*Botanical Journal of the Linnean Society* (1992), *109:* 39–55. With 3 figures

# Floral biology and pollinators of three co-occurring *Cistus* species (Cistaceae)

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*Received June 1990, accepted for publication January 1991*

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BOSCH, J., 1992. **Floral biology and pollinators of three co-occurring *Cistus* species (Cistaceae).** The pollination of three species of *Cistus*, *Cistus albidus* L., *Cistus salvifolius* L. and *Cistus monspeliensis* L. is studied. Insect visitors were censused and some were captured to analyse pollen distribution on their bodies. Floral phenology, breeding systems, some aspects of floral biology (pollen and nectar production, pollen-ovule ratios) and floral morphology were also studied for each species. Flowers of *C. albidus* produce more pollen and nectar than the other two species studied, and attract more insects, especially those with higher nutritional requirements. All three species are highly self-incompatible, but *C. salvifolius* and *C. monspeliensis* show some features that hinder xenogamy, and they have lower pollen-ovule ratios than *C. albidus*. As a result, this latter species apparently receives higher levels of cross-pollination, but at the cost of a higher investment to attract and reward reliable pollinators.

ADDITIONAL KEY WORDS:—Breeding systems – flowering phenology – floral resources – attraction to pollinators.

CONTENTS

0024–4074/92/050039+17 $03.00/0

## INTRODUCTION

Not all the entomophilous plants that flower in the same place and at the same time attract the same insects. Every plant species shows different morphological, physiological and phenological traits that result in different attractiveness towards certain groups of insects.

Caloric rewards offered by flowers to visitors in the form of nectar is a most important parameter; that is, animals with high energy requirements will not forage on flowers with low nectar rewards (Heinrich & Raven, 1972; Heinrich, 1975). Pollen, rich in proteins and amino acids (Kevan & Baker, 1983), is another floral resource exploited by flower visitors, but its nutritional value to foraging insects has proven more difficult to measure. Heinrich (1975) alleges that pollen as a protein source is more important to solitary bees than to social bees, because their energy requirements are lower. In an attempt to demonstrate this, Tepedino & Parker (1982) found that male-fertile cultivars of sunflower, *Helianthus annuus* L., attracted more solitary bees and fewer honey-bees and bumble-bees than male-sterile, nectar-rich cultivars.

In principle, floral attractiveness should bear a relationship with the breeding system of the plant. Thus, plants which cannot set fruit without the mediation of insects should invest more energy in floral rewards and eventually receive more visitors than selfers (e.g. Ehrendfeld, 1979, in a comparison of three *Euphorbia* species).

In the same way, self-incompatible plants should attract highly mobile insects that would better ensure high levels of cross-pollination, a precaution that is not always necessary in species that do not require crossed pollen to set fruit (Heinrich & Raven, 1972).

Species of *Cistus* are highly thermophilous perennial shrubs of variable size (50–150 cm high) common in Mediterranean maquis and scrubland ecosystems (Troumbis & Trabaud, 1986). In Spain, they appear in different plant communities resulting from degradation of live-oak forests (Bonet, Rita & Sebastia, 1985) and they may form almost monospecific populations, especially in the South (Martin & Guinea, 1949).

Despite their abundance, little is known about the pollination ecology of *Cistus* species. Herrera (1985a) studied the floral and fruiting biology of *Cistus salvifolius* L. and *Cistus libanotis* L. in Southern Spain, and *Cistus crispus* L., *Cistus ladanifer* L., and *Cistus salvifolius* L. have been studied by Brandt & Gottsberger (1988) in Portugal.

Pollination studies of three *Cistus* species (*Cistus albidus* L., *Cistus salvifolius* L., and *Cistus monspeliensis* L.), which all occurred in a rosemary scrubland (*Rosmarino-Ericion*) were began in 1985. The flowering periods of these *Cistus* species, overlapped considerably, and this afforded an opportunity to compare the spectra of flower visitors to these co-generic species and to relate these results to their floral biologies.

The aim of these studies was to determine whether three similar species, flowering at the same time and in the same place, differed in their attractiveness to pollinator species. The breeding systems and certain parameters of floral biology (nectar and pollen production, flowering phenology, pollen-ovule ratios, etc.) were also studied in an attempt to decipher how these plants attract pollinators and, in turn, how these pollinators influence the reproductive success of these plants.

## MATERIAL AND METHODS

Field work was initiated in April and ended in mid June, 1985. The study site was located on the grounds of the Public Foundation of Roques Blanques in El Papiol (Barcelona), where the three species grow abundantly.

### *Breeding systems*

To determine if the plants were self-compatible or not, a number of flower buds of each species were bagged in fine-mesh nylon bags to avoid insect visits. When flowers opened, they were hand-pollinated either with pollen from the same flower, or with pollen from another individual. Some flowers were left untreated. Hand pollination was performed by plucking some stamens out with a pair of forceps and by thoroughly rubbing the anthers on the stigma of the flower. Cross-pollinated flowers were partially emasculated to avoid accidental transfer of self pollen.

Additional hand pollinations of *C. salvifolius* were carried out at Taradell, 70 km north of El Papiol.

### *Flowering phenology*

Every 7 days, the number of open flowers was counted on 14 marked plants of each species, chosen at random, to determine floral phenology.

### *Floral biology*

The pistils of nine flowers of each of the three species were dissected under a stereo-microscope and the number of ovules were counted. The number of stamens was also determined on these same flowers. In addition, four buds of each species were collected just prior to anthesis and were preserved in alcohol. An anther from each bud was placed between two glass slides which were gently pressed together until pollen grains were released. The two slides were then observed at × 60 and the number of pollen grains from each anther was counted. The average number of pollen grains per anther of each species was multiplied by the mean number of stamens per flower, as an estimation of the number of pollen grains per flower. From these data, pollen–ovule ratios (P/O) were calculated for the three species.

Pollen grain diameters were measured with an ocular micrometer at × 450. Their volumes were estimated assuming that all pollen grains were perfectly spherical.

*Cistus* flowers produce nectar in a ring-shaped nectary located at the base of the stamens (Herrera, 1985a; Bonet *et al.*, 1985), but in such small quantities that it could not be recovered when micropipettes were used. Herrera (1985b), however, found a positive correlation between dry weight of a flower (FW) and its daily sugar secretion rate (SR): $\log SR = 0.867 \log FW - 1.026$ ($r = 0.825$) in 42 species of southern Spain, and this method was used as an indirect measurement of nectar production in this study. Some flowers of each species were collected the day before opening (when petals first became visible among sepals), air-dried for several weeks, and weighed on a precision balance.

