

Ganglionus, a New Genus of Derelomini (Coleoptera: Curculionidae) Associated with *Carludovica* (Cyclanthaceae)

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ABSTRACT *Ganglionus*, gen. nov., is described for five species: *G. mitigatus*, sp. nov., from Costa Rica; *G. catenatus*, sp. nov., from Costa Rica and Panama; *G. undulatus*, sp. nov., from Costa Rica and Panama; *G. constrictus*, sp. nov., from Ecuador; and *G. spatulatus*, sp. nov., from Colombia. *Ganglionus* is placed in Derelomini and presents the following putative synapomorphies: male with (1) dorsally tumescent rostrum, (2) posteriorly setose sternum VIII, and (3) apically O-shaped tegmen. *Ganglionus* is associated with *Carludovica* Ruiz & Pavón (Cyclanthaceae). Observations on the biology of *G. undulatus* at La Selva, Costa Rica, indicate that the adults are pollinators. The females oviposit into the staminate flowers of the host inflorescences, and the larvae complete their development in the leaf litter. A cladistic analysis—using *Notolomus basalis* LeConte, *Staminodeus vectoris* Franz, and *Perellesschus carludovicae* (Günther) as outgroups—proposes the relationships (*G. mitigatus*, ((*G. catenatus*, *G. undulatus*), (*G. constrictus*, *G. spatulatus*))).

KEY WORDS *Carludovica*, Cyclanthaceae, Derelomini, *Ganglionus*, neotropics, systematics

IN THE NEOTROPICS, the majority of the diversity of “palm flower weevils” (Curculionidae: Curculioninae: Derelomini *sensu* Alonso-Zarazaga and Lyal 1999), as well as their biologies and phylogenetic relationships, remain to be discovered. Recent descriptions of new taxa include *Systemotelus* by Anderson and Gómez (1997), *Staminodeus* by Franz (2001), and a revision of *Perellesschus* Wibmer & O'Brien by Franz and O'Brien (2001). A total of 16 new species of Derelomini was described in these works, however, still larger numbers are already at hand in collections (unpublished data). They are associated with the reproductive organs of Cyclanthaceae (Monocotyledoneae), although the life habits vary considerably (see Franz 1999). The larvae may be detritivorous, as in *Staminodeus*, or herbivorous, as in *Perellesschus* and *Systemotelus*. The adults may be pollinators with behaviors that correspond with the morphology and phenology of cyclanth inflorescences (e.g., *Perellesschus*, for details see Franz and O'Brien 2001), or visitors that neither carry nor transfer pollen among flowers.

In the present paper we describe a new genus of Derelomini, *Ganglionus* Franz & O'Brien, with five new species that are associated with *Carludovica* Ruiz & Pavón (Cyclanthaceae). In addition, we provide a key, natural history notes, and a phylogeny of the species of *Ganglionus*.

Materials and Methods

Morphological Description. The methods are detailed in Franz and O'Brien (2001). Body length was measured from anterior margin of eye to posterior margin of elytron; rostral 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). To homologize the characters of the tibiae, the terms “dorsal, ventral, anterior, and posterior” refer to an idealized anatomical position of 90° from the main body axis for all three pairs of legs. The following abbreviations were used: *l* = length, *w* = width, *r* = rostrum, *P* = pronotum, *t* = protibia, and *f* = profemur. SEM pictures (habitus and detail) were produced with a Hitachi S-4700. We applied the phylogenetic species concept (*sensu* Wheeler and Platnick 2000) to *Ganglionus*. Type labels include the species name, e.g., “*Ganglionus undulatus*,” the type status and gender, e.g., “Holotype, ♂,” and “Franz and O'Brien, 2001.” They are red, blue, and yellow for holotypes, allotypes, and paratypes, respectively. Insect collections codens are used as in Arnett et al. (1993).

Cladistic Analysis. The selected outgroups include the following: (1) *Notolomus basalis* LeConte, a distinct derelomine species that is associated with the cabbage palm *Sabal palmetto* (Walt.) Lodd. ex Schultes (Brown 1976); (2) *Staminodeus vectoris* Franz, a nonpollinating cyclanth derelomine (Franz 2001); and (3) *Perellesschus carludovicae* (Günther), which resembles *Ganglionus* in several aspects of morphology and biology, e.g., in having a perpendicular pygidium in males and being associated with *Carludovica* (Franz and O'Brien 2001, see *Discussion* section).

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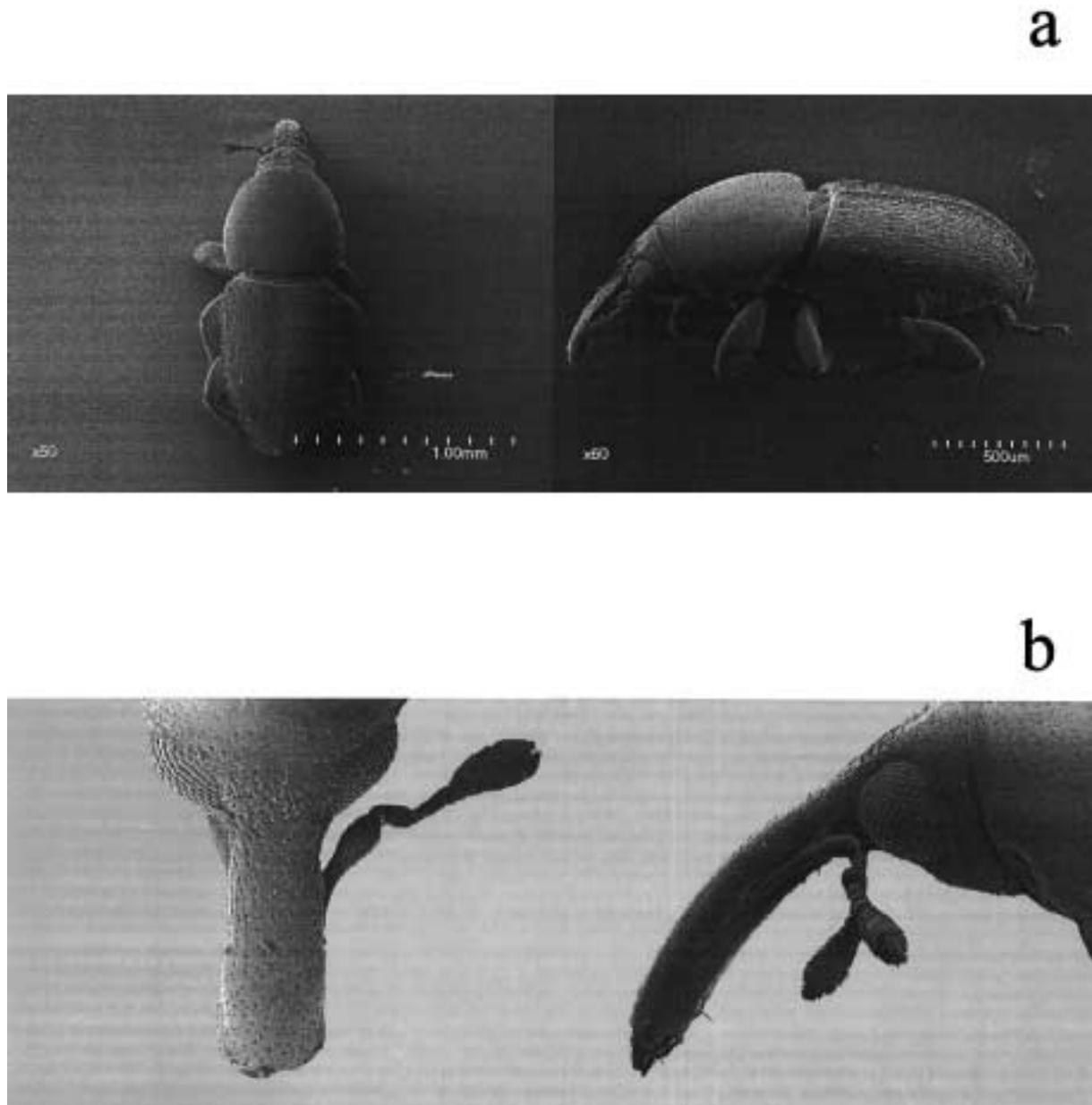


Fig. 1. *Ganglionus undulatus*, dorsal and lateral view. (a) Male, habitus; (b) female, rostrum.

All species of *Ganglionus* were included in the cladistic analysis. 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 the most parsimonious tree). Autapomorphies for the species of *Ganglionus* and for the outgroup taxa were excluded from the matrix. The character arrangement follows the sequence of description.

Ganglionus, gen. nov.

Diagnosis. *Ganglionus* (Fig. 1) keys to *Phyllotrox* Schönherr in Kuschel (1952: 271–273, key to Petalochilinae)—like *Perelleschus*, *Staminodeus*, and *Sys-*

tenotelus—but the former is distinguished from these and all remaining taxa of Derelomini by the putative synapomorphies: (1) male with dorsally tumescent rostrum, (2) posteriorly setose sternum VIII, and (3) apically O-shaped tegmen. Additional characters for diagnosis are the depressed shape (especially in males), the apically broadened protibia which has a row of 7–9 spines along the ventral two-thirds of the posteroventral margin (these are homologous to setae), and the variously shaped sclerite of the median lobe in males (see also *Discussion*). *Perelleschus* has 6–10 spines on the protibia which extend along the entire length of its projecting margin, although the apices of the meso- and metatibia resemble those of *Ganglionus*. However, *Perelleschus* differs from *Ganglionus* by the larger size, compressed shape, reddish

color, lack of tumescences on the rostrum of males, and many other characters (for details see Franz and O'Brien 2001). Whereas the males of *Ganglionus* may be diagnosed immediately by the rostrum, the habitus of females is similar to that of "*Phyllotrox*" (a taxon which is likely to be nonmonophyletic), requiring a more thorough diagnosis.

