

Mating behaviour of *Staminodeus vectoris* (Coleoptera: Curculionidae), and the value of systematics in behavioural studies

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The mating behaviour of *Staminodeus vectoris* Franz (Curculionidae: Curculioninae: Derelomini) is described and discussed in light of a phylogeny of *Staminodeus* Franz. At La Selva, Costa Rica, *S. vectoris* is associated with the staminodes of the inflorescences of *Asplundia uncinata* Harling and several other species of Cyclanthaceae. The males have a row of 6–10 teeth along the margin of the protibia, whereas the females have a small, curved spine on the frons. The adults arrive in numbers at the inflorescences during the pistillate phase of the anthesis of *A. uncinata*, feeding on the staminodes. Eventually, a female detaches a staminode with her mandibles, falls to the ground, and transports it to the site of oviposition in the leaf litter. First, she crawls underneath the staminode, then moves it posteriorly with her legs, and finally returns to its distal end before repeating the process. The female turns on her back and maintains her original position during the movement of the staminode, using her frontal spine as a point of resistance against the substrate. Meanwhile, a male associates with the staminode. The males fight with their prothoracic legs, executing fast blows until their protibial teeth cling and dislodge competitors from the staminode. The positive and negative allometries of the lengths of the male protibia and female spine, are consistent with their functions in the contexts of sexual and natural selection, respectively. The phylogeny of all seven species of *Staminodeus* hypothesises that female transporting behaviour evolved before male fighting behaviour.

KEYWORDS: beetle horns, Cyclanthaceae, Derelomini, mating behaviour, morphology, sexual selection, systematics.

Introduction

Biologists have been fascinated by 'horns' in Coleoptera, and have discussed their function within the context of sexual selection, since the writings of Darwin (1871: 370–378). Arrow (1951) presented the first comprehensive study of these conspicuous modifications, documenting their predominance in males. He concluded

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that they evolved as by-products of allometric growth in body size. Over the past 25 years, however, behavioural observations of several species of horned beetles have become available, along with better-corroborated hypotheses of their adaptive function (see e.g. Eberhard, 1980; Eberhard and Gutiérrez, 1991, Andersson, 1994). Using the terminology of Kuhn (1996), the majority of contemporary studies of beetle horns are conducted under the paradigm that they have evolved and function as weapons in contests among males over females. This includes recent efforts to integrate development with evolution at the level of individuals and populations (Emlen, 2000).

Here I present field observations on the mating behaviour of *Staminodeus vectoris* Franz (Curculionidae: Curculioninae: Derelomini *sensu* Alonso-Zarazaga and Lyal, 1999) that are consistent with the paradigm of weapons functioning in contests among males (i.e. sexual selection). In addition, I emphasise the utility of morphology and systematics in behavioural studies of horned beetles. My arguments complement those by Wenzel (1992) and subsequent authors (e.g. de Quieroz and Wimberger, 1993; Greene, 1994; Wainwright and Friel, 2001) who have discussed the importance of systematics as a means for reconstructing the evolution of behaviour. I begin by reviewing three sources of bias in our knowledge of horns as weapons in beetles.

The first source of bias is related to *taxonomy*. To provide an example, many more observations are available for species of Scarabaeidae, which are often identifiable and comparatively large, than for *Geraeus* Pascoe (Curculionidae: Baridinae: Madopterini), a taxon of small, horned weevils with over 60 species in Mexico alone (O'Brien and Wibmer, 1982). This bias is corroborated by a brief review of the literature on male weapons within Curculionidae (*sensu* Alonso-Zarazaga and Lyal, 1999) in the Neotropics. The two published observations are on *Macromerus bicinctus* Champion (Cryptorhynchinae, with 3487 species in the Neotropics in 1971, species numbers according to O'Brien and Wibmer, 1978) by Wcislo and Eberhard (1989), and on *Parisoschoenus expositus* (Champion) (Baridinae, with 2968 species) by Eberhard and García-C. (2000). Within Curculionoidea (with 12,962 species in the Neotropics), three additional reports have been published on *Cleogonus rubetra* (Fabricius) (Curculionidae, Polak and Brown, 1995), *Rhinostomus barbirostris* (Fabricius) (Dryophthoridae, Eberhard, 1983), and *Brentus anchorago* (Linnaeus) (Brentidae, Johnson, 1982). Allometric horn growth is known from *Centrinaspis* sp. (Baridinae, Eberhard and Gutiérrez, 1991). However, *P. expositus* is the only curculionoid taxon for which the morphology *and* function of horns have been studied in detail (Eberhard *et al.*, 2000). This despite the fact that hundreds of species of Curculionoidea with presumable male weapons are present in research collections (O'Brien, personal communication).

The previous review on Curculionoidea suggests that our knowledge of horned beetles has been and will be restricted to taxonomically accessible, and often large, taxa. Similar arguments could be made by contrasting Scarabaeoidea with Staphyliinoidea or Tenebrionoidea. These biases are likely to persist, considering e.g. the current funding policy for systematics in the USA (Wheeler, 1995), and the geographic concentration of taxonomic research in temperate regions (Cotterill, 1995). This is not to say that additional behavioural studies are likely to reject the hypothesis that beetle horns have evolved and function predominantly as weapons in male contests. But, as will be presented below, the 'horns' in females of *S. vectoris* do not function in this context.

Another source of bias is reflected in an emphasis of function over *homology*.

This is apparent from oversimplifications like the following: '(d)espite this diversity, all beetle horns are used for basically the same thing' (Emlen, 2000: 404). Such statements should be contested by making homology assessments among beetle horns. That horns in Curculionidae and Scarabaeidae have evolved by convergence becomes obvious from comparing the plates in Arrow (1951). Because their morphologies are different from the perspective of common ancestry, studying them separately has logical priority over assuming the same function for all. The levels of homology among beetle horns have yet to be tested with the methods of systematics. And, as has been argued recently, the beetle horn homologies under study have to be included in the cladistic matrices in order to be optimized on the resulting cladograms (Miller and Wenzel, 1995; Grandcolas *et al.*, 2001; McDonald, 2001).

The last source of bias is related to the utility of *phylogeny* in behavioural studies. The precision of questions about processes increases when knowledge of pattern exists (Platnick, 1979). Following this basic tenet, it becomes apparent that our current interpretation of beetle horn evolution will be affected by the pattern of origins, transformations, and losses of horns. Many questions about selection and function could be answered at this pattern level (O'Hara, 1988). Maybe the scepticism that systematists maintain about evolutionary generalizations is founded in part in their extensive knowledge of the diversity of patterns. However, evolutionary history is unique and therefore not amenable to the language of statistics (Wenzel and Carpenter, 1994). Determining whether or not the majority of beetle horns have evolved and function as weapons in contests over females is secondary—logically and chronologically—to the discovery of the *pattern* of beetle horn evolution.

The previous arguments will be substantiated here with a detailed account of the mating behaviour of *S. vectoris*, in light of a phylogeny of *Staminodeus* Franz. *Staminodeus vectoris* (figure 1a) is a small, derelomine weevil (length 1.6–2.3 mm, $n=30$) that occurs in Costa Rica and Panama (Franz, 2001). Six additional species of *Staminodeus* have been described from Colombia, Costa Rica, Ecuador, Panama, and Venezuela. Apparently, all of them are associated with the staminodes of the inflorescences of Cyclanthaceae. The males of *S. vectoris* have a row of 6–10 teeth along the anteroventral margin of the protibia (figure 1b). The females lack this character, but present a small, curved spine (or 'horn') on the frons (figure 1c).

Based on field observations at La Selva, Costa Rica, the morphology and function of both modifications during the mating behaviour of *S. vectoris* are reported here, along with notes on the anthesis of one of its host plants, *Asplundia uncinata* Harling (Franz, 1999).