### *Floral morphology*

The morphology of the flowers of *C. albidus*, *C. salvifolius* and *C. monspeliensis* is very similar, and only the size (diameter) of 15 flowers of each species was measured. The position of the anthers relative to the stigma and the colour patterns of the petals was also noted.

### *Insect visitors*

On different days of the blooming period, a given number of plants of each species were randomly chosen, and the number of open flowers was counted on each plant every hour. These plants were also observed hourly and insects on flowers were counted. Bees were visually identified to the level of genus, and all other insects were identified to the family level. A few specimens of the most commonly occurring insects were collected as voucher material. Insect visitors were grouped into nine 'functional categories' (see Fig. 3) on the presumption that all insects within each category should have similar pollinating abilities. An index was devised to assess the attractiveness of a given plant species for each group of insect visitors: $Aa = Na/Nf.Nc$; where $Na$ is the number of insects of group $a$ censused on a given plant species; $Nf$ is the number of sampled open flowers of that species; and $Nc$ is the number of censuses made.

To examine the presence of pollen on their bodies, some insects were captured and observed under a stereo-microscope. The integument of the insects was divided into 22 regions (see Appendix). For each of these regions, the number of pollen grains found was scored according to the following semi-quantitative scale: 0 = 0–10 pollen grains; 1 = 11–40; 2 = more than 40; 3 = large amounts of pollen grains accumulated on specialized pollen-carrying organs (scopa and corbicula). All scores for each integument region were summed and the result was divided by the number of insects examined. This methodology produced an index ranging from 0–3 which indicated the richness of pollen on each region of the body.

This, together with close observation on the foraging movements of the different insects on the flowers, could offer a comparative method to measure pollination effectivity.

## RESULTS

### *Floral morphology*

The flowers of *Cistus* species are pleiomorphic and have five petals, which are pink to purple in *C. albidus*, and white in *C. salvifolius* and *C. monspeliensis*. In all three species, the petals have a yellow stain at their base. The pistil has five carpels and is surrounded by numerous stamens that produce abundant pollen, and by a basal ring-shaped nectary.

Flowers of *C. albidus* are slightly larger than those of *C. salvifolius* but they are much greater in size than those of *C. monspeliensis*. Fifteen flowers of each species measured demonstrated these differences in diameter length: 4.9 cm (s.d. = 0.33), 4.05 cm (s.d. = 0.49), and 2.2 cm (s.d. = 0.13), respectively.

The style of *C. albidus* flowers is about 4 mm long, so the stigma stands slightly above the anthers. The reverse is true for *C. salvifolius* and *C. monspeliensis* flowers,

TABLE 1. Reproductive characteristics of *Cistus albidus*, *Cistus salvifolius* and *Cistus monspeliensis* flowers. Numbers indicate means ± standard deviations. Figures in parentheses indicate sample size

| | Ovules/ flower (9) | Stamens/ flower (9) | Pollen grains/ anther | Pollen grains/ flower | Pollen grain volume ($\mu dm^3$) (25) | Pollen volume/ flower ($mm^3$) | P/O ratios |
|---|---|---|---|---|---|---|---|
| *C. albidus* | 94.78 ± 14.3 | 176.67 ± 16.18 | (4) 1859.5 ± 145.95 | 328517.86 | 26.90 ± 4.7 | 8.84 | 3466.11 |
| *C. salvifolius* | 76.89 ± 9.42 | 151.33 ± 18.6 | (5) 1051 ± 136.74 | 159047.83 | 36.35 ± 4.0 | 5.78 | 2068.51 |
| *C. monspeliensis* | 20.67 ± 1.83 | 50.67 ± 2.11 | (4) 848 ± 43.15 | 42968.16 | 30.90 ± 3.3 | 1.33 | 2078.77 |

in which the style is very short (0–0.3 mm) and the stigma is positioned below the anthers. However, the stamens of these latter two species are sensitive, and move away from the stigma after being touched at their base by insect visitors (Brandt & Gottsberger, 1988).

### *Floral biology*

At the study site, *C. albidus*, *C. salvifolius* and *C. monspeliensis* flowers last only a few hours. They open in the morning, and in the afternoon they lose their petals, and the sepals move back to their original position enclosing the pistil and stamens.

The data presented in Table 1 show the average number of ovules and stamens per flower, pollen grains per anther, and pollen grains per flower for each of the three species. The highest to lowest order is *C. albidus*, *C. salvifolius* and *C. monspeliensis* for each of these four parameters measured. Thus, *C. albidus* produces roughly twice as many pollen grains per flower as *C. salvifolius*, and eight times as many pollen grains as *C. monspeliensis*.

However, pollen grain volume is higher in *C. salvifolius* and *C. monspeliensis* than in *C. albidus* (Table 1). Nevertheless, results obtained by multiplying average pollen grain volume by the number of pollen grains per flower of each species, show that flowers of *C. albidus* produce more pollen volume than those of *C. salvifolius* and *C. monspeliensis* (Table 1).

The results of calculating P/O ratios are also expressed in Table 1, and they are within the ranges of P/Os found in xenogamous plants (Cruden, 1977). The P/O ratio obtained for *C. salvifolius* (Table 1) coincides closely with results reported by Herrera (1985a) who gives values of between 1158 and 2562 for individual flowers.

The mean dry weight of flowers of the three species were found to be: *C. albidus* 76.04 mg ($N = 7$, S.D. = 4.99), *C. salvifolius* 55.41 mg ($N = 8$, S.D. = 8.01), *C. monspeliensis* 15.38 mg ($N = 8$, S.D. = 2.30). According to Herrera (1985b), *C. albidus* is expected to produce the largest quantity of nectar and *C. monspeliensis* the least.

### *Breeding systems*

Results obtained from hand-pollination studies are shown in Table 2. The three *Cistus* species show a considerable degree of self-incompatibility (most self-pollinated and untreated flowers did not set fruit, whereas most cross-pollinated blossoms produced fruit and abundant seeds). Numbers of seeds per flower were significantly higher in cross-pollinated flowers than in untreated or self-pollinated samples (*C. albidus* and *C. monspeliensis*, ANOVA $P < 0.01$; *C. salvifolius*, Student *t*-test $P < 0.001$). However, some untreated *C. albidus* flowers (21.6%) and some self-pollinated *C. salvifolius* flowers (23.3%) set fruits with numerous seeds. These results suggest that under certain unknown circumstances the incompatibility system may be broken.

