SEXUAL DIMORPHISM IN THE SWEET POTATO WEEVIL, *CYLAS FORMICARIUS* (F.) (COLEOPTERA: BRENTIDAE)

CHRISTOPHER K. STARR[1] and DAVID D. WILSON[2]
Department of Horticulture, University of Georgia, Athens, Georgia, USA 30602

RAY F. SEVERSON[3]
Tobacco Quality and Safety Research Unit, USDA-ARS, Athens, Georgia, USA 30613

and STANLEY J. KAYS
Department of Horticulture, University of Georgia, Athens, Georgia, USA 30602

Abstract

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Cylas formicarius (F.) shows a strong overall sexual monomororphism, with external differences noted in only three organs: (*a*) relative size of the hind wings; (*b*) form of the antennal club and numbers of its different types of sensillum; and (*c*) size of the compound eyes and their individual facets. We relate these to known or predicted behavioural differences. Eye dimorphism is used to test a theoretical rule on the relationship between differences in overall eye size and in the size of individual ommatidia. Some sexually monomorphic features are briefly discussed, including two types of putatively sensory hairs not found on the antennae.

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Résumé

Dans l'ensemble, un monomorphisme sexuel bien évident prévaut chez *Cylas formicarius* (F.) et seulement trois organes externes diffèrent chez les mâles et les femelles, (*a*) la taille relative des ailes postérieures, (*b*) la forme de la massue antennaire et le nombre des différents types de sensilles qui s'y trouvent, (*c*) la taille des yeux composés et de leurs facettes. Nous avons pu établir la relation entre ces caractéristiques et les différences de comportement que l'on suppose en découler. Le dimorphisme des yeux a servi à éprouver un concept théorique sur la relation entre les différences dans la taille des yeux et dans la taille des ommatidies qui les composent. Certaines caractéristiques monomorphes sont examinées brièvement, notammment deux types de poils probablement sensoriels qui ne se trouvent pas sur les antennes.

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Introduction

Cylas is a paleotropical genus of about 25 known species that form a distinctive group within the superfamily of weevils (Coleoptera: Curculionoidea: Brentidae: Cyladinae) (Wolfe 1991; Thompson 1992). A preliminary phylogenetic analysis posits *C. formicarius* (F.) as the sister group of the rest of the genus (Wolfe 1991). This oligophagous species feeds and breeds on *Ipomoea* spp. and other Convolvulaceae (Austin 1991). It has spread throughout much of the world and is the foremost pest of the sweet potato, *Ipomoea batatas* (L.). Because of its economic importance, *C. formicarius* has been subject to much research, including several basic bionomic studies (Sutherland 1986, and references therein).

The adult *C. formicarius* is slender, smooth, and hard-bodied (Figs. 1, 2). Both sexes are functionally winged and active. Although external differences between them are slight, with practice the sexes can be distinguished without magnification. Both are apparently mainly nocturnal, with males more vagile than females (Deen 1940; Howard 1982; Proshold

1983). Females emit a pheromone attractive to males (Louton 1975; Coffelt et al. 1978; Heath et al. 1986).

There have been two major treatments of adult morphology in *C. formicarius*, one in the style of a taxonomic description (Gonzales 1925) and the other in the morphological style of Snodgrass (Ahmad 1964). Neither includes explicit comparison of the sexes, nor were they done with the benefit of scanning electron microscopy, although Gonzales showed remarkable detail in the antennae.

Because external sexual dimorphism in *C. formicarius* is limited to a very few organs, the prospects for relating behavioural differences to particular physical differences seem unusually good. Our main purpose here is to lay the groundwork for such correlations.

Materials and Methods

Our material of *C. formicarius* was all of the "*elegantulus*" colour form, previously treated as a distinct taxon but placed in synonymy by Wolfe (1991). Voucher specimens of this species and *C. puncticollis* (Boh.) are deposited in the University of Georgia's Museum of Natural History and the personal collection of G. William Wolfe. The wing-loading comparison is based on field-caught specimens up to 5 weeks old from southern Florida, USA. All other description is based on laboratory-reared specimens.