Methods

The present study was conducted at the wet tropical forest of the Estación Biológica La Selva (Organización para Estudios Tropicales, OET), Provincia Heredia, Costa Rica (10°26'N, 83°59'W, c.40 m above sea level), from May to October 1998 (Franz, 1999). *Asplundia uncinata* is a terrestrial cyclanth species, c.1.5 m tall, forming dense aggregations in the understory of La Selva (Hammel, 1986), and flowering with fluctuating intensity levels from March to December. Its inflorescence is a monoecious spadix and covered by several spathes (figure 2a). The unisexual flowers are arranged in a regular chessboard mosaic and form a spiral along the central rachis. Four staminate flowers surround and project beyond each pistillate flower, resulting in reticulate spaces above the stigmas. The filiform staminodes of the pistillate flowers are the most conspicuous organs during anthesis. Oil

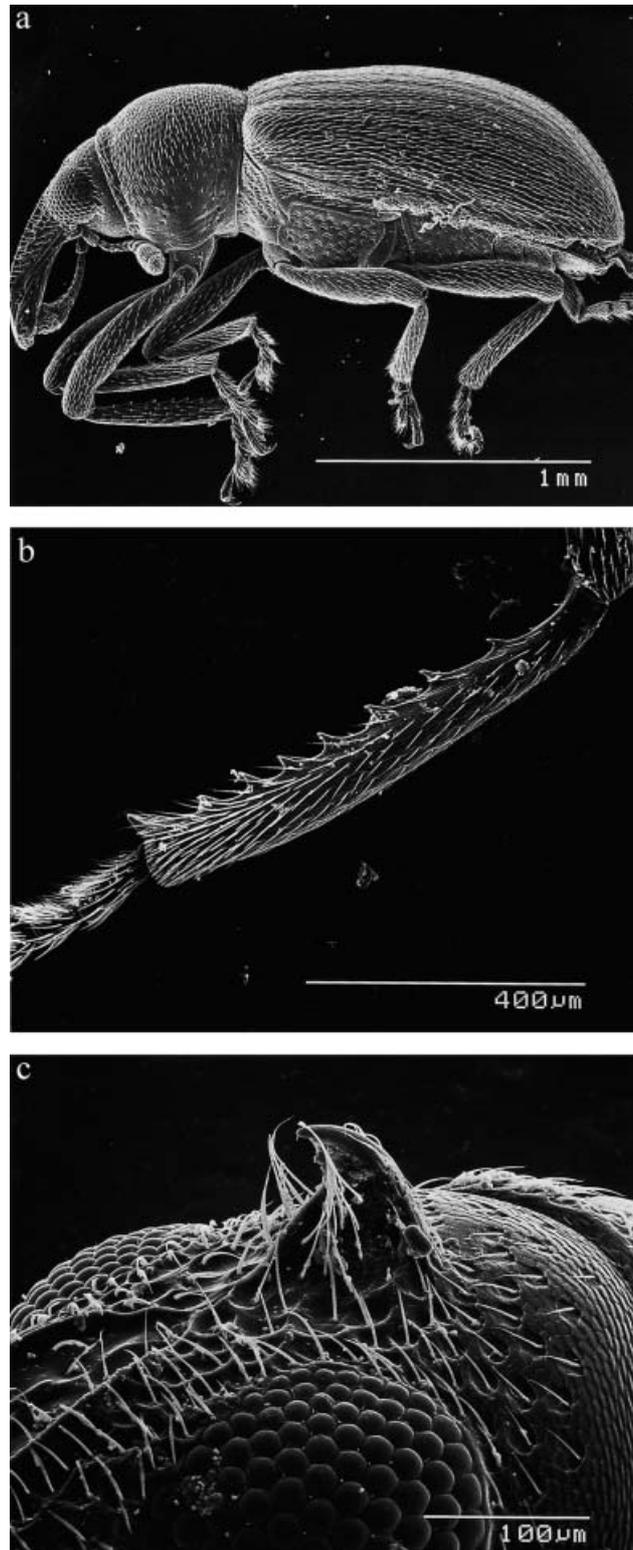


FIG. 1. *Staminodeus vectoris*, habitus: (a) male; (b) protibia of male; (c) spine on frons of female.

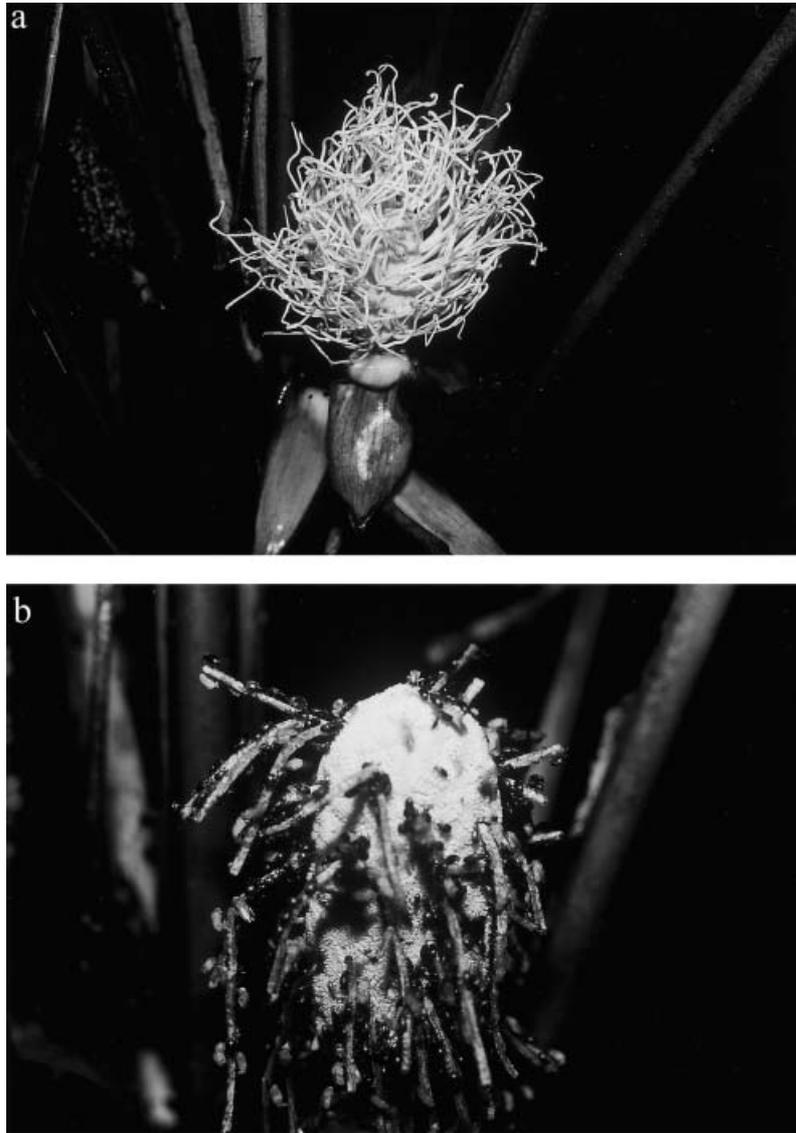


FIG. 2. Inflorescence of *A. uncinata*, pistillate phase: (a) at 03:30 a.m., approximately two hours before arrival of *S. vectoris*, spathes are deflected, staminodes are extended and fragrant; (b) at 06:30 a.m., approximately one hour after arrival of *S. vectoris*, staminodes have been detached by females, some individuals feed and attempt to copulate on remains.

glands may be present on the tepals of both flower types (Harling, 1958). *Asplundia uncinata* is protogynous, and displays facultative geitonogamy. Details on the reproductive biology of this species—and of its pollinator—will be reported elsewhere.

The observations on the mating behaviour of *S. vectoris* were made along the Camino Experimental Norte (CEN) and the Camino Experimental Sur (CES). The abundance of individuals on the inflorescences of *A. uncinata* was sampled by detaching the inflorescence—including the staminodes—with a blade, and collecting

it into a zip-loc[®] bag that was sealed immediately. Three sampling periods were selected: (1) 'pistillate phase', 05:30–06:30 a.m., first day of anthesis; (2) 'intermediate phase', 02:00–05:00 p.m., first day of anthesis; and (3) 'staminate phase', 05:00–08:00 a.m., second day of anthesis. In the laboratory, the individuals were transferred into alcohol at 95%. Initially, they were identified to morphospecies, according to codes by C. W. O'Brien (Florida A&M University, Tallahassee, Florida). Therefore, *S. vectoris* corresponds to 'gen. C2 sp. C1' in Franz (1999). For the purpose of analysing the samples, males and females were distinguished by their sexual dimorphisms, whereas teneral were distinguished from adults by their light colour (for details see Franz, 2001). The variations in abundance throughout the sampling periods, as well as in the ratios between males/females and teneral/adults, were analysed with a nonparametric Mann-Whitney test (Zar, 1999).

Over 20 hours of mating behaviour of *S. vectoris* were observed under a moderate light source, predominantly during the pistillate phase. In order to identify and sex the individuals, a 10 × hand lens was used in combination with a 3 × headband magnifier. Approximately five hours was recorded on video with a Sony CCD-FX 230 camcorder. The recordings were analysed frame by frame in the laboratory. All behavioural drawings were traced from the video images.