### *Flowering phenology*

Data presented in Fig. 1 were derived by summing the number of open flowers of 14 individuals of each species on every sampling day. *Cistus albidus* initiates

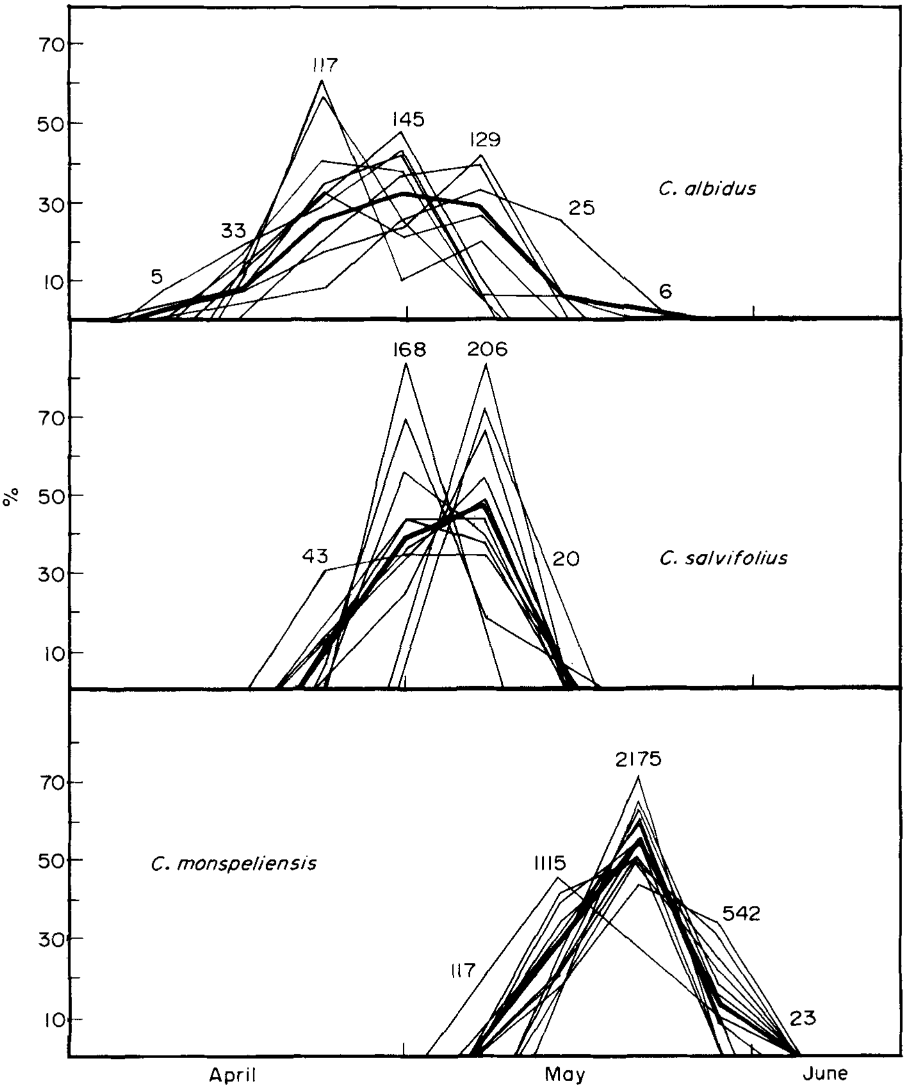

Figure 1. Floral phenology of *Cistus albidus*, *Cistus salvifolius*, and *Cistus monspeliensis* at Roques Blanques. Thick lines: percentage of open flowers (y-axis) on every sampling day (x-axis) with regard to the total number of censused open flowers for 14 individual plants of each species. Numbers indicate total number of open flowers on every sampling day. Thin lines: Percentage of open flowers of 10, 11, and 14 individuals of *C. albidus*, *C. salvifolius*, and *C. monspeliensis*, respectively (plants on which less than ten flowers were counted have been omitted) on every sampling day, with regard to the total number of open flowers censused on each individual plant.

flowering earlier and its flowering is extended over a longer period. The shape of the *C. albidus* mean curve is platikurtic ($g2 = -0.127$), which indicates that the number of open flowers in the population is more or less constant over an extended period. *Cistus salvifolius* and *C. monspeliensis* initiate flowering later in the season, and their blooming periods are shorter (Fig. 1). A high percentage of these flowers open during peak flowering and, as a result, the mean curves for both species are leptokurtic ($g2 = 2.246$ and $g2 = 0.851$ respectively).

Table 2. Fruit and seed-set in manipulated *Cistus albidus*, *Cistus salvifolius* and *Cistus monspeliensis* flowers

| | *N* | Fruits | Seeds/flower | Seeds/fruit |
|---|---|---|---|---|
| *C. albidus* | | | | |
| Untreated | 98 | 19 | 8.31±23.85 | 42.84±38.13 |
| Self-pollinated | 21 | 0 | 0 | 0 |
| Cross-pollinated | 20 | 17 | 40.55±32.79 | 47.70±30.39 |
| *C. salvifolius* | | | | |
| Untreated | 85 | 3 | 0.20± 1.05 | 5.67± 0.47 |
| Self-pollinated | 19 | 2 | 2.95± 8.74 | 28.00± 5 |
| *Self-pollinated | 24 | 8 | 7.71±11.5 | 23.13± 6.35 |
| *Cross-pollinated | 24 | 22 | 32.04±22.31 | 34.95±21.01 |
| *C. monspeliensis* | | | | |
| Untreated | 190 | 25 | 0.37± 1.4 | 2.8 ± 2.86 |
| Self-pollinated | 48 | 10 | 0.23± 0.55 | 1.37± 0.48 |
| Cross-pollinated | 15 | 15 | 13.27± 4.1 | 13.27± 4.1 |

*Taradell, 70 km. N Roques Blanques.

Examination of individual flowering curves of individual plants (Fig. 1) provides additional information on different flowering patterns expressed by the three species. The shape of individual curve lines for *C. albidus* are flatter; thus, every plant opens a few flowers every day. Conversely the individual curve lines for *C. salvifolius* and *C. monspeliensis* show that many more flowers open over a few days. These same data sets also show that individual plants of *C. monspeliensis* produce many more flowers per flowering period than those of *C. salvifolius* and *C. albidus* (Fig. 1).

