# Systematics of Cyclanthura gen. n., a new genus of Derelomini (Coleoptera: Curculionidae) 

NICO M. FRANZ



Franz, N. M.: Systematics of Cyclanthura, a new genus of Derelomini (Coleoptera: Curculionidae). Insect Syst. Evol. 34: 153-198. Copenhagen, June 2003. ISSN 1399-560X.

Cyclanthura, gen. n., is described to accommodate the following 15 new Neotropical species of Derelomini (Coleoptera: Curculionidae: Curculioninae): C. laticola, sp. n.; C. sphaerata, sp. n.; C. cordata, sp. n.; C. dentata, sp. n.; C. pilosa, sp. n.; C. capitulata, sp. n.; C. tenuicola, sp. n.; C. carinata, sp. n.; C. uncinata, sp. n.; C. oculata, sp. n.; C. cultrata, sp. n.; C. striata, sp. n.; C. bipartita, sp. n.; C. crepidula, sp. n.; and C. palmata, sp. n. The monophyly of Cyclanthura is indicated by the putatively synapomorphic elytral elevations and impressions, the posteriorly explanate female tergum VIII, and the posteriorly emarginate female tergum IX. These and various other characteristics - e.g. transformations in the apical region of the male median lobe - distinguish Cyclanthura from Phyllotrox Schönherr to which its species would have been assigned until now. Particular species of Cyclanthura are considered to pollinate and reproduce on the inflorescences of Araceae (Anthurium) and Cyclanthaceae (Asplundia, Carludovica, Sphaeradenia, and Cyclanthus). Several significant host plant transitions appear to have evolved within the genus. These patterns are discussed in the light of a phylogeny of the species of Cyclanthura which is based on an analysis of 22 taxa and 32 characters.
N. M. Franz, Department of Entomology, Comstock Hall, Cornell University, Ithaca, NY 14853 USA (nmf2 @cornell.edu).

## Introduction

The present paper supplements recent contributions to the systematics of derelomine flower weevils from the Neotropics (Franz 2001, Franz \& O'Brien 2001a, 2001b). Under the current conception, Derelomini (Coleoptera: Curculionidae: Curculioninae sensu Alonso-Zarazaga \& Lyal 1999) comprise 220 species and 39 genera, the majority of which are associated with the inflorescences of Arecaceae. Some taxa have economic importance, e.g. Elaeidobius Kuschel whose species pollinate the African oil palm (Syed 1979). Phyllotrox Schönherr is another frequently reported genus in the palm pollination literature (Henderson 1986), although its 47 species differ in many respects. This condition will eventually necessitate revision and reclassification into several monophyletic taxa. Such a project will be beneficial not only from the perspective of systematics,
but also for an efficient communication of the diverse biologies of these species. To illustrate the problem, the type species Phy. semirufus Boheman has been collected in the vicinity of Colonia Tovar, Venezuela (at an altitude of 2000 m ), where it occurs on the flowers of Rubus sp. (Rosaceae, personal observation). Other species that appear to be associated with dicots are Phy. canyonaceris Warner on Aceraceae in the United States (Warner 1976); Phy. crassipes Champion, Phy. mecinoides Champion, and Phy. suturalis on Asteraceae in Mexico (C. W. O'Brien, personal communication); and Phy. melastomataceae Voss on Melastomataceae in Peru (Voss 1954). However, according to the only available key to the Neotropical derelomine genera (Kuschel 1952: 271-273), many described and undescribed palmassociated species would be identified as Phyllotrox. Furthermore, the current conception of Phyllotrox includes various undescribed species
that occur on the inflorescences of Cyclanthaceae, e.g. the pollinators of Asplundia Harling (Franz 1999). Part of the problem is that neither Derelomini nor Phyllotrox have been subjected to modern analyses. Therefore, they have no tested synapomorphies, comprising diverse nonmonophyletic taxa which are referred to partly by their general appearance and partly by similarities in their natural history. While an extensive revision is beyond the present scope, the problem can be reduced by delimiting Phyllotrox from closely related taxa which have distinctive biologies and are evidently not congeneric (under any sensible classification). Such an approach has been adopted in recent contributions on the cyclanth-associated genera Ganglionus Franz \& O'Brien, Perelleschus Wibmer \& O'Brien, Staminodeus Franz, and Systenotelus Anderson \& Gómez (Anderson \& Gómez 1997, Franz 2001, Franz \& O'Brien 2001a, 2001b). Gradual progress in derelomine systematics is appropriate for communicating interesting behavioral observations and for addressing basic evolutionary questions, especially with respect to host plant associations (e.g. Franz 2003).