The morphometric variation was measured with a digital micrometer (Lasico XD) on a dissecting microscope (Wild M5A) at 50–100 × magnification (precision: 5 μm). The following measurements were made: (1) length of male protibia (from base to apex, $n=75$); (2) length of female spine (from base to apex, $n=75$); and (3) length of metepisternum of male and female (from anterior margin to posterior margin, $n=150$ for both sexes combined). Each specimen was measured in lateral view, while the alignment of the respective structure with the visual field resulted in maximum length (figures 6a and 6b). Assuming that the distributions of measurements were unimodal, the deviation from isometry (i.e. $y=Kx^2$, $b \neq 1.0$) was tested on log-transformed values by attempting to fit $y=K_0+K_1x+M$; where y is the natural log of the length of (1) the male protibia or (2) the female spine, x is the natural log of the length of (3) the metepisternum, $K_{0,1}$ are the regression coefficients, and M is the random component with normal variation, zero mean, and common variance (see e.g. Eberhard *et al.*, 2000). The significance of deviation from H_0 (1.0 = isometry) was tested by $t=(K-K_0)/s_K$; where s_K is the standard error of the regression coefficient (Zar, 1999).

Results

Anthesis of A. uncinata

The anthesis of *A. uncinata* has a duration of approximately 24 hours. The pistillate phase begins at 04:55–05:30 a.m. during the first day of anthesis, lasting 3–24 hours, whereas the staminate phase begins at 02:40–04:35 a.m. during the second day of anthesis, lasting 1–3 hours ($n=18$). The staminate flowers decay and detach from the maturing infructescence within 1–5 days after anthesis. In the course of anthesis, the inflorescence of *A. uncinata* displays thermogenesis during the pistillate phase (maximum: 5.5 ± 1.3 °C above ambient temperature, time of maximum: 04:15–05:50 a.m., $n=5$), and during the staminate phase (maximum: 5.2 ± 1.6 °C above ambient temperature, time of maximum: 03:55–04:55 a.m., $n=5$). The floral fragrances are perceptible to humans during the pistillate phase, approximately from 03:30 a.m. to 07:30 a.m. The intensity of volatilization appears

to be correlated with the thermogenesis, its maximum occurring between 05:00 a.m. and 06:00 a.m. The odour is produced by the staminodes and resembles a mixture of raspberry and lemon. The spathes and the staminodes are white, whereas the staminate flowers are pale-yellow (figure 2a).

Abundance of S. vectoris on the inflorescences of A. uncinata

Because the individuals of *S. vectoris* fall with the staminodes to the ground, their abundance on the inflorescences of *A. uncinata* (table 1) displays a significant decrease from the pistillate phase to the staminate phase ($p < 0.05$). They are absent from the inflorescences during the staminate phase. The ratios between males/females and between teneral/adults increase ($p < 0.025$ and $p > 0.05$, respectively).

Mating behaviour of S. vectoris

In addition to *S. vectoris*, three undescribed species of Derelomini are associated with *A. uncinata* at La Selva. All of them arrive from 05:15 a.m. to 06:45 a.m. during the pistillate anthesis, coinciding with the maximum thermogenetic temperature of the inflorescence. Apparently, both the size of the inflorescence and its white appearance increase the number of visitors (Franz, 1999). A species that keys to *Phyllotrox* Schönherr in Kuschel (1952: 271–273, key to Petalochilinae; *Phyllotrox* is probably not monophyletic, O'Brien, personal communication) enters the epistigmatic spaces and functions as the primary pollinator of *A. uncinata*. However, the adults of *S. vectoris* remain on the surface of the inflorescence, associating exclusively with the staminodes (figure 2b). Because they do not contact the stigmas, they do not function as pollinators.

After arriving at the inflorescence, many of the adults of *S. vectoris* immediately begin to feed on the staminodes. Those individuals involved in mating move with high velocity along these organs. Their movements are abrupt, difficult to follow with the eye, and comparable to species of *Mecopus* Schönherr (Curculionidae: Conoderinae: Mecopini), as described by Lyal (1986: 793–794). They change velocity, direction, and position rapidly, flying briefly from staminode to staminode. Therefore, the inflorescence appears 'crowded' and 'hectic' (figure 2b). Within subsequent hours, the mating activities are gradually transferred from the inflorescence to the ground. Other individuals display less activity, remaining on the ephemeral staminodes where they feed and rest. Very little activity occurs from 08:30 a.m. until the next day when other inflorescences are in pistillate phase.

Table 1. Total abundance, ratios between males/females and between teneral/adults of *S. vectoris* on the inflorescences of *A. uncinata* during the pistillate, intermediate, and staminate phase of anthesis. Mean values are listed \pm standard deviations.

	Total abundance (range)	Ratio of males/females (range)	Ratio of teneral/adults (range)
Pistillate phase ($n = 40$)	66.1 ± 199.0 (5–1241)	$45.7 \pm 11.1\%$ (25.0–67.7%)	$30.8 \pm 19.6\%$ (2.0–73.3%)
Intermediate phase ($n = 15$)	17.2 ± 19.8 (0–75)	$61.2 \pm 20.3\%$ (33.3–100.0%)	$47.0 \pm 27.7\%$ (13.3–100.0%)
Staminate phase ($n = 15$)	0.0 (0)	–	–

Shortly after arrival, the sexually active females begin to search for an appropriate staminode (figure 3a), before detaching it from the inflorescence, and transporting it to the site of oviposition in the leaf litter—while making use of the spine on the frons (see details below). During the search, a female moves up and down a section of a staminode and probes it at various times with her mouthparts. This activity lasts from seconds to minutes, as she typically rejects those staminodes damaged by previous visitors. Such damage is caused by feeding, oviposition, and larval development of another undescribed species of Derelomini that infests the staminodes *before*

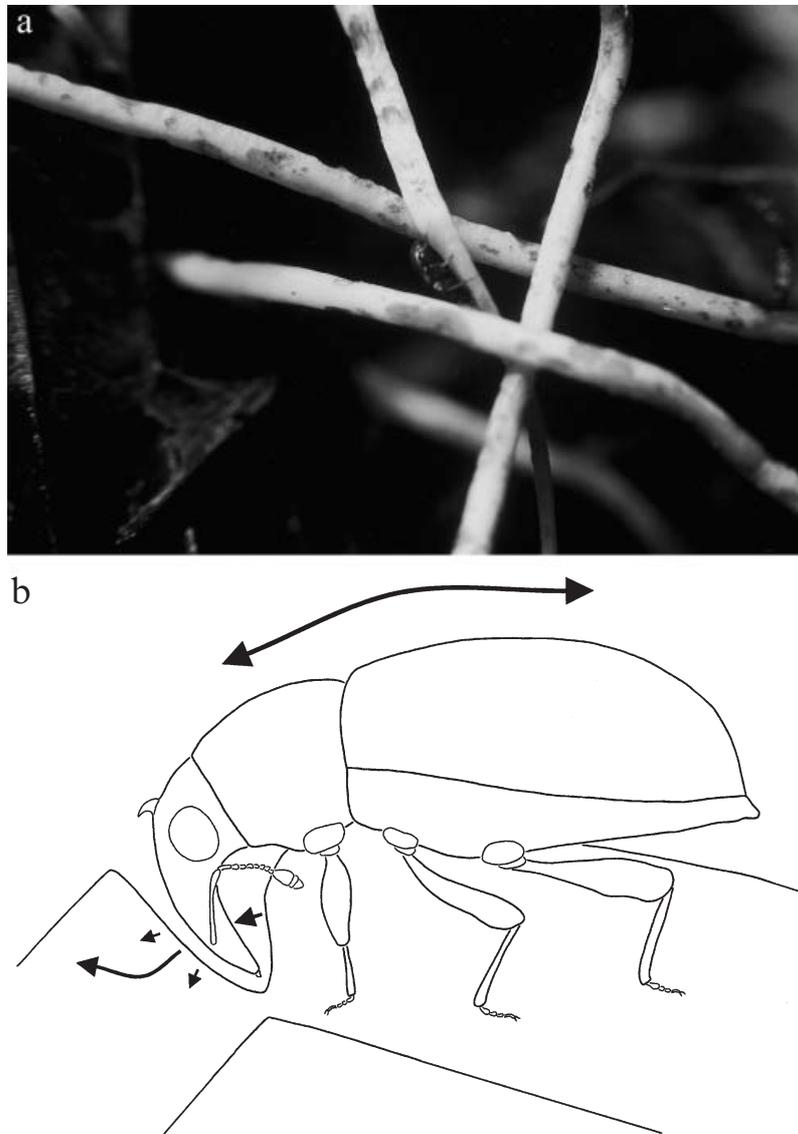


FIG. 3. Female of *S. vectoris*, detachment of staminode: (a) female searching and probing staminode of *A. uncinata*, note damage by previous visitors; (b) female detaching staminode with her mandibles, rocking back and forth and using her rostrum to tear final connections, before falling to ground.