Another difference between flowering strategies of the three species is the simultaneous blooming of most individuals in *C. monspeliensis*, whereas flowering peaks are distributed more randomly in *C. albidus*, with *C. salvifolius* expressing an intermediate pattern. The standard deviation values for peak flowering dates on the three groups of curves (*C. albidus*: 5.715, *C. salvifolius*: 4.433, *C. monspeliensis*: 1.870) indicate that the degree of overlap is lowest in *C. albidus* and highest in *C. monspeliensis*.

### *Insect visitors*

Those insects found visiting flowers of *C. albidus*, *C. salvifolius* and *C. monspeliensis* in Roques Blanques, are listed in Table 3.

The coleopterans represent the highest number of insect visitors to flowers of these three plant species. However, the families visiting these plants vary between the three species. In *C. albidus*, for example, Dastyidae (*Psilothrix* sp., *Dasytes* sp.), Oedemeridae (*Oedemera flavipes* (F.)), and Scarabaeidae (*Tropinota squalida* (Scop.) and *Oxythirea funesta* (Poda)) were the most abundant taxa found. In *C. salvifolius*, Dasytidae, Scarabeidae, Bruchidae (*Bruchus* sp., *Spermophagus* sp.), and Malachidae *Malachius* sp.) are the most abundant families. In *C. monspeliensis*, Bruchidae are, by far, the most important group, followed by Oedemeridae.

Bees, especially *Lasioglossum planulum* (Pér.), *Lasioglossum albomaculatum* (Luc.), *Lasioglossum bimaculatum* (Dours) and *Apis mellifera* (L.), are the second most

TABLE 3. Insect visitors censused on *Cistus albidus*, *Cistus salvifolius*, and *Cistus monspeliensis* flowers in Roques Blanques. In parentheses: % of each taxon

| | *C. albidus* | *C. salvifolius* | *C. monspeliensis* |
|---|---|---|---|
| Diptera | 25 (2.52) | 36 (10.94) | 30 (7.25) |
| Syrphidae | 15 | 10 | 5 |
| Bombyliidae | 2 | 1 | — |
| Empididae | 1 | — | — |
| Unidentified | 7 | 25 | 25 |
| Apoidea | 186 (18.66) | 39 (11.85) | 16 (3.86) |
| *Lasioglossum* | 86 | 14 | 10 |
| *Apis* | 51 | 1 | 2 |
| *Andrena* | 22 | 19 | 1 |
| *Hylaeus* | 14 | — | 1 |
| *Anthidium* | 5 | — | — |
| *Osmia* | 3 | 1 | — |
| *Halictus* | 2 | 2 | 1 |
| *Colletes* | 2 | — | — |
| *Ceratina* | 1 | — | — |
| *Nomada* | — | 2 | 1 |
| Other Hymenoptera | 72 (7.22) | 115 (34.95) | 17 (4.11) |
| Chalcidoidea | 60 | 18 | 5 |
| Ichneumonidae | 5 | 10 | 4 |
| Scoliidae | 5 | — | — |
| Formicidae | 2 | 87 | 4 |
| Chrysididae | — | — | 2 |
| Sphecidae | — | — | 1 |
| Eumenidae | — | — | 1 |
| Lepidoptera | 35 (3.51) | 5 (1.52) | 3 (0.72) |
| Satyridae | 23 | 1 | 2 |
| Zygaenidae | 5 | — | — |
| Lycaenidae | 4 | — | 1 |
| Papilionidae | 1 | — | — |
| Nymphalidae | 1 | 1 | — |
| Pyralidae | 1 | 3 | — |
| Coleoptera | 678 (68.0) | 132 (40.12) | 344 (83.09) |
| Dasytidae | 239 | 44 | 16 |
| Oedemeridae | 178 | 8 | 65 |
| Scarabaeidae | 170 | 23 | 3 |
| Bruchidae | 44 | 20 | 216 |
| Cerambycidae | 22 | 3 | 7 |
| Malachidae | 13 | 24 | 20 |
| Mordellidae | 4 | — | 14 |
| Cleridae | 3 | — | 1 |
| Chrysomelidae | 2 | — | — |
| Alleculidae | 2 | — | — |
| Buprestidae | 1 | 8 | 1 |
| Curculionidae | — | 2 | — |
| Meloidae | — | — | 1 |
| Other insects | 1 (0.1) | 2 (0.6) | 4 (0.97) |
| Orthoptera | 1 | 2 | 4 |
| Total insects | 997 | 329 | 414 |

numerous group in *C. albidus* but are much less represented on flowers of *C. salvifolius* and *C. monspeliensis*.

Other hymenopterans were rarely observed on flowers of *Cistus* in the study area, except for the numbers of ants on *C. salvifolius*. This somewhat unexpected result is attributed to a nest of *Plagiolepis pygmaea* Latr. located adjacent to one of the sampled plants.

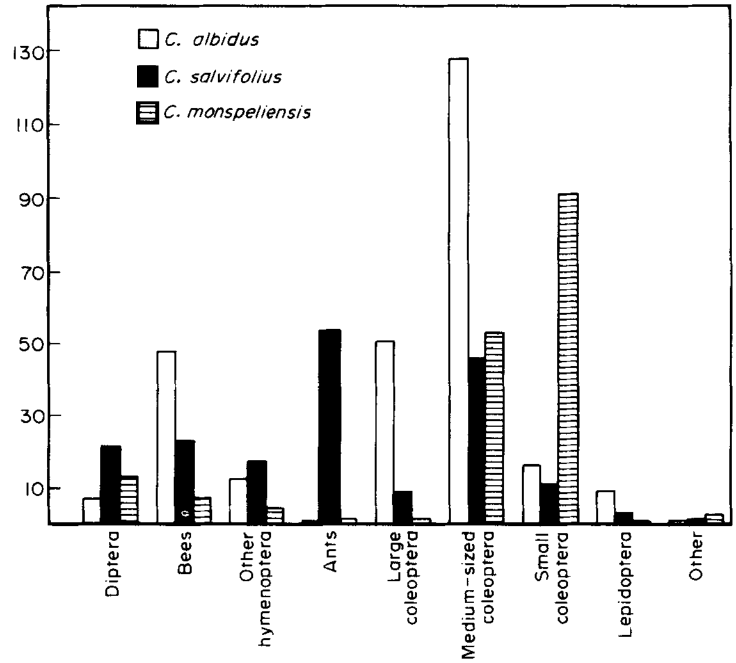

Figure 2. Partitioning of insects belonging to nine functional groups between *Cistus albidus*, *Cistus salvifolius*, and *Cistus monspeliensis*. The length of bars indicates the number of insects of each group × 1000, divided by the number of flowers sampled and the number of censuses made.