Here I describe Cyclanthura gen. n., a new Neotropical genus of Derelomini with 15 new species which are associated with Araceae and Cyclanthaceae. I provide diagnostic characters to distinguish Cyclanthura from Phyllotrox and other derelomine taxa, a key to the species, a phylogeny, and natural history information. Of particular interest to evolutionary biologists is the observation that some species of Cyclanthura have been collected on the inflorescences of Anthurium Schott (Araceae). Consequently, this paper constitutes the first report of an arum-derelomine association. Considering the behaviors of closely related taxa, e.g. Ganglionus and Perelleschus (Franz \& O'Brien 2001a, 2001b), it is likely that these species of Cyclanthura are pollinators of Anthurium, an arum genus with over 800 species in the Neotropics (Mayo et al. 1997). On one previous occasion in Ecuador, unidentified weevils have been documented to visit the inflorescences of Anthurium gualeanum Engler during the period of anthesis (Madison 1979). This pattern has been confirmed, e.g. through personal observations of Cyc. laticola sp. n. on Anthurium sp. at La Selva, Costa Rica. Interestingly, at Golfito, Costa Rica, numbers of individuals of Cyc. bipartita sp. n. have been collected inside the inflorescences of

Cyclanthus bipartitus Poiteau which is sister to all remaining and exclusively derelomine-pollinated cyclanths (Eriksson 1994a, 1994b). Previous reports indicate that it is pollinated by dynastine scarab beetles (Beach 1982). Finally, Cyc. sphaerata sp. n. occurs on the infructescences of Sphaeradenia R. Eriksson and is the first identified species of Derelomini on this cyclanths genus (see Eriksson 1994a). These preliminary observations on host plants associations will be discussed in the light of the phylogeny of Cyclanthura.

## Methods

Morphological description. - The descriptive terminology is in accordance with Nichols (1989) for external morphology, Ting (1936) for the mouthparts, Velázquez de Castro (1998) for the metendosternite, Zherikhin \& Gratshev (1995) for the wing, and Burke (1959) for the male and female genital complex. The apex of the tibia is described using the terms "dorsal/ventral" and "anterior/posterior" as viewed in an idealized anatomical leg position of $90^{\circ}$ from the body axis. The measurements were made with a digital micrometer (Lasico XD) on a dissecting microscope (Wild M5A) at a magnification of 50-100x. The length of the body was measured from the anterior margin of the eye to the posterior margin of the elytron, and the length of the rostrum was measured from the apex of the rostrum to the anterior margin of the eye. The number of measurements is stated in parentheses, e.g. " $(\mathrm{N}=10)$ ", and is valid for all preceding values. These abbreviations are used: $\mathrm{l}=$ length, $\mathrm{w}=$ width, $\mathrm{r}=$ rostrum, $\mathrm{p}=$ pronotum, $\mathrm{t}=$ tibia, and $\mathrm{f}=$ femur. The numbering of the segments of the venter reflects their homology within Curculionoidea (Thompson 1992), i.e. III is the first externally visible segment. The descriptions of the males are followed by those of the females. They complement each other in such a way that identical descriptors among the genus and species, males and females, and serial organs (e.g. legs) are mentioned only once. The habitus photos were generated with a SEM Hitachi S4700. All illustrations of internal morphology were prepared with a drawing tube on a compound microscope (Leitz Dialux 20) at a magnification of 160-250x. The initial pencil drawings were edited with an illustration software program. The type specimen labels include the species name, the type status, gender symbol, author, and year, e.g.
"Cyclanthura, Holotype, ơ, Franz, 2003". They are red for the male holotypes, green for the female allotypes, and yellow for all paratypes. The insect collection codons are stated as in Arnett et al. (1993), and the codon for my personal collection is NMFC.