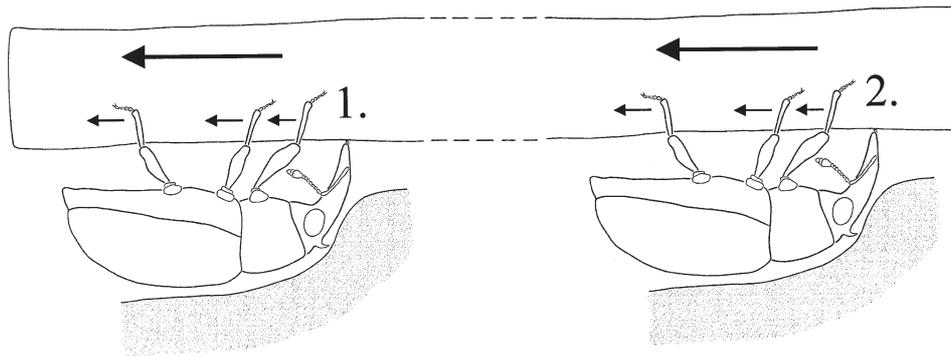
anthesis (for details see Franz, 1999). Once a staminode has been accepted, the female moves close to its base, facing the inflorescence, and begins to detach it with her mandibles. Her rostrum slides from side to side while the incision becomes deeper. The process of separation lasts 62 ± 28 s (range: 26–128 s, $n=25$), and the detached staminodes have a length of 2–8 cm. Prior to separation, the female executes rhythmic pushes against the base of the staminode—rocking back and forth with her body as well as with her rostrum—until the final connections are torn (figure 3b). Because the female is positioned on the detached section, both she *and* the staminode fall to the ground. Occasionally, they become entangled in the inflorescence, which initiates the subsequent transporting behaviour.

On the ground or any other substrate onto which she falls, the female begins to transport the staminode to the site of oviposition. This activity lasts 30–90 minutes, extending in the leaf litter over a distance of up to 1.5 m. From a more distant perspective, the staminodes appear to fall from the inflorescence to the ground, spreading into all possible directions, until they disappear. The spine on the frons of the female functions during the transport. She typically moves up and down and back and forth along the staminode, while examining the substrate that supports it (e.g. earth, leaves, or twigs) with her head and her legs. Eventually, she crawls underneath the end of the staminode that faces the direction of transport. Therefore, prior to transport, she is positioned *between* the staminode and the substrate, while her legs sustain the staminode *above* her (figure 4a). She faces *opposite* to the direction of transport, pushing the staminode backwards and away from her. Lying on her back, the female is able to use the spine on the frons as a ‘barb’—a point of resistance—against the substrate. As she moves her legs in order to transport the staminode backwards, her original position is maintained because the spine exerts resistance against the substrate. The morphology of the spine—i.e. its position, orientation, curvature, and acute apex—facilitates this function. In general, the female is capable of utilizing many irregularities in the substrate in order to maintain her original position while transporting the staminode.

After pushing the staminode backwards for a variable portion of its length, the female crawls up from underneath and returns to the end that faces the direction of transport. Then she repeats the previously described behaviour (figure 4b). The transport is thus an *iterative process* that involves: (1) the examination of the substrate; (2) the orientation of body and spine underneath the staminode; and (3) the transport of the staminode. The maximum velocity that results from this transport is *c.* 10 cm per minute. In general, the female is able to complete the transport of the initially detached staminode in spite of many irregularities in the substrate: loose objects are removed from the direction of transport by pushing them away with the rostrum, the direction is modified to circumvent larger obstacles, and portions of the staminode that have become stuck are detached and abandoned. Eventually, she transports the staminode underneath the surface of the leaf litter into humid areas with abundant detritus. The female oviposits onto the staminode at these cryptic sites, before resting until the next day. Unfortunately, details of the oviposition (e.g. duration, number of eggs, and subsequent female behaviour) are difficult to observe because of its cryptic location and the easily disturbed females.

After arriving at the inflorescence, the males track the females on the staminodes. Apparently, a male attempts to associate with one active female during the entire period that spans from the detachment of the staminode to the oviposition in the leaf litter. He typically flies and/or runs up and down several staminodes until he

a



b

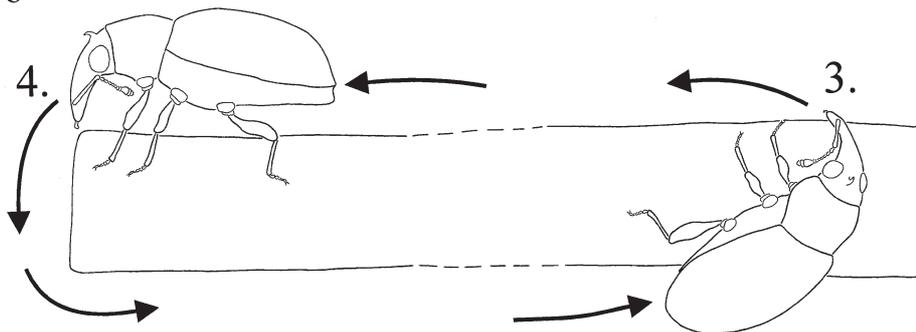


FIG. 4. Female of *S. vectoris*, transport of staminode, sequence of behaviours from 1. to 4. (iteratively); ends of staminode are drawn, dotted lines represent intermediate (omitted) sections of staminode, arrows indicate direction of movement of female, legs, and staminode, respectively: (a) female underneath staminode, using her frontal spine as a 'barb' against substrate and transporting staminode with her legs; (b) female returning to end of staminode.

locates a female in the process of detaching a staminode. Subsequently, he remains on the staminode, apically to the female, while facing her abdomen at a distance of 1–5 mm. Therefore, at the time of separation, *both* the female *and* the male fall to the ground. During the period of transport, he attempts to exclude competitors from the staminode. However, the male neither participates in the transport, nor courts or copulates with the female until they are at the site of oviposition. Males that mount females prior to oviposition are repulsed by intense vibrations that females execute with their entire body for 3–25 s ($n=6$).

There are *conflicts among males* who are associated with staminodes (i.e. the defending male) and those who attempt to replace them (i.e. the attacking male). In general, the female remains undisturbed by these conflicts, while continuing to transport the staminode. Three aggressive behaviours are observed among males.

1. Persecution. The defending male runs from end to end of the staminode. The attacking male approaches from various angles, executing strong vertical pushes with his rostrum in order to dislodge the defending male from the staminode. On some staminodes these aggressions occur every other second,

- involving several competing males. However, often the defending male is able to resist the attack by avoiding, deflecting, and/or countering it. He remains on the staminode in 87.5% of the observations ($n=56$).
2. Intimidation. The defending male and the attacking male oppose head to head on the staminode, at a distance of 2–3 mm (figure 5a). They move abruptly forward and back or left and right, for 1–5 s ($n=78$), maintaining the same distance between them. Meanwhile, each male executes horizontal movements with his abdomen (i.e. from side to side, resembling those of a pendulum), at a frequency of 2–3 oscillations/s.
 3. Fight. The behaviour of intimidation culminates in fights among the two competing males in 61.5% of the observations ($n=78$). During the fights, each male uses his prothoracic legs as weapons with which he attempts to displace the competitor from the staminode (figure 5b). The attacks are launched from various angles: head to head or side to side on the same side of the staminode, or from opposing sides of the staminode. Apparently, the angle of attack conveys advantage during the fight, because it relates to its performers' stability. Each male typically extends and lifts one prothoracic leg in front of his head before executing very fast blows with it, at a frequency of 8–12 blows/s. These blows are delivered at an oblique angle of $\approx 30^\circ$ from the

