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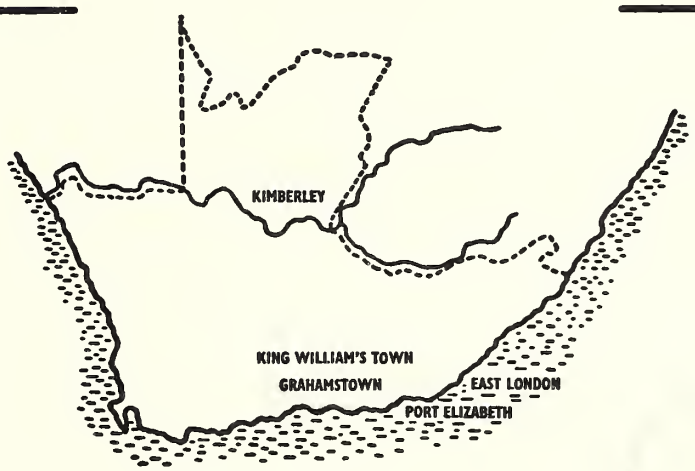

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Prey and nesting sites of some sympatric species of Cerceris (Hymenoptera: Sphecidae) with a review and discussion of the prey diversity of the genus

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CONTENTS

ABSTRACT

Nineteen sympatric *Cerceris* species are examined in relation to frequency of occurrence, nature of nesting sites and of prey. Their nesting sites and prey are discussed in relation to their ecological displacement. There follows a review and discussion of the prey diversity of the genus *Cerceris* which puts forward the hypothesis that *Cerceris* is an Old World genus and that its original prey was hymenopterous. Prey records of a total of twenty Afrotropical species are included of which twelve are new associations and three confirm previously published records.

INTRODUCTION

The genus *Cerceris* Latreille is cosmopolitan in its distribution and with over 850 known species is the largest genus of the Sphecidae. All species are ground-nesting and provision their young with insect prey.

The present paper is based upon observations of sympatric *Cerceris* species made over a period of seven years at Hilton, a farm situated 18 kilometres WNW. of Grahamstown (33°19'S., 26°32'E.) in the Albany Division of the Eastern Cape Province of South Africa.

In view of the large overall number of species and the frequency with which considerable numbers of species often occur together, both spatially and temporally, the ecological displacement of the species—that is the different ways in which the species exploit their habitat—is of great interest. Clearly of importance in such ecological displacement is specificity in such basic ethological factors as the choice of nesting site, and more particularly the choice of prey. It is

these aspects of the ethology of the *Cerceris* species at Hilton which are set forth in the present account.

This is the eighth of a series of publications covering some aspects of the ethology of solitary wasps occurring at Hilton, the climate and vegetation of which have been previously described (Gess and Gess, 1974: 191–192).

Prey records, both published and unpublished, from localities other than Hilton have been included in the account in an attempt to draw together information on the chosen prey of as many Afrotropical *Cerceris* species as possible, little having hitherto been published on the subject.

THE CERCERIS SPECIES PRESENT AT HILTON AND THE RELATIVE FREQUENCY OF THEIR OCCURRENCE

Nineteen species of *Cerceris* have been recorded from Hilton. Arranged in alphabetical order these are: *C. amakosa* Brauns, *C. armaticeps caffrariae* Empey, *C. diodonta diodonta* Schletterer, *C. discrepans discrepans* Brauns, *C. dominicana* Brauns, *C. erythrosoma* Schletterer, *C. holconota holconota* Cameron, *C. hypocritica* Brauns, *C. languida languida* Cameron, *C. latifrons latifrons* Bingham, *C. lunigera* Dahlbom, *C. nasidens obscura* Schletterer, *C. nigrifrons nigrifrons* Smith, *C. oraniensis* Brauns, *C. pearstonensis pearstonensis* Cameron, *C. pictifacies* Brauns, *C. ruficauda ruficauda* Cameron, *C. rufocincta polychroma* Gribodo and *C. spinicaudata spinicaudata* Cameron.

