

# BUTTERFLY POLLINATION OF *CLERODENDRUM INFORTUNATUM* (VERBENACEAE)<sup>1</sup>

T. BYRAGI REDDY AND C. SUBBA REDDI<sup>2</sup>

(With two text-figures)

**Key words:** *Clerodendrum infortunatum*, butterflies, *Papilio polytes*, *P. polymnestor*, *Atrophaneura hector*, pollination

*Clerodendrum infortunatum* L. flowers from February to April. The flowers anthesed during 0600-0700 hr and offer nectar and pollen to insect visitors. Nectar is secreted up to the evening of 3rd day. The nectar sugars are sucrose, glucose and fructose. Sucrose is predominant. Sugar concentration ranges from 6 to 30%. Protein and amino acids are present. The breeding system incorporates both geitonogamy and xenogamy. A total of 17 species of insects are found foraging at the flowers diurnally. Male and female phases of the flowers are separated in time and space. The Papilionoid butterflies (*Papilio polytes*, *P. polymnestor* and *Atrophaneura hector*) approached the flower horizontally, grasped it with their legs and continuously fluttered as they probed for nectar. The wings stroke the anthers/stigma, thereby causing pterigotribic pollination.

## INTRODUCTION

On the basis of observations on wood-white butterfly (*Leptidea sinapis*) and its nectar plants, *Viola canina*, *V. riviniana* and *Lathyrus montanus*; Wiklund *et al.* 1979 hypothesised that butterflies as a group may have evolved to a parasitic mode of life as adults, feeding on the nectar of flowers without pollinating them. However there are certain authentic cases of butterfly pollination *Caesalpinia pulcherrima*, Cruden and Hermann-Parker 1979; *Asclepias syriaca*, Percival 1965; *Aesculus californica*, Moldenke 1976; *Platanthera ciliaris*, Smith and Snow 1976; *Phlox* species, Grant and Grant 1965, Levin and Berube 1972; *Anquria*, Gilbert 1975; *Cnidioscolus urens*, Bawa *et al.* 1983; *Gossypium* species and *Hibiscus esculentus*, Pajni and Sukhwinder Kaur 1979, which does not agree the hypothesis of Wiklund *et al.* 1979.

To shed more light on this aspect, an attempt was made to study the role of butterflies in the pollination of *Clerodendrum infortunatum*, at

Visakhapatnam, a coastal city of India.

## MATERIAL AND METHODS

Observations were made during 1986 and 1987 on the natural populations of *C. infortunatum* L. (Verbenaceae) occurring in Andhra University Campus, Visakhapatnam (17° 42' N, 82° 18' E). Pollen output per anther was assessed by counting all the pollen grains in a sample obtained by gently crushing and tapping the anther on a clean microscope slide, spreading the pollen mass uniformly. The longevity of pollen and stigma was assessed based on the fruit set success from hand-pollination at regular intervals. Pollen loads on stigmas were counted during the female phase. The flowers to be hand-pollinated were emasculated in the bud condition. Tests for apomixis/autogamy, geitonogamy and xenogamy were conducted through controlled pollinations. Apomixis was tested by bagging the emasculated flowers free of pollen, autogamy by pollinating flowers with the pollen of the same flower, for geitonogamy with the pollen of different flowers of conspecific plant, for xenogamy with the pollen of a different conspecific plant.

<sup>1</sup>Accepted February 1995.

<sup>2</sup>Department of Environmental Sciences, Andhra University, Waltair-530003.