Cladistic analysis. - The phylogenetic species concept of was applied to Cyclanthura, emphasizing the diagnosability of species through unique combinations of evolutionarily projectible character states (Wheeler \& Platnick 2000). Reductive coding (Strong \& Lipscomb 1999) was used to assess the primary homology of characters in the male genital complex, but nonadditive multistate characters were coded as well, e.g. for the host plant associations (for discussion see Grandcolas et al. 2001). The following derelomine species were included as outgroup taxa in the character matrix. Derelomus chamaeropsis Fabricius occurs in Europe where it pollinates the dwarf palm Chamaerops humilis Linnaeus (Anstett 1999). Notolomus basalis LeConte is the pollinator of the cabbage palm Sabal palmetto (Walt.) Lodd. ex Schultes in the United States (Brown 1976). Ganglionus undulatus Franz \& O'Brien, Perelleschus carludovicae (Günther), and Systenotelus carludovicae Anderson \& Gómez are Central American species of Derelomini and associated with the inflorescences of Carludovica Ruíz \& Pavón (Cyclanthaceae; Anderson \& Gómez 1997, Franz \& O’Brien 2001a, 2001b). Staminodeus vectoris Franz visits the inflorescences of several species of Asplundia and other cyclanth genera in Central America (Franz 2001). The four latter species key to Phyllotrox in Kuschel (1952: 271273). Finally, Phy. semirufus, the raspberry-associated type species from Venezuela and Brazil was selected to represent this heterogeneous taxon. Other Phyllotrox species were excluded from the analysis because many of them will not remain congeneric after an extensive revision. However, the following 30 species were examined for diagnostic characters and determined to be different from Cyclanthura (see also below): Phy. abdominalis Schaufuss, Phy. aristidis Voisin, Phy. ater Champion, Phy. canyonaceris Warner, Phy. crassipes Champion, Phy. derivatus (Fall), Phy. dimidiatus Faust, Phy. ferrugineus LeConte, Phy. marcidus Champion, Phy. marginellus Faust, Phy. mecinoides Champion, Phy. megalops Champion, Phy. mundus Faust, Phy. nubifer LeConte, Phy.
pallidus Fåhraeus, Phy. posticus Schaufuss, Phy. pusillus Kirsch, Phy. quadricollis Fall, Phy. rubiginosus Faust, Phy. rufipes Faust, Phy. rugirostris Schaufuss, Phy. rutilus (Fall), Phy. schirmi Voss, Phy. sejunctus (Fall), Phy. semirufus, Phy. sericeus Faust, Phy. speculator Kirsch, Phy. subcinctus (Voss), Phy. suturalis (Boheman), and Phy. variabilis Schaufuss. The notion that the sister taxon to Cyclanthura is presently not known should not affect the resulting character polarity and topology of the cladogram (Nixon \& Carpenter 1993). All 15 species of Cyclanthura were included in the analysis.

The character matrix was operated in WinClada (Nixon 2002), and the most parsimonious cladogram was computed with NONA (Goloboff 1999). The numbers of the characters are congruent with the sequence of description. Autapomorphies of the species of Cyclanthura are presented in the diagnoses but were excluded from the character matrix (contra Yeates 1992). The cladistic analysis was performed with the parsimony ratchet (Nixon 1999) as implemented in WinClada, using the following commands: "200 iterations/replication", "2 trees to hold/replication", "5 characters to sample". The single resulting cladogram and character state transformations were examined in WinClada under various optimizations. Branch support values (Bremer 1994) were calculated in NONA with "hold 2000"", "suboptimal 20", and "bsupport 20 ".

## Taxonomy

## Cyclanthura Franz, gen. n.

Diagnosis. - Like several other genera of Derelomini - e.g. Ganglionus, Perelleschus, Staminodeus, Systenotelus, and Terioltes Champion Cyclanthura keys to Phyllotrox in Kuschel (1952: 271-273) by virtue of its inflected mesosternum, the 7 -segmented funicle, and the contiguous and relatively posteriorly positioned procoxal cavities. However, Cyclanthura can be distinguished from these and other derelomine taxa by the following putative synapomorphies: (1) elytron with slight convex elevation near anterior $1 / 8$ of striae (I-III) and posteriorly slightly impressed, (2) posterior margin of tergum VIII in female posteriorly (distinctly) projected and explanate, and (3) posterior margin of tergum IX in female medially slightly to distinctly emarginate. Additional characters for an