Fresh weight was taken from newly frozen individuals. To measure hind wing length and area, elytron length, and head length, we made tracings with a camera lucida on a dissecting microscope. Linear measures were taken from these drawings with an ordinary scale, and hind wing area was determined by running cutout drawings through a leaf-area meter. Elytron length is expressed as the distance from the base of the costal vein to the farthest wing tip.

To count ommatidia, we made camera lucida drawings of one eye from each of 15 females and 15 males, marking the position of each facet. To estimate density, we counted facets in sample areas in the middle part of the drawing. Facet number and density were then used to estimate surface area of the eye. Facet size appears close to uniform in different parts of the eye, and curvature appears regular and similar in females and males.

All other measurements are from SEM graphs made on a Philips 505 scanning electron microscope. Freeze-killed specimens were cleaned in an ultrasonic cleaner for about 2 min, air-dried for at least a day, and coated with 60 nm of gold palladium. Most scans were at 20 kV with spot sizes of 20 and 50 nm.

Results

Wings. The hind wings are well developed, with no obvious differences between those of females and males. In comparing wing loading, i.e. body weight per unit area of the flying wings, we applied five measures (Table 1). Elytron length and head length were chosen as separate indices of overall body size. Given the extensive folding of the hind wings, it is reasonable to treat the size of elytra as independent of hind wing length or area.

TABLE 1. Weight, hind wing size, and indices of overall body size in adult *Cylas formicarius*. Sample sizes are for each sex. Figures are means ± 2 SE

	Fresh weight (mg) $n = 16$	Hind wing area (mm^2) $n = 16$	Hind wing length (mm) $n = 16$	Head length (mm) $n = 12$	Elytron length (mm) $n = 12$
Females	5.3 ± 0.44	6.3 ± 0.42	5.0 ± 0.16	1.9 ± 0.04	3.1 ± 0.06

The average area of the hind wing is greater in males than in females (*t*-test for two means; $p < 0.05$), but we found no significant sexual difference in any of the other four measures ($p > 0.05$). Wing loading is significantly greater in females than in males ($p << 0.01$; all comparisons of ratios use a *t*-test of arcsine-transformed values), as is variance in wing loading. Similarly, the length ratios of hind wing:elytron and hind wing:head are each less in females ($p = 0.005$ and 0.001, respectively).

We found no convenient direct measure of hind wing width. However, the ratio of the square root of wing area to wing length is significantly greater in males than in females ($p = 0.001$), indicating that males have relatively broader wings for use in flight.

Antennae. Each 10-segmented antenna is about 1.2–1.3 mm long in the female and 1.6–1.7 mm in the male. It comprises a simple scape, a funicle of eight fairly uniform segments, and a one-segmented terminal club (Fig. 2). Neither the funicle nor club shows notable dorsoventral or anterioposterior differentiation, so that the following description applies equally to all sides.

The surface of the scape and funicle is covered with reticulating ridges (Fig. 7). Similar reticulation is found on parts of the head, much of the tibiae and tarsi, and a short (0.04–0.06 mm) basal ring of the club. Funicular segments have a maximum diameter of about 0.11 mm in both sexes. However, they are shorter in males, so that the entire funicle has a length of about 0.50 mm, compared with about 0.61 mm in females.

The most striking gross difference in the antennae is in the shape of the terminal club. In the female the club is a long ovoid (Figs. 2, 3), about 0.45–0.50 mm long and 0.21–0.22 mm wide in the middle. Aside from the basal ring, its surface is relatively smooth except around the bases of hairs. The male club is cylindrical (Fig. 4), 0.95–1.10 mm long and 0.16–0.17 mm wide in the middle. Aside from the basal ring, it is covered with short, low longitudinal ridges, giving it a rugose appearance.

Three distinct types of sensory hairs are found on the antennae. These and the other two types described below are usually 2.5–4.0 μm thick along the middle part of the hair.

Type I hairs (Fig. 5) are usually enclosed at the base in a short sleeve. They are semi-recumbent, rising in a low, even curve, with a smoothly round shaft and pointed tip (Fig. 8). Type II hairs (Fig. 6) are similarly sleeved at the base, with the sleeve usually extending about 2–3 μm from the substrate surface. They are distinctly longer than types I and III and rise in a low S-shaped curve which projects farther and ends in a rounded tip (Fig. 9). Type III hairs (Figs. 5, 7) are more loosely held at the base, with at most a very short sleeve. Like type I, they are semi-recumbent, but the shaft is sculptured with low, longitudinal ridges. Their most salient feature is a truncate tip, with round lobes projecting along the rim (Fig. 10).