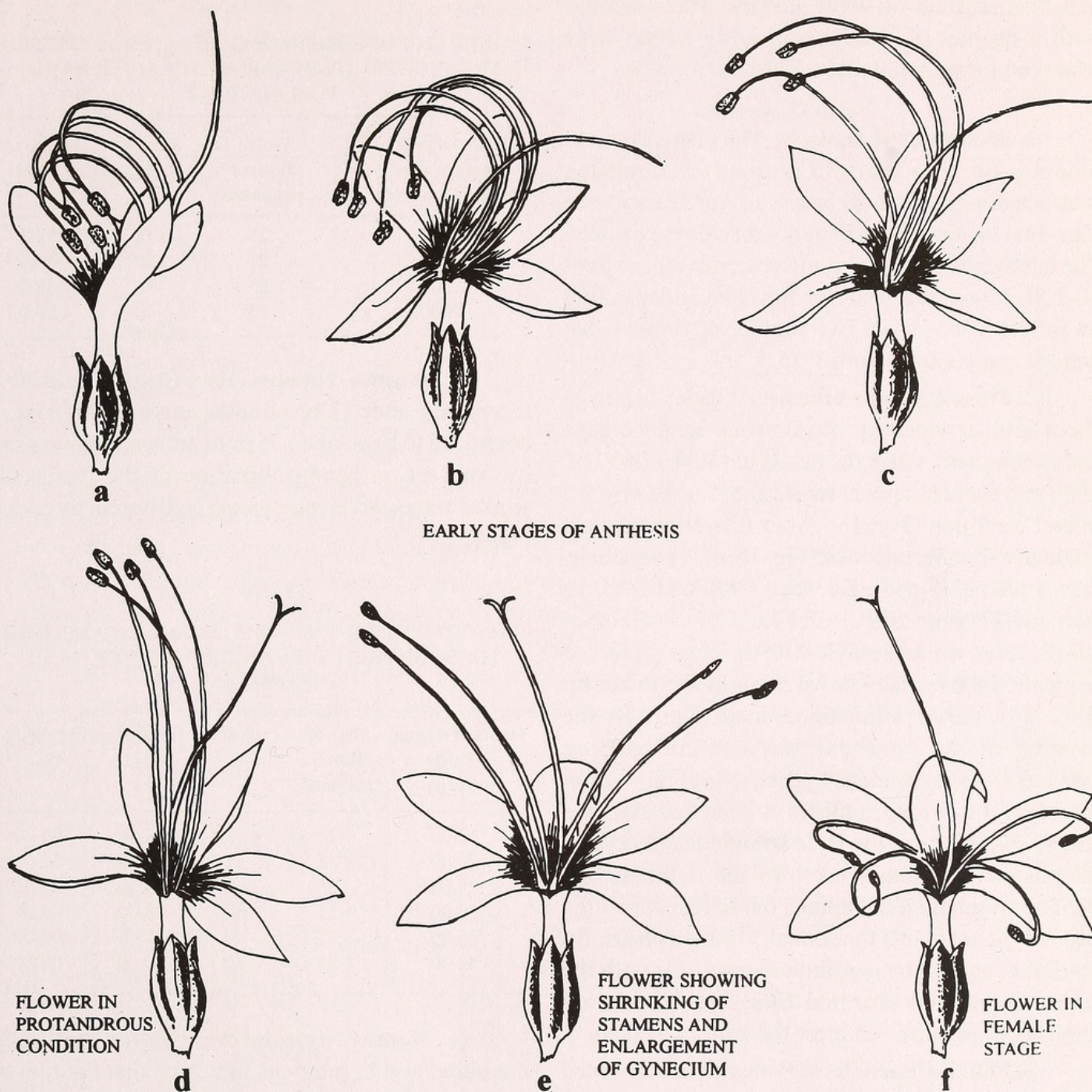


Fig. 1. Different phases of *C. infortunatum* flower.

Nectar produced in flowers protected from insects for 3 hr period was measured using disposable micropipettes. Sugar concentrations were determined with a pocket refractometer and sugar composition was analysed by paper-chromatography and spectrophotometry (Horborne 1973). Proteins and amino acids were identified by the method of Baker and Baker (1973).

The butterflies caught over the flowers were identified with the help of Wynter-Blyth (1957) and the nomenclature used is after Varshney (1983). The behaviour of visitors, the length of a visit and flowers visited in a unit time, using a stop watch, were carefully studied. The more frequent visitors were caught and examined under a stereomicroscope for the pollen adhering to the body

and then washed off with alcohol. The washings with a droplet of lactophenol aniline-blue were observed for pollen under a light microscope.

### RESULTS

**1. Blooming phenology:** The plants begin to bloom soon after the cold season, the flowering season extending from February to April every year. Each branch terminates in a sub-corymbose panicle. The number of flowers per inflorescence ranges from 10-100. Flowering lasts for 5-32 days, depending on inflorescence size. The number of flowers that anthesis daily varies from 1-15.