Figure 1. Cyclanthura laticola, habitus. (A) male, dorsal view; (B) male, lateral view; (C) head of male, dorsal view; (D) head of female, lateral view.
efficient diagnosis include: (1) the (dark) reddishbrown color, shallow frontal impression, distinct arcuate sulcus along the posterior margin of the eye, fairly slender legs, fairly deep striae, and the association with Araceae (Anthurium) in the lati-cola-uncinata clade (see details below); and (2) the medioventrally narrowly emarginate posterior margin of the male pygidium in combination with
an apically acutely narrowed, sinuate, ventrally carinately projected median lobe in the oculatapalmata clade. With these diagnostic characters, Cyclanthura can be rather easily differentiated from the holotype species of Phyllotrox (i.e. Phy. semirufus) which lacks the elytral and genitalic characters and is associated with Rosaceae. The same is true for almost all other Phyllotrox
species, possibly with the exception of Phy. dimidiatus and Phy. speculator. The single male type specimens of the latter two species were examined for their external characters (although only briefly while visiting CWOB), and had very slight elytral elevations and posterior impressions. At the time it was noted that Phy. dimidiatus has an apically transversely broadened median lobe, whereas Phy. speculator has relatively large eyes (as described by Kirsch 1874: 406). Both characteristics could be homologous to those of particular species of Cyclanthura and might eventually warrant transfer to this new genus when Phyllotrox is revised.

Description. - Male (Figs. 1A-1C). Fairly small, length $1.8-4.1 \mathrm{~mm}$, width $0.8-1.8 \mathrm{~mm}$, oval to elongate, $1 / \mathrm{w}=1.8-2.4$, greatest width near central region of elytron, slightly compressed, dorsally convex, ventrally slightly convex, color light to dark (reddish-) brown, sculpture punctulate, vestiture short, fine, appressed, aurate.

Head. Mouthparts (Figs. 4A-4C). Mandible (Fig. 4A) with 2 dentes, outer dens slightly larger, slightly superposed, inner dens arcuate, angulate, subbasally with deep, narrow indentation, outer margin with 2-3 small setae near basal $1 / 3$, inner margin rotundate, explanate. Maxilla (Fig. 4B) with cardo basally bilobed, arcuate, apically distinctly broadened, centrally with 1 fairly small seta; stipes triangular, fairly narrow, slightly angulate, subbasally with 1 fairly large seta; galea + lacinia + palpiger fused, obliquely transversely sutured, elongate, outer margin subcentrally with 1 fairly large, arcuate seta, subapically with 1 fairly small seta, inner $1 / 3+$ apical margin with dense, long, fine setation, inner margin ventrally with 2-8 larger, broad, slightly arcuate, weakly sclerotized lacinial dentes, dorsally with 1-2 subcentral $+1-2$ subapical, smaller, narrow, arcuate, heavily sclerotized lacinial dentes; maxillary palp 2 -segmented, protruded from apex of palpiger; I large, slightly shorter than II, transverse, clavate, subapically with 1 small seta; II large, elongate, subbasally with 1 small seta, apically papillate. Labium (Fig. 4C) with prementum equilateral to subcircular, basal margin subrectate, lateral margins slightly rotundate, subcentrally with 1 very large seta, apical margin subrectate; median tendon fairly large, elongate-triangular, apically broadened, dorsally projecting to apical margin of prementum, with dense, long, fine setation; labial palp 3-segmented,
protruded from apical margin of prementum; I fairly large, slightly longer than II, elongate, clavate, centrally with 1 very large seta; II nearly 2 x as long as III, basally equilateral, clavate, apicolaterally with distinct, triangular, angulate, acute projection, projecting beyond apex of III; III small, globular, apically papillate; postmentum elongate, apically slightly broadened.

Rostrum. In lateral view fairly short to fairly long, $0.6-1.1 \mathrm{~mm}$, slightly shorter to slightly longer than pronotum, $\mathrm{r} / \mathrm{p}=0.8-1.3$, dorsally and ventrally slightly arcuate, apically slightly narrowed; in dorsal view fairly narrow, breadth similar throughout (apically slightly broadened); in cross-section subquadrate, apical $2 / 5$ slightly depressed; dorsally with 1 elongate, shallow, median impression, nearly $1 / 3$ as long as rostrum, extending along central region, basal $1 / 3$ rugulose, apically glabrate; ventrally with 2 median sulci, shallow, extending from base to subapex of rostrum, subparallel; antennal insertion near apical $1 / 3$ to central region; scrobe fairly narrow, fairly shallow, subrectate, basally slightly broadened, angulate, oblique, vaguely defined, apically narrow, shallow, acuminate, extending to subapex of rostrum, position lateral throughout.

