

**DESCRIPTION AND PHYLOGENY OF *STAMINODEUS*,
A NEW GENUS OF DERELOMINI (COLEOPTERA: CURCULIONIDAE)
ASSOCIATED WITH CYCLANTHACEAE**

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Abstract

Staminodeus, **new genus**, is described for seven species: *S. inermis*, **new species**, from Panama; *S. curvibtibialis*, **new species**, from Colombia and Venezuela; *S. denticulatus*, **new species**, from Costa Rica and Panama; *S. bispinosus*, **new species**, from Panama; *S. forcipis*, **new species**, from Costa Rica; *S. dilatatus*, **new species**, from Panama; and *S. vectoris*, **new species**, from Costa Rica and Panama. *Staminodeus* is placed in Derelomini, and is characterized by the putative synapomorphies: carinate rostrum, male with prothoracic leg ventrally denticulate (excepting *S. inermis*) as well as median lobe internally with complex structures, and female with frontal spine. All species are hypothesized to be associated with the staminodes of the inflorescences of Cyclanthaceae. Field observations on the reproductive behavior of *S. vectoris* at La Selva, Costa Rica, indicate that the protibia in males is used to displace competitors, whereas the spine in females was used as a point of support while transporting the detached staminodes to oviposition sites on the forest floor. A cladistic analysis with *Notolomus basalis* LeConte, *Perellesschus carludovicae* (Günther), and *Systemotelus costaricensis* Anderson & Gómez as out-group taxa hypothesizes the phylogenetic relationships (*S. inermis*, ((*S. curvibtibialis*, *S. denticulatus*), ((*S. bispinosus*, *S. forcipis*), (*S. dilatatus*, *S. vectoris*)))).

Resumen

Staminodeus, **género nuevo**, se describe para siete especies: *S. inermis*, **especie nueva**, de Panamá; *S. curvibtibialis*, **especie nueva**, de Colombia y Venezuela; *S. denticulatus*, **especie nueva**, de Costa Rica y Panamá; *S. bispinosus*, **especie nueva**, de Panamá; *S. forcipis*, **especie nueva**, de Costa Rica; *S. dilatatus*, **especie nueva**, de Panamá; y *S. vectoris*, **especie nueva**, de Costa Rica y Panamá. *Staminodeus* se coloca en Derelomini, y se caracteriza por las sinapomorfías putativas: rostro carinado, macho con pata protorácica ventralmente denticulada (exceptuando *S. inermis*) así como lóbulo mediano internamente con estructuras complejas, y hembra con espina frontal. Se hipotetiza que todas las especies están asociadas con los estaminoides de las inflorescencias de Cyclanthaceae. Observaciones de campo sobre el comportamiento reproductivo de *S. vectoris* en La Selva, Costa Rica, indican que la protibia en machos es usada para desplazar competidores, y que la espina en hembras es usada como un punto de apoyo durante el transporte de los estaminoides separados a los sitios de oviposición en el piso del bosque. Un análisis cladístico con *Notolomus basalis* LeConte, *Perellesschus carludovicae* (Günther), y *Systemotelus costaricensis* Anderson & Gómez como grupos externos hipotetiza las relaciones filogenéticas (*S. inermis*, ((*S. curvibtibialis*, *S. denticulatus*), ((*S. bispinosus*, *S. forcipis*), (*S. dilatatus*, *S. vectoris*)))).

The Neotropical association between derelomine weevils (Curculionidae: Curculioninae *sensu* Kuschel 1995) and Cyclanthaceae presents many questions to be addressed in a phylogenetic context. Derelomini consist of approximately 40 genera with over 200 species in the literature (Alonso-Zarazaga

and Lyal 1999), among them *Celetes* Schönherr, *Derelomus* Schönherr, and *Phyllotrox* Schönherr. Although the tribe is cosmopolitan, the majority of species occur in tropical regions and are associated with palms, cyclanths, and arums. Some species, e.g., *Elaeidobius kamerunicus* (Faust), are considered to be important pollinators of cultivated palms (for review see Henderson 1986). The only genera that have been described with explicit reference to Cyclanthaceae are *Perelleschus* Wibmer & O'Brien and *Systemotelus* Anderson & Gómez, each with three species (Wibmer and O'Brien 1986; Anderson and Gómez 1997). Meanwhile, a large number of undescribed taxa have been observed to pollinate and reproduce in the reproductive organs of several genera of Cyclanthaceae (Gottsberger 1991; Eriksson 1994a; Seres and Ramírez 1995; Anderson and Gómez 1997; Franz 1999). At La Selva, Costa Rica, 13 species of Derelomini are associated with 11 species of Cyclanthaceae (Franz 1999). This monocot host family consists of 12 genera with 230 species which occur in wet forests throughout the Neotropical region (Harling *et al.* 1998); a generic phylogeny has been proposed by Eriksson (1994b). An extensive revision of Derelomini, including the description and phylogeny of its genera, is necessary before attempting to reconstruct the biological history of this association. In the present paper I begin by describing a new genus, *Staminodeus* Franz, with seven species from Colombia, Costa Rica, Panama, and Venezuela. I provide field observations on the reproductive behavior of *S. vectoris* Franz, as well as a cladistic analysis of *Staminodeus* using the following outgroups: *Notolomus basalis* LeConte, *Perelleschus carludovicae* (Günther), and *Systemotelus costaricensis* Anderson & Gómez.

Methods

Morphological Description. The entomological terminology follows Nichols (1989), as well as Ting (1936) for the mouthparts, Crowson (1944) for the metendosternite, Zherikhin and Gratshev (1995) for wing venation, and Burke (1959) for the genital complex in both sexes. Measurements were made using the ocular scale of a dissecting microscope (Wild M5A) at 50 × magnification or a compound microscope (Leitz Dialux 20) at 160 × magnification. Body length was measured from anterior margin of eye to posterior margin of elytron; rostrum length was measured from apex of rostrum to anterior margin of eye (number of measurements in parentheses, e.g., N = 15 for the preceding values). These abbreviations were used: l = length, w = width, r = rostrum, p = pronotum, t = tibia, and f = femur. Ventrites are numbered according to their homology within the curculionoid condition (e.g., see Thompson 1992), i.e., the first externally visible ventrite is ventrite III. Male descriptions are followed by those of females. Morphological descriptions are complementary, i.e., the shared features between genus and species, male and female, and serial homologs (e.g., legs) are not repeated after being mentioned for the first time. Illustrations were prepared using the drawing tube of either microscope, and SEM pictures of *S. vectoris* were produced with a Hitachi S-2360N. Type labels include the species name, e.g., "*Staminodeus vectoris*," the type status and gender, e.g., "Holotype, ♂," and "N. M. Franz, 2000." They are red, green, and yellow for holotypes, allotypes, and paratypes, respectively. Insect collections are coded as in Arnett *et al.* (1993).

Cladistic Analysis. The present lack of phylogenetic resolution and the large number of undescribed taxa within Derelomini are confining conditions for the choice of outgroups for *Staminodeus*, although these conditions are

acceptable as long as the character homologies are applicable to the ingroup taxa (*e.g.*, see Nixon and Carpenter 1993). Using the key to the Petalochilinae by Kuschel (1952) as the best currently available reference, *Not. basalis* was chosen as a distinctive taxon which is associated with the cabbage palm *Sabal palmetto* (Walt.) Lodd. ex Schultes (Brown 1976), whereas *Per. carludovicae* and *Sys. costaricensis* were chosen because they are associated with Cyclanthaceae and would key out to the same couplet as *Staminodeus*, namely *Phyllotrox*. Described species of *Phyllotrox* were excluded because this genus is probably not monophyletic and in need of revision. All species of *Staminodeus* were included as ingroup taxa. The data matrix was operated in Winclada (Nixon 1999), and the tree search was performed with NONA (Goloboff 1993), using the following commands: “whennig” and “mswap+” which found all most parsimonious trees. Bremer branch support values (Bremer 1994) were calculated in NONA with “hold 5000,” “suboptimal 20,” and “bsupport 20.” The resulting trees and character distributions were examined in Winclada. Autapomorphies for the species of *Staminodeus* (see descriptions) and for the outgroup genera were excluded from the matrix. The character arrangement follows the sequence of description.

Staminodeus, new genus

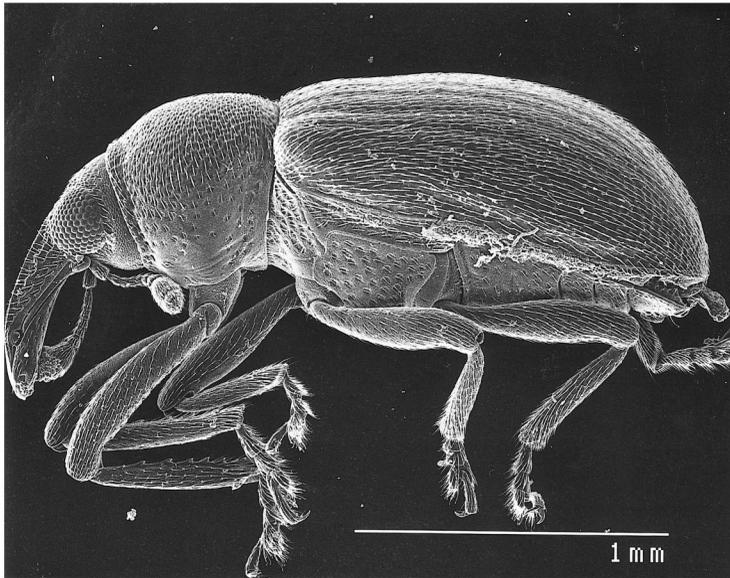
Diagnosis. Like *Perelleschus* and *Systemotelus*, *Staminodeus* keys out to *Phyllotrox* in Kuschel (1952). However, *Staminodeus* (Fig. 1a) is distinguished from these taxa and all other presently known Derelomini by the carinate rostrum in both sexes and the frontal spine in females (Fig. 1b). With the notable exception of *S. inermis* Franz, the prothoracic leg in all males is ventrally denticulate.