Male (Fig. 1a). Small, length 1.5–2.3 mm, width 0.6–1.0 mm, oval to elongate, $l/w = 2.1$ – 2.5 , greatest width near middle of pronotum and/or anterior one-third of elytron, depressed, dorsally and ventrally slightly convex, color dark brown (to black), sculpture punctulate (but see rostrum), vestiture fairly short, fine, appressed, shiny, ventrally more dense.

Head. Mouthparts. Mandible (Fig. 2a) with two dentes, inner dens subapically with obtuse projection, outer dens superposed, subapically with obtuse projection, outer margin with two setae. Maxilla (Fig. 2b) with cardo basally bifurcate, apically broadened; stipes+galea+lacinia+palpiger fused, outer margin subapically with one seta, inner margin setose in apical three-fourths, basal setae longer, with 3–6 lacinial dentes; maxillary palp 2-segmented; I slightly longer than II, distinctly expanded, transverse, clavate, apically with one small seta; II elongate, apically papillate. Labium (Fig. 2c) with prementum elongate, margins subrectate, apicodorsally with setose region, extending to maxillary palps, and two large setae; labial palp 3-segmented; I shorter than II, elongate, clavate, ventrally with one small seta; II longer than III, elongate, clavate, outer region protruding beyond III; III equilateral, clavate, retracted into II, apically papillate; postmentum elongate.

Rostrum (Fig. 3). In lateral view fairly short, 0.4–0.5 mm, shorter than pronotum, $r/p = 0.5$ – 0.7 , dorsally and ventrally slightly arcuate, breadth similar throughout or distinctly narrowed in basal one-third, apical one-sixth light brown; in dorsal view fairly broad, slightly narrowed in basal one-fourth; in cross-section subrectangular, depressed; dorsally tumescent, basal one-third to two-thirds with tuberculi or carinulae, laterodorsal margin with or without row of tuberculi along basal one-third or two-thirds, and with or without distinctive tuberculus near basal two-fifths (small or large, projecting dorsally or laterally), with one tuberculus near inner margin of each eye; antennal insertion near apical two-fifths; scrobe fairly slender and deep, slightly arcuate, apically acuminate, basally vaguely defined.

Antenna. Eleven-segmented, extending to anterior margin of pronotum, fairly stout, light brown; scape extending to eye, slightly shorter than funicle+club, slightly arcuate, clavate; 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; club 3-segmented, similar in length to IV–VII of funicle, oval to elongate, compact; I longer than II; II shorter than III; funicle+club pubescent.

Eye. Fairly small, elliptical to subcircular, slightly protruded, distant from anterior margin of pronotum

by one-third to two-thirds diameter of eye, separated by distance similar to apex of rostrum, black.

Head. Fairly small, transverse, globular, ventrally with median suture, posterior to eyes light brown.

Thorax. Pronotum in dorsal view large, globular, $l/w = 0.9$ – 1.0 , greatest width near middle, anteriorly narrowed, slightly convex, anterior margin explanate, lateral margins rotundate, posterior margin bisinuate, anteriorly light brown; in lateral view conical, narrowed in posterior one-third.

Epipleura. Mesepisternum triangular; mesepimeron small; metepisternum anteriorly broadened, posteriorly narrowed; metepimeron extending above posterior one-fourth of metepisternum.

Sterna. Prosternum longer than mesosternum, transverse, slightly convex, with long vestiture, procoxal cavities inserted near posterior margin (anterior region nearly 4 times as long as posterior region), contiguous; mesosternum shorter than metasternum, equilateral, slightly convex and retracted from ventral plane, posteriorly projecting between mesocoxae, mesocoxal cavities separated by distance nearly two-thirds as broad as mesocoxa; metasternum transverse, laterally convex, centrally subplane, medially canaliculate, anterior margin projecting between mesocoxae, truncate, posterior margin with triangular projection near inner margin of each metacoxa, metacoxal cavities separated by distance nearly one-half as broad as metacoxa.

Metendosternite (Fig. 4a). Stalk shorter than furcal arms, ventrally broadened, medially emarginate, separated by median flange; ventral flange broader than stalk; laterally concave; lamina nearly one-sixth as long as central sclerotization; lateral projections apically broadened; anterior tendons inserted near base of furcal arms; furcal arms diverging, dorsally narrowed, bifurcate.

Legs. Prothoracic leg similar in length to mesothoracic leg, stout; procoxa globular, in cross-section subcircular, inner margin with one subapical foveola, apically obliquely truncate, with dense vestiture; procoxa transverse, apically broadened, oblique; profemur shorter than pronotum, $f/p = 0.5$ – 0.7 , stout, slightly sinuate, in cross-section elliptical, distinctly compressed, greatest width near middle; protibia (Fig. 4b) slightly shorter than profemur, $t/f = 0.7$ – 0.9 , stout, slightly sinuate, in cross-section subcircular, slightly compressed, apically broadened, pubescent in anteroventral three-fifths, apically obliquely truncate, anteroventral margin with row of setae, posteroventral margin with row of 7–9 spines, extending along ventral two-thirds of projecting margin, inermous; protarsus 5-segmented, nearly three-fourths as long as protibia, light brown, I–III dorsally with dark median stripe; I slightly longer than II, equilateral, clavate; II slightly shorter than III, transverse, clavate; III bilobed, equilateral, ventrally with long vestiture; IV nearly one-half as long as III, equilateral; V similar in length to I–III, elongate, clavate; protarsal claw nearly two-fifths as long as V, paired, simple. Mesothoracic leg slightly shorter than metathoracic leg; mesocoxa transverse, in cross-section elliptical; mesotibia (Fig. 4c) short, lack-

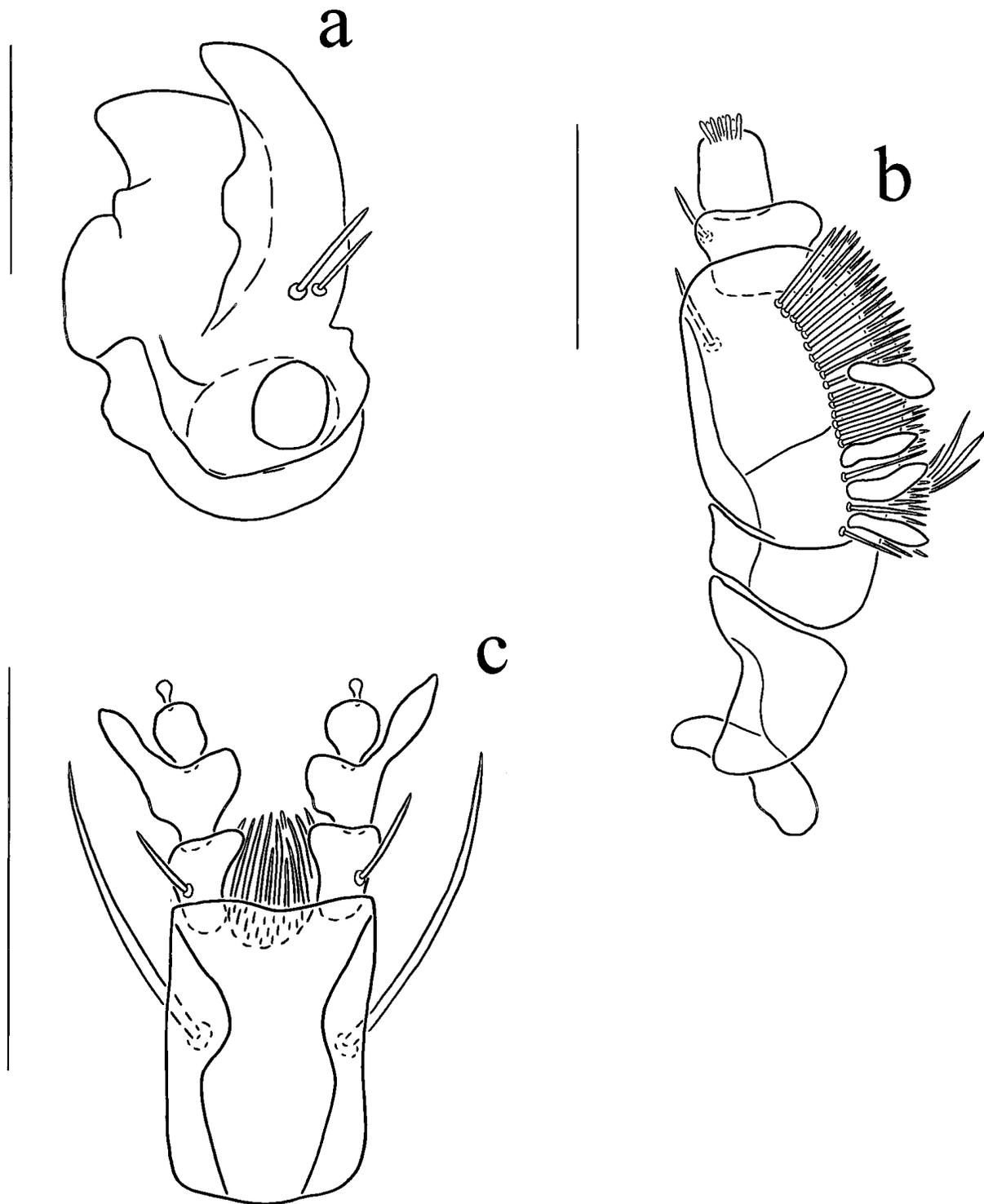


Fig. 2. *Ganglionus undulatus*, mouthparts of male, ventral view. (a) Left mandible; (b) right maxilla; (c) labial prementum. Scale bar = 0.05 mm.

ing anteroventral pubescence, anteroventral margin with row of 8–10 spines, extending along entire length of projecting margin, posteroventral margin with row of setae; mesotarsus similar in length to mesotibia, I longer than II, elongate. Metacoxa transverse, in cross-section elliptical, medially canaliculate; metatibia (Fig. 4d) fairly short, otherwise as mesotibia; meta-

tarsus similar in length to metatibia, I similar in length to II+III, elongate.