Antenna (Fig. 4D). 11-segmented, extending beyond anterior margin of pronotum, slender; scape extending to eye, slightly shorter than funicle + club, slender, slightly arcuate, clavate, glabrate; funicle 7 -segmented, with short pubescence; I large, similar in length to II-IV, elongate, clavate; II small, similar in length, gradually progressing from elongate to transverse, clavate; club 3 -segmented, similar in length to IV-VII of funicle, oval, compact, with dense, short pubescence; I longer than II; II slightly shorter than III.

Eye. Fairly small, subcircular, posterior margin slightly rotundate, protruded, distant from anterior margin of pronotum by nearly $2 / 3$ diameter of eye, separated by distance slightly smaller to slightly greater than breadth of apex of rostrum, argentate to black.

Head. Fairly small, transverse, globular, frons with fairly shallow impression (rostrum + head in lateral view slightly angulate, dorsal margin slightly concave), posterior to eyes (dorsolaterally) slightly constricted, posterior margin of eye slightly projected, with distinct, arcuate sulcus.

Thorax. Pronotum. In dorsal view fairly small, equilateral, $1 / w=0.8-1.1$, anterior margin nearly


Figure 2. (A) Cyclanthura dentata, habitus of male, lateral view, including smaller picture of profemoral dens; (B) Cyclanthura carinata, habitus of male, lateral view; (C) Cyclanthura oculata, habitus of female, lateral view.


Figure 3. (A) Cyclanthura striata, habitus of male, lateral view; (B) Cyclanthura bipartita, habitus of male, lateral view; (C) Cyclanthura crepidula, habitus of male, lateral view.


Figure 4. Cyclanthura laticola, mouthparts of male, ventral view, scale bars 0.05 mm . (A) left mandible; (B) right maxilla, with dorsal setation indicated; (C) labial prementum, with dorsal setation indicated. (D) left antenna (outline of segments), scale bar 0.1 mm .
$2 / 3$ as broad as posterior margin, greatest width near central region, anteriorly narrowed, slightly convex, anterior margin subrectate, explanate, lateral margins rotundate, anteriorly gradually converging, posterior margin slightly bisinuate, medially slightly projected, densely punctulate, vestiture anterolaterally directed; in lateral view conical, anterior margin explanate, centrally slightly projected, posterior margin explanate, emarginate.

Epipleura. Mesepisternum trapezoidal. Mesepimeron fairly narrow, triangular, dorsally projecting to pronotum. Metepisternum tetragonal, extending beyond lateral margins of metasternum, anteriorly abruptly broadened, transverse, posteriorly gradually narrowed. Metepimeron fairly small, narrow,
triangular, extending above posterior $1 / 4$ of metepisternum, ventral margin undulate.

Sterna. Prosternum slightly longer than mesosternum, equilateral to transverse, slightly convex, anterior margin slightly emarginate, posterior margin medially narrowly emarginate, centrally (anterior + posterior to procoxal cavities) with short, dense vestiture, posteriorly distinctly longer, laterally glabrate; procoxal cavities inserted near posterior $2 / 5$ (anterior region nearly 3 x as long as posterior region), contiguous. Mesosternum nearly $1 / 2$ as long as metasternum, transverse, slightly convex, inflected (retracted from ventral plane), posteriorly projecting between mesocoxae, equate with metasternum, margin rotundate, densely punctulate, with fairly short vestiture; mesocoxal
cavities inserted at posterior margin, separated by distance nearly as broad as mesocoxa. Metasternum transverse, laterally distinctly convex, centrally subplane (anteriorly) to concave (posteriorly), medially canaliculate along posterior $1 / 2$, anterior margin projecting between mesocoxae, slightly concave, posterior margin projected near inner margin of each metacoxa; metacoxal cavities inserted at posterior margin, separated by distance nearly as broad as metacoxa.

Metendosternite (Fig. 5A). Stalk slightly shorter than furcal arms, transverse, ventral margin emarginate, separated by median flange; ventral flange broader than stalk, lateral margins slightly emarginate, dorsally gradually converging; lamina nearly $1 / 4$ as long as central sclerotization; lateral projections fairly small, lateroventrally projected, apically broadened; anterior tendons inserted near base of furcal arms, slender, converging; furcal arms dorsally diverging, subrectate to slightly arcuate, apically gradually narrowed, bifurcate, inner bifurcation short.