Male. Small, length 1.2–2.7 mm, width 0.6–1.2 mm, oval to elongate, $l/w = 1.9–2.5$, greatest width near anterior 2/5 of elytron, slightly compressed, dorsally convex, ventrally slightly convex, dark reddish-brown, sculpture punctate, vestiture short, fine, appressed, shiny.

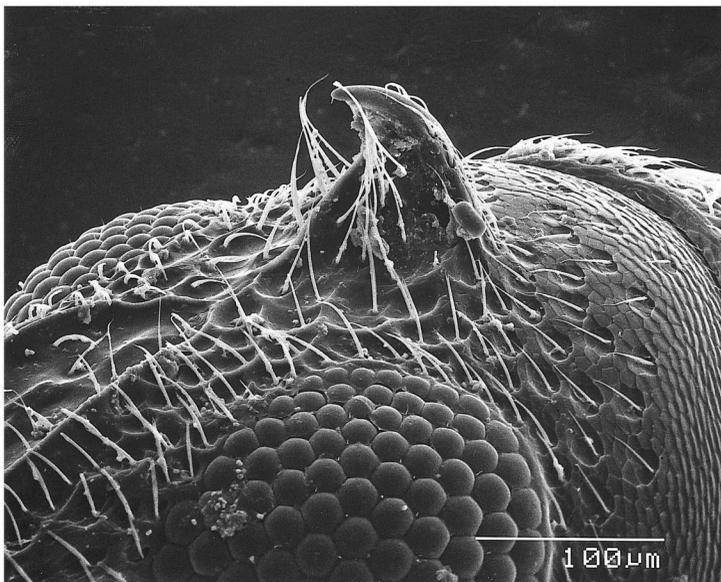
Head. *Mandible* (Fig. 2a). With 2 large dentes, inner dens with triangular emargination, outer dens slightly superposed. *Maxilla* (Fig. 2b). Cardo basally bilobed, apically broadened; stipes apically narrowed, outer margin with 1 large seta; galea+lacinia+palpiger fused, outer margin with 1 large seta, inner 1/3 setose, inner margin with 4–10 lacinial dentes (*sensu* Ting 1936); maxillary palps 3-segmented, extending beyond apex of palpiger; I longer than II, transverse; II shorter than III, transverse; III equilateral, apically papillate. *Labium* (Fig. 2c). Prementum with lateral margins apically diverging, apical margin with 2 triangular projections, median tendon triangular, dorsally and ventrally with 2 large setae; labial palps 2-segmented, extending beyond apex of prementum; I+II similar in length, equilateral; II apically papillate. Postmentum ventrally with 2 large setae.

Rostrum. In lateral view fairly short, 0.3–0.6 mm, slightly shorter than pronotum, $r/p = 0.7–1.0$, dorsally slightly arcuate, narrowed in apical 1/3, ventrally subrectate; in dorsal view fairly broad, breadth similar throughout; in cross-section subquadrate; dorsally with 2 marginal carinae, extending from frons to subapex of rostrum, slightly diverging, and 2 central carinulae, extending from basal 1/4 to apical 1/3 of rostrum, diverging; glabrate or carinulate in laterobasal 1/3; ventrally with 2 median sulci, extending from base to basal 2/5 of rostrum, subparallel; antennal insertion near apical 1/3; scrobe extending to eye, narrow, deep, subrectate, apically acuminate, shallow, basally vaguely defined.

Antenna. 11-segmented, extending to anterior 1/2 of pronotum, fairly slender; scape extending to eye, slightly shorter than funicle+club, slender, slightly arcuate, clavate in apical 1/4; funicle 7-segmented; I large, similar in length to II+III, elongate, clavate; II–VII small, similar in length, gradually progressing from elongate to transverse, clavate;



a



b

Fig. 1. *Staminodeus vectoris*, **a)** male, habitus; **b)** female, frons.

club 3-segmented, similar in length to III/IV–VII of funicle, oval, compact; I distinctly longer than II+III; II+III similar in length; funicle+club with short pubescence.

Eye. Fairly large, subcircular, slightly protruded, distant from anterior margin pronotum by 1/4–1/2 diameter of eye, separated by distance greater than breadth of antennal club, black.

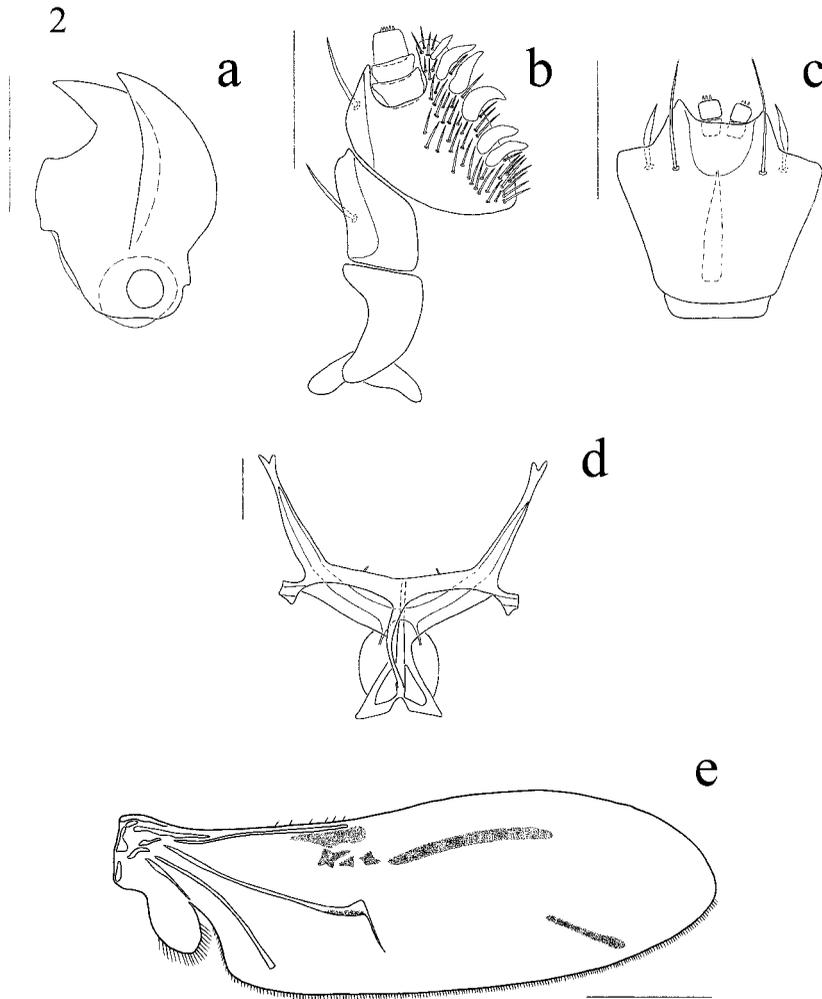


Fig. 2. *Staminodeus vectoris*, male, **a)** left mandible, ventral view; **b)** right maxilla, ventral view; **c)** labial prementum, ventral view; **d)** metendosternite, posterior view; **e)** right wing, dorsal view. Scale bar 0.05 mm for a), b), and c); 0.1 mm for d); and 0.5 mm for e).

Head. Fairly small, globular, transverse, frons glabrate or with 1 spinule.

Thorax. Pronotum. In dorsal view large, globular, $l/w = 0.8-1.1$, greatest width near central region, anteriorly narrowed, slightly to distinctly convex, anterior margin explanate, lateral margins rotundate, posterior margin bisinuate, sculpture densely punctate, vestiture medially converging; in lateral view conical, tumescent above procoxal cavities, narrowed in posterior 1/3, posterior margin lateroventrally explanate.

Epipleura. Mesepisternum triangular; mesepimeron pentagonal, dorsally broadened, projecting to pronotum+elytron; metepisternum tetragonal, extending beyond lateral

margin of metasternum, anteriorly broadened, posteriorly narrowed; metepimeron extending above posterior 1/4 of metepisternum.

Sterna. Prosternum fairly long, equilateral, convex, procoxal cavities inserted near central region, contiguous; mesosternum nearly 1/2 as long as metasternum, transverse, convex, retracted from ventral plane, mesocoxal cavities inserted at posterior margin, separated by distance nearly 1/5 as broad as mesocoxae; metasternum transverse, laterally convex, centrally plane, medially canaliculate, anterior margin with nodulate projection between mesocoxae, posterior margin with small, triangular projection near inner margin of each metacoxa, metacoxal cavities inserted at posterior margin, separated by distance similar to length of ventrite IV.

Metendosternite. (Fig. 2d). Stalk slightly shorter than furcal arms, ventrally broadened, emarginate, separated by median flange; ventral flange broader than stalk, laterally convex; lamina nearly 1/4 as long as central sclerotization; lateral projections apically expanded; anterior tendons inserted near lateral 1/3 of dorsal margin of lamina, slender, converging; furcal arms diverging, dorsally bifurcate.