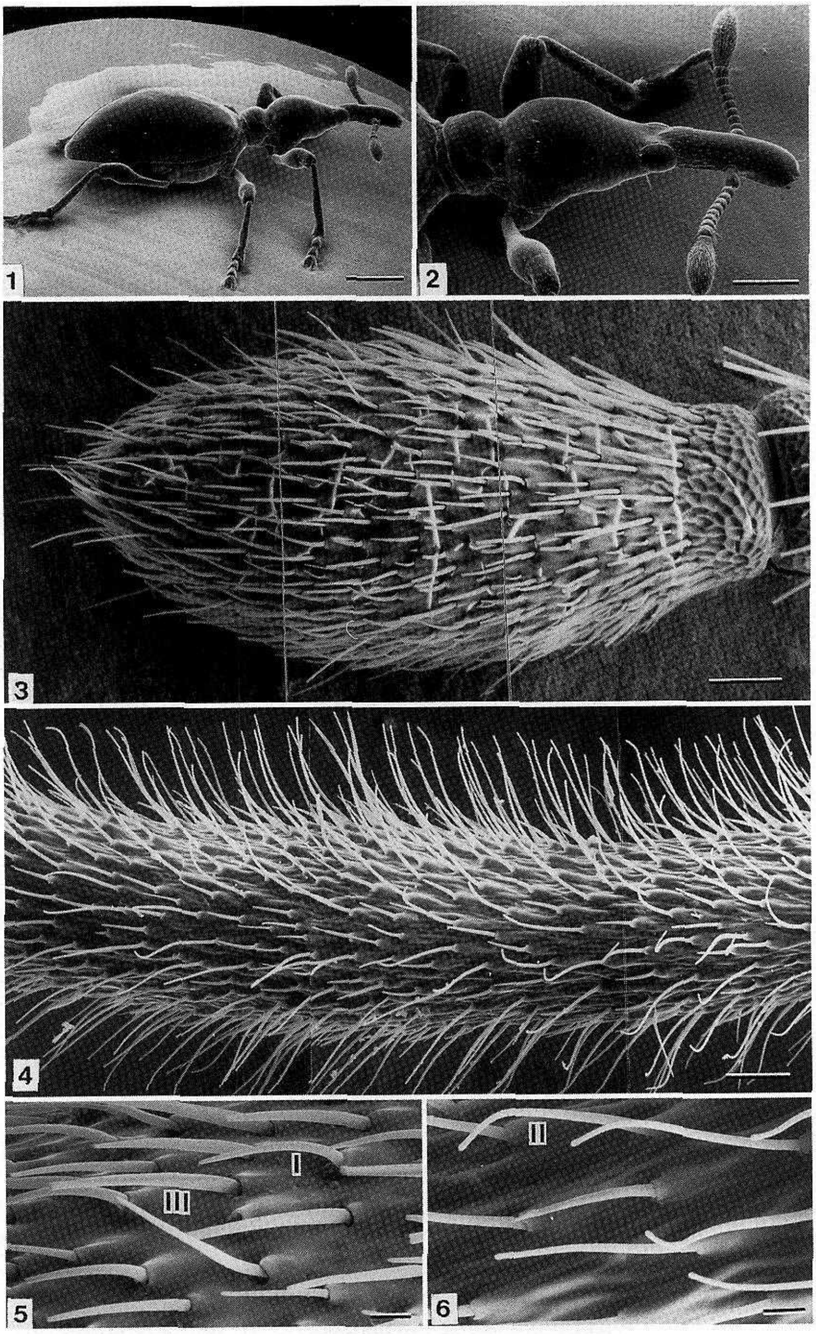
These and other features of the different sensory hair types are summarized in Table 2. It is perplexing that we could not find pores along the sides or terminally in any of them, even scanning apparently very clean specimens at 40 000×.