Dipterans were far less abundant than bees, but the highest percentage of flies was found on *C. salvifolius*.

Lepidopterans and Orthopterans were very scarce and accounted for less than 4% of insect visitors to any one species.

*Cistus albidus* attracts considerably more visitors per flower than the two other species. Indeed, considering all insects together, the index of attractiveness equals 0.27 for *C. albidus*, 0.18 for *C. salvifolius*, and 0.17 for *C. monspeliensis*. The result of applying the same index to each "functional group" of visitors is shown in Fig. 2. These results indicate which groups of insects were preferentially attracted to each *Cistus* species in Roques Blanques. The number of dipterans attracted per flower is significantly higher in *C. salvifolius* than in *C. albidus* and *C. monspeliensis* (Chi-square, $P < 0.05$), and the same is true for ants ($P < 0.001$). On the other hand, bees and large (mainly Scarabaeidae) and medium-sized (Oedemeridae, Dasytidae, Malachidae, etc.) coleopterans were most attracted to *C. albidus* ($P < 0.001$); and small coleopterans (mainly bruchids) were preferentially attracted to flowers of *C. monspeliensis* ($P < 0.001$).

It is important to note that the most abundant groups (coleopterans and ants) have poor mobility as a common trait. These insects remain for long periods of time on the same flower, so it is likely that many individuals were counted more than once, as censuses were carried out at intervals of 1 h. Thus, the importance of these particular insects may be overestimated. At any rate, this does not contradict the fact that different insect taxa preferentially visit different species of *Cistus* in the study site.

TABLE 4. Bees censused on *Cistus albidus*, *Cistus salvifolius* and *Cistus monspeliensis* flowers grouped according to size. In parentheses: % of each group

| | *C. albidus* | *C. salvifolius* | *C. monspeliensis* |
|---|---|---|---|
| Bees $>12$ mm | 79 (42.47) | 6 (15.4) | 3 (18.75) |
| Bees $8 \leqslant x \leqslant 12$ mm | 40 (21.51) | 3 ( 7.7) | 3 (18.75) |
| Bees $<8$ mm | 67 (36.02) | 30 (76.9) | 10 (62.5) |

Bees were further subdivided into three categories according to size: (a) bees larger than 12 mm (*A. mellifera*, *Andrena limbata* War., *Andrena hispana* War., *Halictus scabiosae* Rossi, etc.); (b) bees between 12 and 8 mm (*L. albomaculatum*, *L. bimaculatum*, *Andrena humilis* Imh., *Nomada* spp., etc.); and (c) bees smaller than 8 mm (*L. planulum*, *Hylaeus gibbus* Saund., *Andrena* spp., etc.) and then compared for visitation rates on *Cistus* spp. The results are presented in Table 4, and demonstrate that a considerable number (64%) of the bees attracted to *C. albidus* flowers belong to categories (a) and (b), whereas most of the bees that visited *C. salvifolius* and *C. monspeliensis* (77% and 62% respectively) are small-sized.

## *Foraging behaviour of insect visitors*

### *Bees*

In the first hours of the morning, bees that visit flowers of *Cistus* forage for both pollen and nectar, but they abandon pollen collection at midday, as pollen resources are depleted.

Honey-bees, *A. mellifera*, collect nectar and pollen simultaneously. They stand on the stamens and introduce the proboscis among the staminal filaments while they brush the anthers with their legs. In this way, they repeatedly contact the stigmatic surface with the frons, legs and ventral parts of their body. Some *Andrena*, *L. albomaculatum* and other large-sized bees behave in a similar way, but their movements are slower.

Bees of smaller size (*L. planulum* and others) are not able to collect nectar and pollen at the same time, since they have to plunge their whole body among the stamens to reach the nectary. Individuals often stand on the base of a petal as they extend the proboscis through the staminal filaments to reach the nectar. This behaviour strongly reduces any contact of insect's body with anthers or stigmata. Small bees collect pollen by scratching the anthers with their fore legs and mandibles. Contact with the stigma during these pollen collecting activities is not as frequent as in the case of larger bees.

Pollen was found on virtually every part of bees' bodies, but the largest amounts were observed mainly on the legs and ventral region (Fig. 3). As expected from differences in foraging behaviour, large-sized bees had more pollen on their bodies than medium sized-bees, and small-sized bees had the least amount of pollen.

### *Dipterans*

Flies that visit *Cistus* spp. (Calliphoridae, Muscidae, Tachinidae and the hover fly *Eristalis tenax* L.) are more stationary than bees when they alight on flowers. They sometimes simply lick petals, where they find numerous pollen grains, or they lick anthers by walking on them or by holding some of them with