Legs. Prothoracic leg distinctly longer than mesothoracic leg, slender; procoxa elongate, conical, apically obliquely truncate, inner margin with 1 subapical foveola; protrochanter transverse, apically broadened, oblique; profemur similar in length to pronotum, $f/p = 0.9-1.3$, slender, in cross-section subcircular, ventrally inermous or denticulate; protibia similar in length to profemur, $t/f = 0.8-1.2$, slender, in cross-section subquadrate, width similar throughout, anteroventral margin inermous or denticulate/dentate, apically truncate, posteriorly narrowed, with row of setae ventrally ascending beyond condyle, inermous or mucronate; protarsus 5-segmented, nearly 3/5 as long as protibia; I longer than II, elongate, clavate; II shorter than III, equilateral, clavate; III bilobed, equilateral, lobes slender, diverging; IV nearly 1/4 as long as III, equilateral; V similar in length to II+III, elongate, clavate; protarsal claws nearly 2/5 as long as V, paired, simple; I-IV ventrally with long vestiture. Mesothoracic leg slightly shorter than metathoracic leg, fairly slender; mesocoxa equilateral, subcircular; mesofemur fairly slender, slightly sinuate, in cross-section subcircular, slightly compressed, greatest with near apical 2/5, ventrally inermous; mesotibia short, anteroventral margin inermous, apically slightly broadened, inermous or mucronate. Metacoxa transverse, elliptical, medially canaliculate; metatibia fairly long, apically inermous.

Scutellum. Exposed by elytron, intermediate in size, pentagonal.

Elytron. In dorsal view oval to elongate, $l/w = 1.3-1.6$, greatest width near anterior 2/5, broader than posterior margin of pronotum, humeri subquadrate, anterior margin bisinuate, lateral margins subparallel in anterior 1/2, gradually converging in posterior 1/2, posterior margin rotundate, subcontiguous; in lateral view convex, lateral margin slightly sinuate; 10-striate; striae similar in breadth to intervals, punctate, shallow, maculations dark brown, equilateral, subcontiguous; intervals light brown; III+VI merging before posterior margin, VII-IX ascending in anterior 1/3, X contiguous with lateral margin; vestiture parallel.

Wing. (Fig. 2e). Slightly longer than body, $wing/body = 1.2-1.5$, elliptical to elongate, $l/w = 2.6-3.7$, greatest width near apical 1/3, anterior margin sinuate, posterior margin slightly convex, anal lobe large; C, Sc, R, Cu, Cu1, 2A, and 4A present; with 1 small, triangular maculation in radial field and 2 large, elongate maculations in apical field; radial sclerites and 1 radiomedial sclerotization present; stigmal patch with 2 short macrosetae (see Zherikhin and Gratshev (1995:756); long macrosetae along apical margin of anal lobe; short macrosetae sparse along apical 1/2 of R, dense along posterior margin; microsetae throughout surface.

Abdomen. *Venter*. Nearly $2 \times$ as long as lateral margin of metasternum, laterally convex, centrally plane, posteriorly gradually converging; III+IV fused, V-VII separated; III similar in length to IV, transverse, anterior margin with large, triangular, acuminate projection between metacoxae, anterior edges projected; IV longer than V, transverse; V+VI similar in length, transverse; VII similar in length to IV, transverse, posterior margin rotundate, cristulate; vestiture fairly long, semierect. *Pygidium*. Indistinct (covered by elytron), shorter than VII, transverse, slightly convex, narrow, parallel to orientation of tergum. *Tergum VIII*. Nearly 1/2 as long as spiculum gastrale, transverse,

convex, anterior margin subrectate, anterior edges projected, posterior margin subrectate, plicate, setose. *Sternum VIII*. Consisting of 2 elongate, plicate, posteriorly diverging sclerites, nearly 1/3–1/2 as long as tergum VIII. *Spiculum gastrale*. Similar in length to median lobe, narrow, subrectate, medially flanged, basally with irregular expansion, apically bifurcate, with short, slender, perpendicular projections (T-shaped). *Tegmen*. Nearly 1/3 as long as median lobe, fairly slender, Y-shaped; tegminal apodeme slightly shorter than lateral apodemes, subrectate; lateral apodemes arcuate, projecting to lateral region of median lobe. *Aedeagus*. Median lobe in dorsal view elongate, l/w = 2.2–3.5, basal margin irregular, lateral margins subrectate, subparallel, apical margin rotundate; in lateral view fairly broad, slightly sinuate, apically narrowed, slightly deflexed, porose; internally with 2 elongate, laterobasal sclerites, extending from basal region to central region of median lobe; with 1 elongate, median sclerite, extending along laterobasal sclerites; with 2 apical rami; and extended, denticulate regions; aedeagal apodemes shorter or longer than median lobe, narrow.

Variation. Color variation occurs in all species, *i.e.*, teneral individuals are pale yellow to light-reddish brown. Morphometrical variation occurs to a remarkable extent in male individuals of all species (excepting *S. inermis*). Apparently, larger males display positive allometry in the shape of the prothorax, *i.e.*, the pronotum is distinctly expanded, the prothoracic leg is very long, and anteroventral margin of the protibia bears more and larger dentes (Franz 1999).

Female. Length 1.1–2.4 mm, width 0.6–1.2 mm, l/w = 1.8–2.4. Rostrum 0.3–0.7 mm, subequal in length to pronotum, r/p = 0.8–1.2; antennal insertion near apical 2/5. Frons with 1 basally triangular, apically acute, arcuate spine, nearly 1/4–3/4 as long as diameter of eye, anteriorly with long, fine, erect setae. Pronotum fairly large, fairly globular, l/w = 0.7–1.1, slightly convex. Prothoracic leg longer than mesothoracic leg, fairly slender; procoxa anteriorly with long vestiture; f/p = 0.9–1.3, profemur fairly slender, slightly sinuate, in cross-section subcircular, slightly compressed, greatest with near apical 2/5, ventrally inermous; t/f = 0.7–1.1, protibia fairly slender, anteroventral margin inermous, apically slightly broadened, inermous; mesotibia apically inermous. Elytron l/w = 1.2–1.6. Wing/body = 1.2–1.5, wing l/w = 3.0–3.6. Posterior margin of ventrite VII glabrate. *Tergum VIII* nearly 2/5 as long as sternum VIII, transverse, convex, anterior margin subrectate, posterior margin rotundate, plicate, setose; *tergum IX* weakly sclerotized, similar in length to sternum VIII, elongate, anteriorly irregular, posteriorly narrowed; *sternum VIII* narrow, subrectate, medially flanged, apically bifurcate (Y-shaped); *coxites* nearly 1/2 as long as sternum VIII, elongate, apically setulose, styli elongate, apically with 1 seta; *vagina+bursa copulatrix* large, elongate, longer than sternum VIII, with common oviduct; *spermathecal duct* apically papillate; *spermatheca* elongate, abruptly deflexed (C-shaped), basally rugose, apically narrowed; basally with large, elongate gland reservoir.

Variation. Apparently, the frontal spine displays negative allometry (Franz 1999, in prep.). The morphometrical variation of the prothorax is less remarkable than in males.

Type Species. *Staminodeus vectoris*, by present designation.

Etymology. Named for the association with the staminodes of the inflorescences of Cyclanthaceae (see below). Gender masculine.

Key to the Species of *Staminodeus*

1. Length 1.1–1.4 mm, light reddish-brown; male with eyes separated by distance similar to breadth of antennal club, frons glabrate, profemur ventrally inermous, anteroventral margin of protibia apically mucronate (Fig. 3a); female with eyes separated by distance slightly greater than breadth of antennal club, frontal spine nearly 1/3 as long as diameter of eye, protibia apically mucronate *S. inermis* n. sp.

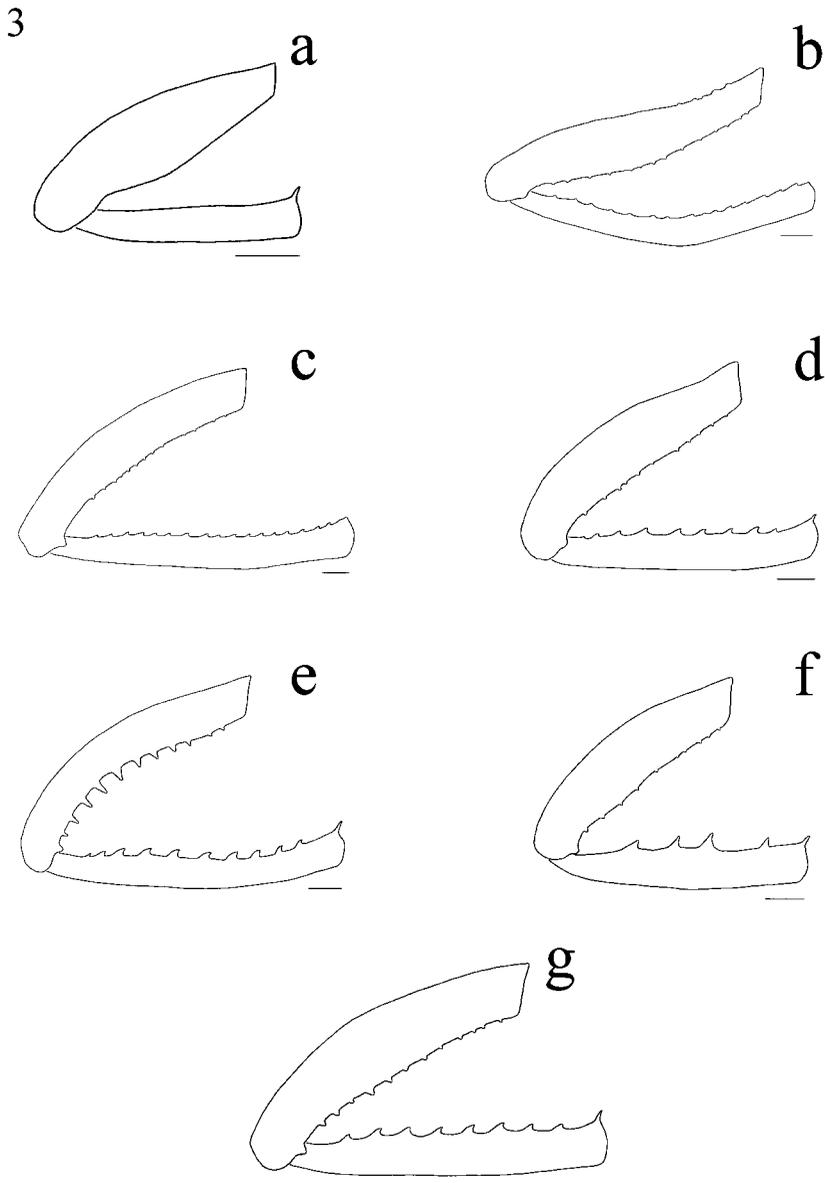


Fig. 3. *Staminodeus*, male, right profemur and protibia, anterior view, a) *S. inermis*; b) *S. curvittibialis*; c) *S. denticulatus*; d) *S. bispinosus*; e) *S. forcipis*; f) *S. dilatatus*; g) *S. vectoris*. Scale bar 0.1 mm.