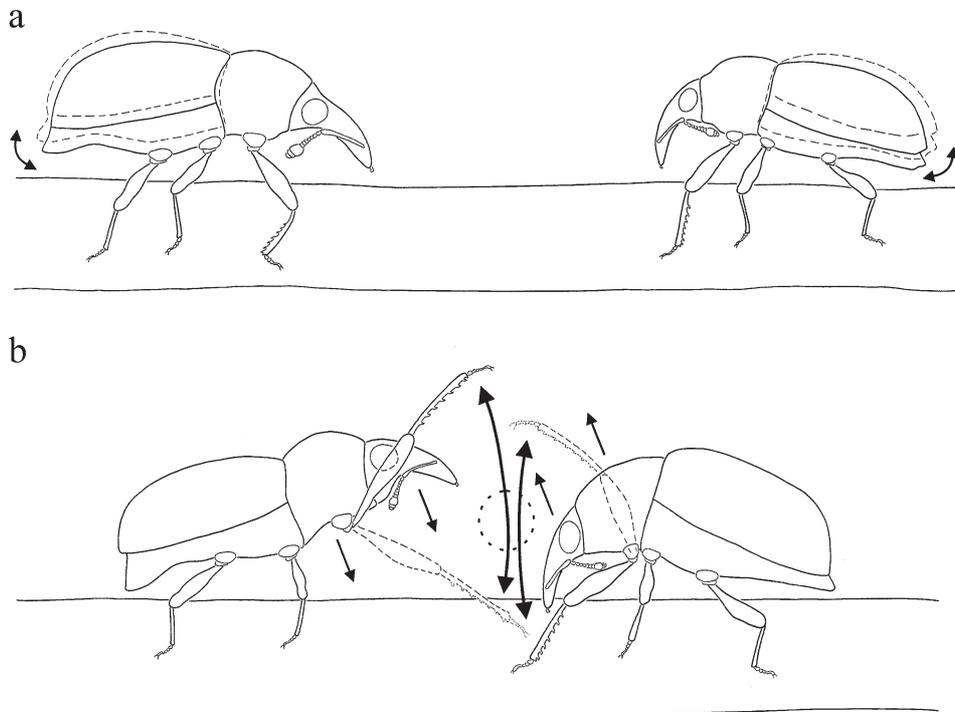


FIG. 5. Males of *S. vectoris*, conflict behaviour; dotted lines indicate alternative positions of body parts during sequence of movement, arrows indicate directions of movements: (a) intimidation behaviour, two males are opposed on staminode, their abdomens moving horizontally; (b) fighting behaviour, two males execute fast blows with their prothoracic legs, sustained by prothoracic movements, until their protibiae cling (dotted ring) and dislodge inferior male.

longitudinal vertical plane, i.e. from central upwards to lateral downwards and vice versa. Because of the fully extended condition of the prothoracic legs, they resemble the movements of two accelerated, interlocking windshield-wipers. Each male sustains the force of his blows with phasic movements of his prothorax (figure 5b). Eventually, the anteriorly directed teeth along the anteroventral margin of the protibia *cling*, and *transfer* the lifting power among both competitors. Immediately, the inferior male is dislodged and falls from the staminode. Some fights involve 3–4 males. They last 20 ± 17 s (range: 5–82 s, $n=40$), and are interrupted by periods of intimidation. Apparently, the inferior male remains undamaged in the majority of the fights, although $\approx 10\%$ of the males lack 1–2 of their protibial teeth.

Morphometrical variation of S. vectoris

Compared to the length of the metepisternum, used as an indicator of overall body size, the length of the protibia in males displays *positive allometry* with $y = 0.21 + 1.36x$ (figure 6a; $r^2 = 91.1\%$, $p < 0.001$). The regression coefficient is greater than 1.0, with a significance of $p < 0.0005$ ($t = 7.217$; $t_{0.05(1), 74} = 1.666$). Contrastingly, the length of the spine in females displays *negative allometry* with $y = -0.73 + 0.89x$ (figure 6b; $r^2 = 47.6\%$, $p < 0.001$); although it is not significantly smaller than 1.0, with $p > 0.10$ ($t = 1.027$; $t_{0.05(1), 74} = 1.666$).

Natural history of Staminodeus

At La Selva, the adults of *S. vectoris* have been collected on species of cyclanths throughout the year, including *A. euryspatha* Harling, *A. sleeperae* Grayum & Hammel, *A. uncinata*, *A. utilis* (Oerst.) Harling, *A. vagans* Harling, *Carludovica rotundifolia* H. Wendl. ex Hook. fil., *C. sulcata* Hammel, *Chorigyne pendula* (Hammel) R. Erkiesson, *Dicranopygium umbrophilum* Hammel, *D. wedelii* Harling, and *Evodianthus funifer* (Poit.) Lindman (Franz, 1999). Apparently, *Cyclanthus bipartitus* Poit. is the only cyclanth species from which *S. vectoris* is absent; it is sister to all remaining cyclanths and lacks their characteristic staminodes (Harling, 1958). However, according to the observations presented here, the mating behaviour of *S. vectoris* at La Selva is restricted to *Asplundia* and *Evodianthus*. The adults visit other cyclanth species, feeding on the staminodes *without* detaching them. Typically, there are up to 100 individuals of *S. vectoris* on the inflorescences of *Asplundia* and *Evodianthus*, but fewer than ten individuals on those of *Carludovica*, *Chorigyne* and *Dicranopygium* ($n = 3\text{--}40$ inflorescences per species of cyclanth, according to Franz, 1999). Therefore, although the adults of *S. vectoris* visit many cyclanth species at La Selva, they concentrate on those species used for feeding *and* mating.

The eggs of *S. vectoris* appear to hatch shortly after oviposition, because third instar larvae are present in the leaf litter as soon as five days after anthesis. Presumably, they begin to feed along the deteriorating staminode, before moving into the detritus and completing their development under humid conditions in the leaf litter. They are detritivorous and display fast negative phototaxis when disturbed. Pupation occurs in the top 1.0 cm layer of the ground. The entire life cycle lasts 12–20 days ($n \approx 25$, according to Franz, 1999).

Brief notes on the natural history of two additional species of *Staminodeus* are available (Franz, 2001). *Staminodeus curvitibialis* is associated with *Sphaeradenia hamata* Harling in La Planada, Nariño, Colombia, and with *Asplundia caput-medusae* (Hook. fil.) Harling in Portachuelo and Rancho Grande, Aragua, Venezuela.

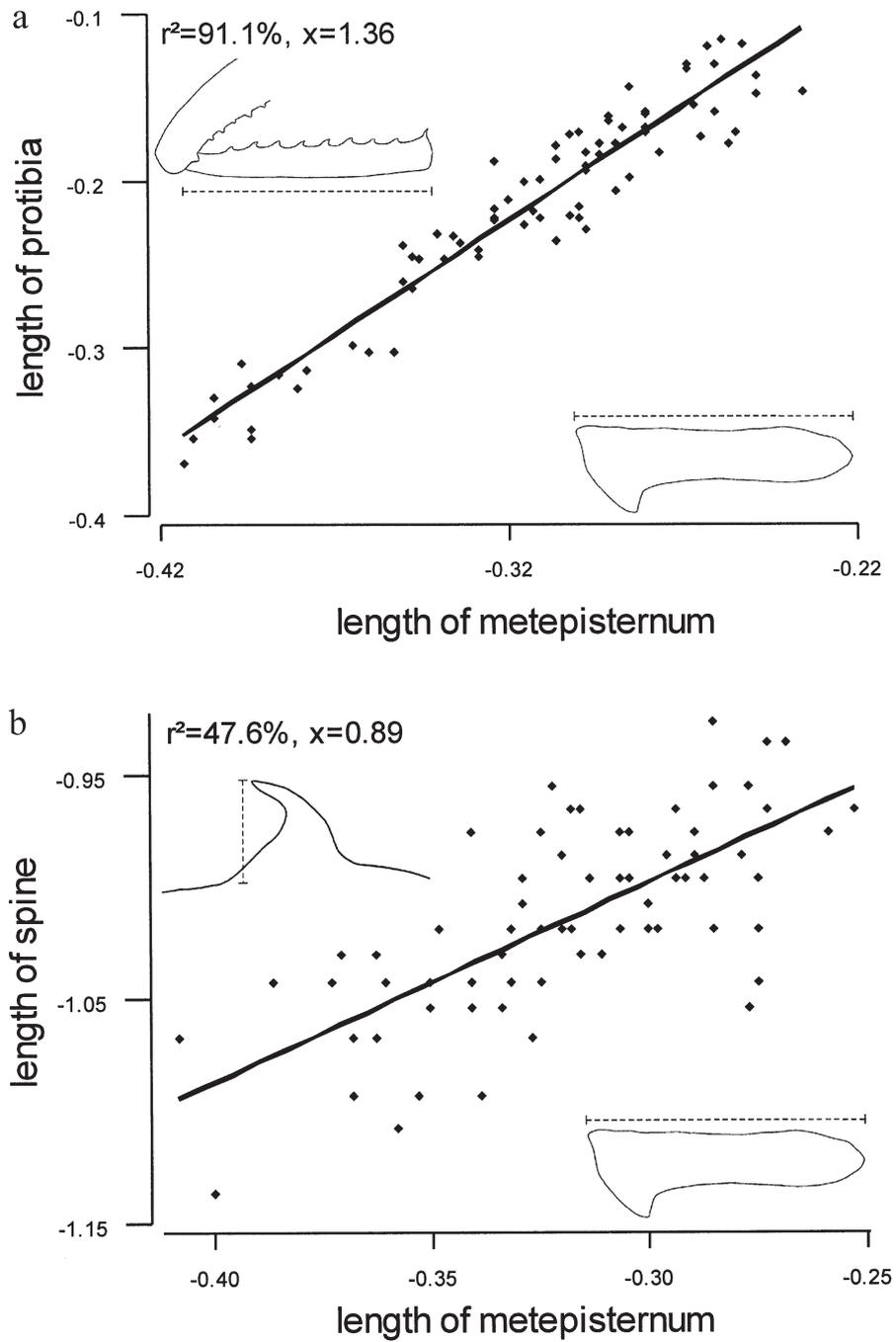


FIG. 6. Linear regression of morphological characteristics of *S. vectoris* in comparison to length of metepisternum; values are transformed to log, r^2 and regression coefficient are indicated: (a) length of male protibia; (b) length of female spine.