Legs. Prothoracic leg slightly longer than mesothoracic leg, fairly slender; procoxa fairly large, conical, laterally obliquely truncate, apically slightly convex, inner margin with 1 subapical foveola; protrochanter transverse, triangular, apically broadened, oblique; profemur similar in length to pronotum, $\mathrm{f} / \mathrm{p}=0.8-1.2$, fairly slender, slightly sinuate, in cross-section elliptical, compressed, greatest width near apical 2/5, basally and apically narrowed; protibia (Fig. 5B) slightly shorter than profemur, $\mathrm{t} / \mathrm{f}=0.8-1.0$, slender, subrectate to slightly sinuate, in cross-section subcircular, apically slightly compressed, apically slightly broadened, slightly angulate, ventrally with dense vestiture along apical $1 / 4$, apically obliquely truncate, antero-/posteroventral margin with row of 25-35 spines (fairly long, narrow, acute, homologous to setae), ascending beyond condyle, inermous; protarsus 5-segmented, nearly $2 / 3$ as long as protibia, I-III dorsally with dark, median stripe, ventrally with dense vestiture, long near apex of III; I slightly longer than II, elongate, clavate; II shorter than III, equilateral to transverse, clavate; III bilobed, equilateral to elongate, lobes slender, apically slightly diverging; IV nearly $1 / 2$ as long as II, equilateral, retracted into III; V longer than II+III, elongate, slender, arcuate, apically gradually broadened; protarsal claw near $2 / 5$ as long as V , paired, simple. Mesothoracic leg slightly shorter than metathoracic leg, slender; mesocoxa trans-
versely globular; mesofemur slightly shorter than metafemur, slender; mesotibia fairly short, ventrally without dense vestiture along apical $1 / 4$. Metacoxa transverse, in cross-section elliptical, laterally acutely narrowed, medially slightly sulcate; metatibia fairly long.

Scutellum. Exposed by elytron, fairly small, triangular.

Elytron. In dorsal view oval to elongate, $1 / \mathrm{w}=$ 1.2-1/6, greatest width near central region, slightly broader than posterior margin of pronotum, humerus convex to subquadrate, protruded, anterior margin slightly emarginate, lateral margin rotundate, subparallel to slightly diverging along anterior $1 / 2$, converging along posterior $1 / 2$, posterior margin rotundate, subcontiguous; in lateral view convex (undulate along anterior $1 / 4$, see also below), lateral margin slightly sinuate; 10-striate; striae slightly broader than intervals, I-VIII fairly deep, IX+X deep, III+VIII merging before posterior margin, X along lateral margin; with 1 slight, transverse, convex elevation near anterior $1 / 8$ of IIII, posteriorly slightly impressed (near anterior 1/4 of I-III); maculations fairly large, punctate, subcircular, subcontiguous, dark reddish-brown, glabrate; intervals lighter, with fairly short, posteriorly directed vestiture.

Wing (Fig. 5C). Slightly longer than body, wing/body=1.1-1.5, elliptical to elongate, $1 / w=2.6-$ 3.4, greatest width near central region, anterior margin slightly sinuate, posterior margin slightly convex, narrowed along basal $1 / 5$, anal lobe indistinct; $\mathrm{Sc}, \mathrm{R}, \mathrm{Cu}, \mathrm{Cu}$, and 2 A present, C and 4 A obsolete; anterior margin with slight brown pigmentation, with 1 large, elongate, apically broadened maculation in radial field, with 2 large, elongate, narrow maculations in apical field; 2 radial sclerites, 1 radiomedial sclerotization present; long macrosetae along basal $1 / 5$ of posterior margin, short macrosetae sparse along basal $1 / 2$ of anterior margin, dense along posterior margin, microsetae throughout surface.

Abdomen. Venter. Nearly 2 x as long as lateral margin of metasternum, laterally slightly convex, centrally subplane, posteriorly gradually converging; III+IV fused, ventrally slightly elevated, angulate, V-VII separated; III longer than IV, transverse, centrally slightly concave, anterior margin with large, broad, rotundate projection between metacoxae, anterolateral edges projected, acute; IV slightly shorter than V+VI, transverse, posterolat-


Figure 5. Cyclanthura laticola, male thoracic morphology. (A) metendosternite, posterior view, scale bar 0.1 mm ; (B) left protibia, anterior view, scale bar 0.1 mm ; (C) right wing, dorsal view, scale bar 0.5 mm . Lighter shading indicates maculations, and darker shading indicates sclerites and veins.
eral edges slightly projected; V+VI similar in length, transverse, posterior margin of VI slightly emarginate; VII slightly to distinctly longer than $\mathrm{V}+\mathrm{VI}$, lateral margins posteriorly gradually converging, posterior margin subrectate to slightly rotundate, with short, fine setation.