- 1'. Length 1.4–2.7 mm, dark reddish-brown; male with eyes separated by distance (slightly) greater than breadth of antennal club, frons glabrate or spinulose, profemur ventrally denticulate/dentate, anteroventral margin of protibia denticulate/dentate, protibia apically inermous or mucronate (Fig. 3b–g); female with eyes separated by distance greater than breadth of antennal club, frontal spine nearly 1/2–3/4 as long as diameter of eye, protibia apically inermous 2
- 2(1). Male with laterobasal 1/3 of rostrum carinulate, anteroventral margin of protibia with 12–18 denticuli, protibia apically inermous (Fig. 3b–c) 3
- 2'. Male with laterobasal 1/3 of rostrum glabrate, anteroventral margin of protibia with 3–10 dentes, apically mucronate (Fig. 3d–g) 4
- 3(2). Male with greatest width near humeri, rostrum slightly broadened in apical 1/3, frons glabrate, procoxal cavities inserted near anterior 1/3 of prosternum, profemur sinuate, posterolaterally denticulate, protibia distinctly arcuate (Fig. 3b); female with laterobasal 1/3 of rostrum carinate, frontal spine nearly 1/2 as long as diameter of eye *S. curvitalis* n. sp.
- 3'. Male with greatest width near anterior 2/5 of elytron, breadth of rostrum similar throughout, frons spinulose, procoxal cavities inserted near central region of prosternum, profemur slightly arcuate, posterolaterally glabrate, protibia slightly arcuate (Fig. 3c); female with laterobasal 1/3 of rostrum carinulate, frontal spine nearly 2/3–3/4 as long as diameter of eye *S. denticulatus* n. sp.
- 4(2). Male with frons spinulose 5
- 4'. Male with frons glabrate 6
- 5(4). Male with frontal spine nearly 1/5 as long as diameter of eye, profemur slightly sinuate, ventrally denticulate, protibia subrectate, anteroventral margin of protibia with 6–10 dentes (Fig. 3d) *S. bispinosus* n. sp.
- 5'. Male with frontal spine nearly 2/5 as long as diameter of eye, profemur (distinctly) arcuate, ventrally denticulate/dentate, protibia slightly arcuate, anteroventral margin of protibia with 8–10 dentes (Fig. 3e) *S. forcipis* n. sp.
- 6(4). Male with anteroventral margin of protibia with 3–6 subrectate dentes (Fig. 3f) *S. dilatatus* n. sp.
- 6'. Male with anteroventral margin of protibia with 6–10 arcuate dentes (Fig. 3g) *S. vectoris* n. sp.

Staminodeus inermis, new species

Diagnosis. *Staminodeus inermis* is distinguished from the other species of *Staminodeus* by the small size, the light reddish-brown color (but see section on variation in generic description); the short distance between the eyes, the ventrally inermous prothoracic leg in males; and the fairly short frontal spine in females.

Male. Very small, length 1.2–1.3 mm, width 0.6–0.7 mm, l/w = 1.9–2.0, light reddish-brown. Rostrum 0.3 mm, r/p = 0.9–1.0. Eyes separated by distance similar to breadth of antennal club. Frons glabrate, slightly protruded. Pronotum l/w = 0.8, slightly convex. Prosternum similar in length to mesosternum, slightly convex. Profemur (Fig. 3a) slightly sinuate, f/p = 1.0–1.3, greatest width near apical 2/5, ventrally inermous; protibia (Fig. 3a) subrectate, t/f = 0.8–0.9, anteroventral margin inermous, apically mucronate, pro-

mucron nearly 2/3 as long as protarsal claw; mesotibia apically mucronate, mesomucron nearly 1/4 as long as mesotarsal claw. Elytron l/w = 1.3–1.5 (N = 15). Wing/body = 1.3–1.5, wing l/w = 2.9–3.7. Median lobe (Fig. 4a) l/w = 2.6–3.0 (N = 5), laterobasal sclerites apically broadened, denticulate, median sclerite plicate, apical rami basally diverging, apically fused into triangular projection, basal 1/3 of median lobe denticulate, aedeagal apodemes shorter than median lobe.

Female. Length 1.1–1.4 mm, width 0.6–0.7 mm, l/w = 1.9–2.0. Rostrum 0.3–0.4 mm, r/p = 1.0–1.2. Eyes separated by distance slightly greater than breadth of antennal club. Frontal spine nearly 1/3 as long as diameter of eye. Pronotum l/w = 0.7–0.8. F/p = 0.9–1.3; t/f = 0.7–1.0, protibia apically mucronate, promucron nearly 1/4 as long as protarsal claw. Elytron l/w = 1.3–1.5 (N = 15). Wing/body = 1.4–1.5, wing l/w = 3.1–3.6 (N = 5). Spermatheca (Fig. 5a) deflexed nearly 135°, apex acute.

Type Information. Male holotype “PANAMA, Bocas del Toro, Corriente Grande, Rio Changuinola/ 9°17'30"N, 82°32'41"W, H. Wolda, Feb. 28, 1980” (CWOB); female allotype, same label as male holotype with different date “Feb. 12, 1980” (CWOB); male paratypes, same labels as male holotype with different dates “Jan. 22, 1980” (AMNH, 1), “Jan. 23, 1980” (AMNH, 2), “Jan. 25, 1980” (AMNH, 1), “Jan. 26, 1980” (AMNH, 1; BMNH, 1), “Jan. 29, 1980” (BMNH, 1), “Feb. 6, 1980” (BMNH, 1), “Feb. 8, 1980” (BMNH, 1), “Feb. 10, 1980” (BMNH, 1), “Feb. 11, 1980” (CMNC, 1), “Feb. 12, 1980” (CMNC, 1), “Apr. 3, 1980” (CMNC, 1), “Apr. 10, 1980” (CMNC, 1), “Apr. 12, 1980” (CMNC, 1), “Apr. 16, 1980” (CWOB, 1); “Panama, Bocas del Toro, Cor. Grande, Rio Changuinola, 9°17'30"N, 82°32'41"W, leg. H. Wolda, II-06-1980” (CWOB, 2), same labels as previous specimens with different dates “II-14-1980” (CWOB, 1), “II-15-1980” (CWOB, 1; INBC, 1), “II-17-1980” (INBC, 1), “II-26-1980” (INBC, 2), “III-25-1980” (INBC, 1), “III-27-1980” (MIUP, 2), “IV-04-1980” (MIUP, 1), “IV-19-1980” (MIUP, 1), “IV-24-1980” (MIUP, 1; MUCR, 3), “IV-25-1980” (MUCR, 1), “V-05-1980” (MUCR, 1); female paratypes, same labels as male holotype with different dates “Jan. 30, 1980” (AMNH, 1), “Feb. 2, 1980” (AMNH, 1), “Feb. 3, 1980” (AMNH, 1), “Feb. 4, 1980” (AMNH, 1), “Feb. 7, 1980” (AMNH, 1), “Feb. 12, 1980” (BMNH, 2), “Feb. 14, 1980” (BMNH, 1), “Feb. 25, 1980” (BMNH, 1), “March 7, 1980” (BMNH, 1), “Apr. 15, 1980” (CMNC, 1), “Apr. 27, 1980” (CMNC, 1), “Apr. 28, 1980” (CMNC, 1); “Panama, Bocas del Toro, Cor. Grande, Rio Changuinola, 9°17'30"N, 82°32'41"W, leg. H. Wolda, II-04-1980” (CMNC, 1), same labels as previous specimen with different dates “II-06-1980” (CMNC, 1), “II-07-1980” (CWOB, 2), “II-14-1980” (CWOB, 1), “II-15-1980” (CWOB, 2; INBC, 1), “II-21-1980” (INBC, 3), “II-26-1980” (INBC, 1), “III-27-1980” (MIUP, 1), “III-29-1980” (MIUP, 2), “IV-02-1980” (MIUP, 1), “IV-20-1980” (MIUP, 1; MUCR, 2), “IV-24-1980” (MUCR, 2), “IV-25-1980” (MUCR, 1).

Etymology. Named for the male plesiomorphy of lacking ventral denticulation on the prothoracic leg—*inermis* signifying “unarmed” (Nichols 1989).

Distribution. *Staminodeus inermis* has been collected on the Caribbean slope of Panama, Provincia Bocas del Toro, Río Changuinola (Fig. 6).

Natural History. Unknown.