The species varied greatly in the frequency of occurrence, as reflected by catches and sightings. The most commonly met with species, in decreasing order, were *C. latifrons, C. languida* and *C. rufocincta polychroma, C. holconota, C. spinicaudata* and *C. pearstonensis.* Less commonly met with species were *C. nigrifrons* and *C. ruficauda, C. lunigera, C. nasidens obscura* and *C. oraniensis.* Rare were *C. hypocritica, C. amakosa, C. diodonta* and *C. pictifacies, C. dominicana* and *C. erythrosoma, C. discrepans* and *C. armaticeps.*

The flight periods of all the *Cerceris* species at Hilton fall between mid-October and mid-April.

IDENTIFICATION OF THE NESTING SITES

Nests belonging to ten species were located at Hilton. All were constructed in level or nearly level bare ground which was sufficiently friable to allow the females to excavate their burrows using their mandibles and legs but no water. The ground was firm though in sandy situations the firm underlying sand was sometimes overlain by a layer of loose material.

Six species were found to nest in sandy soil, two sites being particularly favoured: a sandpit (see Gess and Gess, 1980: Fig. 1) and the area adjacent to it, and a very gently sloping bank margining a car track where the latter crosses the bed of a seasonal tributary of the New Year's River. The sand, light coloured and fine grained, is derived from the weathering of Witteberg Quartzite and is of alluvial origin having been deposited upon its flood plain by the above seasonal water course.

The species found nesting in these sites were: *C. holconota* (seven nests; both in the sandpit and on the gently sloping bank where it nested in company with *Bembix albofasciata*); *C. languida* (many nests; in the sandpit in very fine sand where it nested in company with *Bembecinus braunsii* and *B. haemorrhoidalis*); *C. latifrons* (many nests; as for *C. holconota*); *C. oraniensis* (4 nests; on level ground immediately above and below the lip of the sandpit); *C. rufocincta* (several nests; in the sandpit where it sometimes nested in company with *Bembecinus braunsii* and *B. haemorrhoidalis*); and *C. spinicaudata* (three nests; as for *C. holconota*).

Four species were found to nest in disturbed clayey soil immediately adjacent to a water furrow (see Gess and Gess, 1976: Plate 2). The clayey soil, reddish-brown in colour, is derived

from the weathering of Upper Witteberg Shales previously known as Lower Dwyka Shales and referred to as such by Gess and Gess (1974: 192 and 1975: 24). Though less compacted than undisturbed clayey soil the substrate nested in by the four species was nevertheless less friable than the soil in sandy areas. The species concerned were: *C. lunigera* (1 nest); *C. pearstonensis* (1 nest); *C. ruficauda* (1 nest) and *Cerceris* sp. A (1 nest). The last listed species is unidentified owing to the unfortunate escape during the opening up of the nest of the female nest builder. Whereas it is very probable that the species was one of the nineteen recorded from Hilton, it is clear, knowing its chosen nesting substrate and prey, that it was not one of the named species recorded above as having been found nesting.

IDENTIFICATION OF THE PREY

The identity of the prey of thirteen of the nineteen species of *Cerceris* recorded from Hilton is known. Prey identifications for nine of these species were made at Hilton, seven of the associations having been previously unknown and the other two confirming previously recorded associations. For four of the ten species for which prey identifications were not made at Hilton information as to the nature of the prey taken is available from other sources. The *Cerceris* species are dealt with individually below.

Cerceris sp. A.

In a nest excavated on 6.xii.1974 and containing forty-one uneaten prey this species was found to have provisioned its cells solely with a 3,5–4,0 mm long metallic-green species of PTEROMALIDAE (Hymenoptera: Chalcidoidea).

Cerceris erythrosoma Schletterer

This species was not associated with its prey at Hilton but is known to provision with beetles of the family CURCULIONIDAE. Brauns (1911: 239 and 1926: 278) recorded the prey as a species of *Tanymecus*. Similarly, prey associated with females collected by Jacot Guillarmod at Mamathes in Lesotho and now in the collections of the Albany Museum consist in one instance of a 10 mm long specimen of *Tanymecus makkaliensis* Fhs. (det. G. A. K. Marshall) and in five instances of 6,8–7,6 mm long specimens of *Protostrophus* sp. near *sceleratus* H. v. S. (det. R. T. Thompson).