**2. Phenology of anthesis:** Anthesis begins at about 0500 hr with the protrusion of essential organs and is complete, when the petals unfold by 0600 hr. Pistil and stamens appear twisted and curled upward in bud condition (Fig. 1a). After flower opens they gradually become uncoiled (Fig. 1b, c). The stamens uncoil after the pistil. Between 0700 and 0900 hr stamens become linear and face the horizontal corolla tube, while the style with the closely pressed stigmatic lobes is bent down towards the lower lip (Fig. 1d). This is a functional male phase. By the evening of the same day stamens are bending sideways — two stamens to each side (Fig. 1e). On the second morning, anthers wither and stamens still bend sideways, the style straightens to occupy the position previously taken by the stamens (Fig. 1f). The stigmatic lobes spread out to receive pollen and the flower is in a functionally female phase. By the 3rd evening, the corolla withers along with the style, stigma and staminal filaments. Sepals are persistent, and turn red after the fruit is formed.

**3. Pollen Characters:** Pollen grains are freed through longitudinal anther dehiscence when stamens become linear at about 0700 hr. They are of three sizes: large grains 68.2  $\mu\text{m}$ , and medium 58.5  $\mu\text{m}$  and small 47.0  $\mu\text{m}$ , spheroidal, deep violet in colour and exine spiny. Their output per anther ranges from 1400-2600 ( $\bar{x}$  = 2000), out of which 63% are fertile. The fertile grains remained viable for 26 hr after anther dehiscence, as indicated by the fruit set on hand-pollination using stored pollen (Table 1). Pollen-ovule ratio is 2000:1.

TABLE 1

LONGEVITY OF POLLEN OF *C. infortunatum* ASSESSED THROUGH FRUIT SET CAPABILITY AFTER HAND-POLLINATIONS

| Hours of pollen storage after anther dehiscence | No. of flowers pollinated | Fruit set (%) | Seed set (%) |
|-------------------------------------------------|---------------------------|---------------|--------------|
| 12.00                                           | 25                        | 72            | 98.85        |
| 24.00                                           | 25                        | 52            | 55.00        |
| 26.00                                           | 25                        | 28            | 38.00        |
| 28.00                                           | 25                        | 0             | 00.00        |

**4. Stigma receptivity:** Stigma attained receptivity after 12 hr of anthesis (at 0700 hr) and continued to be so up to 35 hr of anthesis as assessed by fruit set on hand-pollination of the pistils (at similar stages of development) at different intervals (Table 2).

TABLE 2

LONGEVITY OF STIGMA OF *C. infortunatum* ASSESSED THROUGH FRUIT SET CAPABILITY AFTER HAND-POLLINATIONS

| Hours of stigma life after maturity | No. of flowers pollinated | Fruit set (%) | Seed set (%) | Fecundity (%) |
|-------------------------------------|---------------------------|---------------|--------------|---------------|
| 12.00                               | 25                        | 72            | 93.00        | 93.00         |
| 24.00                               | 25                        | 72            | 57.00        | 57.00         |
| 28.00                               | 25                        | 60            | 87.00        | 87.00         |
| 32.00                               | 25                        | 60            | 83.00        | 83.00         |
| 35.00                               | 25                        | 40            | 100.00       | 100.00        |
| 48.00                               | 25                        | 40            | 00.00        | 00.00         |

**5. Nectar dynamics:** Nectar volumes measured at 3 hr intervals indicated that the rate of production varies throughout flower life (Table 3). Secretion on the day of flower opening began in the hypogaeal disc from 0630 hr and continued up to the 3rd evening. It was small in the forenoon, increased from noon and amounted to over 2  $\mu\text{l}$  for a 3 hr period. Next morning the secretion was considerably reduced, and on the third day it was in traces. Sugar concentration was also low (6-12%) in the forenoon, but was maximum (20-30%) at 1300-1600 hr and then declined 14% by 1900 hr.

TABLE 3

NECTAR VOLUMES MEASURED AT 3-HOURLY INTERVALS IN *C. infortunatum*

| Time (h)        | Nectar volume<br>R | ( $\mu$ l)<br>$\bar{x}$ | Sugar<br>Concentration<br>(%) | Temp.<br>(°C) | RH<br>(%) |
|-----------------|--------------------|-------------------------|-------------------------------|---------------|-----------|
| 0700 (anthesis) | 0.87-1.00          | 0.93                    | 06                            | 25.0          | 82        |
| 1000            | 0.93-1.06          | 0.99                    | 12                            | 27.0          | 77        |
| 1300            | 2.00-2.40          | 2.18                    | 30                            | 29.0          | 65        |
| 1600            | 1.00-3.66          | 2.25                    | 20                            | 27.0          | 69        |
| 1900            | 1.47-2.60          | 2.12                    | 14                            | 26.5          | 75        |
| Second day      |                    |                         |                               |               |           |
| 0700            | 0.32-0.50          | 0.41                    | 12                            | 25.5          | 80        |
| 1000            | 0.12-0.35          | 0.25                    | 14                            | 28.0          | 75        |
| 1300            | 0.10-0.20          | 0.15                    | 17                            | 29.6          | 69        |
| 1600            | Traces             |                         |                               |               |           |