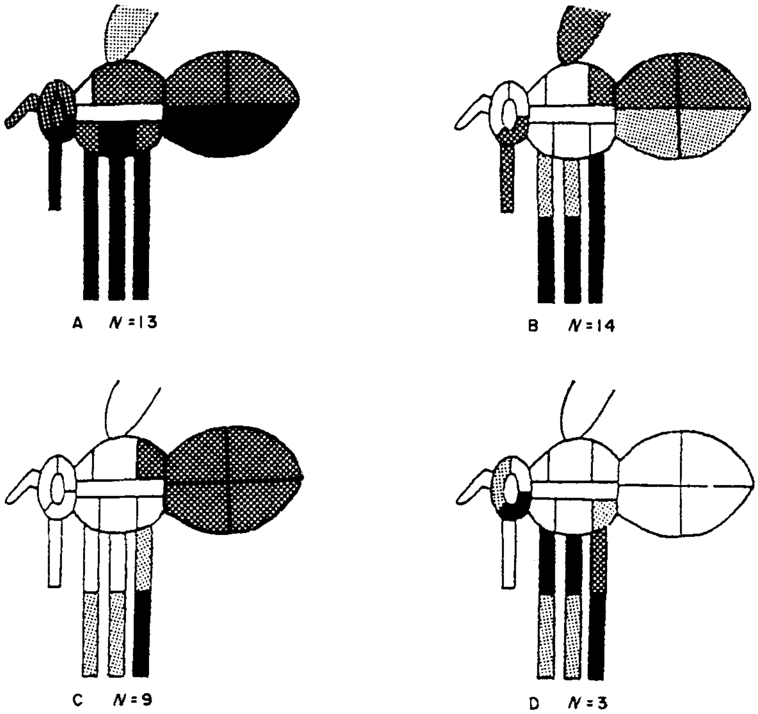

Figure 3. Distribution of *Cistus* pollen on the bodies of insect visitors. A. Large-sized bees. B. Medium-sized bees. C. Small-sized bees. D. *Eristalis tenax*. $N$ = Number of studied specimens. Index of pollen richness: □ $x < 0.5$ no pollen; ▨ $0.5 < x < 1$ pollen scarce; ▩ $1 < x < 1.5$ pollen abundant; ■ $x > 1.5$ pollen very abundant.

their forelegs. On some occasions, they extend their proboscis through the stamens to suck nectar. Contact with the stigma is less aggressive than in the case of bees. Pollen is limited to the legs and the head of these flies (Fig. 3D), and although they may carry considerable numbers of grains, they do not visit as many flowers per unit time as bees.

### *Coleopterans*

Beetles feed on *Cistus* pollen by holding the anthers with their fore legs. Nectar is consumed when they crawl through the stamens or standing on the petals. They are similar to dipterans observed when they contact the stigma by walking over the stamens.

During morning hours when pollen resources are abundant, beetles normally carry considerable quantities of pollen (21 beetle samples seen), but not as much as bees, since their integument is much less hairy. Furthermore, beetles may stay on the same flower for hours, thus effecting little cross-pollination.

## DISCUSSION

### *Insect visitors*

The possibility of a positive correlation between the quantity of nectar produced by a flower and the energetic demands of its pollinators has been suggested by Heinrich & Raven (1972) and Heinrich (1975). Thus, large and mobile insects tend to forage preferentially on flowers or inflorescences that produce large amounts of nectar. The nutritional value of pollen is more difficult to evaluate, but it seems also logical to presume that foragers with higher pollen requirements will visit the most productive species (Tepedino & Parker, 1982).

Non-parasitic bees should have higher nutritional requirements than other flower-visiting insects, since they collect pollen and nectar for both their own consumption and to feed their larvae (Faegri & van der Pijl, 1978). Among bees, those of larger size have a higher absolute cost of flight and provision their nests with greater amounts of food. In social species, nutritional costs are increased because workers, queens and drones are produced (Schaffer *et al.*, 1979), and additional energy is required in heating and cooling nest temperatures (Heinrich, 1975).

Of the three species of *Cistus* occurring in Roques Blanques, *C. albidus* produces the most pollen and probably the most nectar. This species should, therefore, attract pollinators with higher food requirements (the social honey-bee, and large-sized solitary bees). Indeed, *C. albidus* not only attracted most of the insects observed, but it is the only *Cistus* species that attracted honey bees (Table 3). It also attracted more larger-sized solitary bee species than either of the two other *Cistus* (Table 4).

The absence of *A. mellifera* on *C. salvifolius* and *C. monspeliensis* does not necessarily mean that it cannot forage profitably on these two plants. In fact, *A. mellifera* has been found elsewhere visiting flowers of these same *Cistus* species (Bonet *et al.*, 1985; Herrera, 1985a; Brandt & Gottsberger, 1988). That this is not the case in Roques Blanques may be due to a greater attractiveness of *C. albidus* and other plants that grow near the study site, including *Diplotaxis erucoides* (L.) DC. and *Erucastrum nasturtiifolium* (Poiret) O. E. Schulz, on which large numbers of honey-bees were observed.

As shown in Fig. 3, most other groups of visitors are also preferentially attracted to only one or two of the three *Cistus* species. Bruchids are small seed-eating beetles that appear late in the flowering season. This may be the reason why they are more abundant on the later flowering *C. monspeliensis*. Why other coleopterans prefer *C. albidus* to *C. salvifolius* may be related to nutritional values. Since *C. albidus* flowers are the most productive, they would attract not only more bees, but also more beetles.

Beetles have traditionally been considered to be less adapted to exploit floral resources than other groups of anthophilous insects that visit the same flowers (Proctor & Yeo, 1973; Faegri & van der Pijl, 1978). It was, therefore, surprising to learn that the coleopteran visitors on *Cistus* are partitioned by flower type and plant species. Even when species instead of groups of beetles were considered, partitioning was evident (*Psilothrix* sp. predominates on *C. albidus* (Chi-square, $P < 0.001$), *Malachius* sp. on *C. salvifolius* and *C. monspeliensis* ($P < 0.05$), *Dasytes* sp. on *C. albidus* and *C. salvifolius* ($P < 0.05$), and *O. flavipes* on *C. albidus* and *C. monspeliensis* ($P < 0.001$)). These comparative results demonstrate that beetles distinguish between flowers of the three *Cistus* species. This is potentially important because it may prevent heterospecific pollination that would occur if partioning was not expressed. Further research is necessary to ascertain whether preferences may be explained in terms of energetic balance as for bees or from other causes, such as an innate preference for specific odours, colours, etc. expressed at the specific level of flowering plants.

Another factor that could reinforce the general attractiveness of *C. albidus* may be its early flowering period. Bees and other insects would first be attracted to *C. albidus* and then remain oriented to this species after other *Cistus* initiated flowering, especially if resource rewards remain higher in *C. albidus* blossoms. Wells & Wells (1983) have demonstrated that this type of conditioning was expressed when honey-bees continued to visit artificial blue flowers after artificial yellow flowers were introduced, even when these yellow flowers contained larger nectar rewards.

### *Breeding systems*

Results on hand-pollination studies (Table 2) and P/O ratios demonstrate that these three *Cistus* species are highly self-incompatible, and each is insect pollinated.

If beetles are not important pollinators, *C. monspeliensis* would depend almost exclusively on the few bees that visit these plants for pollination. On the other hand, *C. albidus* would receive maximum pollination because it is attractive to bees. Finally, *C. salvifolius* would represent an intermediate situation where some bees and flies act as main pollinator agents. However, the fact that the spectrum of pollinators reported for *C. salvifolius* and *C. monspeliensis* in areas where *C. albidus* is not present, significantly differ from results found in Roques Blanques, indicates that the two former species might be receiving less crossed pollen then they would if they grew in isolation from *C. albidus*. In fact, *C. albidus* normally grows on limestone-derived soils, while *C. salvifolius* and *C. monspeliensis* are most often found on siliceous substrates (Bonet *et al.*, 1985).