Cerceris holconota holconota Cameron

Six females seen transporting prey were captured, four after they had revealed their nests which were subsequently excavated to recover the prey stored in the caches. The thirteen prey obtained were representative of six families of Hymenoptera as detailed below: BRACONIDAE, ?Genus & sp. (1 female, 13.i.1975); BETHYLIDAE, ?Genus & sp. (1 female, 20.xii.1974); TIPHIIDAE, *Anthobosca* sp. (1 male, 13.i.1975), *Braunsomeria* sp. (4 males, 13.i.1975 and 1 male, 16.xi.1977), *Mesa incisa* (Cameron) (2 females, 20.xii.1974); MUTILLIDAE, *Dasylabris eunyce* (Péringuey) (1 male, 13.i.1975); FORMICIDAE, ?*Camponotus* sp. (1 winged male, 11.xii.1975); HALICTIDAE, *Lasioglossum* sp. (1 female, 20.xii.1974).

Cerceris languida languida Cameron

A female transporting prey was captured on each of the following three dates: 24.xi.1977, 10.i.1978 and 23.ii.1978. The first female was allowed to enter her nest which was subsequently excavated and yielded 32 prey from the cache. All 34 prey obtained from the three females were beetles of the family PHALACRIDAE and represented a single, 1,7 mm long, black *Olibrus* sp.

Cerceris latifrons latifrons Bingham

Females transporting prey were captured on 19.xi.1973 (1), 20.xii.1974 (1), 10.i.1975 (1),

9.xii.1975 (4), 2.xii.1977 (3) and 2.i.1978 (1). All eleven prey obtained were beetles of the tribe Hopliini, SCARABAEIDAE: MELOLONTHINAE. Two 4,4–4,7 mm long species were represented. The prey taken at Hilton agrees with that recorded by Arnold (1940: 106) for the subspecies *C. latifrons sedula* Arnold from Rhodesia, namely "an unidentified species of beetle (Hoplinae)".

Cerceris lunigera Dahlbom

One female seen transporting prey on 6.xii.1974 was captured after revealing her nest. The two prey obtained from the cache in the excavated nest were bees of the family HALICTIDAE, namely *Halictus* sp. (female) and *Lasioglossum* sp. (female).

Cerceris nasidens obscura Schletterer

This species was not associated with its prey at Hilton but according to E. McC. Callan (*pers. comm.*) it has been found provisioning nests in Grahamstown with "small melolonthid beetles", SCARABAEIDAE: MELOLONTHINAE. The tribe to which the beetles belong is apparently not Hopliini.

Cerceris nigrifrons nigrifrons Smith

This species was not associated with its prey at Hilton. However, Brauns (1926: 320) reported the prey to be beetles of the family BUPRESTIDAE, for instance *Sphenoptera* sp. in Rhodesia.

Cerceris oraniensis Brauns

Four females, each carrying a single prey, were captured at or near their nest entrances on 16.ii.1978. A fifth prey was obtained from the cache of a nest excavated on the same day. All the prey were beetles of the family CURCULIONIDAE and represented a single, 7,0–7,4 mm long *Protostrophus* species.

Cerceris pearstonensis pearstonensis Cameron

This species was not associated with its prey at Hilton but was found at other localities to provision with beetles of the family CURCULIONIDAE. At Strowan, near Grahamstown, on 30.xi.1970, a female was caught when flying with a 4,6 mm long *Protostrophus* sp. Prey associated with two females collected by Jacot Guillarmod at Mamathes, Lesotho, and now in the collections of the Albany Museum are likewise small weevils. The larger of the two, 4,4 mm long, is a *Protostrophus* sp., the smaller, 4,2 mm long, belongs to some other genus.

Cerceris ruficauda ruficauda Cameron

A nest of this species excavated on 10.xii.1974 was found to contain twenty-six uneaten prey, beetles of the family CHRYSOMELIDAE: CRIOCERINAE. A single 3,4 mm long blackish-bronze species was represented.

Cerceris rufocincta polychroma Gribodo

Eight females seen transporting prey were captured, one after it had revealed its nest which was subsequently excavated to recover the prey stored in the cache. The ten prey obtained were representative of two families of Hymenoptera as detailed below: TIPHIIDAE, *Anthobosca rufithorax* (Cameron) (1 female, 2.i.1978), *Tiphia* sp. (1 male, 13.xii.1977 and 1 male, 2.i.1978); MUTILLIDAE, *Chrestomutilla* sp. (1 male, 24.i.1978), *Dasylabroides caffra* (Kohl) (1 female !!, 13.xii.1977; 1 male, 17.i.1978; 2 males, 24.i.1978), *Psammotherma flabellata* (F.) (1 male, 20.xii.1974; 1 male, 13.i.1975).