Staminodeus curvitibialis, new species

Diagnosis. *Staminodeus curvitibialis* is distinguished from the other species of *Staminodeus* in general, and from *S. denticulatus* in particular, by the glabrate frons, the anterior insertion of the procoxal cavities, and the high number

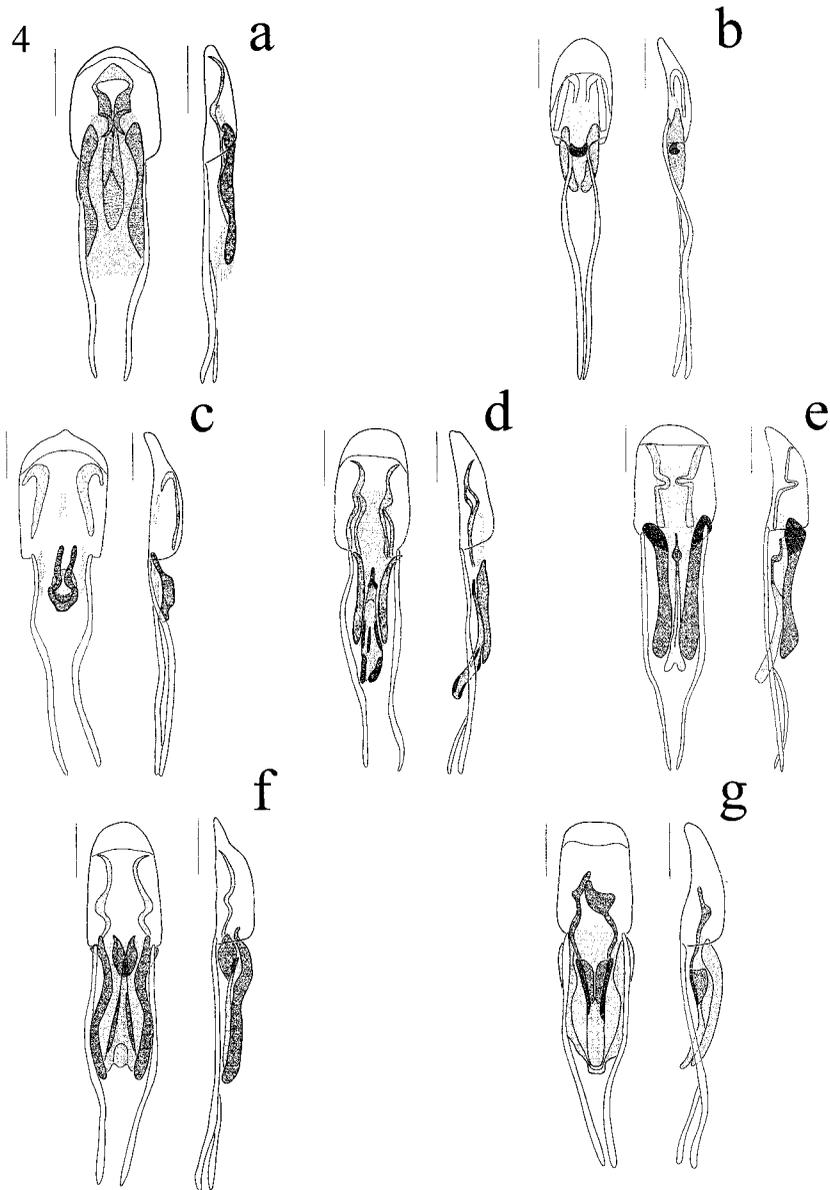


Fig. 4. *Staminodeus*, male, aedeagus, ventral and lateral view, **a)** *S. inermis*; **b)** *S. curvifibialis*; **c)** *S. denticulatus*; **d)** *S. bispinosus*; **e)** *S. forcipis*; **f)** *S. dilatatus*; **g)** *S. vectoris*. Illustrations are interpretative: denticulation and setation are omitted. Scale bar 0.1 mm.

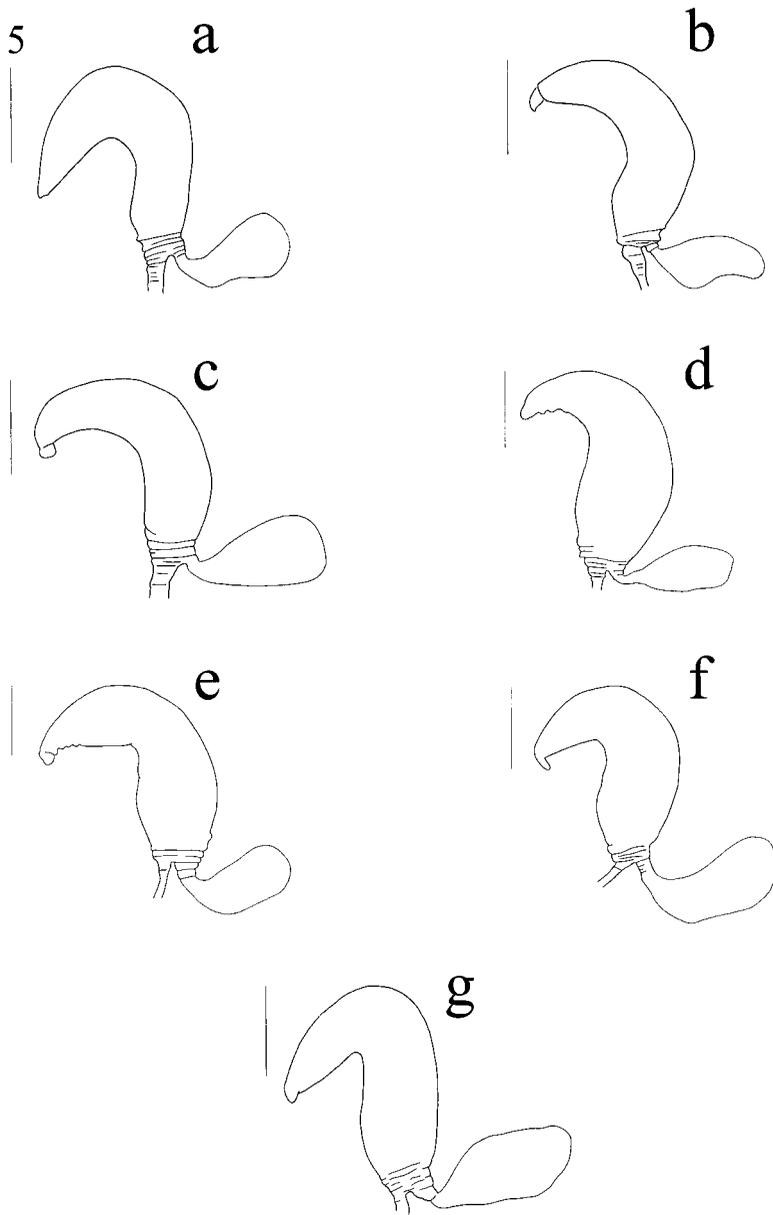


Fig. 5. *Staminodeus*, female, spermatheca and gland reservoir, **a)** *S. inermis*; **b)** *S. curvittibialis*; **c)** *S. denticulatus*; **d)** *S. bispinosus*; **e)** *S. forcipis*; **f)** *S. dilatatus*; **g)** *S. vectoris*. Scale bar 0.05 mm.



Fig. 6. Distribution of *Staminodeus* in Costa Rica, Panama, and Venezuela, ● *S. bispinosus*; ○ *S. curvitalis* (distributional record for Colombia, Provincia Nariño, La Planada is omitted); ■ *S. denticulatus*; □ *S. dilatatus*; ▲ *S. forcipis*; △ *S. inermis*; ▽ *S. vectoris*.

of small denticuli along the distinctly arcuate protibia in males; as well as the laterobasal carina along the base of the rostrum in females.

Male. Length 1.9–2.7 mm, width 0.8–1.1 mm, l/w = 2.1–2.5, greatest width near humeri. Outer basal margin of mandible with rotundate projection. Rostrum 0.5–0.6 mm, r/p = 0.6–0.7, slightly broadened in apical 1/3, laterobasal 1/3 carinulate. Eyes separated by distance slightly greater than breadth of antennal club. Head small, frons glabrate. Pronotum l/w = 0.9–1.1, distinctly convex. Prosternum distinctly longer than mesosternum, elongate, distinctly convex, medially with duplicate carina, extending from procoxal cavities to posterior margin, procoxal cavities inserted near anterior 1/3. Profemur (Fig. 3b) very slender, sinuate, f/p = 1.0–1.2, slightly compressed, greatest width near apical 2/5, posterolaterally and ventrally denticulate; protibia (Fig. 3b) very slender, distinctly arcuate, t/f = 1.0–1.1, anteroventral margin with row of 12–18 denticuli, apically inermous; mesotibia apically inermous. Elytron l/w = 1.4–1.6 (N = 15), greatest width of elytron near humeri. Wing/body = 1.2–1.5, wing l/w = 2.6–3.4 (N = 5). Posterior margin of ventrite VII subrectate. Median lobe (Fig. 4b) l/w = 2.4–2.8 (N = 5), laterobasal sclerites denticulate, median sclerite heavily sclerotized, very short, rotundate, impressed, apically spinulose, apical rami weakly sclerotized, apically deflexed, basal 1/2 of median lobe denticulate, aedeagal apodemes longer than median lobe.

Female. Length 1.8–2.3 mm, width 0.8–1.0 mm, l/w = 1.9–2.2, greatest width near anterior 2/5 of elytron. Rostrum 0.5–0.7 mm, r/p = 1.0–1.1, laterobasal 1/3 carinate, laterobasal carina contiguous with dorsolateral carina. Head fairly small, frontal spine nearly 1/2 as long as diameter of eye. Pronotum l/w = 0.8–1.0, greatest width near anterior 1/3. Prosternum longer than mesosternum, equilateral, pleurosternal suture anteriorly with short projection, procoxal cavities inserted near central region. F/p = 1.0–1.1; t/f = 0.8–1.0. Elytron l/w = 1.3–1.6 (N = 15). Wing/body = 1.4–1.5, wing l/w = 3.1–3.6 (N = 5). Spermatheca (Fig. 5b) deflexed nearly 90°, apex separated, acute.