On the second day, the volume was small (0.15-0.41  $\mu$ l) and the concentrations were 12-17%.

Proteins and amino acids were present; the score on histidine scale was 6. The sugars present were sucrose, glucose and fructose, sucrose being dominant.

#### 6. Flower-visitor activity dynamics:

Altogether 17 species of insects foraged at the

flowers (Table 4). Of these, three were bees and 14 Lepidoptera. The latter consisted of 13 butterfly species and one hawkmoth. Census at the initial, peak and final phases of the blooming season revealed that *Amegilla* among the bees, *Papilio polytes*, *Atrophaneura hector*, *Valeria valeria anais* and *Barbo cinnara* among the butterflies were consistent and made repeated visits at the two study sites, and in the two consecutive years of study. *Papilio polymnestor* was more frequent at Botany Garden site and sporadic at the V.P. Hall site. *Pelopidas mathias*, *Graphium agamemnon* were conspicuous at the V.P. Hall site in 1986. *Pseudapis oxybeloides* made repeated visits in 1987. *Ceratina* appeared in 1987 at V.P. Hall site only (Fig. 2).

The bees exclusively collect pollen from these flowers. *Amegilla* collected pollen by touching the dehiscent anthers several times. It never alighted on the anther. It touched the dehiscent anther, then hovered and groomed pollen from the body, and then repeated the action. Other bees alighted on the anther and collected pollen.

The butterflies probed for nectar without any bias to the functional sex phase of the flower. The Papilionids approached the horizontally oriented flowers frontally, supported by their legs on the petals/staminal filaments/style, and took nectar while constantly fluttering their wings. The wings and body touch the essential flower parts. The

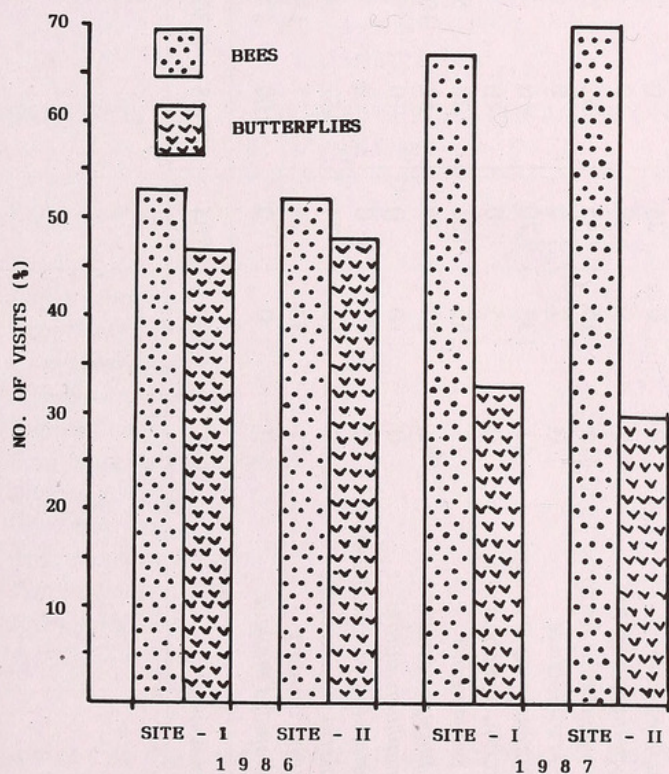


Fig. 2. Insect group abundance on *C. infortunatum* flowers at two study sites.