Cerceris spinicaudata spinicaudata Cameron

Three females seen transporting prey were captured after revealing their nests which were subsequently excavated to recover the prey stored in the caches. The nine prey obtained were all

small bees of the family HALICTIDAE. Species of two genera were represented: *Lasioglossum* spp. (4 females representative of 3 species, 20.xii.1974; 1 female, 10.i.1975) and *Nomioides* sp. (probably *N. halictoides* Blüthgen) (4 females, 20.xii.1974).

Prey associated with two females collected by Jacot Guillarmod, one at Strowan, near Grahamstown (27.ii.1972) and the other at Mamathes, Lesotho, and now in the collections of the Albany Museum are likewise females of species of *Lasioglossum*. The present records confirm the association given by Brauns (1926: 337) who wrote: "I found it carrying *Halictus* sp. for larval food".

It should be noted that, though the genus *Halictus* occurs in southern Africa, most species at one time allocated to it are now included in the closely related genus *Lasioglossum*. Brauns' record may thus apply to either *Halictus* or *Lasioglossum*.

PROVENANCE OF THE PREY

For some species at least it was established where the prey taken by them was to be found, therefore allowing the situation to be identified in which the wasps hunt and respond to prey of certain size and behaviour. For other species it is possible to speculate concerning the identity of the situation by using circumstantial evidence.

Olibrus sp. (Phalacridae) the sole prey of *C. languida* was found to be very common in the flowers of *Lasiospermum bipinnatum* (Compositae), an annual herb growing in the sandpit and elsewhere. Recorded from this plant in October and November during the first weeks of the wasp's flight period, the beetle was undoubtedly present both then and later in the summer in the flowers of other herbaceous composites as well. The flowers of species of *Senecio*, a genus of common occurrence at Hilton, were found by H. Andreae (*pers. comm.*) to be frequented by three *Olibrus* species at the Cape. The beetle is associated throughout its life with its host plant, the egg being laid in the flower and the larva feeding in the capitulum until full-grown when it bores down the stem to pupate in the ground. In European species there may be six generations in the year (Imms, 1957: 801). From the above it is apparent that *C. languida* must hunt for its prey in the flowers of Compositae, probably all small annuals like *L. bipinnatum*. The commonness of such plants and the large number of generations of *Olibrus* probably developing upon them makes possible the extended flight and nesting period—continuously from the first half of October to the beginning of March—established at Hilton for *C. languida*.

The Hopliini (Scarabaeidae) which constitute the prey of *C. latifrons* are as a tribe characteristically found in the flowers of Compositae so that this wasp may be expected to hunt in a similar though not necessarily the same situation as that pertaining to *C. languida*.

The *Protostrophus* sp. (Curculionidae) found to be the prey of *C. oraniensis* was common on the foliage of the annual herbaceous weed *Conyza bonariensis* (Compositae) during the only period, mid-February, during which this wasp was observed nesting. The beetle infested plants, growing in the sandpit, were in close proximity to the nests.

Protostrophus, recently monographed by Van Schalkwyk (1968) is a very commonly met with genus, the majority of the 136 recognized species being found in South Africa. The species are inconspicuous, mostly dull coloured and are unable to fly. In body length they range from 3–9mm. The beetles are apparently not restricted to any particular plants, the eggs being dropped to the ground where ever the females are feeding. The larvae lead a subterranean life, probably feeding upon decaying vegetable matter. Mass emergences of thousands of adults have been recorded when great damage may be done by their feeding on the foliage of many different plants including seedling trees. From the observed presence at Hilton of *Protostrophus* sp. on the foliage of *Conyza* and the known biology of the weevil genus it would appear that *C. oraniensis* hunts for its prey amongst foliage at no great height above the ground. It is probable that the

other two *Cerceris* species known to prey at least partly upon *Protostrophus* and occurring at Hilton, *C. erythrosoma* and *C. pearstonensis* hunt in similar situations.