Scutellum. Exposed, fairly small, triangular.

Elytron. In dorsal view oval to elongate, $l/w = 1.2$ – 1.5 , greatest width near anterior one-third, similar in breadth to posterior margin of pronotum, humeri subquadrate, anterior margin concave, lateral margins

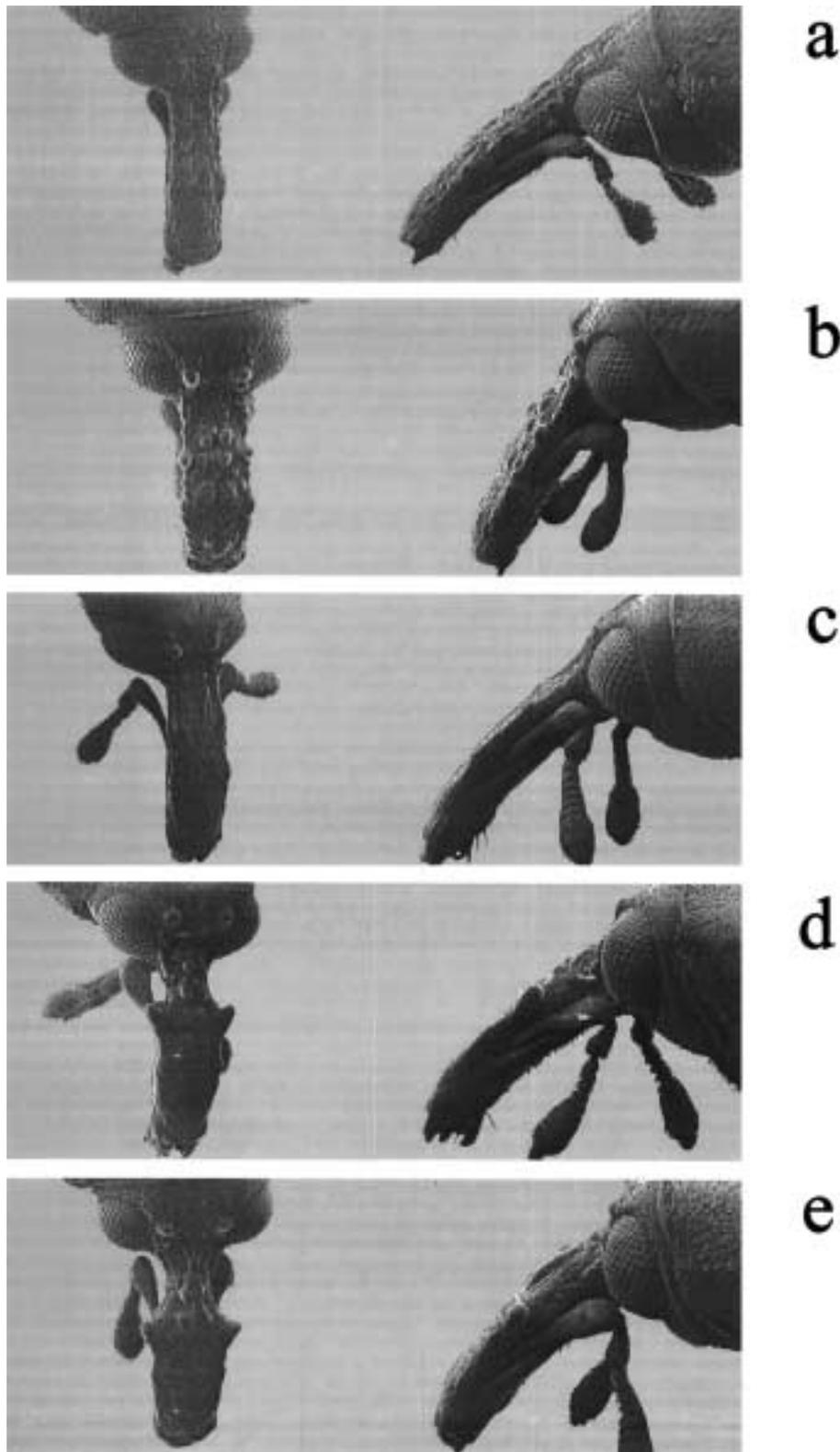


Fig. 3. *Ganglionus*, rostrum of male, dorsal and lateral view. (a) *G. mitigatus*; (b) *G. catenatus*; (c) *G. undulatus*; (d) *G. constrictus*; (e) *G. spatulatus*.

subparallel in anterior one-third, gradually converging in posterior two-thirds, posterior margin rotundate, subcontiguous; in lateral view convex, lateral margin

sinuate; with long vestiture; 10-striate; striae nearly one-fifth as broad as intervals, punctulate, shallow (or even indistinct), maculations dark brown, subcircular,

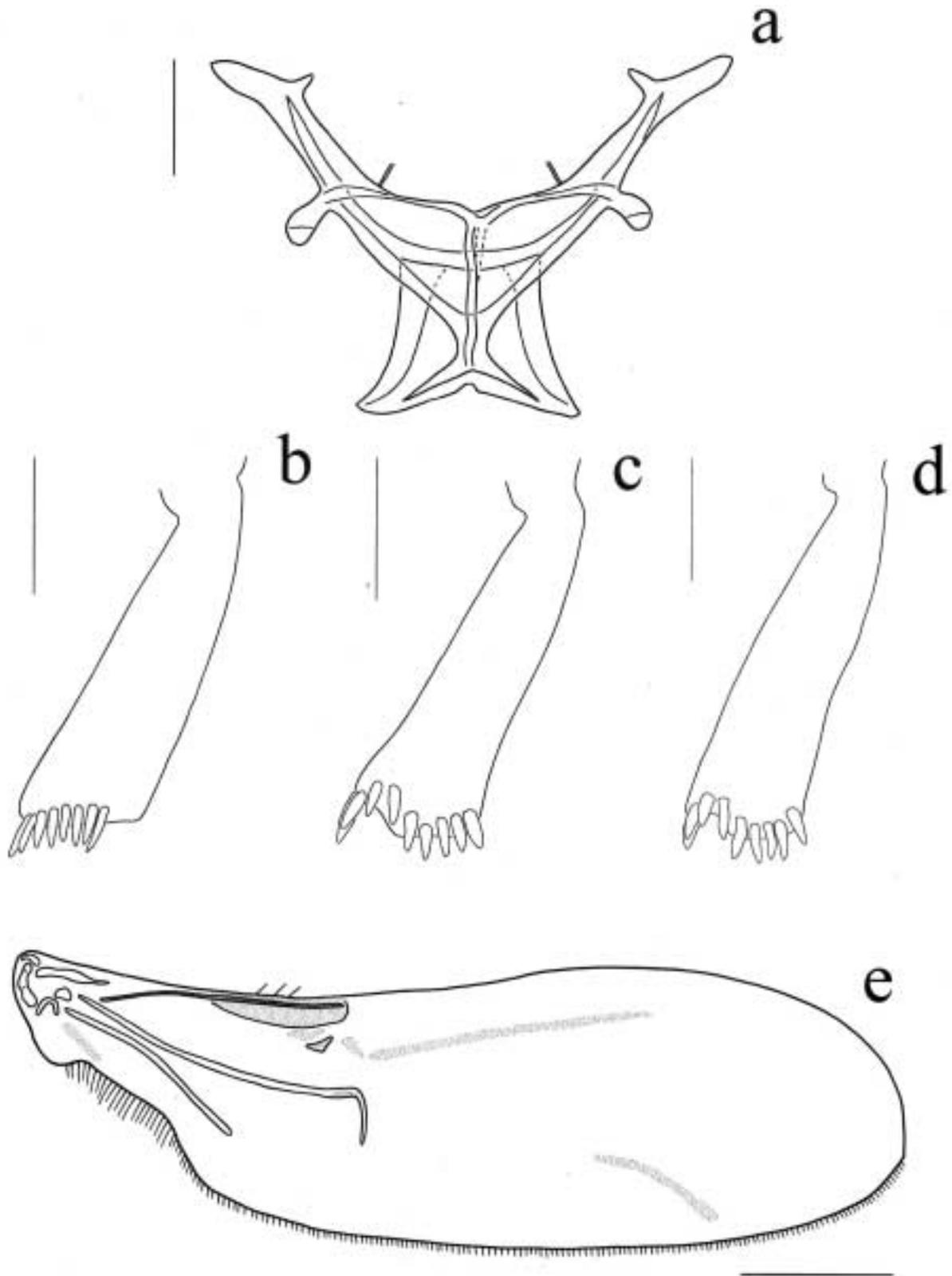


Fig. 4. *Ganglionus undulatus*, male. (a) Metendosternite, posterior view; (b) protibia, posterior view; (c) mesotibia, anterior view; (d) metatibia, anterior view; (e) right wing, dorsal view. Scale bar = 0.1 mm (a-d), 0.5 mm (e).

separated; intervals lighter; III+VIII merging before posterior margin.

Wing. (Fig. 4e). Slightly longer than body, wing/body = 1.2–1.4, elliptical to elongate, $l/w = 3.0\text{--}3.5$, greatest width near apical one-third, anterior margin slightly sinuate, posterior margin slightly convex, lobulate near base (anal lobe indistinct); Sc, R, Cu, Cu1, and 2A present, C and 4A obsolete; with one large, elongate, apically broadened maculation in radial field, and two large, elongate maculations in apical field; two radial sclerites and one radiomedial sclerotization present; long macrosetae along basal one-fifth of posterior margin; short macrosetae sparse along apical one-third of R, dense along posterior margin; microsetae throughout surface.

Abdomen. Venter similar in length to 2 times lateral margin of metasternum, laterally convex, centrally subplane, posteriorly gradually converging; III+IV fused, V–VII separated, VI+VII light brown; III longer than IV, anterior margin with triangular projection between metacoxae, anterior edges projecting; IV–VI similar in length; VII longer than VI, posterior margin rotundate.