Type Information. Male holotype “Venezuela, Aragua, Rancho Grande, 1,400 m, on *Asplundia caput-medusae*, leg. H. Escalona, VI-06–1999” (IZAV); female allotype, same label as male holotype (IZAV); male paratypes, same labels as male holotype (AMNH, 5; BMNH, 5; CMNC, 5; CWOB, 5; IZAV, 5; MIUP, 5; MUCR, 5); female paratypes, same labels as male holotype (AMNH, 5; BMNH, 5; CMNC, 5; CWOB, 5; IZAV, 5; MIUP, 5; MUCR, 5).

Etymology. Named for the male apomorphy of having an arcuate protibia—*curvus* signifying “bent” and *tibialis* signifying “of the tibia” (Brown 1956).

Distribution. *Staminodeus curvitalis* has been collected in Colombia, Provincia Nariño, La Planada: 01°05'N, 77°57'W; in Venezuela, Provincia Aragua, Portachuelo and Rancho Grande; in Venezuela, Provincia Carabobo, Morón; and in Venezuela, Provincia Falcón, Capadare (Fig. 6).

Natural History. *Staminodeus curvitibialis* is associated with *Sphaeradenia hamata* Harling in Colombia, and with *Asplundia caput-medusae* (Hooker fil.) Harling in Venezuela (H. Escalona, pers. comm.).

Staminodeus denticulatus, new species

Diagnosis. *Staminodeus denticulatus* is distinguished from the other species of *Staminodeus* in general, and from *S. curvitibialis* in particular, by the frontal spinule and the high number of small denticuli along the apically inermous protibia in males; as well as the fairly long and abruptly deflexed frontal spine in females.

Male. Length 1.8–2.4 mm, width 0.9–1.2 mm, l/w = 1.9–2.2. Rostrum 0.4–0.6 mm, r/p = 0.7–0.8, laterobasal 1/3 carinulate. Eyes separated by distance slightly greater than breadth of antennal club. Frons with 1 apically directed, arcuate spinule, nearly 1/4 as long as diameter of eye, anteriorly with long, fine, erect setae. Pronotum l/w = 0.8–0.9, anteriorly distinctly narrowed, distinctly convex. Prosternum distinctly longer than mesosternum, equilateral, distinctly convex. Profemur (Fig. 3c) slightly arcuate, f/p = 1.0/1.3, width similar throughout, ventrally denticulate; protibia (Fig. 3c) slightly arcuate, t/f = 1.0, anteroventral margin with row of 12–18 apically directed, arcuate, acute denticuli, apically inermous; mesotibia apically inermous. Elytron l/w = 1.3–1.5 (N = 4). Median lobe (Fig. 4c) l/w = 2.3–2.3 (N = 3), apical margin medially projected, laterobasal sclerites weakly sclerotized, short, spinulose, median sclerite heavily sclerotized, short, basally rotundate, impressed, apically spinulose, with 2 elongate, slightly diverging projections, apical rami broad, apically deflexed, with small, elongate, spinulose region between apical rami, aedeagal apodemes slightly longer than median lobe.

Female. Length 1.9–2.4 mm, width 1.0–1.2 mm, l/w = 1.8–2.0. Rostrum 0.5–0.7 mm, r/p = 0.9–1.0, laterobasal 1/3 carinulate. Frontal spine nearly 2/3–3/4 as long as diameter of eye, basally subrectate, perpendicular to frons, apically abruptly deflexed (not gradually arcuate). Pronotum l/w = 0.8–0.9, greatest width near anterior 1/3. Prosternum longer than mesosternum. F/p = 0.9–1.2; t/f = 0.9–1.1. Elytron l/w = 1.2–1.5 (N = 12). Spermatheca (Fig. 5c) deflexed nearly 90°, apex slightly separated, obtuse.

Type Information. Male holotype “Costa Rica, Puntarenas, Las Cruces, 1,100 m, on *Carludovica subpalmata*, leg. L. Gómez, XII-1994” (CMNC); female allotype, same label as male holotype (CMNC); male paratypes “PANAMA, Chiriquí, Fortuna, (8°44'N, 82°15'W), UV trap, Apr. 22, 1978/ H. Wolda, Collector” (CWOB, 2), same label as previous specimens with different date “Aug. 9, 1977” (MIUP, 1); same label as male holotype (MUCR, 1); “Costa Rica, Puntarenas, Las Cruces, 1,000 m, on *Evodiantus funifer*, leg. L. Gómez, XII-29–1994” (MUCR, 1); female paratypes, same label as male holotype (CMNC, 1); “Costa Rica, Puntarenas, Las Cruces, 1,000 m, on *Evodiantus funifer*, leg. L. Gómez, XII-29–1994” (CMNC, 1; MUCR, 3); “PANAMA, Chiriquí, Fortuna, (8°44'N, 82°15'W), UV trap, Apr. 22, 1978/ H. Wolda, Collector” (CWOB, 1), same labels as previous specimen with different dates “May 2, 1978” (CWOB, 1), “July 11, 1978” (CWOB, 1), “Aug. 2, 1978” (MIUP, 2).

Etymology. Named for the denticulate protibia in males—*denticulatus* signifying “with small teeth” (Brown 1956).

Distribution. *Staminodeus denticulatus* has been collected in the Cordillera de Talamanca de Costa Rica, Provincia de Puntarenas, San Vito: 08°47'N, 82°57'W; on the Caribbean slope of Panama, Provincia Bocas del Toro, Chiriquí Grande; and on the Pacific slope of Panama, Provincia Chiriquí, Fortuna (Fig. 6).

Natural History. *Staminodeus denticulatus* is associated with *Carludovica*

palmata Ruíz & Pavón and *Evodianthus funifer* (Poit.) Lindman in Costa Rica, and with *Asplundia* sp. in Panama, Provincia Bocas del Toro, Chiriquí Grande (label information by Windsor & Stockwell, X-13-1996).

Staminodeus bispinosus, new species

Diagnosis. *Staminodeus bispinosus* is distinguished from *S. forcipis* by the fairly short frontal spinule and the slightly sinuate profemur in males. It is problematic to separate the females from *S. forcipis*, *S. dilatatus*, and *S. vectoris* by the slight differences in spermathecal characters. The actual association of males and females of *S. bispinosus* has to be reconfirmed by field observations.

Male. Length 1.5–1.9 mm, width 0.7–1.0 mm, l/w = 2.0–2.3. Rostrum 0.4–0.5 mm, r/p = 0.8–1.0. Frons with 1 apically directed, arcuate spinule, nearly 1/5 as long as diameter of eye, anteriorly with long, fine, erect setae. Pronotum l/w = 0.8–0.9, convex. Prosternum longer than mesosternum. Profemur (Fig. 3d) slightly sinuate, f/p = 1.0–1.2, width similar throughout, ventrally denticulate; protibia (Fig. 3d) subrectate, t/f = 0.8–1.1, anteroventral margin with row of 6–10 apically directed, arcuate dentes, apically mucronate, promucron nearly 2/3 as long as protarsal claw; mesotibia apically inermous. Elytron l/w = 1.3–1.6 (N = 15). Median lobe (Fig. 4d) l/w = 2.8–3.1 (N = 10), laterobasal sclerites apically denticulate, median sclerite heavily sclerotized, basally projected, deflexed, apically acuminate, glabrate, apically rami basally divided, undulate, basal 3/4 of median lobe denticulate, aedeagal apodemes shorter than median lobe.

Female. Length 1.9 mm, width 0.7–1.0 mm, l/w = 1.9–2.1. Rostrum 0.5–0.6 mm, r/p = 1.0–1.2. Frontal spine nearly 3/5 as long as diameter of eye. Pronotum l/w = 0.8–0.9. F/p = 1.1–1.3; t/f = 0.8–0.9. Elytron l/w = 1.3–1.5 (N = 15). Spermatheca (Fig. 5d) deflexed nearly 90°, subapically undulate, apex rotundate.

Type Information. Male holotype “PANAMA, Chiriqui, Fortuna, (8°44'N, 82°15'W), UV trap, June 27, 1978/ H. Wolda, Collector” (CWOB); female allotype, same label as male holotype with different date “July 17, 1978” (CWOB); male paratypes, same labels as male holotype with different dates “Apr. 17, 1978” (CWOB, 1), “Apr. 24, 1978” (CWOB, 1); “PANAMA, Bocas del Toro, Corriente Grande, Rio Changuinola/ 9°17'30"N, 82°32'41"W, H. Wolda, Jan. 20, 1980” (CWOB, 1), same labels as previous specimen with different dates “Jan. 23, 1980” (CWOB, 1), “Feb. 9, 1980” (CWOB, 1), “Feb. 13, 1980” (MIUP, 1), “Feb. 24, 1980” (MIUP, 1), “Apr. 8, 1980” (MIUP, 1); “Panama, Bocas del Toro, Cor. Grande, Rio Changuinola, 9°17'30"N, 82°32'41"W, leg. H. Wolda, II-21-1980” (MIUP, 1), same label as previous specimen with different date “III-26-1980” (MIUP, 1); female paratypes, same labels as male holotype with different dates “Apr. 22, 1978” (CWOB, 1), “May 5, 1978” (CWOB, 2), “May 17, 1978” (CWOB, 1), “June 27, 1978” (CWOB, 1; MIUP, 1), “July 25, 1978” (MIUP, 3), “Aug. 22, 1978” (MIUP, 1).

Etymology. Named for the frontal spine which is present in both sexes—*bis* signifying “twice” and *spinosus* signifying “thorny” (Brown 1956).

