits indicate that they are not ordinarily pollinators.

Sexual reproduction through autogamy and allogamy in *H. suaveolens* is absolutely dependent

upon a biotic or abiotic vector for the explosion of the carinal-lobe and subsequent placement of pollen on the stigma. The flower has about two hours lifespan and needs to be pollinated during that period. The abiotic vector, the wind does not always blow at particular speed in natural conditions and hence its role in activating carinal-explosion is limited during that short period of flower life. The wind-activated carinal-explosion however results in only self-pollination. It is the insect foraging activity that brings about cross- as well as self-pollination. As a result, the plant may have confined anthesis to daylight hours when the flower-visitors are active. The total anthesis period correlates with the foraging period of insects on *H. suaveolens*. Furthermore, the peak period of anthesis also coincides with the intensive foraging period of insects. Such a coincidence insures completion of pollination process in most of the flowers anthesed in a day by insects which are usually most active foraging when air temperature is relatively higher and relative humidity lower. The natural pollination thus is a function of insects collecting floral resource and periodical occurrence of appropriate wind. As already stated, the mere carinal-explosion does not insure 100% pollination success in terms of seed output. The production of seed from each of the two ovules in the flower is then dependent on the rate of enough self- or foreign-pollen deposition on the stigma and not directly on the rate of flower tripping. The low natural seed output in *H. suaveolens* is a surprising result that differs from expectations despite its being self- and cross-compatible. This might have been due to the behavior or small bees collecting pollen from stigma and limited role of wind. There is no information on natural fecundity of other allied species and hence the speciality of *H. suaveolens* cannot be observed. The low rate of natural seed set however does not affect the plant being a ruderal occupying varying habitats in tropical or subtropical regions. The plant is a perennial and can reproduce sexually by seed as well as asexually by vegetative growth from perennating root stock. The sexual process brings about the required change in genetic material through insect-mediated pollination that is essential for weediness. The asexual process on the other hand permits perpetuation of the plant in times of poor yields. Therefore, such a dual reproductive behavior exhibited by *H. suaveolens* is a ruderal character for perpetuation of the plant.

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References

- ADAMS, C. D. 1972. Flowering Plants of Jamaica. University of the West Indies Press, Mona, Jamaica.
- ALURI, R. J. S. 1988. Pollination ecology of *Jasminum angustifolium* Vahl. (Oleaceae). Proc. Indian natn. Sci. Acad. **B54**: 165–169.
- . 1989. Reproductive ecology of *Ocimum americanum* L. and *O. basilicum* L. (Lamiaceae). Plant Species Biol. **4**: 107–116.
- and SUBBA REDDI, C. 1989. Pollination biology of *Anisomeles indica* and *A. malabarica* (Lamiaceae). Plant Species Biol. **4**: 157–167.
- ANONYMOUS 1978. Flora of Taiwan. Vol. IV. Epoch Publishing Company Ltd., Taipei, Taiwan.
- BLAKE, S. T. 1971. A revision of *Plectranthus* (Labiatae) in Australasia. Cont. Queensl. Herb. **9**: 1–120.
- BRANTJES, N. B. M. and DE VOS, O. C. 1981. The explosive release of pollen in flowers of *Hyptis* (Lamiaceae). New Phytol. **87**: 425–430.
- BURKART, A. 1939. El mecanismo floral de la labiade *Hyptis mutabilis* y su convergencia hacia la flora papilionoidea. Darwiniana **3**: 425–427.
- DAVEY, J. E. 1975. Note on the mechanism of pollen release in *Bruguiera gymnorhiza*. J. S. Afr. Bot. **41**: 269–272.
- DAVIS, M. A. 1987. The role of flower visitors in the explosive pollination of *Thalia geniculata* (Marantaceae), a Costa Rican marsh plant. Bull. Torrey Bot. Club **114**: 134–138.
- DOCTERS VAN LEEUWEN, W. M. 1931. Uit het leven von enkele javaanoche Lorantheaceae. De Tropische Natuur **6**: 103–118.
- . 1954. On the biology of some Javanese Lorantheaceae and the role birds play in their life history. Beaufortia **4**: 105–208.
- FAEGRI, K. and VAN DER PIJL, L. 1979. The Principles of Pollination Ecology. Pergamon Press, Oxford.
- FEEHAN, J. 1985. Explosive flower opening in ornithophily: a study of pollination mechanisms in some Central African Lorantheaceae. Bot. J. Linn. Soc. **90**: 129–144.
- GILBERT, M. 1981. A *Loranthus* and its birds. East Afr. Nat. Hist. Soc. Bull. **96**–97.
- GOEBEL, K. V. 1920. Die Entfaltungsbewegungen der Pflanzen und deren teleologische Deutung. Gustav Fischer, Jena.
- HARBORNE, J. B. 1973. Phytochemical Methods. Chapman and Hall, London.
- HARLEY, R. M. 1971. An explosive mechanism in *Eriope crassipes*, a Brazilian labiate. Biol. J. Linn. Soc. **3**: 159–164.
- . 1976. A review of *Eriope* and *Eriopidian* (Labiatae). Hooker's Icones Plantarum **38**, Kew.
- HEDGE, I. C. 1972. The pollination mechanism of *Aeollanthus njassae*. Notes R. Bot. Gard. Edin. **32**: 45–48.
- HICKEY, M. and KING, C. 1988. 100 Families of Flowering Plants. Cambridge University Press, Cambridge.
- KELLER, S. and ARMBRUSTER, S. 1989. Pollination of *Hyptis capitata* by Eumenid wasps in Panama. Biotropica **21**: 190–192.
- MARIE-VICTORIN, F. 1942. Flore Laurentienne. Les Freres des ecoles Chretiennes, Montreal.
- MEEUSE, B. J. D. 1961. The Story of Pollination. The Ronald Press Co., New York.
- MOSQUIN, T. 1985. The explosive pollination mechanism in the Pop flower, *Chamaepericlymenum* (Cornaceae). Can. Field-Nat. **99**: 1–5.
- NOWICKE, J. W. and EPLING, C. C. 1969. Part IX, Family 169, Labiatae. Ann. Mo. Bot. Gard. **56**: 71–111.
- PLITMANN, U., RAVEN, P. H. and BREEDLOVE, D. E. 1973. The systematics of Lopezieae (Onagraceae). Ann. Mo. Bot. Gard. **60**: 478–563.
- PROCTOR, M. and YEO, P. 1972. The Pollination of Flowers. Taplinger, New York.
- SCOTT-ELLIOT, G. F. 1891. Notes on the fertilization of South Africa and Madagascar flowering plants. Ann. Bot. **5**: 333–405.
- TANAKA, H. 1972. Pollination of *Plectranthus inflexus*. J. Jpn. Bot. **47**: 249–254.
- TAYLOR, N. 1942. The Practical Encyclopedia of Gardening. Garden City Publ. Co., New York.
- VAN DER PIJL, L. 1972. Functional considerations and observations on the flowers of some Labiatae. Blumea **20**: 92–103.
- VOGEL, S. T. 1954. Blütenbiologische Typen als Elemente der Sippengliederung. Bot. Stud. **1**: 1–338.
- WIENS, D. and TOLKEN, H. R. 1979. Lorantheaceae. In: Leistner, O. A. (ed.), Flora of Southern Africa, **10**: 1–41. Botanical Research Institute, Department of Agricultural Technical Services, Pretoria.

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