Only type III hairs are found on the scape and funicle. They form a single ring of about 12 hairs around the middle of each funicular segment. They are also sparse on the scape and not so regularly arranged.

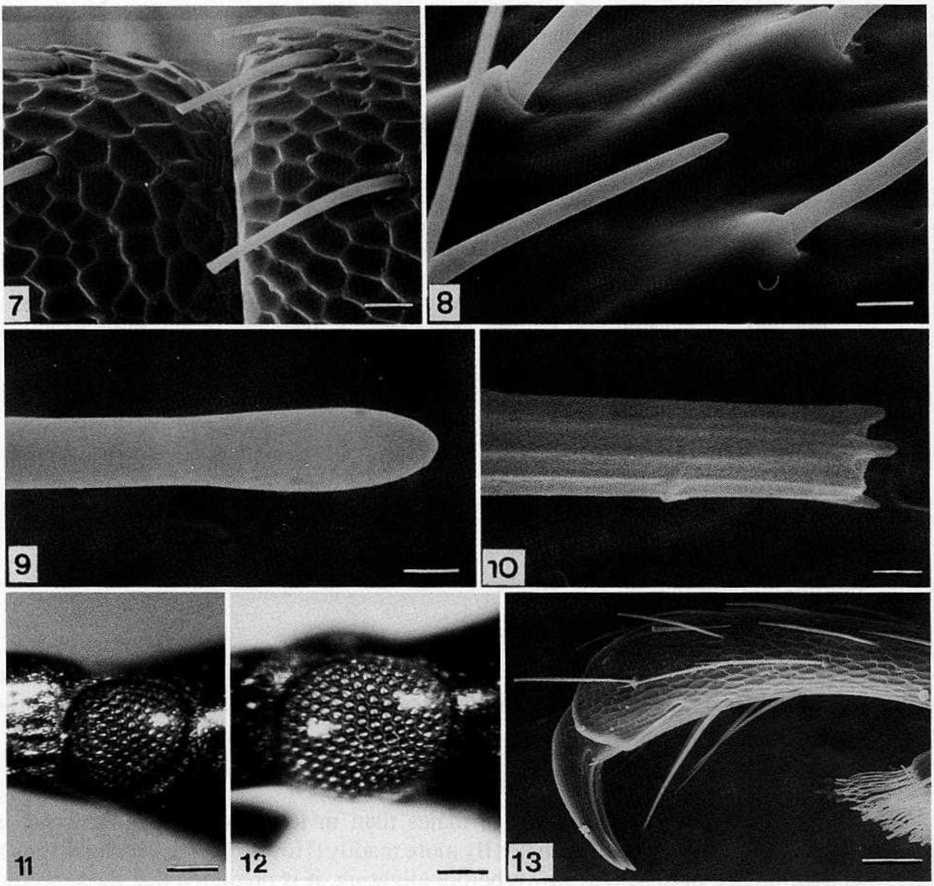
As seen in Figures 3 and 4 and Table 3, there is a clear sexual dimorphism in the representation of different hair types on the antennal club. The mass of long, projecting, type II hairs gives the male antenna its overall fuzzy appearance.

Eyes. The compound eye surface is quite smooth, so that facets are obscured in coated specimens. Males have strikingly larger eyes, more ommatidia, and somewhat larger facets than females (Figs. 11, 12). Eye dimensions are summarized in Table 4.

Other Features. Some sexually monomorphic features of *C. formicarius* merit comment. The cuticle is smooth and shiny over most of the body, not clothed in scales but with a sparse



FIGS. 1–6. *Cylas formicarius*: 1, female, scale bar = 1 mm; 2, head and prothorax of female, scale bar = 0.5 mm; 3, terminal antennal club of female, scale bar = 0.05 mm; 4, middle part of terminal antennal club of male, scale bar = 0.05 mm; 5–6, surface details of terminal antennal club of female (5) and male (6), Roman numerals indicate examples of the three sensory hair types, each directly above the numeral, scale bars = 0.01 mm.