Distribution. *Staminodeus bispinosus* has been collected on the Caribbean slope of Panama, Provincia Bocas del Toro, Río Changuinola; and on the Pacific slope of Panama, Provincia Chiriquí, Fortuna (Fig. 6).

Natural History. Unknown.

Staminodeus forcipis, new species

Diagnosis. *Staminodeus forcipis* is distinguished from *S. bispinosus* by the fairly large frontal spinule and the distinctly arcuate, apically dentate profemur in males. See diagnosis of *S. bispinosus* for females.

Male. Length 2.1 mm, width 1.0 mm, $l/w = 2.1$. Rostrum 0.5 mm, $r/p = 0.8$. Frons with 1 apically directed, arcuate spinule, nearly $2/5$ as long as diameter of eye, anteriorly with long, fine, erect setae. Pronotum $l/w = 0.9$, convex. Prosternum longer than mesosternum. Profemur (Fig. 3e) (distinctly) arcuate, $f/p = 1.2$, width similar throughout, each ventrolateral margin with row of denticuli/dentes, larger towards apex; protibia (Fig. 3e) slightly arcuate, $t/f = 1.0$, anteroventral margin with row of 8–10 apically directed, arcuate dentes, apically mucronate, promucron nearly $2/3$ as long as protarsal claw; mesotibia apically inermous. Elytron $l/w = 1.4$. Median lobe (Fig. 4e) $l/w = 2.9$ ($N = 1$), laterobasal sclerites apically heavily sclerotized, broadened, denticulate, median sclerite basally projected, apically acuminate, glabrate, apical rami distinctly undulate in central region, basal $3/4$ of median lobe denticulate, aedeagal apodemes shorter than median lobe.

Female. Length 1.9–2.0 mm, width 1.0 mm, $l/w = 1.9$ –2.0. Rostrum 0.5 mm, $r/p = 1.0$. Frontal spine nearly $3/5$ as long as diameter of eye. Pronotum $l/w = 0.8$ –0.9. $F/p = 1.1$ –1.2; $t/f = 0.9$ –1.0. Elytron $l/w = 1.4$ ($N = 2$). Spermatheca (Fig. 5e) deflexed nearly 90° , subapically undulate, apex slightly separated, rotundate.

Type Information. Male holotype “COSTA RICA, S. J., Zurqui de Moravia, 1,600 m, XI-1995, malaise trap, Hanson & Godoy” (CWOB); female allotype “COSTA RICA, S. Jose, Zurqui de Moravia, 1,600 m, malaise trap, III-1992, P. Hanson” (CWOB); female paratype “COSTA RICA, S. Jose, Zurqui de Moravia, 1,600 m, malaise trap, II-1993, P. Hanson” (MUCR, 1: teneral).

Etymology. Named for the dentate profemur and protibia in males which resemble a pair of tongs—*forceps* signifying “nippers, tongs” (Brown 1956).

Distribution. *Staminodeus forcipis* has been collected in the Cordillera de Tilarán of Costa Rica, Provincia Puntarenas, Monteverde; and in the Central Valley of Costa Rica, Provincia San José, Zurquí de Moravia (Fig. 6).

Natural History. Unknown.

Staminodeus dilatatus, new species

Diagnosis. *Staminodeus dilatatus* is distinguished from *S. vectoris* by the lower number of larger, subrectate dentes in males, in addition to differing from *S. bispinosus* and *S. forcipis* by the glabrate frons. See diagnosis of *S. bispinosus* for females.

Male. Length 1.4–1.9 mm, width 0.7–0.9 mm, $l/w = 1.9$ –2.2. Rostrum 0.4–0.5 mm, $r/p = 0.7$ –1.0. Frons glabrate. Pronotum $l/w = 0.8$ –0.9, convex. Prosternum longer than mesosternum. Profemur (Fig. 3f) slightly arcuate, $f/p = 0.9$ –1.1, width similar throughout, ventrally denticulate; protibia (Fig. 3f) subrectate, $t/f = 0.9$ –1.1, anteroventral margin with row of 3–6 apically directed, subrectate dentes, apically mucronate, promucron nearly $2/3$ as long as protarsal claw; mesotibia apically mucronate, mesomucron nearly $1/4$ as long as mesotarsal claw. Elytron $l/w = 1.3$ –1.4 ($N = 15$). Median lobe (Fig. 4f) $l/w = 3.0$ –3.5 ($N = 5$), laterobasal sclerites apically setose, median sclerite basally projected, apically bifurcate, setose, apical rami undulate, basal $2/3$ of median lobe denticulate, aedeagal apodemes shorter than median lobe.

Female. Length 1.5–1.9 mm, width 0.8–1.0 mm, $l/w = 1.9$ –2.0. Rostrum 0.4–0.6, $r/p = 1.0$ –1.1. Frontal spine nearly $3/5$ as long as diameter of eye. Pronotum $l/w = 0.8$. $F/p = 1.0$ –1.2; $t/f = 0.8$ –1.0. Elytron $l/w = 1.3$ –1.4 ($N = 3$). Spermatheca (Fig. 5f) deflexed nearly 120° , apex narrowly projected.

Type Information. Male holotype “PANAMA, Bocas del Toro, Corriente Grande, Rio Changuinola/ $9^\circ 17' 30''$ N, $82^\circ 32' 41''$ W, H. Wolda, Feb. 3, 1980” (CWOB); female allotype, same label as male holotype with different date “Feb. 9, 1980” (CWOB); male paratypes, same labels as male holotype with different dates “Jan. 20, 1980” (CWOB, 1), “Feb. 11, 1980” (CWOB, 1),

“Feb. 26, 1980” (CWOB, 1), “Mar. 13, 1980” (CWOB, 1), “Mar. 18, 1980” (CWOB, 1), “Mar. 28, 1980” (MIUP, 1); “Panama, Bocas del Toro, Cor. Grande, Río Changuinola, 9°17'30"N, 82°32'41"W, leg. H. Wolda, III-15-1980” (MIUP, 1), same labels as previous specimen with different dates “III-26-1980” (MIUP, 2), “III-29-1980” (MIUP, 1); female paratypes, same label as male holotype with different date “March 4, 1980” (CWOB, 1); “Panama, Bocas del Toro, Cor. Grande, Río Changuinola, 9°17'30"N, 82°32'41"W, leg. H. Wolda, IV-24-1980” (MIUP, 1).

Etymology. Named for the diagnostic character of the male protibia with respect to *S. vectoris*, *i.e.*, less and larger dentes—*dilatatus* signifying “spread out, enlarged, extended” (Brown 1956).

Distribution. *Staminodeus dilatatus* has been collected on the Caribbean slope of Panama, Provincia Bocas del Toro, Río Changuinola (Fig. 6).

Natural History. Unknown.

Staminodeus vectoris, new species

Diagnosis. *Staminodeus vectoris* is distinguished from *S. dilatatus* by the higher number of smaller, arcuate dentes in males, in addition to differing from *S. bispinosus* and *S. forcipis* by the glabrate frons. Males and females were associated by field observations (see below).

Male. Length 1.6–2.3 mm, width 0.7–1.0 mm, l/w = 2.1–2.4. Rostrum 0.4–0.5 mm, r/p = 0.7–0.9. Frons glabrate. Pronotum l/w = 0.8–1.0, convex. Prosternum longer than mesosternum. Profemur (Fig. 3g) slightly arcuate, f/p = 0.9–1.2, width similar throughout, ventrally denticulate; protibia (Fig. 3g) subrectate, t/f = 0.9–1.2, anteroventral margin with row of 6–10 apically directed, arcuate dentes, apically mucronate, promucron nearly 2/3 as long as protarsal claw; mesotibia apically mucronate, mesomucron nearly 1/4 as long as mesotarsal claw. Elytron l/w = 1.3–1.6 (N = 15). Wing/body = 1.2–1.3, wing l/w = 3.0–3.4 (N = 8). Median lobe (Fig. 4g) l/w = 2.5–3.3 (N = 15), laterobasal sclerites apically setose, median sclerite basally projected, apically bifurcate, setose, apical rami undulate, apically spatulate, basal 3/4 of median lobe denticulate, aedeagal apodemes shorter than median lobe.

Female. Length 1.8–2.2 mm, width 0.8–1.0 mm, l/w = 2.1–2.4. Rostrum 0.5 mm, r/p = 0.8–1.1, laterobasal 1/3 carinulate. Frontal spine nearly 3/5 as long as diameter of eye. Pronotum l/w = 0.8–1.1 (N = 15). F/p = 0.9–1.2; t/f = 0.8–1.0. Elytron l/w = 1.4–1.6 (N = 15). Wing/body = 1.2–1.3, wing l/w = 3.0–3.4 (N = 8). Spermatheca (Fig. 5g) deflexed nearly 135°, apex rotundate.

Type Information. Male holotype “Costa Rica, Heredia, La Selva, 40 m, on *Asplundia uncinata*, leg. N. Franz, VII-03-1997” (MUCR); female allotype, same label as male holotype (MUCR); male paratypes, same labels as male holotype (AMNH, 5; BMNH, 5; CMNC, 5; CWOB, 5; INBC, 5; MIUP, 5; MUCR, 5); female paratypes, same labels as male holotype (AMNH, 5; BMNH, 5; CMNC, 5; CWOB, 5; INBC, 5; MIUP, 5; MUCR, 5).

Etymology. Named for the female behavior of transporting the detached staminodes (see below)—*vectoris* signifying “carrier” (Brown 1956).

Distribution. *Staminodeus vectoris* has been collected at the Volcán Arenal in Costa Rica, Provincia Alajuela, Los Lagos: 10°29'N, 84°43'W; on the Caribbean slope of Costa Rica, Provincia Heredia, Parque Nacional Braulio Carrillo, La Selva and Rara Avis; in the Central Valley of Costa Rica, Provincia San José, Zurquí de Moravia; and on the Caribbean slope of Panama, Provincia Bocas del Toro, Río Changuinola (Fig. 6).