In addition, there are certain morphological and phenological characteristics which tend to facilitate the transfer of pollen between individuals in *C. albidus* and to obstruct it in *C. salvifolius* and *C. monspeliensis*. For example, individual plants of *C. albidus* and *C. salvifolius* produce approximately the same number of flowers, but flowering periods are longer for the former than for the latter. Individual plants of *C. monspeliensis* produce many more flowers, and as in *C. salvifolius*, they follow a strategy near to mass-flowering. It has already been demonstrated (Pyke, 1982; Geber, 1985; Andersson, 1988) that the greater the number of flowers on a plant, the greater number will be visited by a bee during a single bout. This behaviour favours pollination between flowers in the same individual, but not between individuals (Augspurger, 1980; Wyatt, 1982; Geber, 1985; Andersson, 1988), as found in *Catalpa speciosa* Engelm., where trees receive more crossed pollen at the end of their blooming period when flowers are scarce than during the peak of flowering (Stephenson, 1982). Furthermore, mean distances between individual plants and its five nearest conspecific neighbours are shorter for *C. albidus* than for *C. salvifolius* and *C. monspeliensis* (unpublished data). However, it is also important to note here that synchrony of flowering among individual *C. monspeliensis* plants (and to a lesser extent among individual *C. salvifolius* plants) (Fig. 1), could play an important role to increase the probability of these plants receiving crossed pollen (Bawa, 1983). Although mass-flowering appears to be a disadvantageous pollination strategy for xenogamous plants, it may be a useful mechanism to avoid interspecific pollen exchanges or to reduce flower predation by insects, birds, etc. (Bawa, 1983).

This study shows that some of the traits traditionally accepted as adaptive for self-incompatible species (Ordnuff, 1969) are more accentuated in *C. albidus* than in *C. salvifolius* or *C. monspeliensis*. Thus, the larger flowers of *C. albidus*, that produce more nectar and pollen, contain more ovules, and have anthers widely separated from the stigma, are characteristics that work in concert to constrain selfing. Similarly, the lower P/O ratios for *C. salvifolius* and *C. monspeliensis* (Table 1) are nearer to those of facultatively xenogamous species (see Cruden, 1977) than the P/O ratio recorded for *C. albidus*.

The increased number of pollen grains, ovules (Table 1) and seeds (Table 2) produced per flower in *C. albidus* requires that either additional pollinators are attracted to these plants or that these plants produce more pollen grains to ensure sufficient pollen dispersal. Results presented above suggest that both strategies are practiced.

The number of pollen grains produced per ovule (P/O ratios) also varies between the three species, although all of them are mainly crossers. Pollen–ovule ratios are inversely related to the likelihood that a pollen grain reaches a stigma, thus, cleistogamous flowers have the lowest P/Os, and xenogamous flowers the highest (Cruden, 1977). According to Cruden & Miller-Ward (1981), P/Os are also negatively correlated with the ratio of stigmatic area to the pollen bearing area on the bodies of pollinators, because the greater the pollen bearing area, the more grains of pollen need to be produced by the plant to achieve the same density of grains on the body of the pollinator. Results obtained with *Cistus spp.* are consistent with this hypothesis, since *C. albidus*, the species with the highest P/O, attracts most of the larger-sized insects (with greater pollen bearing areas) and has a stigmatic surface area slightly smaller than the other two species (personal observation). Cruden & Miller-Ward (1981) also predicted that pollen grain surface area is inversely correlated with P/O ratios. Again, results obtained with *C. albidus*, *C. salvifolius* and *C. monspeliensis* (Table 1) support this hypothesis.

Normally, to attain a maximum seed-set, more than one pollen grain per ovule needs to be placed on the stigma. The number of grains necessary to fertilize each ovulum ranges from two to 20, depending on the plant species (Cruden, 1977; Silander & Primack, 1978; Shore & Barrett, 1984; Waser & Fugate, 1986; Snow, 1986). If *C. albidus* requires higher numbers of pollen grains on a stigma to set a seed, this would explain why it produces more pollen grains per ovulum than other *Cistus* species studied.

For every pollen grain deposited on a stigma, a number of 'additional' grains need to be produced to attract pollinators (Faegri & van der Pijl, 1978). Since *C. albidus* receives visits of nectar and pollen-seeking insects with high nutritional requirements (bees), its flowers should produce larger amounts of nectar and pollen than the other two *Cistus* species studied. This increases investment in flower production that is compensated by higher rates of pollinator visitation.

## ACKNOWLEDGEMENTS

I am grateful to A. Bonet and A. Alsina for their assistance in field work, to J. Retana for his help with statistical treatment of data, and to E. Bellet for allowing me to work in the grounds of the Public Foundation of Roques Blanques. I thank E. Asensio, C. Plateaux-Quénu and X. Vázquez who helped me with insect identification. Finally, I am indebted to C. M. Herrera and P. F. Torchio, who reviewed an early draft of the manuscript, made numerous suggestions for its improvement and helped with English translation.

## REFERENCES

ANDERSSON, S., 1988. Size-dependent pollination efficiency in *Anchusa officinalis* (Boraginaceae): causes and consequences. *Oecologia, 76:* 125–130.

AUGSPURGER, C. K., 1980. Mass-flowering of a tropical shrub (*Hybanthus prunifolius*): influence on pollinator attraction and movement. *Evolution, 34:* 475–488.

BAWA, K. S., 1983. Patterns of flowering in tropical plants. In C. E. Jones & R. J. Little (Eds), *Handbook of Experimental Pollination Biology:* 394–410. New York: Van Nostrand.

BEATTIE, A. J., BREEDLOVE, D. E. & EHRLICH, P. R., 1973. The ecology of the pollinators and predators of *Frasera speciosa. Ecology, 54:* 81–91.

BONET, A., RITA, J., SEBASTIA, M., 1985. *La flora mel. lifera de la circumscripcio de Barcelona. [Honey plants of Barcelona.]* Barcelona: Estudis i monografies de la Diputació de Barcelona, No 7.