Pygidium. Exposed, longer than ventrite VII, subcircular, slightly convex, broad, posterior margin ventrally emarginate, perpendicular to orientation of venter.

Genital Complex. Tergum VIII (Fig. 5a) slightly shorter than spiculum gastrale, equilateral, slightly convex, anterior edges projecting, posterior margin rotundate, medially emarginate. Sternum VIII (Fig. 5b) consisting of two small, narrow, transverse, posteriorly converging sclerites, nearly one-third as long as tergum VIII, posteriorly with large setae, anterior one-half separated, margins arcuate. Spiculum gastrale (Fig. 5c) slightly shorter than median lobe, slender, subrectate, medially flanged, basally broadened, apically bifurcate (Y-shaped). Tegmen (Fig. 5d) one-third to two-fifths as long as median lobe, slender, O-shaped; tegminal apodeme fairly short, subrectate; lateral apodemes connected, forming ring around aedeagus. Aedeagus (Fig. 6) with median lobe in ventral view elongate, $l/w = 2.8\text{--}4.0$, ventrally plicate, plicae extending from apical one-third to basal one-fourth, merging from lateral to medial, basal margin with two triangular projections, medially distinctly emarginate, lateral margins subparallel, slightly concave in basal one-third, apical margin acuminate, apex small, projecting, rotundate; in lateral view fairly broad, apically gradually narrowed, slightly deflexed; apical one-half to two-thirds tubulose, tubuli increasing toward apex; internally membranous (i.e., with internal sac), weakly sclerotized, with small, equilateral, apically variously shaped sclerite (Fig. 7), nearly one-fourth as long as median lobe, positioned in apical one-half, and with denticulate region extending along or beyond apical sclerite (i.e., small or large); aedeagal apodemes slightly shorter than median lobe, narrow, slightly broadened in basal one-third, apically angulate.

Variation. The level of pigmentation varies among individuals: the color of teneral specimens is more or less light brown and homogeneous, whereas com-

pletely developed specimens have a dark brown color with a characteristically heterogeneous pattern, e.g., of the head. Often the pronotum is darker than the elytron. The color of the elytron in *G. mitigatus*, sp. nov., and *G. undulatus*, sp. nov., is homogeneous (i.e., dark brown), however, in *G. catenatus*, sp. nov., *G. constrictus*, sp. nov., and *G. spatulatus*, sp. nov., there is variation on the elytron in the amount of pale yellow-brown and the characteristic dark color (see species descriptions).

The sculptures (i.e., tumescences) of the rostrum in larger males are more distinct (in number, size, and shape), and the pronotum is expanded (broader than the abdomen). Both morphometrical features, although not quantified, appear to display positive allometry (for comparison see variation of *Staminodeus* in Franz 2001).

For our present purpose, we consider the tumescences as expressed in most larger males to represent genotypic species characters (rather than traits, for a review of the distinction between characters and traits see Wheeler and Platnick 2000) which are valid to use to reconstruct the phylogeny of the species of *Ganglionus*. The phenotypic morphometrical variation may be due to variable nutritional conditions during the development of the larvae (as has been observed, e.g., in some scarab beetles; for review see Emlen 2000; for an example of weevils see Eberhard et al. 2000).

Female (Fig. 1b). Length 1.3–2.0 mm, width 0.6–0.9 mm, $l/w = 2.0\text{--}2.4$, greatest width near anterior one-third of elytron, slightly depressed, light brown. Rostrum fairly long, 0.4–0.7 mm, similar in length to pronotum, $r/p = 0.7\text{--}1.2$; in lateral view dorsally arcuate, breadth similar throughout; in dorsal view fairly narrow, breadth similar throughout; in cross-section subquadrate; sculpture dorsally indistinct; antennal insertion near middle. Pronotum in dorsal view fairly large, equilateral, $l/w = 0.8\text{--}1.0$. Mesocoxal cavities separated by distance similar to breadth of mesocoxa, metacoxal cavities separated by distance nearly three-fourths as broad as metacoxa. $F/p = 0.5\text{--}0.8$, profemur less distinctly compressed, $t/f = 0.7\text{--}1.0$. Elytron $l/w = 1.2\text{--}1.5$, slightly broader than posterior margin of pronotum. Venter slightly longer than 2 times lateral margin of metasternum, centrally slightly convex, VII similar in length to V+VI. Pygidium covered, similar in length to ventrite VII, transverse, narrow, lateral margins posteriorly converging, posterior margin rotundate, subparallel to orientation of tergum.

Genital Complex. Tergum VIII nearly one-half as long as sternum VIII, equilateral to transverse, slightly convex, lateral margins posteriorly converging, posterior margin subrectate, setose. Tergum IX shorter than sternum VIII, triangular, weakly sclerotized (indistinct). Sternum VIII (Fig. 5e) narrow, subrectate, medially slightly flanged, apically broadened, circular to elliptical, explanate (O-shaped), sparsely setulose, apical margin rotundate. Coxites nearly one-half as long as sternum VIII, elongate, posteriorly converging, sparsely setulose, styli elongate, slender, apically se-

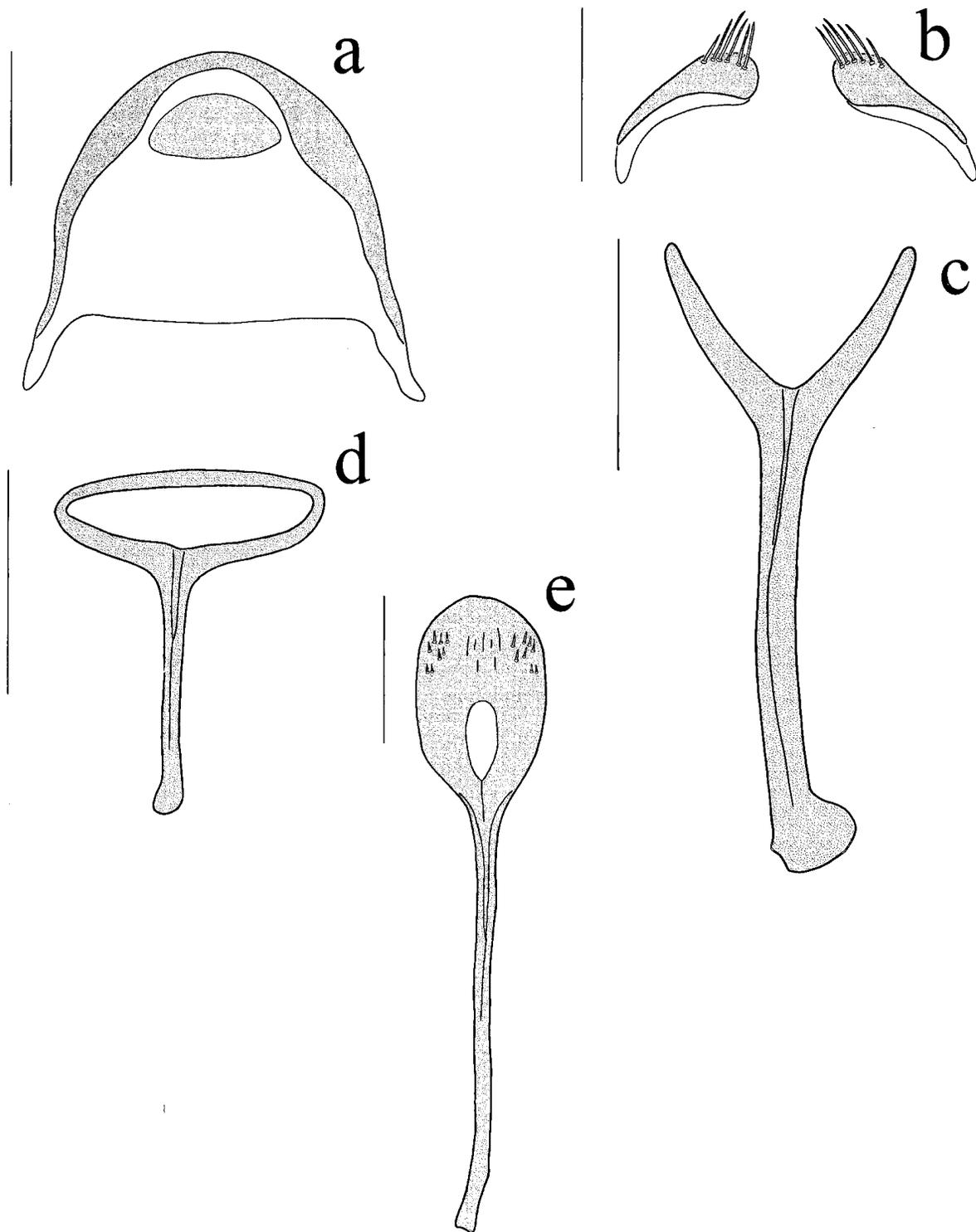


Fig. 5. *Ganglionus undulatus*, genitalia of male and female, ventral view. (a) Tergum VIII of male; (b) sternum VIII of male; (c) spiculum gastrale of male; (d) tegmen of male; (e) sternum VIII of female. All genitalia illustrations are interpretative; details are omitted. Scale bar = 0.1 mm.

tose. Vagina+bursa copulatrix large, elongate, longer than sternum VIII, with common oviduct. Duct inserted at base of spermatheca; spermatheca (Fig. 7) elongate, abruptly deflexed ($\approx 90-150^\circ$) near apical two-fifths (C-shaped), basally oblique, undulate, api-

cally gradually narrowed; reservoir inserted near base of spermatheca, very large, elongate.