Staminodeus denticulatus is associated with *Carludovica palmata* Ruíz & Pavón, with *E. funifer* in San Vito, Puntarenas, Costa Rica, and with *Asplundia* sp. in Chiriquí Grande, Bocas del Toro, Panama. Therefore, all *Staminodeus* species for which hosts are known have been collected on cyclanths.

Morphology and phylogeny of Staminodeus

The male prothoracic legs display considerable morphological variation among the seven described species of *Staminodeus*, providing external diagnostic characters for the recognition of species (Franz, in press). *Staminodeus inermis* Franz lacks the row of teeth along the anteroventral margin of its mucronate protibia. *Staminodeus curvibialis* Franz and *S. denticulatus* Franz have 12–18 small teeth along an apically inermous protibia; whereas *S. bispinosus* Franz, *S. forcipis* Franz, *S. dilatatus* Franz, and *S. vectoris* have 3–10 large teeth along an apically mucronate protibia (figure 7). The male protibia of *S. curvibialis* is curved. The male profemur of *S. forcipis* is curved, and has larger ventral teeth, e.g. in comparison to *S. vectoris*. Finally, the males of *S. denticulatus*, *S. bispinosus* and *S. forcipis* have a small, curved spine on the frons, resembling that of the females, except for its smaller size.

The female frontal spines are similar among all seven species of *Staminodeus*. The only notable exception is *S. denticulatus*, which has a slightly larger spine (Franz, 2001). The female prothoracic legs lack the row of teeth, and the protibia is inermous at the apex.

A phylogeny of the species of *Staminodeus* has been proposed by Franz (2001), using *Notolomus basalis* LeConte, *Perrelleschus carludovicae* (Günther) and *Systemotelus costaricensis* Anderson & Gómez as outgroup taxa (figure 8). The cladistic analysis for ten taxa and 18 characters yielded a single most parsimonious cladogram ($L=22$, $CI=86$, $RI=90$). Those characters with apparent relevance for the mating behaviour of *Staminodeus* are mapped according to fast optimization (for explanation see table 2). Most remaining characters are generated from the male genitalia. The cladogram optimises the presence of the female frontal spine as a synapomorphy for *Staminodeus*. As the result of a reversal, the promucron in males is absent in *S. curvibialis* + *S. denticulatus*. The synapomorphies of the clade inside of *S. inermis* are the ventrally toothed profemur and protibia in males. The size, shape, and number of teeth along the anteroventral protibial margin support *S. curvibialis* + *S. denticulatus* and its sister taxon, the clade of *S. bispinosus* to *S. vectoris*. Finally, the small frontal spine in males is convergent in *S. denticulatus* and *S. bispinosus* + *S. forcipis*.

Discussion

Specialization and specificity

The behaviour of *S. vectoris* involves a series of characteristics that appear to be *specializations* for using the staminodes of cyclanths for feeding, mating, and oviposition. The behaviour of the adults is synchronized with the anthesis of *A. uncinata*. Such synchronization is observed in other cantharophilous plants (see e.g. Young, 1986 on the pollination of an arum by several dynastine species), as well as in cyclanths in general (Eriksson, 1994). Olfaction facilitates long distance attraction to the staminodes, although thermoreception, vision, or even pheromones cannot be dismissed. However, unlike other derelomine taxa, e.g. *Perrelleschus* Wibmer and O'Brien (for details see Franz and O'Brien, 2001), *S. vectoris* is not a pollinator of

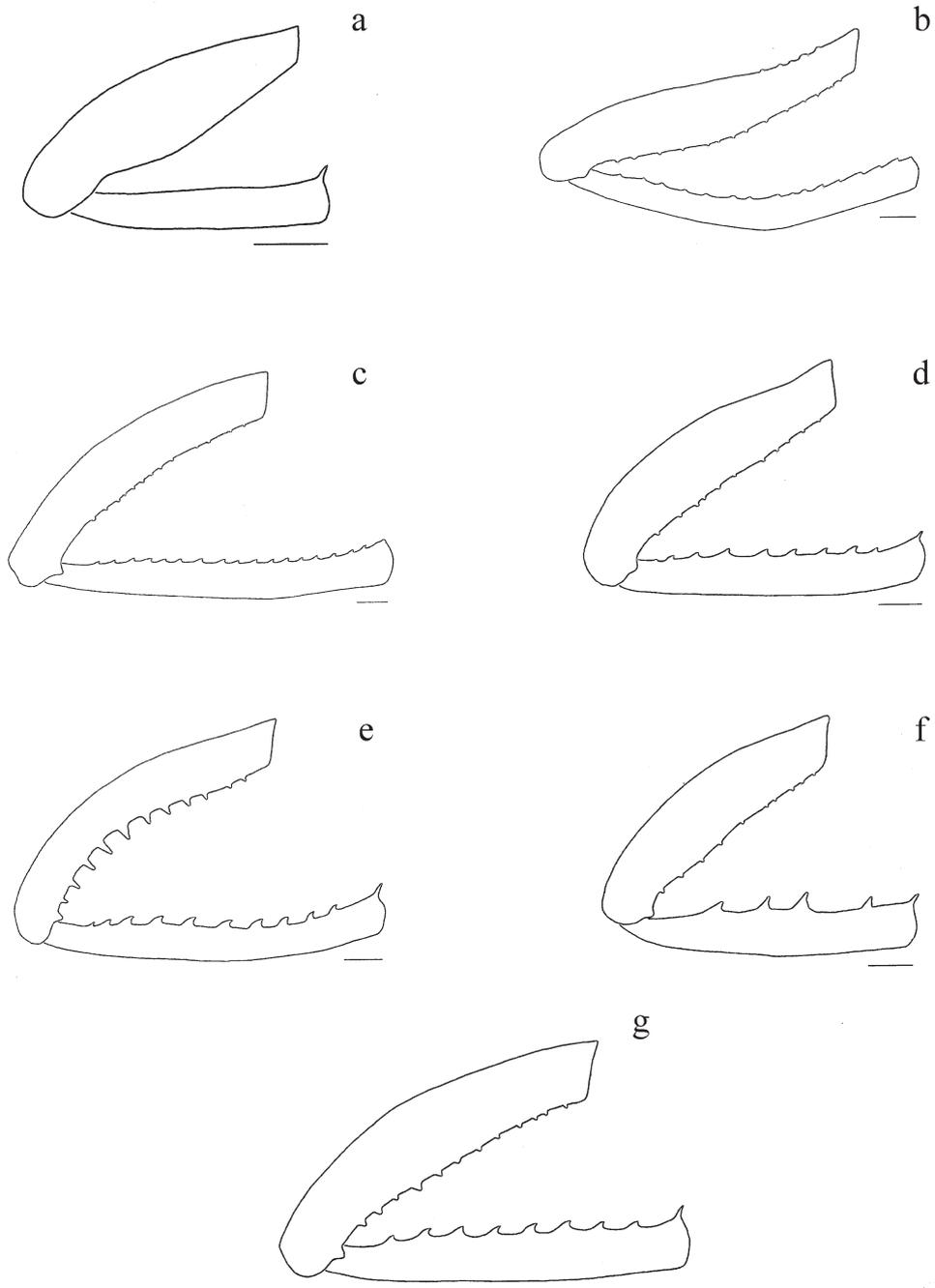


FIG. 7. Males of *Staminodeus*, prothoracic legs, anterior view, scale bar 0.1 mm: (a) *S. inermis*; (b) *S. curvitalis*; (c) *S. denticulatus*; (d) *S. bispinosus*; (e) *S. forcipis*; (f) *S. dilatatus*; (g) *S. vectoris*. Adapted from Franz (2001), with permission of The Coleopterists Bulletin.