TABLE 4  
CENSUS OF FLOWER VISITORS ON *C. infortunatum*

| Insect species                   | BOTANY GARDEN SITE I |       |       |       |       |       | V. P. HALL SITE II |       |      |       |       |       |
|----------------------------------|----------------------|-------|-------|-------|-------|-------|--------------------|-------|------|-------|-------|-------|
|                                  | 1986                 |       |       | 1987  |       |       | 1986               |       |      | 1987  |       |       |
|                                  | 13/2                 | 27/2  | 14/3  | 15/3  | 24/3  | 5/4   | 15/2               | 23/2  | 16/3 | 3/3   | 13/3  | 28/3  |
| BEEES                            |                      |       |       |       |       |       |                    |       |      |       |       |       |
| <i>Amegilla</i> sp.              | 745                  | 603   | 635   | 742   | 1,134 | 680   | 547                | 542   | 514  | 508   | 494   | 353   |
| <i>Ceratina</i> sp.              | 0                    | 0     | 0     | 0     | 0     | 0     | 0                  | 0     | 0    | 86    | 71    | 72    |
| <i>Pseudapis oxybeloides</i>     | 0                    | 163   | 0     | 52    | 305   | 222   | 0                  | 0     | 0    | 452   | 550   | 419   |
| MOTH                             |                      |       |       |       |       |       |                    |       |      |       |       |       |
| <i>Macroglossum gyrans</i>       | 0                    | 0     | 0     | 0     | 171   | 0     | 0                  | 123   | 0    | 0     | 0     | 0     |
| BUTTERFLIES                      |                      |       |       |       |       |       |                    |       |      |       |       |       |
| <i>Euploea core</i>              | 0                    | 0     | 24    | 0     | 0     | 0     | 26                 | 26    | 0    | 0     | 0     | 13    |
| <i>Hypolimnas bolina</i>         | 0                    | 0     | 0     | 0     | 0     | 0     | 0                  | 13    | 0    | 0     | 0     | 0     |
| <i>Atrophaneura hector</i>       | 15                   | 15    | 45    | 52    | 17    | 19    | 27                 | 130   | 41   | 79    | 107   | 78    |
| <i>A. aristolochiae</i>          | 0                    | 7     | 0     | 0     | 0     | 0     | 0                  | 27    | 0    | 0     | 0     | 0     |
| <i>Graphium agamemnon</i>        | 42                   | 135   | 70    | 0     | 0     | 0     | 0                  | 141   | 82   | 0     | 0     | 0     |
| <i>Papilio demoleus</i>          | 0                    | 5     | 0     | 0     | 0     | 0     | 0                  | 6     | 0    | 0     | 0     | 0     |
| <i>P. polynnector</i>            | 72                   | 255   | 121   | 28    | 57    | 25    | 0                  | 80    | 0    | 0     | 0     | 0     |
| <i>P. polytes romulus</i>        | 42                   | 74    | 39    | 52    | 102   | 35    | 56                 | 108   | 73   | 54    | 45    | 46    |
| <i>Anaphaeis aurota</i>          | 0                    | 0     | 0     | 0     | 0     | 0     | 0                  | 7     | 0    | 0     | 0     | 0     |
| <i>Catopsilia crocale pomona</i> | 0                    | 0     | 0     | 0     | 0     | 0     | 0                  | 14    | 0    | 0     | 0     | 0     |
| <i>Valeria valeria anais</i>     | 39                   | 19    | 71    | 152   | 63    | 64    | 54                 | 65    | 80   | 87    | 78    | 98    |
| <i>Borbo cinnara</i>             | 31                   | 33    | 99    | 127   | 183   | 0     | 54                 | 21    | 93   | 71    | 64    | 75    |
| <i>Pelopidas mathias</i>         | 0                    | 0     | 0     | 100   | 272   | 0     | 0                  | 0     | 0    | 133   | 113   | 119   |
| Total visits                     | 986                  | 1,309 | 1,104 | 1,305 | 2,304 | 1,045 | 764                | 1,303 | 883  | 1,470 | 1,522 | 1,273 |

number of flowers visited per minute and the length of a visit by the Papilionids set out in Table 5 show that *P. polymnestor* spent less time at a flower and

They always kept their wings folded and static while sucking the nectar and seldom contacted the anthers/stigma. The hawkmoth characteristically hovered