Variation. Color variation is apparent (although not as considerable as in males) because of differences in the level of pigmentation. With the exception of *G.*

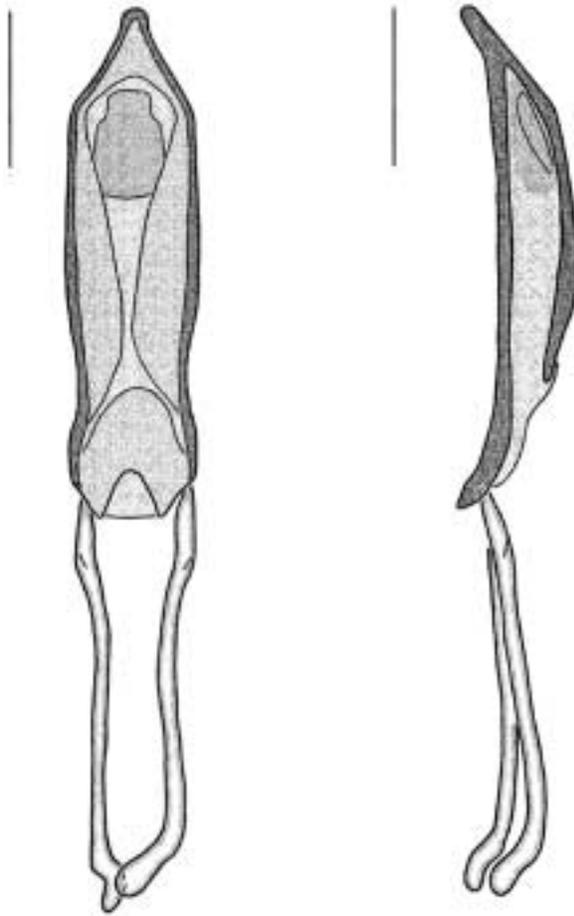


Fig. 6. *Ganglionus undulatus*, aedeagus, ventral and lateral view. Stippling indicates the level of sclerotization. Scale bar = 0.1 mm.

undulatus, the pronotum and/or elytron (especially along the margins) may be darker. The most conspicuous variation is observed in *G. mitigatus*.

Type Species. *Ganglionus undulatus*, by present designation.

Etymology. Named for the dorsal appearance of the rostrum in males; the distinctive arrangement of the laterodorsal tuberculi resembles generalized arthropod ganglia (as depicted, e.g., in figure 245 in Snodgrass 1993, p. 475)—ganglion signifying “swelling, knot of nerves” (Brown 1956). Gender masculine.

Key to the Species of *Ganglionus*

- 1. Male with rostrum slightly broadened in apical one-half, without distinctive tuberculus near basal two-fifths of laterodorsal margin (Fig. 3a), apical sclerite of median lobe rhomboidal (Fig. 7a); female with apical margin of sternum VIII medially distinctly emarginate *G. mitigatus* sp. nov.
- 1'. Male with breadth of rostrum similar throughout or distinctly narrowed in basal one-third, with distinctive tuberculus near basal two-fifths of laterodorsal margin (Fig. 3 b-e); fe-

- male with apical margin of sternum VIII roundedate 2
- 2(1'). Male with breadth of rostrum similar throughout, laterodorsal margin with row of tuberculi along basal one-third to two-thirds, with small tuberculus near basal two-fifths, projecting dorsally (Fig. 3 b and c), apical sclerite of median lobe rectangular (Fig. 7 b and c); female with pronotum centrally concolorous 3
- 2'. Male with rostrum distinctly narrowed in basal one-third, laterodorsal margin without row of tuberculi, with large tuberculus near basal two-fifths, projecting laterally (Figs. 3 d and e), apical sclerite of median lobe spathulate (Figs. 7 d and e); female with pronotum centrally darker 4
- 3(2). Male with row of tuberculi of laterobasal margin of rostrum extending along basal two-thirds (Fig. 3b), elytron yellowish brown, apical sclerite of median lobe apically roundedate (Fig. 7b); female with spermatheca L-shaped (Fig. 7b) *G. catenatus* sp. nov.
- 3'. Male with row of tuberculi of laterobasal margin of rostrum extending along basal one-third (Fig. 3c), elytron dark brown, apical sclerite of median lobe apically subrectate (Fig. 7c); female with spermatheca C-shaped (Fig. 7c) *G. undulatus* sp. nov.
- 4(2'). Male with basal one-third of rostrum tuberculate (Fig. 3d); denticulate region of median lobe small, extending along apical sclerite (Fig. 7d); female with spermatheca as in Fig. 7d *G. constrictus* sp. nov.
- 4'. Male with basal one-third of rostrum carinulate (Fig. 3e); denticulate region of median lobe large, extending beyond median lobe (Fig. 7e); female with spermatheca as in Fig. 7e *G. spatulatus* sp. nov.

***Ganglionus mitigatus*, sp. nov.**

Diagnosis. Distinguished by the lack of a distinctive tuberculus near the basal two-fifths of the laterodorsal margin of the rostrum, the rhomboidal apical sclerite of the median lobe in males; as well as the characteristic color pattern, the comparatively long rostrum, and the medially distinctly emarginate apical margin of sternum VIII in females. In larger males the tuberculi of the rostrum extend beyond the antennal insertion and comparatively are larger than in smaller males. Color variation in females is considerable on the elytron, ranging from light to dark brown.

Male. Length 1.6–2.0 mm, width 0.7–0.9 mm, l/w = 2.2–2.5. Rostrum (Fig. 3a) 0.4–0.5 mm, r/p = 0.6–0.8, slightly broadened in apical one-half, basal two-thirds tuberculate. Pronotum l/w = 0.8–1.0. F/p = 0.6–0.8; t/f = 0.8–1.0, protibia light brown along basal one-third. Elytron l/w = 1.3–1.5 (N = 15). Median lobe l/w = 3.5–3.8 (N = 3), apical sclerite (Fig. 7a) rhom-

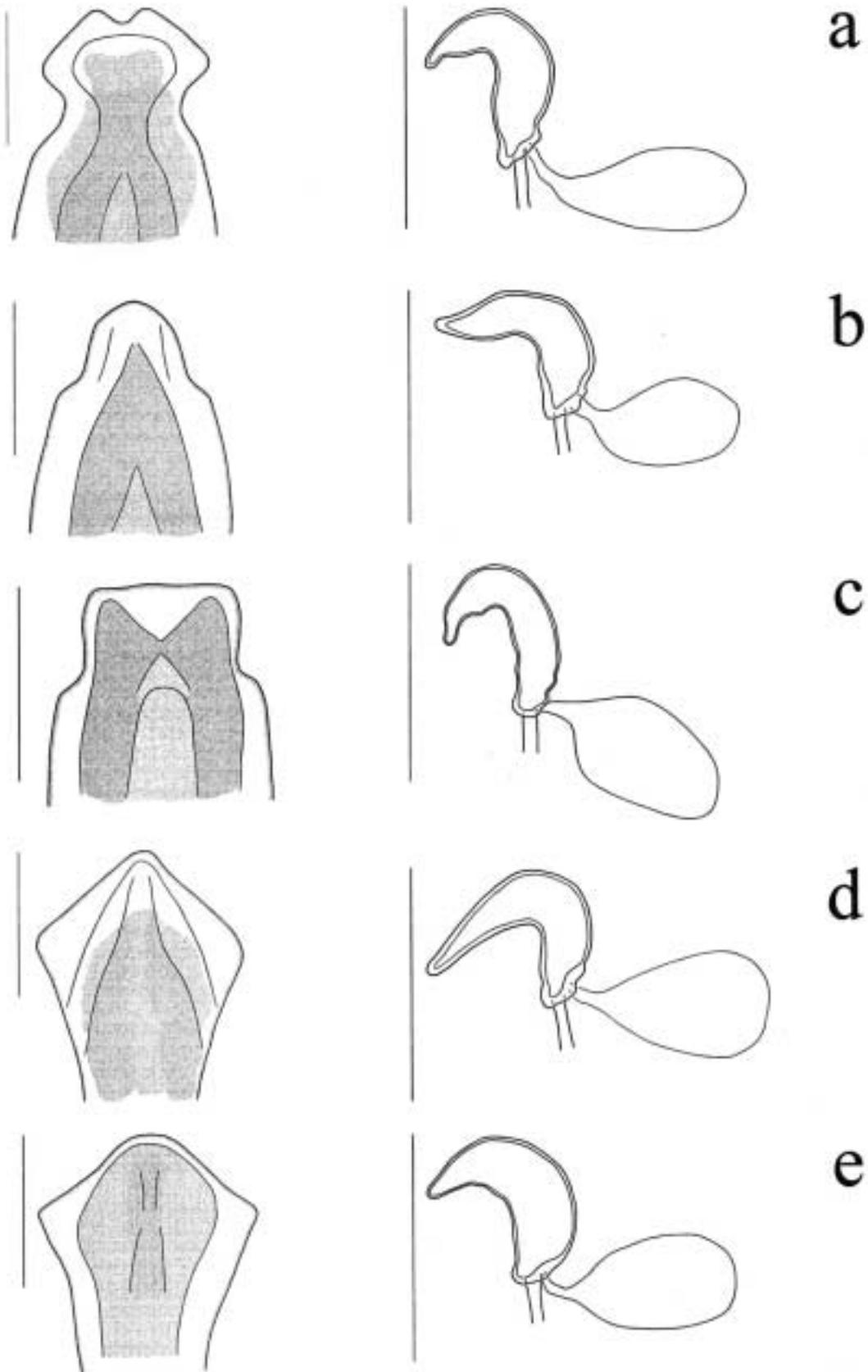


Fig. 7. *Ganglionus*, apical sclerite of median lobe of male, ventral view, and spermatheca with gland reservoir of female. (a) *G. mitigatus*; (b) *G. catenatus*; (c) *G. undulatus*; (d) *G. constrictus*; (e) *G. spatulatus*. The stippling indicates the extension and density of the denticulation. Scale bar = 0.05 mm.

boidal, centrally narrowed, apically emarginate, denticulate region large, extending from apex of sclerite to base of median lobe, broad, denticuli fairly large.