FIGS. 7–13. *Cylas formicarius*: 7, details of antennal funicle, to show surface sculpture and the ring of type III hairs on each segment, scale bar = 0.01 mm; 8–10, details of sensory hairs on antennal club [8, tip and bases of type I hairs, scale bar = 5 μm; 9, tip of type II hair, scale bar = 1 μm; 10, tip of type III hair, scale bar = 1 μm]; 11–12, compound eyes of female (11) and male (12), scale bar = 0.1 mm; 13, tarsal segment 5, in side view, to show truncate type III hairs above and sharply pointed type IV hairs below, scale bar = 0.05 mm.

covering of short (about 23–28 μm), acute, semi-recumbent hairs. Their presence on the elytra in about the same density as over the rest of the body suggests that they are not sensory.

Both females and males have functional walking legs, with little difference between pairs. Tarsal segments 1–3 have footpads of long, erect hairs. These are especially prominent on segment 3, which is strongly lobed below. As noted above, the cuticle of the tibiae and tarsi is largely of the rugose-reticulate type found on the antennal scape and funicle. The tibiae and tarsi likewise have a sparse scattering of type III hairs above. The 5th tarsal segment below has three pairs of longer, sharply pointed hairs designated as type IV (Fig. 13; Table 2), with usually another two along each side. At least some of these project away from the surface more than do type III hairs.

We found no sexual differences in the mouthparts. At each outer corner of the labrum and toward each hind corner of the labium is a pair of very long hairs. These resemble type IV hairs, but their curve is less regular, as in type II hairs. For present purposes we designate them as type V (Table 2).

TABLE 2. Features of putatively sensory hairs of *Cylas formicarius*. All lengths are means from at least eight hairs

Type	Length	Shaft surface	Base	Tip	Locations
I	40 µm	Smooth	Usually with a definite sleeve	Pointed	Antennal club
II	87 µm	Smooth, rounded	With a pronounced sleeve	Rounded	Antennal club
III	52 µm (antenna) 95 µm (legs)	With low longitudinal ridges	With at most a low, loose sleeve	Truncate, outer rim lobed	Antennal funicle, antennal club (female), tibiae and tarsi above
IV	120 µm	Nearly smooth	With a slight sleeve	Sharply pointed	Tarsal segment 5 below and at sides
V	104 µm	Apparently smoothly rounded	With no sleeve	Tapering to sharp point	Two pairs on labium, two pairs on labrum

A brief overview of another species, *C. puncticollis*, showed no notable gross-structural differences from *C. formicarius*. Sexual dimorphism of the antennae and eyes is much the same in the two species.

Discussion

The finding of lower wing loading in males than in females of *C. formicarius* is consistent with indirect evidence that males fly more readily (Howard 1982; Proshold 1983). If there is a difference in distances flown before alighting, it is predicted that those would likewise be greater in males. The difference in wing loading is not, evidently, a simple result of different average body densities, e.g. a result of gravid females in the sample. Neither fresh weight nor overall body size differs significantly between the sexes, and males have longer hind wings relative to each of the two body size indices.

At least 21 species of curculionoid beetles have been the subject of SEM studies, with special attention to the antennae (Borden and Wood 1966; Borden 1968; Moeck 1968; Borg and Norris 1971; Mustaparta 1973; Payne et al. 1973; Hatfield et al. 1976; Smith et al. 1976; Dickens and Payne 1978; Bland 1981; Whitehead 1981). Moeck (1968) reported moderate sexual dimorphism in the shape of the antennal club and total number of sensilla in *Trypodendron lineatum* (Olivier) (Scolytidae). Otherwise, if both sexes were studied, the authors either stated or implied that they were much the same. *Cylas formicarius*'s marked sexual dimorphism in the antennae and eyes, together with measurable dimorphism in the hind wings and apparent monomorphism in all other external features, represents a marked

TABLE 3. Mean numbers of types I, II, and III sensory hairs on the antennal club in *Cylas formicarius*. Based on counts from one side of one antenna in each specimen

	Type I	Type II	Type III	Total
Female ($n = 3$)	292	48	159	499
Male ($n = 2$)	230	702	12	944

TABLE 4. Compound eye dimensions in *Cylas formicarius*, given as means ± 2 SE. Facet and eye size are linear indices expressed as the square roots of their respective areas. Eye surface area is estimated from the number and mean area of facets

	Ommatidia per eye	Facet area (μm^2)	Facet size	Eye area (mm^2)	Eye size
Female ($n = 15$)	128 ± 4	527 ± 14	22.9 ± 0.4	0.067 ± 0.003	0.259 ± 0.006
Male ($n = 15$)	185 ± 10	840 ± 61	28.9 ± 1.0	0.156 ± 0.015	0.393 ± 0.018

departure from this pattern. If *C. formicarius* is the sister group of the rest of its genus (Wolfe 1991), then the similar pattern of sexual dimorphism in *C. puncticollis* indicates that this is part of the groundplan for *Cylas*.