The species of Criocerinae (Chrysomelidae), the sole recorded prey of *C. ruficauda* may be expected to occur on foliage as is characteristic for the subfamily and it is there that the wasp undoubtedly does its hunting.

For the species of *Cerceris* which hunt Hymenoptera two possible hunting situations immediately present themselves: at flowers and young growth visited by the prey for purposes of foraging for nectar or glandular exudates, or at the nests of the prey.

It was noted at the time when the nest of *C. lunigera* and those of *C. spinicaudata* were excavated that they were situated in close proximity to the nests of various small bees some of which at least were those of species represented amongst the prey of the wasps. This was particularly striking with respect to *C. spinicaudata* and *Nomioides* sp. (probably *N. halictoides*) which nested next to one another in the sand. It therefore seems possible that the hunting of these two *Cerceris* species may take place at or near the nest entrances of their prey and in close proximity to the entrances of their own nests. The fact that only female bees are recorded as prey would lend support to this hypothesis. The latter would be in accord with the findings of Marchal (1887) as reported by Hamm and Richards (1930: 106) on the behaviour of *C. rybyensis* (L.) (= *C. ornata* Fabr.) in France. That wasp nested in a garden path in close proximity to innumerable nests of *Andrena* and *Halictus* on which species it was preying. The *Cerceris* was reported to circle round the nests, every now and then dropping to the ground, or even entering a burrow. Only bees returning home laden with pollen were attacked, and these were knocked down and stung as they hovered over their nests before entering.

With respect to *C. holconota* and *C. rufocincta polychroma* on the other hand, the wide range of unrelated prey of both sexes and of very diverse habits and behaviour makes it likely that the only situation in which these *Cerceris* species in hunting would meet all the prey species would be at flowers and young growth to which the latter would go for foraging purposes. In the areas in which the two *Cerceris* species nested—in and near the sandpit—the flowering plants known to have been visited by a mixed company of Braconidae, Tiphiidae, Mutillidae and others were *Selago corymbosa* (Selaginaceae) and various low-growing Compositae including *Helichrysum* and *Lasiospermum*. It therefore appears that *C. holconota* and *C. rufocincta polychroma* hunt for their prey on and around flowers of low-growing herbaceous plants.

DISCUSSION OF THE NESTING SITES AND THE PREY IN RELATION TO ECOLOGICAL DISPLACEMENT.

The existence at Hilton of two basically very different soil types, one clayey and the other sandy, and the specificity shown by the wasps in their choice of nesting substrate has resulted in the *Cerceris* species of that locality being divided for the purposes of nesting into two distinct non-competitive groups, indicating that an area with more than one type of friable soil can support a larger number of *Cerceris* species than one with a uniform soil type.

Other factors, for example the depth of the friable soil, will be limiting. The species nesting in sand place their caches at depths ranging from 60 ± mm in *C. rufocincta* to 500 + mm in *C. latifrons*. Therefore, whereas *C. latifrons* can only nest in relatively deep sand *C. rufocincta* and other shallow-nesters are less restricted.

Hunting by *Cerceris* species at Hilton appears to take place at no great distance from the nest. This being so, competition for prey between species such as for example the clay-nesting *C. lunigera* on the one hand and the sand-nesting *C. spinicaudata* on the other is avoided as, although both hunt halictine bees, their hunting areas are distinct. This is especially true for these species which are believed to prey upon bees nesting in close proximity to their own nests.

All the species are highly prey specific with the exception of *C. rufocincta* and more

particularly *C. holconota* which, with their recorded prey representing respectively two and six families of Hymenoptera, appear to be catholic in their choice. With the high prey specificity generally shown competition for prey is effectively avoided despite the fact that a number of species nesting in the same soil type may hunt in very similar situations. The most commonly taken prey recorded or known for *Cerceris* species occurring at Hilton are species of Halictidae and Curculionidae, notably *Protostrophus* species. With respect to the three species hunting *Protostrophus* weevils, differences in preferred size range of prey either alone or in conjunction with differences in substrate-determined nest situation are likely factors of importance in the avoidance of competition.

REVIEW AND DISCUSSION OF THE PREY DIVERSITY OF THE GENUS CERCERIS

The most interesting aspect of the behaviour of *Cerceris* concerns the diversity of insects taken as prey by the genus and the specificity shown by individual species.