Female. Length 1.6–2.0 mm, width 0.7–0.9 mm, $l/w = 2.1\text{--}2.4$, reddish brown. Rostrum 0.5–0.7 mm, $r/p = 0.9\text{--}1.2$. Pronotum $l/w = 0.9\text{--}1.0$, posterior margin darker. $F/p = 0.6\text{--}0.8$; $t/f = 0.8\text{--}1.0$. Elytron $l/w = 1.3\text{--}1.5$ ($N = 10$), yellowish brown to dark brown, striae I–III and margins darker. Apical margin of sternum VIII medially distinctly emarginate. Spermatheca (Fig. 7a) deflexed $\approx 120^\circ$, apically projecting.

Type Information. Male holotype “COSTA RICA, S. J., Braulio Carillo N. P. Hwy., VIII-30-1998, N. Franz, CWOB/on *Carludovica palmata* flowers” (CWOB); female allotype, same label as male holotype (CWOB); male paratypes, same labels as male holotype (CMNC, 5; CWOB, 5; MUCR, 5); female paratypes, same labels as male holotype (CMNC, 3; CWOB, 5; MUCR, 3).

Etymology. Named for the comparatively inconspicuous sculpture of the rostrum in males—*mitigatus* signifying “calmed” (Brown 1956).

Distribution. *Ganglionus mitigatus* has been collected on the Caribbean slope of Costa Rica, Provincia San José, Parque Nacional Braulio Carillo (sympatric with *G. undulatus*) (Fig. 8a).

Natural History. Although the label information indicates an association with *C. palmata* Ruíz & Pavón, this host record is most likely incorrect; subsequently acquired knowledge of all *Carludovica* species by one of us (N.M.F.) suggests that *G. mitigatus* is associated with *C. rotundifolia* H. Wendl. ex Hook. fil. H. Wendl. ex Hook. fil. The adults were collected during the pistillate anthesis, around 1000 hours. Typically, they occupied the epistigmatic spaces between the staminate flowers, and remained hidden until these were removed.

Ganglionus catenatus, sp. nov.

Diagnosis. Distinguished by the row of tuberculi which extends along the basal two-thirds (beyond the antennal insertion, for comparison see *G. undulatus*) of the laterodorsal margin of the rostrum, the dorsally projecting tuberculus near the basal two-fifths, and the apically rotundate sclerite in the median lobe of males; as well as the L-shaped spermatheca in females. The rostral tumescences are difficult to diagnose in the smallest males; however, the yellowish brown color of the elytron—although varying in intensity and extension—distinguishes them from *G. undulatus*. Similarly, the dark brown color on the elytron in females is absent in *G. undulatus*.

Male. Length 1.5–2.0 mm, width 0.6–0.9 mm, $l/w = 2.1\text{--}2.4$. Rostrum (Fig. 3b) 0.4–0.5 mm, $r/p = 0.5\text{--}0.7$, breadth similar throughout, basal one-half tuberculate, laterodorsal margin with row of tuberculi along basal two-thirds, with small, distinctive tuberculus near basal two-fifths, projecting dorsally. Pronotum $l/w = 0.9\text{--}1.0$. $F/p = 0.5\text{--}0.7$; $t/f = 0.7\text{--}0.9$. Elytron $l/w = 1.2\text{--}1.4$ ($N = 15$), striae I–II and IX–X dark brown, striae III–VIII yellowish brown. Wing/body =

1.2–1.4, wing $l/w = 3.2\text{--}3.5$. Median lobe $l/w = 3.6\text{--}4.0$ ($N = 5$), apical sclerite (Fig. 7b) rectangular, apically narrowed, rotundate, denticulate region small, extending along apical sclerite.

Female. Length 1.5–1.9 mm, width 0.6–0.9 mm, $l/w = 2.0\text{--}2.3$. Rostrum 0.4–0.5 mm, $r/p = 0.7\text{--}1.0$. Pronotum $l/w = 0.8\text{--}0.9$. $F/p = 0.5\text{--}0.7$; $t/f = 0.7\text{--}0.9$. Elytron $l/w = 1.3\text{--}1.5$ ($N = 15$), striae I–II darker. Spermatheca (Fig. 7b) deflexed $\approx 90^\circ$ (L-shaped).

Type Information. Male holotype “Costa Rica, Puntarenas, Río Claro Pavones (# 97139), on *Carludovica palmata*, leg. L. Gómez, 1997” (CMNC); female allotype, same label as male holotype (CMNC); male paratypes, same labels as male holotype (CMNC, 15; CWOB, 15; INBC, 10), “Costa Rica, Puntarenas, Coto Brus, Fila de Cal, 560 m, $08^\circ 43' 16''$ N, $82^\circ 57' 25''$ W, on Cyclanthaceae, leg. L. Gómez, XII-1994” (IZAV, 5; MIUP, 10), “Costa Rica, Puntarenas, Coto Brus, Las Cruces, 1,100 m, on Cyclanthaceae (#94395), leg. L. Gómez, X-01-1994” (MUCR, 10), “Costa Rica, Puntarenas, C. Brus, Las Cruces, 1,150 m, $08^\circ 47' 03''$ N, $82^\circ 57' 36''$ W, on *Carludovica palmata*, leg. R. Anderson, VI-21-1998” (QCAZ, 5; UNCB, 5); female paratypes, same labels as male holotype (CMNC, 10), “Costa Rica, Puntarenas, Coto Brus, Fila de Cal, 560 m, $08^\circ 43' 16''$ N, $82^\circ 57' 25''$ W, on Cyclanthaceae, leg. L. Gómez, XII-1994” (CMNC, 5; CWOB, 15; INBC, 10; IZAV, 5), “Costa Rica, Puntarenas, Coto Brus, Las Cruces, 1,100 m, on Cyclanthaceae (#94395), leg. L. Gómez, X-01-1994” (MIUP, 10), “Costa Rica, Puntarenas, C. Brus, Las Cruces, 1,150 m, $08^\circ 47' 03''$ N, $82^\circ 57' 36''$ W, on *Carludovica palmata*, leg. R. Anderson, VI-21-1998” (MUCR, 10; QCAZ, 5; UNCB, 5).

Etymology. Named for the appearance of closely aligned tuberculi along the laterodorsal margin of the rostrum in males—*catena* signifying “chain” (Brown 1956).

Distribution. *Ganglionus catenatus* has been collected in the Cordillera de Talamanca of Costa Rica, Provincia Puntarenas, Fila de Cal, Las Cruces, and Río Claro Pavones; and in Panama (label information: “Panama, #5151, H. Pittier/on Cyclanthaceae”) (Fig. 8a).

Natural History. In Costa Rica, Las Cruces, the adults have been collected on *C. palmata*.

Ganglionus undulatus, sp. nov.

Diagnosis. Distinguished by the row of tuberculi that extends along the basal one-third of the laterodorsal margin of the rostrum, the dorsally projecting tuberculus near the basal two-fifths, and the apically subrectate sclerite in the median lobe of males; as well as the C-shaped spermatheca in females. The vestiture of the elytron is comparatively coarse and dense (especially in males). Compare with *G. catenatus* for additional diagnostic characters.

Male. Length 1.6–2.0 mm, width 0.7–0.9 mm, $l/w = 2.2\text{--}2.4$. Rostrum (Fig. 3c) 0.4–0.5 mm, $r/p = 0.6\text{--}0.7$, breadth similar throughout, basal one-half tuberculate, laterodorsal margin with row of tuberculi along basal one-third, with small, distinctive tuberculus near