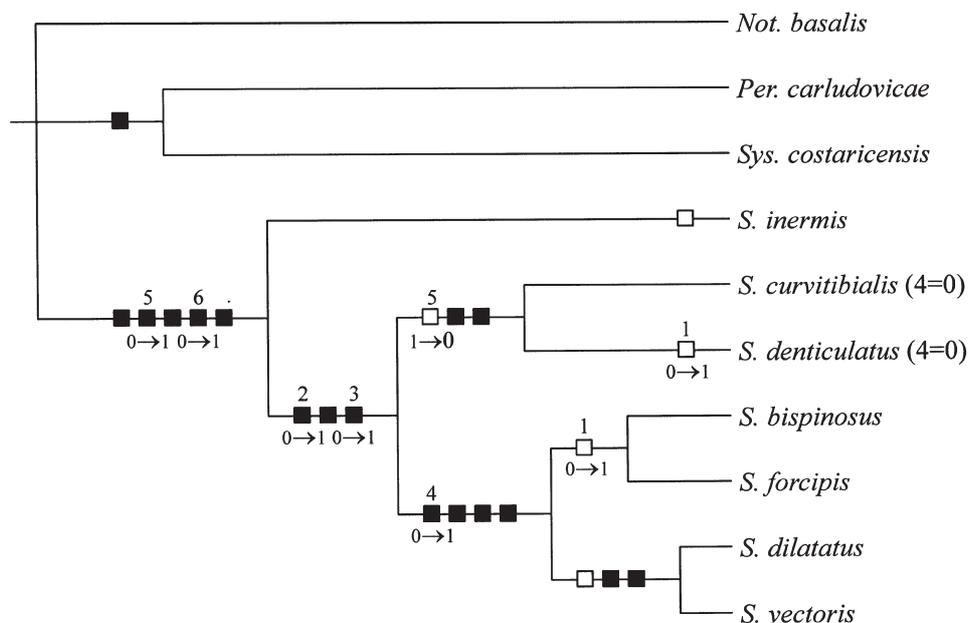


FIG. 8. Phylogenetic relationships among the seven species of *Staminodeus*, with *Not. basalis*, *Per. carludovicae* and *Sys. costaricensis* as outgroup taxa; behaviourally relevant characters are mapped (according to fast optimization), homology is indicated by black rectangles and homoplasy by white rectangles; character numbers and state transformations (table 2) are displayed above and below each rectangle, respectively. Adapted from Franz (2001), with permission of The Coleopterists Bulletin.

Table 2. Explanation of cladistic characters of *Staminodeus* with apparent relevance to the mating behaviour (for details see Franz, 2001).

Character	Explanation
1	male with small frontal spine: (0) absent, (1) present
2	male with ventrally toothed profemur: (0) absent, (1) present
3	male with ventrally toothed protibia: (0) absent, (1) present
4	male protibia with row of: (0) 12–18 small teeth, (1) 3–10 large teeth
5	male with promucron: (0) absent, (1) present
6	female with large frontal spine: (0) absent, (1) present

its host plant. The adults remain on the surface of the inflorescence, where contacting the stigmas is impossible, and leave before the pollen is released. The majority of individuals, especially those involved in reproduction, are associated with the staminodes that the females detach before falling to the ground. This is congruent with a relative increase in males and teneral (who are presumably not mating) on the inflorescence during the intermediate phase (table 1).

The *specificity* of *S. vectoris* to its host plants has to be considered in the context of host plant use. At La Selva, many cyclanth species are visited by the adults, but mating and oviposition appear to be restricted to *Asplundia* and *Evodianthus*. Empirical evidence for an evolutionary explanation of this pattern is unavailable at the moment. However, if the staminodes attract pollinators—and detaching them decreases the attractiveness of the inflorescence—then mutations that increase the

resistance of the staminodes against damage by *S. vectoris*, either structurally or chemically, could be adaptive. Until adaptations to the potentially detrimental behaviour of the adults are evident in *A. uncinata* or other cyclanth species that host *S. vectoris*, this association represents an example of specialization by the parasite to the host, i.e. *unidirectional* adaptation. According to Thompson (1994), coevolution involves *reciprocal* adaptation.

Behaviour, morphology and selection

Arguably, the behavioural complexity (figures 3 and 4) that the females of *S. vectoris* display while detaching and transporting the staminodes of *A. uncinata* is *unique* among Curculionoidea. Attelabid leaf rollers have complex oviposition behaviours (Vogt, 1992), in contrast with most observed curculionoids (for review see Howden, 1995). To my best knowledge, active female transport of an oviposition substrate is unique to *S. vectoris*. The same is true within Derelomini, although many Neotropical species remain to be studied (Franz, 2001).

Among the more salient characteristics of *S. vectoris* is the *velocity* with which the females operate after arriving at the inflorescence of *A. uncinata*. The period of arrival in itself is short: most individuals are on the inflorescence within half an hour of the initial colonization. Those females involved in reproduction spend little feeding time on the inflorescence, since staminodes are on the ground within minutes. The females use them exclusively for themselves, rejecting previously damaged staminodes. The best available explanation for the putative evolutionary increase in their velocity is that staminodes represent a *limited resource*. Damage by feeding or detachment results in very rapid decay. Although the detached staminodes do not constitute the principal source of larval nutrition, it appears that the females prefer less damaged staminodes for transport and oviposition. The ephemeral nature of the staminodes and their central function during the mating behaviour, are conditions under which competitively high velocity could be beneficial for the females. Halffter and Edmonds (1982) report on an analogy in dung beetle behaviour. To contrast this, the primary pollinator of *A. uncinata* has a longer reproductive period and moves at a much lower velocity.

The *complexity* and *efficiency* with which the females detach and transport the staminodes is, again, unique among Curculionoidea (figure 4). The mode of transport resembles dung rolling beetles (see Fabre, 1949: 93–107, with notes on *Canthon pilularius* (Linnaeus)), or ants (see Hölldobler and Wilson, 1990: 279–285, with notes on *Camponotus sericeus* (Fabricius)). However, the females of *S. vectoris* differ from these by turning on their backs, and maintaining their original position while transporting the staminode with their legs. The iterativeness of the transport represents another unique characteristic. Quantitative observations are required before hypotheses about the evolution of this behaviour should be formulated.

The female frontal spine (figure 1c) functions in the context of transporting the staminodes—rather than in sexually mediated contests. The negative allometry ($x < 1.0$, figure 6b) of the spine length is consistent with this: it occurs in many morphological characters that have evolved under *natural selection*, and perform a function with a mean optimal size (Harvey and Pagel, 1991; Eberhard *et al.*, 1998; Palestini *et al.*, 2000). It is conceivable that such an optimum exists for the size of the female frontal spine of *S. vectoris*, because of the relatively fixed diameter of the staminodes. Using the frontal spine, the females are able to move the staminodes laterally and modify the direction of transport. The curvature of the spine

approximates that of the staminode, and facilitates grasping it without slipping. However, an equally plausible explanation for the size of the spine could be made by reference to the observation that females oviposit in the leaf litter. Any larger spine would probably restrict their mobility. The frontal position, anterior orientation, and acute apex of the spine, are efficient in the context of providing a point of resistance against the substrate. They compensate for the directional momentum that females generate when moving the staminodes with their legs. An obtuse projection would be much less effective. Whether the long setae on the anterior half of the frontal spine perform any sensory function during the transport remains unknown.

Hypotheses about the historical selective conditions that favoured the evolution of oviposition behaviour in *S. vectoris* are speculative and difficult to corroborate (O'Hara, 1988). However, the available natural history information may be relevant for such a venture. The larvae of *S. vectoris* are detritivorous, and the females oviposit onto an ephemeral substrate that exposes them to the environment. This life history occurs in several derelomine species (O'Brien, personal communication), but is apomorphic within Curculioninae (Kuschel, 1995; plesiomorphically, the larvae of Curculioninae are endophytic). If the exposure to the environment causes high rates of larval mortality, then the ability of the females to *select specific oviposition sites* could be adaptive. The high larval mobility and short life cycle of *S. vectoris* confer additional protection from these putative pressures.

Several characteristics of the male behaviour suggest that *sperm precedence* (Parker, 1970) occurs in the females of *S. vectoris*: each male competes in order to be the last mate before oviposition. Sufficient conditions for sexual selection are met if the operational sex ratio is biased (Andersson, 1994). During the pistillate phase, males and females visit the inflorescences of *A. uncinata* in similar numbers. However, the females oviposit *once* per staminode, and many of them are not even involved in reproduction. Therefore, sexually active males predominate and access to females is limited. Empirical evidence for sperm precedence is absent in any derelomine species, but exists in other curculionid taxa (e.g. the boll weevil *Anthonomus grandis* Boheman, Bartlett *et al.*, 1968; the alfalfa weevil *Hypera postica* (Gyllenhal), LeCato and Pienkowski, 1972; and the plum curculio *Conotrachelus nenuphar* (Herbst), Huettel *et al.*, 1976). Behavioural observations of other curculionoids have been interpreted within the same context (Johnson, 1982; Eberhard, 1983; Wcislo and Eberhard, 1989; Polak and Brown, 1995; Eberhard and García-C., 2000). In addition, sperm competition has been documented in diverse insect taxa (Parker, 1970; Ridley, 1988; Birkhead, 1996).