TABLE 5

NUMBER OF FLOWERS VISITED FOR UNIT TIME AND LENGTH OF A VISIT BY PAPILIONIDS ON *C. infortunatum*

| Papilionid species         | No. of flowers visited/minute |       |           |        | Length of a visit in seconds |         |           |       |
|----------------------------|-------------------------------|-------|-----------|--------|------------------------------|---------|-----------|-------|
|                            | n                             | R     | $\bar{x}$ | S.D.   | n                            | R       | $\bar{x}$ | S.D.  |
| <i>Atrophaneura hector</i> | 10                            | 17-20 | 18.4      | ± 1.2  | 10                           | 3.0-3.5 | 3.1       | ± 0.5 |
| <i>Graphium agamemnon</i>  | 10                            | 30-60 | 48.2      | ± 10.8 | 10                           | 1.0-2.0 | 1.4       | ± 0.5 |
| <i>Papilio demoleus</i>    | 10                            | 30-60 | 46.0      | ± 9.8  | 10                           | 1.0-2.0 | 1.7       | ± 0.3 |
| <i>P. polymnestor</i>      | 10                            | 45-60 | 50.0      | ± 12.5 | 10                           | 1.0-1.5 | 1.1       | ± 0.3 |
| <i>P. polytes romulus</i>  | 10                            | 18-25 | 20.0      | ± 3.2  | 10                           | 2.5-4.0 | 3.8       | ± 1.1 |

as a result covered more flowers in an unit time. Thus it proved to be more active. As its proboscis length (38 mm) exceeded the corolla tube length (av. 25 mm), it got at the nectar with ease. Species with proboscis shorter than the corolla length had to push their heads into the tube and took more time in foraging (Table 6).

Butterflies other than Papilionids used to land

TABLE 6

PROBOSCIS LENGTH OF BUTTERFLIES FORAGING ON *C. infortunatum*

| Butterfly species            | N | Mean Proboscis length (mm) |
|------------------------------|---|----------------------------|
| <i>Barbo cinnara</i>         | 5 | 08                         |
| <i>Anaphaeis aurota</i>      | 5 | 10                         |
| <i>Catopsilia pyranthe</i>   | 5 | 14                         |
| <i>Hypolimnas bolina</i>     | 4 | 14                         |
| <i>Euploea core</i>          | 5 | 15                         |
| <i>Graphium agamemnon</i>    | 5 | 15                         |
| <i>Papilio demoleus</i>      | 5 | 16                         |
| <i>Valeria valeria anais</i> | 5 | 17                         |
| <i>Atrophaneura hector</i>   | 5 | 18                         |
| <i>Papilio polymnestor</i>   | 3 | 38                         |
| <i>P. aristolochiae</i>      | 4 | 17                         |
| <i>P. polytes romulus</i>    | 5 | 18                         |

on the corolla lobes, insert their proboscids either from above or below the essential floral parts and take nectar pushing their heads into the corolla tube.

a little above the essential flower parts in front of the flower, and thus made no contact with the anthers/stigma.

All the flower-visitors recorded are diurnal. *Amegilla* appeared between 0730-1800 hr, but was more frequent between 0800 and 1200 hr. Hawkmoth foraged at around dawn and dusk. The butterflies displayed no regularity in the time of their visits, but were relatively more common in the forenoon.

Although flowers secreted nectar throughout the day and night, no noctuid was observed at the flowers at the biotope studied.

**7. Stigmatic pollen loads:** On the day of the female phase, stigmas were collected at the Botany Garden and the pollen grains on them were counted. The mean pollen load for 60 stigma was 6. Most stigma with pollen also contained butterfly scales.

**8. S/P Ratio:** The area of stigma relative to the area of wing over which the pollen of *C. infortunatum* got smeared, was calculated for five of the Papilionids. The ratio for *P. demoleus* and *G. agamemnon* was 0.089, that for *P. Polytes* 0.084, for *A. hector* 0.076 and for *P. polymnestor* 0.062 (Table 7).

**9. Breeding systems:** The flowers are compatible only to geitono- and xeno-pollen. Fruit set, seed set and fecundity realised on hand-

TABLE 7

S/P RATIO OF THE PAPILIONIDS ON *C. infortunatum*

| Papilionid species             | N | S/P ratio |
|--------------------------------|---|-----------|
| <i>Papilio demoleus</i>        | 5 | 0.0889    |
| <i>Graphium agamemnon</i>      | 5 | 0.0882    |
| <i>Papilio polytes romulus</i> | 5 | 0.0842    |
| <i>Atrophaneura hector</i>     | 5 | 0.0762    |
| <i>Papilio polymnestor</i>     | 5 | 0.0615    |

pollinaion with the former pollen type was 73%, 66% and 46% respectively; those with the latter type was 52%, 53% and 28% respectively.