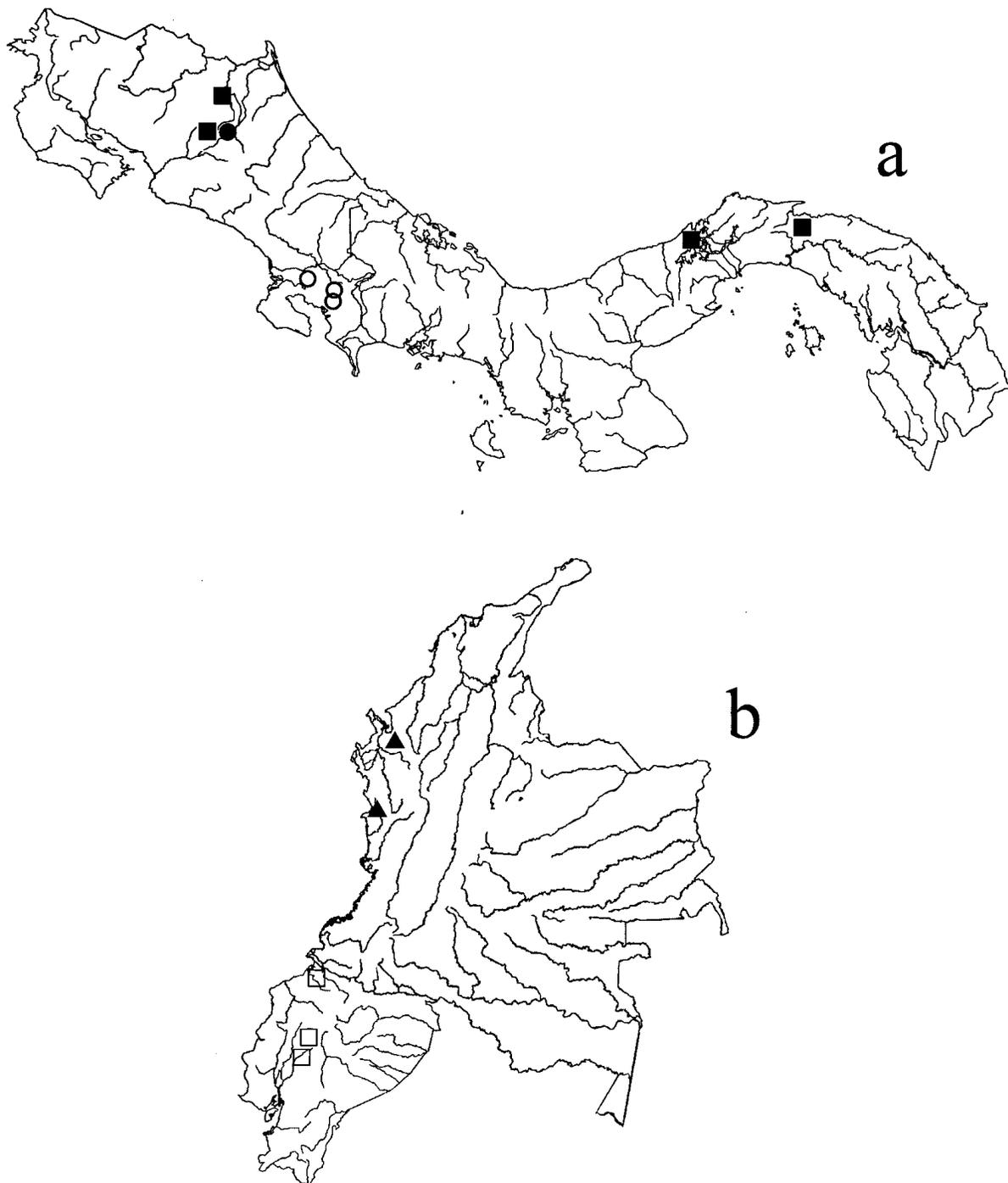


Fig. 8. Distribution of *Ganglionus*; (a) Costa Rica and Panama; (b) Colombia and Ecuador; ● *G. mitigatus*; ○ *G. catenatus*; ■ *G. undulatus*; □ *G. constrictus*; ▲ *G. spatulatus*.

basal two-fifths, projecting dorsally. Pronotum l/w = 0.9–1.0. F/p = 0.5–0.7; t/f = 0.7–0.9. Elytron l/w = 1.2–1.5 ($N = 15$). Wing/body = 1.2–1.4, wing l/w = 3.0–3.3 ($N = 5$). Median lobe l/w = 3.1–3.7 ($N = 8$), apical sclerite (Fig. 7c) rectangular, apically narrowed, subrectate, denticulate region small, extending along apical sclerite.

Female. Length 1.5–1.8 mm, width 0.7–0.8 mm, l/w = 2.1–2.3. Rostrum 0.5–0.6 mm, r/p = 0.8–1.0.

Pronotum l/w = 0.8–1.0. F/p = 0.6–0.8; t/f = 0.8–0.9. Elytron l/w = 1.3–1.5 ($N = 15$). Spermatheca (Fig. 7c) deflexed $\approx 150^\circ$, apically projecting.

Type Information. Male holotype “Costa Rica, Heredia, La Selva, 40 m, on *Carludovica sulcata*, leg. N. Franz, IX-09-1997” (MUCR); female allotype, same label as male holotype (MUCR); male paratypes, same labels as male holotype (CMNC, 15; CWOB, 15; INBC, 10; IZAV, 5; MIUP, 10; MUCR, 10; QCAZ, 5; UNCB, 5);

female paratypes, same labels as male holotype (CMNC, 15; CWOB, 15; INBC, 10; IZAV, 5; MIUP, 10; MUCR, 10; QCAZ, 5; UNCB, 5).

Etymology. Named for the appearance of the dorsal rostrum sculpture in males in lateral view—*undulatus* signifying “wavy” (Brown 1956).

Distribution. *Ganglionus undulatus* has been collected on the Carribbean slope of Costa Rica, Provincia Heredia, La Selva, and Provincia San José, Parque Nacional Braulio Carillo (sympatric with *G. mitigatus*); and in the Canal Zone of Panama, Provincia Colón, Fort Sherman; and on the Carribbean slope of Panama, Provincia Panamá, El Llano-Cartí (Fig. 8a).

Natural History. In Panama, El Llano-Cartí and Fort Sherman, the adults have been collected on the inflorescences of *C. drudei* Masters (label information: C. W. & L. B. O'Brien, VII-28-1995 and VII-31-1995, respectively). At La Selva, Costa Rica, *G. undulatus* is associated with *C. rotundifolia* and *C. sulcata* Hammel (for an account of cyclanth inflorescence morphology see Harling 1958, pp. 24–33). Here we present a summary of the observations on the latter species by Franz (1999), part of which were provided for *P. carludoviccae* (as well as *P. sulcatae* Franz & O'Brien) in Franz and O'Brien (2001). Except for the substrate for oviposition (see also below), the behavior of the adults of *G. undulatus* and those two species appears to be similar. They arrive at the inflorescences around 0530 hours during the pistillate phase of anthesis (≈ 50 – 150 individuals per inflorescence, $N = 5$), flying to the staminodes, and entering the epistigmatic spaces between the staminate flowers. Apparently, they are covered with pollen and function as co-pollinators of *C. sulcata*. After remaining inside during the day, the majority depart after the pollen is released, nearly 24 h later, for other fragrant inflorescences.

On the inside, they feed on the floral organs, mate, and oviposit into the basal region of the staminate flowers. These detach after anthesis and fall to the ground within 24 h. Therefore, the larvae are not strictly herbivorous but in part detritivorous (for comparison see notes on *S. vectoris* in Franz 2001), and their development continues in the leaf litter. Apparently, the adults emerge from the pupae after 3–5 wk, but more detailed studies are necessary to understand the biology of the immatures. *Ganglionus undulatus* was coded as “*Perelleschus* sp. C4” in Franz (1999). Because the females were often erroneously assigned to “*Phyllotrox* sp. C1,” the actual number of adult specimens was underestimated in that work by $\approx 100\%$.

Ganglionus constrictus, sp. nov.

Diagnosis. Distinguished by the basally narrowed and tuberculate rostrum (for comparison see *G. spatulatus*), the laterally projecting tuberculus near the basal two-fifths of the laterodorsal margin, and the small denticulate region of the median lobe in males; as well as the characteristically shaped spermatheca in females. The rostral characters (i.e., constriction and laterally projecting tuberculi) vary to the extent that

they are difficult to diagnose in the smallest males, requiring examination of genital characters (i.e., apically spathulate sclerite and small denticulate region in median lobe). Their color variation (yellow to brown) on the elytron may be similar to that of *G. spatulatus*. The centrally dark color of the pronotum is absent in more teneral females.

Male. Length 1.6–2.3 mm, width 0.7–1.0 mm, l/w = 2.1–2.3. Rostrum (Fig. 3d) 0.4–0.5 mm, r/p = 0.6–0.7, distinctly narrowed in basal one-third, apical two-thirds nearly 2 times as broad as basal one-third, apically gradually narrowed, basal one-third tuberculate, laterodorsal margin with large, distinctive tuberculus near basal two-fifths (triangular, greatest breadth of rostrum), projecting laterally. Pronotum l/w = 0.9–1.0. F/p = 0.5–0.7; t/f = 0.7–0.9. Elytron l/w = 1.2–1.4 ($N = 15$), yellowish brown, striae I–II and margins dark brown. Median lobe l/w = 3.4–3.8 ($N = 3$), apical sclerite (Fig. 7d) spathulate, apically broadened, triangular, denticulate region small, extending along apical sclerite.

Female. Length 1.3–2.0 mm, width 0.7–0.9 mm, l/w = 2.0–2.2. Rostrum 0.4–0.6 mm, r/p = 0.8–0.9. Pronotum l/w = 0.8–0.9, centrally darker. F/p = 0.5–0.7; t/f = 0.7–1.0. Elytron l/w = 1.2–1.4 ($N = 15$), striae I–II darker in anterior one-half. Spermatheca (Fig. 7d) deflexed $\approx 120^\circ$, apical region long.

Type Information. Male holotype “Ecuador, Pichincha, 16 km, SE Sto. Domingo, 680 m, on palm flowers, leg. S. & J. Peck, VI-27-1975” (CMNC); female allotype, same label as male holotype (CMNC); male paratypes, same labels as male holotype (CMNC, 15; CWOB, 15; INBC, 10; IZAV, 5; MIUP, 10; MUCR, 10; QCAZ, 5; UNCB, 5); female paratypes, same labels as male holotype (CMNC, 15; CWOB, 15; INBC, 10; IZAV, 5; MIUP, 10; MUCR, 10; QCAZ, 5; UNCB, 5).

Etymology. Named for the basal constriction of the rostrum in males—*constrictus* signifying “tightened” (Brown 1956).

Distribution. *Ganglionus constrictus* has been collected on the Pacific slope of Ecuador, Departamento Esmeraldas, San Lorenzo; and Departamento Pichincha, Santo Domingo de los Colorados and Río Palenque (Fig. 8b).

Natural History. The mention of “palm flowers” most likely refers to *C. palmata*; for comparison see notes (on *P. biventralis* Franz & O'Brien and *P. variabilis* Franz & O'Brien) in Franz and O'Brien (2001).

Ganglionus spatulatus, sp. nov.

Diagnosis. Distinguished by the basally narrowed and carinulate rostrum, the laterally projecting tuberculus near the basal two-fifths of the laterodorsal margin, and the large denticulate region of the median lobe in males; as well as the characteristically shaped spermatheca in females. The rostral characters (i.e., constriction and laterally projecting tuberculi) vary to the extent that they are difficult to diagnose in the smallest males, requiring examination of genital characters (i.e., apically spathulate sclerite and large denticulate region in median lobe). The centrally dark

color of the pronotum is absent in more teneral females. Compare with *G. constrictus* for additional diagnostic characters.