Provisioning is with adult Coleoptera or Hymenoptera, depending upon the *Cerceris* species. From data presented by Bohart and Menke (1976: 576) and by Iwata (1976: 150–151) it appears that eleven families of Coleoptera have so far been recorded as prey: Anthribidae, Bruchidae, Buprestidae, Cerambycidae, Chrysomelidae, Coccinellidae, Curculionidae, Nitidulidae, Phalacridae, Scarabaeidae and Tenebrionidae. Published records of Hymenoptera taken as prey mostly concern Apoidea.

Coleoptera appear to be the more commonly taken order and have been recorded as prey of *Cerceris* from many parts of the world. North American species of *Cerceris* provision exclusively with Coleoptera and the few records pertaining to South America concern prey of the same order. The few prey records for Australian *Cerceris* similarly concern Coleoptera. In the Palaearctic, Oriental and Afrotropical Regions of the Old World, however, there are, in addition to species provisioning with Coleoptera, a minority of species that utilize Hymenoptera. Thus the Palaearctic *C. rybyensis* (L.), *C. hortivaga* Kohl and *C. sabulosa* (Panzer) and the Oriental *C. pictiventris* Dahlbom provision with Apoidea, especially Halictidae and some in addition with Colletidae and Andrenidae.

Though Apoidea appear to be the most commonly taken non-coleopterous prey, four records of the use of Hymenoptera other than bees have been published (see Bohart and Menke, 1976: 576). In the Palaearctic, *C. stratiotes* Schletterer is believed to prey only on the chalcid, *Stilbula cynipiformis* (Rossi), a *Cerceris* species provisioning with halictid and andrenid bees was found to have also in its brood cells a species of *Psen* (Sphecidae), and a female *C. pekingensis* Tsuneki was reported to have taken a species of *Pison* (Sphecidae) into her burrow. The fourth record concerns the Oriental *C. langkasukae* Pagden which was reported carrying a species of *Hingstoniola* (Sphecidae) although her regular prey were buprestids.

The prey of eight Afrotropical *Cerceris* species has been recorded in print. On the African mainland, Curculionidae are taken by *C. chirindensis* Arnold (Arnold, 1932: 13), *C. emeryana varilineata* Cameron (Brauns, 1926: 322, as *C. varilineata* Cam.) and *C. erythrosoma* Schletterer (Brauns, 1911: 239 and 1926: 278); Buprestidae are taken by *C. nigrifrons* Smith (Brauns, 1926: 320); and Scarabaeidae are taken by *C. latifrons sedula* Arnold (Arnold, 1940: 106, as *C. sedula* Arnold). On Malagasy, Curculionidae are taken by *C. clypearis* Saussure; Chrysomelidae and Buprestidae by *C. albotegula* Arnold; and nomiine bees (Halictidae) by *C. nenitra* Saussure (all Arnold, 1945: 23, 41 and 42 respectively).

Additional records (all C. F. Jacot Guillarmod's and unpublished) obtained from the Albany Museum collections concern *C. bothavillensis* Brauns and *C. emeryana multicolor* Arnold (both from Mamathes, Lesotho) and *C. multipicta fuscifacies* Empey (from the Transvaal Lowveld) all of which took Curculionidae, in the case of the first named species, *Leurops sublineata* Marshall.

With the addition of the records from Hilton, the prey of a total of 20 (i.e. 10,6%) of the 189

Afrotropical species of *Cerceris* recognized by Empey (1969) is known. The corresponding figures for America north of Mexico are 21 (i.e. 27%) of 78 species (see Scullen, 1965 and Evans, 1971: 509). Of the twenty Afrotropical species concerned, fourteen species prey upon Coleoptera and six upon Hymenoptera whereas, as previously noted, all North American prey recorded comprised Coleoptera. With respect to both regions the most commonly taken prey are species of Curculionidae, 40% and 48% of the species for which prey is known taking this family in the Afrotropical Region and in America north of Mexico respectively.

Cerceris is most unusual though not unique (see *Bembix*) in the Sphecidae in provisioning with prey belonging to more than one order, with, as has been shown, a majority of species utilizing Coleoptera and a minority utilizing Hymenoptera. It is therefore of interest to examine which of these two orders constitutes the original prey taken by the genus.