10. **Natural fruit set:** Fruit set, seed set and fecundity observed on natural pollination was 21%, 55% and 26% respectively.

#### DISCUSSION

Floral morphology and behaviour, and the flower-visitors guild composition and their behaviour undoubtedly showed that the flowers of *C. infortunatum* are tailored for manipulation and pollination exclusively by butterflies. Further, such characteristics of nectar as small quantities in the forenoon hours when the butterflies were active, low sugar concentration, sucrose dominance and richness in amino acids conform to the characters of typical butterfly flowers (Baker 1973, 1975, 1978).

Of the different butterfly visits recorded on *C. infortunatum*, those of *Papilio polytes*, *Atrophaneura hector* and *Papilio polymnestor* were consistent and substantial. The presence of butterfly scales and the presence of pollen of *C. infortunatum* on the underside of butterfly wing was also demonstrated, and this substantiated the role of butterflies in the pterigotribic pollination of *C. infortunatum*. The manner in which pollination efficiency is achieved is similar to that described for *Caesalpinia pulcherrima* by Cruden and Hermann-Parker (1979).

Both selfing through geitonogamy and out-crossing appear to play a role in the reproduction of *C. infortunatum* as revealed by hand-pollination experiments, but to a varying degree. The flowers

are strongly protandrous, male and female phases of the flowers are separated in time and space, probably to avoid deposition of auto-pollen on the stigma, or to avoid damage to the immature stigma by the visitor's wing in the male phase.

The pollinators were seen repeatedly visiting all the opened flowers in an inflorescence, and also making inter-inflorescence and inter-plant movements. It is thus likely that pollinator foraging may result in both geitonogamy and xenogamy. But the small number of flowers opening each day should help to maximise xenogamy (see Cruden 1976). However, controlled experiments revealed that in terms of fruit set, seed set and fecundity the success of geitonogamous mode of reproduction is significantly better than that of xenogamous mode. Apparently this taxon has primarily adapted for selfing through geitonogamy, but with a greater provision for xenogamy, and the attendant genetic variability.

Observations of daily foraging revealed that the pollinator species did not forage continuously. In a single bout they visited several flowers in a population of *C. infortunatum* and flew away, sometimes to nearby *Anacardium occidentale*, *Antigonon leptopus* to forage on their flowers. Such behaviour is expected on the basis of energy considerations of butterflies (Heinrich and Raven 1972, Heinrich 1975), and has been reported by Cruden and Hermann-Parker (1979), Schmitt (1980), Subba Reddi *et al.* (1981, 1983), Reddi & Subba Reddi (1983) and Meera Bai (1987). The behaviour of pollinators greatly influences the breeding structure of populations and population structure, and thus influences the amount and organisation of genetic variability within the plants (Levin 1978). The drifting behaviour of butterflies then assumes much significance and contributes to inter-population movement of pollen. Such pollen transfers are necessary to have genetic variability because *C. infortunatum* has clonal populations.

Based on their work with wood-white butterfly *Leptidea sinapis* and its nectar plants, Wiklund *et al.* (1979) hypothetically stated that butterfly feeding

on nectar plants is only a parasitic relationship. Here is an instance of mutualism where *C. infortunatum* may be considered to have co-evolved with butterflies and whose sexual reproduction is totally dependent on the activity of Papilionids. The study suggested that the relationship, whether parasitic or mutualistic, depends on the flower size and architecture, and on the butterfly size and its behaviour. Thus all the butterfly visitors to *C. infortunatum* have not proved to be pollinators. *Valeria valeria anais* and *Barbo cinnara* failed to contact the essential flower parts because of their small size and behaviour.

Pollen-collecting by the bee component of the flower-visitor guild, particularly by the voracious *Amegilla* sp. is highly detrimental to the reproduction of *C. infortunatum* as it causes a shortage in the availability of pollen for the pterigotribic pollination by the Papilionid butterflies.

#### ACKNOWLEDGEMENTS

We thank R.E. Schultes, Botanical Museum of Harvard university, Cambridge, Massachusettes for his critical comments, and also Dr. E.U.B. Reddi for his constant encouragement and suggestions.

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