Male. Length 1.5–2.1 mm, width 0.7–1.0 mm, l/w = 2.1–2.4. Rostrum (Fig. 3e) 0.4–0.5 mm, r/p = 0.6–0.7, distinctly narrowed in basal one-third, apical two-thirds nearly 2 times as broad as basal one-third, apically gradually narrowed, basal one-third carinulate, laterodorsal margin with large, distinctive tuberculus near basal two-fifths (triangular, greatest breadth of rostrum), projecting laterally. Pronotum l/w = 0.8–1.0. F/p = 0.5–0.7; t/f = 0.7–0.9. Elytron l/w = 1.3–1.4 (N = 15), posterior one-fourth to three-fourths yellowish brown, anterior margin, striae I–II and IX–X darker. Median lobe l/w = 2.8–3.3 (N = 3), apical sclerite (Fig. 7e) spatulate, apically broadened, triangular, denticulate region large, extending from apex of sclerite beyond base of median lobe, narrow, denticuli fairly small, aedeagal apodemes similar in length to median lobe.

Female. Length 1.4–1.9 mm, width 0.6–0.9 mm, l/w = 2.0–2.2. Rostrum 0.4–0.6 mm, r/p = 0.7–1.0. Pronotum l/w = 0.8–1.0, centrally darker. F/p = 0.6–0.7; t/f = 0.8–0.9. Elytron l/w = 1.2–1.4 (N = 15), striae I–II darker in anterior one-half. Spermatheca (Fig. 7e) deflexed $\approx 120^\circ$.

Type Information. Male holotype “COLOMBIA, Chocó D., Río Sanpichí, 4-IV-1994, B&E 103, R. Bernal & F. Ervik/on inflorescence *Carludovica palmata* at female anthesis” (UNCB); female allotype, same label as male holotype (UNCB); male paratypes, same labels as male holotype (UNCB, 2), “COLOMBIA, Chocó D., Río Sanpichí, 12-III-1994, B&E 104, R. Bernal & F. Ervik/on inflorescence *Carludovica palmata* at male anthesis” (UNCB, 6), “COLOMBIA, Chocó, Nuquí, 35 m, Est. Biol. El Amargal, 28-II-1999, L. Nuñez, R. Bernal/on *Carludovica palmata* Cur 31” (CMNC, 5; CWOB, 10; UNCB, 2); female paratypes, same labels as male holotype (UNCB, 2), “COLOMBIA, Chocó D., Río Sanpichí, 12-III-1994, B&E 104, R. Bernal & F. Ervik/on inflorescence *Carludovica palmata* at male anthesis” (CMNC, 5; CWOB, 5; UNCB, 8).

Etymology. Named for the appearance of the rostrum in males in dorsal view—*spatula* signifying “spade” (Brown 1956).

Distribution. *Ganglionus spatulatus* has been collected on the Pacific slope of Colombia, Departamento Chocó, Estación Biológica El Amargal (Nuquí) and Río Sanpichí (Fig. 8b).

Natural History. In Colombia, Río Sanpichí, the adults have been collected on *C. palmata*. They remain on the inflorescences until the staminate anthesis when the pollen is released.

Cladistic Analysis

Characters. The following characters were used to construct the data matrix (Table 1). Except for character 10, all are binary.

1. Male with dorsally tumescent rostrum: (0) absent; (1) present.

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

Taxon/character	5	10
<i>Not. basalis</i>	00000	0000–
<i>Sta. vectoris</i>	00000	0000–
<i>Per. carludovicae</i>	00000	1100–
<i>G. mitigatus</i>	10000	11110
<i>G. catenatus</i>	11010	11111
<i>G. undulatus</i>	11010	11111
<i>G. constrictus</i>	11101	11112
<i>G. spatulatus</i>	11101	11112

2. Male rostrum with distinctive tuberculus near basal two-fifths of laterodorsal margin: (0) absent; (1) present.
3. Male rostrum with laterally projecting tuberculus near basal two-fifths of laterodorsal margin: (0) absent; (1) present.
4. Male rostrum with row of tuberculi along laterobasal margin: (0) absent; (1) present.
5. Male rostrum with distinctive constriction in basal one-third: (0) absent; (1) present.
6. Male (as well as female) with triangular scutellum: (0) absent; (1) present.
7. Male with perpendicular pygidium: (0) absent; (1) present.
8. Male with posteriorly setose sternum VIII: (0) absent; (1) present.
9. Male with apically O-shaped tegmen: (0) absent; (1) present.
10. Male with apical sclerite of median lobe: (0) rhomboidal; (1) rectangular; (2) spatulate. Coded as nonadditive. Inapplicable in outgroup taxa.

Analysis. The cladistic analysis for eight taxa and ten characters yields one most parsimonious cladogram with L = 11, CI = 100, and RI = 100 (Fig. 9). None of

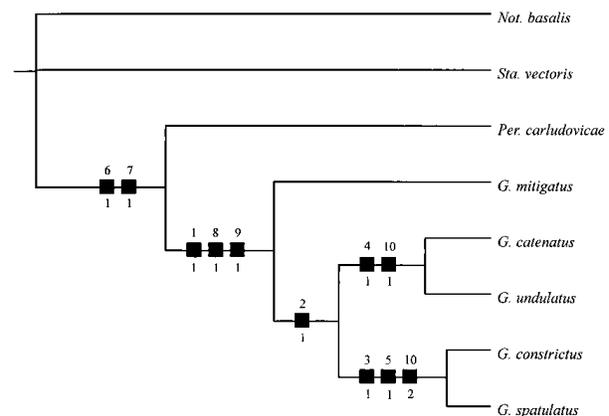


Fig. 9. Most parsimonious cladogram depicting phylogenetic relationships among the five species of *Ganglionus*, with *Not. basalis*, *Sta. vectoris*, and *Per. carludovicae* as outgroup taxa. Character transformations are hypothesized according to DELTRAN optimization. Homology is indicated by black rectangles (homoplasy is absent, for details see discussion). Character numbers and character states (Table 1) are displayed above and below each rectangle, respectively.

the characters are considered to be homoplasious (see discussion below).

Discussion

The monophyly of *Ganglionus* is indicated by the dorsally tumescent rostrum, the posteriorly setose sternum VIII, and the apically O-shaped tegmen in males (Fig. 9). Additional putative synapomorphies are the setose mandible, the first expanded segment of the maxillary palp, the second protruded segment of the labial palp, the apically broadened protibia which has a row of 7–9 spines along the ventral two-thirds of the posteroventral margin; as well as the acuminate apex, the apical sclerite, and denticulate region of the median lobe in males. However, their respective generality has to be determined by a more comprehensive analysis of Derelomini. If the natural history notes on *G. undulatus* at La Selva, Costa Rica, are applicable to all the species, then the combination of an association with *Carludovica*, pollinator function, oviposition/development in staminate flowers/leaf litter, and (at least partly) detritivorous larvae may be apomorphic for *Ganglionus*. Contrastingly, the larvae of *Perelleschus* and *Systemotelus* are herbivorous and consume the pulp and seeds of the infructescences of *Carludovica* (Anderson and Gómez 1997, Franz and O'Brien 2001). The homology of these behavioral characters has to be tested in a future cladistic analysis.

The placement of *Ganglionus* within Derelomini is based on the following putative synapomorphies it shares with *Perelleschus* and *Systemotelus*: ventrally pubescent protibia, triangular scutellum, perpendicular pygidium in males, and association with *Carludovica*. However, it is important to note that the present lack of phylogenetic resolution inside and outside of Derelomini precludes satisfactory assessments of global polarity for the taxon (for review see Nixon and Carpenter 1993). Since the erection of Derelomini by Lacordaire in 1866 (p. 9), the tribe—which today comprises ≈40 genera with over 200 species (according to Alonso-Zarazaga and Lyal 1999, and C.W.O.B., unpublished data)—has not been revised, although several Asian taxa of Derelomini are currently under study to redefine Acalyptini and Derelomini (H. Kojima, in a letter). As suggested by an examination of undescribed derelomine species in collections, neither *Perelleschus* nor *Systemotelus* are sister to *Ganglionus*.

The relationships within *Ganglionus* are based on characters of the rostrum and aedeagus in males. The monophyly of the clade that is sister to *G. mitigatus* is supported by the distinctive tuberculus near the basal two-fifths of the laterodorsal margin of the rostrum. This single character is congruent with additional putative homologies (presently not coded in the matrix), i.e., a slightly larger tuberculus near the inner margin of each eye, more acute projections along the basal margin of the median lobe, as well as similarities in the shape and denticulation of the apical sclerite (Fig. 7). The denticulate regions of *G. mitigatus* and *G. spatulatus* are considered to be nonhomologous because

they differ in the extension, breadth, and size of the denticuli. The monophyly of the clade (*G. catenatus*, *G. undulatus*) is indicated by the row of tuberculi along the laterobasal margin of the rostrum and the rectangular apical sclerite of the median lobe; whereas (*G. constrictus*, *G. spatulatus*) is supported by the laterally projecting tuberculus near the basal two-fifths of the laterodorsal margin of the rostrum, its distinctive constriction, and the spatulate apical sclerite of the median lobe. The females of the latter two species share a distinctive color pattern on the pronotum and elytron.

More comprehensive studies on the biologies of all *Ganglionus* species are necessary before attempting an explanation of their evolutionary history. Specifically, it remains unknown what their distributional patterns are, whether each of them is restricted to only some species of *Carludovica*, and if the male rostral tumescences are functional during mating (as has been reported of other morphological features in *Staminodeus*, see Franz 2001). The considerable sexual dimorphism and allometry in males would be congruent with the hypothesis of fighting among males (e.g., Emlen 2000). In comparison with *Perelleschus* (both are pollinators; see Franz and O'Brien 2001), it appears that the reproductive costs that individuals of *Ganglionus* represent for their hosts may be lower, because their development occurs in the staminate flowers—without causing damage to the seeds of *Carludovica*. Comparatively 'inocuous' reproduction has been observed in other derelomine species that pollinate Arecaceae (e.g., *Derelomus chamaeropsis* F., see Anstett 1999, and references therein) and Cyclanthaceae (see Franz 1999). With respect to those that are associated with *Carludovica*, again, the historical sequence that explains these behaviors remains to be tested with cladistics.

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