Natural History. *Staminodeus vectoris* is associated with the staminodes of the inflorescences of Cyclanthaceae. At La Selva, both sexes visit several spe-

Table 1. Character matrix for the cladistic analysis of *Staminodeus*.

Taxon/character	5	10	15	
<i>Not. basalis</i>	0000-	00000	-----	-00
<i>Per. carludovicae</i>	0000-	00100	-----	-00
<i>Sys. costaricensis</i>	0000-	00100	-----	-00
<i>S. inermis</i>	1000-	11011	000-0	-01
<i>S. curvitibialis</i>	10110	00011	00101	011
<i>S. denticulatus</i>	11110	00011	00101	011
<i>S. bispinosus</i>	11111	10011	01011	101
<i>S. forcipis</i>	11111	10011	01011	101
<i>S. dilatatus</i>	10111	11011	11021	101
<i>S. vectoris</i>	10111	11011	11021	101

cies of *Asplundia* Harling, *Carludovica* Ruiz & Pavón, *Chorigyne* R. Eriksson, *Dicranopygium* Harling, and *Evodianthus* Oersted. The following observations were made for the most part on *Asplundia uncinata* Harling. The adult beetles arrive at dawn during the pistillate anthesis when the floral fragrances are volatilized. The females detach the staminodes and fall to the floor where they transport them with their legs—by turning upside down and using the frontal spine to support their position against the surface underneath. Meanwhile, the males associate with the moving staminodes. If several males occur on the same staminode, short fights are observed during which the prothoracic legs are used to displace competing males with fast blows. Presumably, the dentate protibiae interlock and translate the lifting power among them. Copulation and oviposition occur above the forest floor; the reproductive behavior is described with more detail in Franz (1999, in prep.). The ephemeral staminodes serve as an oviposition substrate. The larvae are detritivores in the leaf litter, and the pupae emerge from the forest floor after 10–20 days. The adult beetles are not pollinators because they do not touch the pistillate flowers of the host inflorescence and leave before the staminate anthesis. *Staminodeus vectoris* was coded (by C. W. O'Brien) as “gen. C2 sp. C1” in Franz (1999).

Cladistic Analysis

Characters. The following characters were used to construct the data matrix (Table 1).

1. Carinate rostrum: (0) absent; (1) present.
2. Male with spinulose frons: (0) absent; (1) present.
3. Male with denticulate profemur: (0) absent; (1) present.
4. Male with denticulate/dentate protibia: (0) absent; (1) present.
5. Male protibia with: (0) 12–18 denticuli; (1) 3–10 dentes. Inapplicable in *S. inermis* and in outgroup taxa.
6. Male with promucron: (0) absent; (1) present.
7. Male with mesomucron: (0) absent; (1) present.
8. Male with exposed, broad, perpendicular pygidium: (0) absent; (1) present.
9. Male with complex sclerites in median lobe: (0) absent; (1) present.
10. Male with denticulation in median lobe: (0) absent; (1) present.
11. Male with apical setation in laterobasal sclerites of median lobe: (0) absent; (1) present. Inapplicable in outgroup taxa.

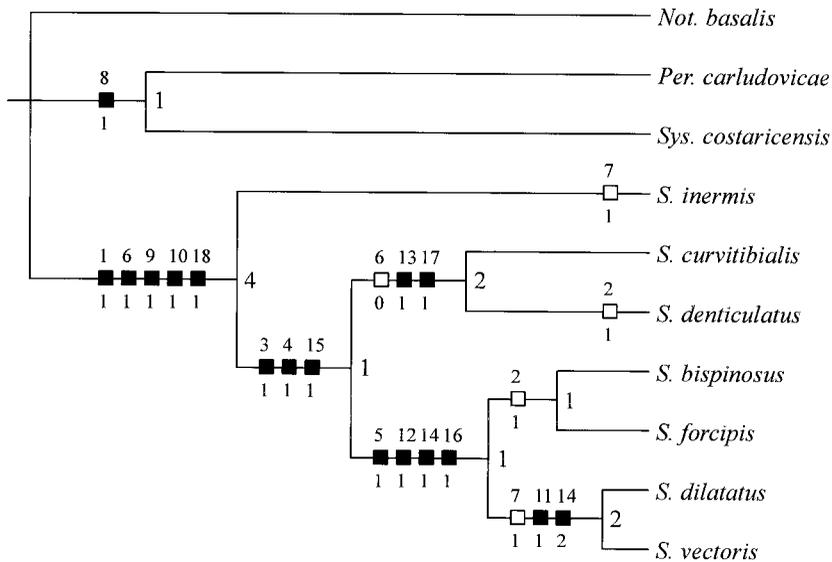


Fig. 7. Phylogenetic relationships among the seven species of *Staminodeus*, with *Not. basalis*, *Per. carlundovicae*, and *Sys. costaricensis* as outgroup taxa. Character transformations are hypothesized according to ACCTRAN optimization. Homology is indicated by black rectangles, whereas homoplasy (for details see discussion) is indicated by white rectangles. Character numbers and character states (Table 1) are displayed above and below each rectangle, respectively, and Bremer support is indicated at the right end of each branch.

12. Male with basal projection of median sclerite of median lobe: (0) absent; (1) present. Inapplicable in outgroup taxa.
13. Male with median sclerite of median lobe: (0) longer than apical rami; (1) shorter than apical rami. Inapplicable in outgroup taxa.
14. Male with median sclerite of median lobe apically: (0) acuminate; (1) impressed; (2) bifurcate. Coded as non-additive. Inapplicable in *S. inermis* and in outgroup taxa.
15. Male with apical rami of median lobe: (0) fused; (1) separated. Inapplicable in outgroup taxa.
16. Male with apical rami of median lobe: (0) deflexed; (1) undulate. Inapplicable in outgroup taxa.
17. Male with aedeagal apodemes: (0) shorter than median lobe; (1) longer than median lobe.
18. Female with spinose frons: (0) absent; (1) present.

Analysis. The cladistic analysis for ten taxa and 18 characters yields a single most parsimonious cladogram with $L = 22$, $CI = 86$, and $RI = 90$ (Fig. 7). Bremer values indicate support by synapomorphies for the monophyly of *Staminodeus*, as well as that of (*S. curvibtibialis*, *S. denticulatus*) and (*S. dilatatus*, *S. vectoris*). Homoplasy is hypothesized for character 2 (male with spinulose frons), character 6 (male with promucron), and character 7 (male with mesomucron). Fast optimization (ACCTRAN) proposes character 6 as a synapomorphy for *Staminodeus* and a reversal (secondary loss) for (*S. curvibtibialis*,

S. denticulatus), whereas slow optimization (DELTRAN) proposes convergent transformations for *S. inermis* and ((*S. bispinosus*, *S. forcipis*), (*S. dilatatus*, *S. vectoris*)).

Discussion

The monophyly of *Staminodeus* within Derelomini is indicated by the carinate rostrum; the complex structures (sclerites, denticulation) of the median lobe in males; and the frontal spine in females. ACCTRAN optimization preserves the primary homology of the male promucron for *Staminodeus* (cf. de Pinna 1991), and I prefer this optimization because the secondary loss of this character in *S. curvittibialis* and *S. denticulatus* corresponds to the general morphology of the male protibia in these species, *i.e.*, they have smaller denticuli which may not interlock among competing males as observed for *S. vectoris*. *Staminodeus inermis* is the sister taxon to the remaining species which share the ventrally denticulate/dentate prothoracic leg in males and the separated apical rami in the median lobe. The dark color and positive allometry of the male prothorax appear as further evidence for this divergence. *Staminodeus curvittibialis* and *S. denticulatus* are the sister taxon to the remaining species because of the shared characters of the male protibia (denticulate, inermous), the median sclerite of the median lobe (central position, short extension, apical impression with spinulose margin), and the fairly long aedeagal apodemes. The spinulose frons in *S. denticulatus* is interpreted as a single homoplasy. Conversely, the basal projection of the median sclerite and the distinctive undulation of the apical rami characterize the other clade with four species. The sister relationship of *S. bispinosus* and *S. forcipis* has weak support (spinulose frons in males, median sclerite of median lobe apically acuminate and glabrate), whereas I consider the apical setation of the laterobasal sclerites and the bifurcate apex of the median sclerite as stronger evidence for the sister relationship of *S. dilatatus* and *S. vectoris*.

Characters 5 and 11–16 are inapplicable to the outgroup taxa. Apparently, *Staminodeus* has evolved highly apomorphic male genitalia. However, the present hypotheses of genitalic homology may have to be reconsidered when closer relatives than the present outgroups are discovered; an undescribed species from Panama is a potential candidate. Cyclanthaceae occur throughout the Neotropical region, and field work in presently underrepresented geographic areas, *e.g.*, Colombia, is likely to yield additional species which will serve to refine previous assessments.

If the natural history of *S. vectoris* is—within reasonable limits—applicable to the remaining species, then *Staminodeus* is the first genus of Derelomini for which the association with the staminodes of the inflorescences of Cyclanthaceae has been reported. *Perelleschus* and *Systemotelus* have different biologies, since their larvae develop in the maturing infructescences rather than in the leaf litter (Anderson and Gómez 1997; Franz 1999, in prep.). A detailed account of the remarkable behavior of *S. vectoris* will be given elsewhere. *Staminodeus inermis* is an interesting candidate for field observations: its males lack the morphological synapomorphies for fighting, but may have similar behaviors to *S. vectoris*. This condition would refute the present hypothesis that fighting in males evolved *after* the specialized behavior of transporting staminodes in females.

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