Suggested relationships within the subfamily Philanthinae based entirely upon consideration and evaluation of morphological characters of presumed phylogenetic value have been discussed by Bohart and Menke (1976: 557–558) and shown by them in a dendrogram (Fig. 183). On the basis of the number of advanced characters appearing in each genus, *Cerceris* is seen as a highly advanced genus, surpassed only by the North American *Eucerceris*.

If on Bohart and Menke's dendrogram are entered details of the prey for each of the included genera (unknown for *Eremiasphecium, Odontosphex* and *Philanthinus*) it is seen that the species of Philanthinae prey pre-eminently upon Hymenoptera and that only *Cerceris* (partly) and *Eucerceris* (wholly) prey upon Coleoptera.

It therefore appears that within the Philanthinae the use of Hymenoptera as prey is primitive or unspecialized and that the use of Coleoptera is advanced or derived. In this case *Cerceris* in its prey selection represents the transitional stage between the less advanced condition and that shown by *Eucerceris*. In this connection Pagden's record (see Bohart and Menke, 1976: 576) of *C. langkasukae* carrying a hymenopteran although her regular prey were Buprestidae may represent atavistic behaviour in time of shortage of the coleopterous prey.

The change from Hymenoptera to Coleoptera by *Cerceris* can be shown to have been advantageous for two reasons. Firstly, it enabled that fraction which made the change to avoid competition with related genera (e.g. *Philanthus*) and possibly others (e.g. *Palarus*) for hymenopterous prey, and secondly, it made available to *Cerceris* as potential prey vast numbers of species of many families belonging to an order which at least in its adult stage was not being exploited by any other wasps.

The vast possibilities opened up by the adoption of the new prey may be considered to have led to an outburst of speciation in the fraction of *Cerceris* concerned, leading to the predominance of Coleoptera-preying species over Hymenoptera-preying species and to the overall magnitude of the genus *Cerceris*, which with a total of over 850 known species (Bohart and Menke, 1976: 575) is the largest genus of the Sphecidae.

Within the range of Coleoptera preyed upon, the most commonly taken by *Cerceris* appear to be species of Curculionidae and species of this family constitute the sole prey of *Eucerceris*. The preference for weevils may be attributable to the overwhelmingly greater number of species in the Curculionidae than in other families.

With respect of those Philanthinae which utilize Hymenoptera as prey, some interesting trends relevant to the prey taken by the various genera are apparent. Thus the sole recorded prey for *Pseudoscolia* and the most characteristic prey of *Trachypus, Philanthus* and the Hymenoptera-preying species of *Cerceris* are species of Halictidae though species of all three latter genera may also utilize other families of bees as well as wasps of several aculeate and non-aculeate families. On the other hand prey taken by three of the four genera of the Aphilanthopsini (prey is not known for the fourth genus) consists in each case of a single genus of Formicidae.

It is clear that the genera of the Aphilanthopsini are greatly specialized in their choice of prey (as is indicated also by the presence in *Clypeadon* and *Listropygia* of an "ant clamp" formed of

the pygidial plate and the hypopygium) whereas the other genera represent the more unspecialized or primitive condition. In those species which utilize a wide spectrum of prey, the prey taken at any locality or time is probably dependant upon its abundance in the area and upon its size relative to the provisioning wasp. The frequency with which Halictidae are taken by species of *Trachypus, Philanthus* and the Hymenoptera-preying *Cerceris* species is undoubtedly due to the commonness of species and individuals of this bee family. There does, however, appear to be a tendency towards restriction in the range of prey taken. This may be seen in those of the Hymenoptera-preying *Cerceris* occurring at Hilton for which a number of prey records is available. Thus, in contrast to *C. holconota* for which six families including Halictidae are recorded as prey, *C. spinicaudata* appears to be restricted to Halictidae and *C. rufocincta polychroma* appears to specialize in Tiphiidae and Mutillidae.

Finally, from the fact that both Hymenoptera- and Coleoptera-preying species of *Cerceris* occur in the Old World but only Coleoptera-preying forms occur in the New World it may be speculated that *Cerceris* was originally an Old World Genus.

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