The following characteristics have to be considered in an evolutionary discussion of the male behaviour of *S. vectoris*. The males attempt to associate with the females immediately after arriving at the inflorescence. Initially, each male associates with one female, and subsequently defends her staminode until both are at the site of oviposition. Typically, the males neither court nor copulate with the females until oviposition in the leaf litter. Those that do are rejected. It is unlikely that the males are able to associate with several ovipositing females and copulate more than once per day. This suggests that being the *last mating partner* represents the most successful male reproductive strategy, rather than mating with the highest possible number of females.

Staminodeus vectoris represents another curculionoid example of *conflicts among males* that involve the use of *weapons* (figure 5) in contests over females (for

comparison see Eberhard, 1983 on *R. barbirostris*, Weislo and Eberhard, 1989 on *M. bicinctus* and Eberhard and García-C., 2000 on *P. expositus*). The fights are analogous to *M. bicinctus*, because in both species the prothoracic legs (figure 1b) are used to execute the blows. However, rather than 'ritually', the inferior male is *dislodged* from the oviposition substrate *by force* in *S. vectoris*. The intimidation behaviour appears to communicate the male disposition to defend the staminode against competitors, and prevents the escalation of fights in over a third of the conflicts.

Other derelomine species display male fighting behaviour (Franz, 1999). Interestingly, the period of reproduction of *S. vectoris* is the shortest of all. But the males may be able to 'predict' the female disposition for oviposition, since this involves the acceptance, detachment, and transport of staminodes.

Apparently, the three decisive factors during male fights of *S. vectoris* are the angle, extension, and force of attack. Comparatively larger males may be superior competitors, because of the greater reach and stronger force of their prothoracic legs. However, their mobility may be reduced, resulting in less effective angles of attack. These hypotheses have to be tested by additional observations. The positive allometry ($x > 1.0$, figure 6a) of the male protibia is consistent with its function as a weapon in the context of *sexual selection* (Harvey and Pagel, 1991; Andersson, 1994; Eberhard *et al.*, 1998). Similar interpretations have been provided for the rostrum of *R. barbirostris* (Eberhard, 1983), the prothoracic legs of *M. bicinctus* (Weislo and Eberhard, 1989), the prothoracic horns of *P. expositus* (Eberhard and García C., 2000), and for many other species of insects (see Emlen and Nijhout, 2000 for a recent comprehensive review). Unlike *P. expositus* in which males are dimorphic for horn length and sheath length (Eberhard *et al.*, 2000), the scaling relationships of the male protibia are linear in *S. vectoris*.

Systematics

The previous discussion indicates that, to a degree, systematic contributions to behavioural studies are feasible *without* precise knowledge of taxonomy, homology and phylogeny. Accordingly, the comparison of taxa facilitates the hypothesis that many characteristics of the mating behaviour of *S. vectoris* are autapomorphies. This includes the transport of staminodes by females and the fights among males. The same is true for the morphology and function of the female frontal spine and the male protibial teeth. However, as stated by Wenzel (1992: 373): '(t)he search for species-specific units is not only useless from the point of view of phylogenetic analysis (assuming the species are already identified), but it may also be ill-advised on the grounds that it deliberately or inadvertently obscures phylogenetically informative elements common to several species'. Here I apply the arguments of Wenzel (1992) to *S. vectoris*, in order to illustrate how knowledge of systematics (figures 7 and 8) *complements* the present study (see table 3 for a summary). The following questions and levels of analysis are addressed.

1. *Level of homology*. How are the morphological characters with apparent relevance to the mating behaviour of *S. vectoris* distributed among other derelomine species? The female frontal spine is a synapomorphy for *Staminodeus*. The male protibial teeth are absent in *S. inermis*, but present as a synapomorphy in all remaining species of *Staminodeus*.
2. *Extent of transformation*. How do these morphological characters vary among

Table 3. Summary of conclusions on mating behaviour of *Staminodeus* as inferred from evidence of behaviour and systematics (for details see *Discussion*).

Behaviour	Systematics
1. <i>S. vectoris</i> is specialized to feed, mate, and oviposit on the staminodes of <i>Asplundia</i> and <i>Evodianthus</i> , but evidence for coevolution is lacking.	1. The frontal spine in females in homologous for all seven species of <i>Staminodeus</i> , whereas the protibial teeth in males are homologous for the clade that is sister to <i>S. inermis</i> .
2. The frontal spine in females of <i>S. vectoris</i> is used in the context of transporting the staminode to the site of oviposition (negative allometry of length of spine suggests evolution through natural selection).	2. Particularly the morphology of males varies among the species of <i>Staminodeus</i> , e.g. the number, size, and shape of the protibial teeth and the presence/absence of the frontal spine. These characters are aut- and/or synapomorphies, although one convergence and one reversal occur.
3. The ability of females of <i>S. vectoris</i> to select specific oviposition sites in the leaf litter could be adaptive.	3. The evolution of the frontal spine in females precedes that of the protibial teeth in males (several additional patterns).
4. The mating behaviour of males seems to indicate that sperm precedence occurs in females of <i>S. vectoris</i> .	4. Hypothesis: the evolution of female transporting behaviour evolved before that of male fighting behaviour (several additional hypotheses).
5. The prothoracic legs in males of <i>S. vectoris</i> are used in the context of fighting (positive allometry of length of protibia suggests evolution through sexual selection).	5. Testability: <i>S. inermis</i> has females that transport staminodes and males that fight (several additional tests)?

species? The female frontal spine is consistent among all seven species of *Staminodeus*. Within the clade that is sister to *S. inermis*, the male protibial teeth vary in number, size, and shape, conferring information for the definition of species and their phylogenetic relationships. Interestingly, the males of *S. denticulatus*, *S. bispinosus* and *S. forcipis* have small frontal spines, and those of *S. curvitibialis* + *S. denticulatus* lack the promucron.

3. *Sequence of transformation*. How have these morphological characters evolved sequentially? Within *Staminodeus*, the evolution of the female frontal spine has *preceded* that of the male protibial teeth. The evolutionary sequence of the number, size, and shape of the protibial teeth remains unknown, although the small number and large size in *S. dilatatus* appear to be autapomorphic. The same is true for the curvature of the protibia in males of *S. curvitibialis*, the large size of the profemoral teeth in males of *S. forcipis*, and the large frontal spine in females of *S. denticulatus*. The evolution of the small frontal spine in males is *convergent* in *S. denticulatus* and *S. bispinosus* + *S. forcipis*. Finally, the absence of the promucron is a *reversal* in *S. curvitibialis* + *S. denticulatus*.
4. *Hypothesis of behaviour*. How is the morphological evolution within *Staminodeus* useful for generating hypotheses about the behavioural evolution? (1) Since the evolution of the female frontal spine has preceded that of the male protibial teeth, it is conceivable that female transporting behaviour has evolved *before* male fighting behaviour (Franz, 2001). (2) Because

the protibial teeth are small and the promucron is absent in males of *S. curvibtibialis* + *S. denticulatus*, their fighting behaviour may be different from their sister clade. It is difficult to imagine how their prothoracic legs cling during fights. However, they could be used to grasp and lift competitors from the staminode. (3) The functions of the large profemoral teeth in males of *S. forcipis* and of the small frontal spines in males of *S. denticulatus* and *S. bispinosus* + *S. forcipis* remain unknown.

5. *Testability of morphology*. How are the morphological hypotheses testable by behavioural studies? (1) The hypothesis that male fighting evolved after female transporting is testable by studying the mating behaviour of *S. inermis*. (2) Whether the male prothoracic legs of *S. curvibtibialis* are used for grasping and lifting may be tested by direct observation. (3) Again, behavioural observations are necessary.

Returning to the introductory comments, it becomes apparent that knowledge of morphology and systematics contributes to future studies of the mating behaviour of *Staminodeus*. Observations of all seven species will be necessary to generate behavioural homologies among them, in order to test the present phylogenetic hypothesis. As stated by Wenzel (1992: 361), '(b)ehavior is not special, it is only more difficult to characterize'. In addition to generating accurate hypotheses about the levels of homology of the adaptations under study (Coddington, 1988), systematics provides their patterns of transformation, convergence, and reversal—none of which are apparent in absence of phylogeny. To provide an example, the loss of horns has been undocumented in beetles. The evolution of prothoracic horns and fighting behaviour in Baridinae is as fascinating as it remains unstudied. Detailed research of behaviour and systematics is rare in Curculionoidea (Anderson, 1993; but see Donaldson, 1992 for an exception), although it should be favoured over ecologically motivated generalizations at much higher levels (e.g. Farrell, 1998).

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