BRANDT, U. & GOTTSBERGER, G., 1988. Flower phenology, pollinating insects, and breeding systems in *Cistus*, *Halimium*, and *Tuberaria* species in Portugal. *Lagascalia, 15:* 625–634.

CRUDEN, R. W., 1977. Pollen-ovule ratios: a conservative indicator of breeding systems in flowering plants. *Evolution, 31:* 32–40.

CRUDEN, R. W. & MILLER-WARD, S., 1981. Pollen-ovule ratio, pollen size, and the ratio of stigmatic area to the pollen bearing area of the pollinator: an hypothesis. *Evolution, 35:* 964–974.

EHRENDFELD, J. G., 1979. Pollination of three species of *Euphorbia* subgenus *Chamaesyce*, with special reference to bees. *American Midland Naturalist, 101:* 87–98.

FAEGRI, K. & VAN DER PIJL, L., 1978. *The Principles of Pollination Ecology.* London: Pergamon Press.

GEBER, M. A., 1985. The relationship of plant size to self-pollination in *Mertensia ciliata. Ecology, 66:* 762–772.

HEINRICH, B., 1975. Energetics of pollination. *Annual Review of Ecology and Systematics, 6:* 139–170.

HEINRICH, B. & RAVEN, P. H., 1972. Energetics and pollination ecology. *Science, 176:* 597–602.

HERRERA, J., 1985a. *Biología reproductiva del matorral de Doñana.* [Reproductive biology in the Doñana scrubland.] Unpublished Ph.D. thesis of the University of Sevilla.

HERRERA, J., 1985b. Nectar secretion patterns in Southern Spanish Mediterranean scrubland. *Israel Journal of Botany, 34:* 47–58.

KEVAN, P. G. & BAKER, H. G., 1983. Insects as flower visitors and pollinators. *Annual Review of Entomology, 28:* 407–453.

MARTIN, M. & GUINEA, E., 1949. *Jaras y jarales. [Rock roses and rock rose scrublands.]* Madrid: Ministerio de Agricultura, Instituto forestal de investigación y experiencias, No 20.

ORDNUFF, R., 1969. Reproductive biology in relation to systematics. *Taxon, 18:* 121–133.

PROCTOR, M. & YEO, P., 1973. *The Pollination of Flowers.* Glasgow: Collins.

PYKE, G. H., 1982. Foraging in bumble-bees: rule of departure from an inflorescence. *Canadian Journal of Zoology, 60:* 417–428.

SCHAFFER, W. M., JENSEN, D. B., HOBBS, D. E., GUREVITCH, J., TODD, J. R., VALENTINE-SCHAFFER, M., 1979. Competition, foraging energetics and the cost of sociality in three species of bees. *Ecology, 60:* 976–987.

SHORE, J. S. & BARRET, S. C. H., 1984. The effect of pollination intensity and incompatible pollen on seed set in *Turnera ulmifolia* (Turneraceae). *Canadian Journal of Botany, 62:* 1298–1303.

SILANDER, J. A. & PRIMACK, R. B., 1978. Pollination intensity and seed set in the evening primrose (*Oenothera fruticosa*). *American Midland Naturalist, 100:* 213–216.

SNOW, A. A., 1986. Pollination dynamics in *Epilobium canum* (Onagraceae): consequences for gametophytic selection. *American Journal of Botany, 73:* 139–151.

STEPHENSON, A. G., 1982. When does out-crossing occur in a mass-flowering plant? *Evolution, 36:* 762–767.

TEPEDINO, V. J. & PARKER, F. D., 1982. Interspecific differences in the relative importance of pollen and nectar to bee species foraging on sunflowers. *Environmental Entomology, 11:* 246–250.

TROUMBIS, A. & TRABAUD, L., 1986. Comparison of reproductive biological attributes of two *Cistus* species. *Acta Oecologica (Oecologia Plantarum), 7:* 235–250.

WASER, N. M. & FUGATE, M. L., 1986. Pollen precedence and stigma closure: a mechanism of competition for pollination between *Delphinium nelsonii* and *Ipomopsis aggregata. Oecologia, 70:* 573–577.

WELLS, H. & WELLS, P. H., 1983. Honey-bee foraging ecology: optimal diet, minimal uncertainty or individual constancy? *Journal of Animal Ecology, 52:* 829–836.

WYATT, R., 1982. Inflorescence architecture: how flower number, arrangement, and phenology affect pollination and fruit-set. *American Journal of Botany, 69:* 585–594.

## APPENDIX

Regions of integument utilized to determine distribution of pollen on the bodies of insect visitors. (Modified from Beattie, Breedlove & Erhlich, 1983.)

### HYMENOPTERA

Head.
1. Proboscis.
2. Vertex, ocellar triangle, dorsal occiput.
3. Eyes.
4. Antennae.
5. Frons, clypeus.
6. Mandibles, labrum, genae.

Thorax.
7. Dorsal cervix, pronotum.
8. Mesonotum.
9. Scutellum, postscutellum, dorsal propodeum.
10. Tegulae, wings.
11. Ventral cervix, prosternum.
12. Mesosternum.
13. Metasternum.
14. Pleural thoracic plates.

Abdomen.
15. Terga of segments 2–3.
16. Terga of remaining segments.
17. Sterna of segments 2–3.
18. Sterna of remaining segments.

Legs.
19. Coxae, trochanters, femora of pairs 1–2.
20. Coxae, trochanters, femora of pair 3.
21. Tibiae, tarsi of pairs 1–2.
22. Tibiae, tarsi of pair 3.

### DIPTERA

Head.
1. Proboscis.
2. Vertex, ocellar triangle, dorsal occiput.
3. Eyes.
4. Antennae.
5. Orbit, frons, parafacialia.
6. Proboscis fossa.

Thorax.
7. Dorsal cervix, prescutum, humeri.
8. Mesonotum.
9. Scutellum, metanotum.
10. Tegulae, wings.
11. Ventral cervix, prosternum.
12. Mesosternum.
13. Metasternum.
14. Pleural thoracic plates.

Abdomen.
15. Terga of segments 1–3 or 4.
16. Terga of remaining segments.
17. Sterna of segments 1–3 or 4.
18. Sterna of remaining segments.

Legs.
19. Coxae, trochanters, femora of pairs 1–2.
20. Coxae, trochanters, femora of pair 3.
21. Tibiae, tarsi of pairs 1–2.
22. Tibiae, tarsi of pair 3.