As in other curculionoids studied, the antennal sensilla in *C. formicarius* are concentrated on the terminal club, although in a simpler pattern than in most. Sensilla are not arranged in distinct zones or bands in *C. formicarius*, and the three types found on the antennae are fewer than in other studied genera. Furthermore, the three types of unbranched hairs are relatively similar to each other. Where counts of antennal sensilla are reported from other curculionoids (Moeck 1968; Hatfield et al. 1976; Dickens and Payne 1978; Bland 1981), they are comparable to what we report for the males and about double or triple that for the females of *C. formicarius*.

Although the structural differences between antennae of females and males are clear, their functional significance is not. It is not certain whether or not type III hairs are flexibly socketed, but types I and II evidently are not. On the assumption that the antennae and tarsi are mechanoreceptive, we suggest that mechanoreception is among the functions of type III hairs. It is perplexing that we did not find pores—indicative of an olfactory function (Chapman 1982; Zacharuk 1985)—on any hair type, even though it seems certain that some must have this function. As noted by Chapman (1982), male insects often have many more olfactory sensilla on the antennae than do females and are attracted to females by volatile pheromones. Given such attraction in *C. formicarius* (Louton 1975; Coffelt et al. 1978; Heath et al. 1986) and the presumption that females require superior taste discrimination for the choice of oviposition sites, together with the observed sexual differences in numbers of type I and type II hairs, we conjecture that the first are gustatory and the second olfactory.

In form and placement, type IV hairs closely resemble others shown to be mechanoreceptive in two chrysomelid beetles (Stürkow and Quadbeck 1958; Stürkow 1959; Rees 1969).

The greater number of ommatidia and greater individual facet size in males gives them about twice the total eye area of females (Table 4). The small size of insect eyes imposes severe constraints on both light-gathering capacity and resolving power, resulting in differences between eyes of differing size. Analysis of the built-in design conflict between resolution and sensitivity has led to scaling rules for compound eyes and their component ommatidia (Land 1981, 1985; Wehner 1981). An overall enlargement of the eye can produce an increase in either resolution or sensitivity or a compromising increase in both. Improved resolution is relatively more "expensive" than improved sensitivity, which varies approximately in proportion to outer surface area (Land 1981, 1985). A broadening of individual ommatidia requires that their number be increased if the eye's overall resolving power is to be maintained. Specifically, for similar eyes the scaling rule predicts that the linear size of individual facets varies according to the square root of linear size of the eye surface as a whole. Comparisons between species corroborate this rule (Land 1981, 1985; Wehner 1981). Sexual eye dimorphism in *C. formicarius* allows the first within-species test of this expected

For present purposes, the scaling rule may be formulated as the hypothesis that the ratio of linear size of the eye to number of facets is equal in females and males. A comparison of means of this ratio (Table 4) shows only a 5% difference between the sexes (*t*-test of arcsine-transformed ratios; $p = 0.66$). The rule is thus corroborated. Accordingly, females and males are expected to have similar resolving power, but male eyes should be more sensitive. This is consistent with observations that males are most active in dim light and are more vagile (Howard 1982; Proshold 1983). It also predicts that sexual differences in flight activity will be most marked in dim light.

Cylas formicarius shows moderate within-sex variation in eye dimensions. This suggests either that (*a*) the scaling rule likewise applies within a sex, in which case individuals with larger facets should have more of them, or (*b*) there is a tendency toward standardization of overall eye size, in which case the opposite is expected. Regrettably, the rank correlation coefficients for facet area and facet number in our samples are too low (−0.09 for females and 0.13 for males) to allow us to discriminate against either prediction.

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