Pygidium. Covered in part by elytron, similar in length to VII of venter, subcircular, broad, slightly convex, posterior margin rotundate, medioventrally broadly to distinctly narrowly emarginate, perpendicular to orientation of venter, centrally with 1 obscure impression (see also below).

Genital complex (Figs. 6A-6F). Tergum VIII (Fig. 6A) similar in length to slightly shorter than spiculum gastrale, equilateral to subcircular, distinctly convex, with or without 1 slight, fairly small, elliptical impression in posterior $1 / 2$, posterior $2 / 3$ with short, unifid setation, anterolateral edges distinctly projected, elongate, oblique, posterior margin rotundate, medially broadly to distinctly narrowly emarginate. Sternum VIII (Fig.

6 B) with 2 small, transverse, triangular, separated sclerites, nearly $1 / 8$ as long as tergum VIII, inner margins subrectate to slightly emarginate, anterior/posterior margins sinuate, laterally acutely converging, posterior margin with $4-8$ fairly large, subrectate, unifid setae. Spiculum gastrale (Fig. 6 C) shorter than median lobe, fairly stout, slightly deflexed, basally capitate-explanate, medially slightly to distinctly flanged, apically bifurcate (Yshaped), with 2 subrectate, apically slightly clavate projections. Tegmen (Fig. 6D) nearly 3/5 as long as median lobe, fairly slender, bifurcate (Y-shaped), tegminal apodeme longer than lateral apodemes, slightly deflexed, lateral apodemes slightly sinuate, dorsally sclerotized, ventrally membranous, connected, forming ring around median lobe. Aedeagus with median lobe in dorsal view (Fig. 6E) slightly to distinctly elongate, l/w=3.2-7.5, basal margin centrally distinctly rotundately or triangularly emarginate, basilateral edges triangular, acute to rotundate, lateral mar-


Figure 6. Cyclanthura laticola, male genital complex, scale bars 0.1 mm . All genitalia illustrations are interpretative in order to facilitate an understanding of the structural homologies. With respect to the median lobe, lighter shading indicates membranous regions, and darker shading indicates denticulate regions (the degree of darkness and the density of denticulation are proportionate to each other). (A) tergum VIII, ventral view; (B) sternum VIII, ventral view; (C) spiculum gastrale, ventral view; (D) Tegmen, ventral view; (E) aedeagus, ventral view (with dark ampullate sclerite); (F) aedeagus, lateral view.
gins slightly sinuate to subrectate to slightly emarginate, subparallel to apically slightly to distinctly converging, apex broad to narrow, rotundate to distinctly narrowly projected, acuminate-cultrate, margins with heavy sclerotization, porose along apical $1 / 2$, pori dense near apex; in lateral view (Fig. 6F) slightly to distinctly deflexed, fairly narrow to fairly broad, apically variously narrowed, apex narrow to distinctly transversely broadened
(capitate), angulate, slightly to distinctly deflexed or reflexed; with membranous internal sac, with or without various denticulate regions and/or sclerites, with 2 small, narrow, elongate, apically variously directed, weakly sclerotized rami along apical orifice, apical orifice extending along subapex, elliptical-elongate, apical margin inflected; aedeagal apodemes slightly shorter than median lobe, narrow, apically slightly angulate.

Female (Fig. 1D). Length $2.0-4.3 \mathrm{~mm}$, width $0.9-1.9 \mathrm{~mm}, 1 / \mathrm{w}=1.9-2.3$. Rostrum in lateral view fairly long, $0.7-1.1 \mathrm{~mm}$, similar in length to slightly longer than pronotum, $\mathrm{r} / \mathrm{p}=0.8-1.4$; in dorsal view with median impression indistinct, basally not rugulose; antennal insertion from apical $2 / 5$ to central region (towards basal 2/5). Scape shorter than funicle + club. Pronotum $1 / w=0.8-1.2$. Metasternum centrally subplane. Profemur similar in length to pronotum, $\mathrm{f} / \mathrm{p}=0.8-1.2$; protibia slightly shorter than profemur, $\mathrm{t} / \mathrm{f}=0.8-1.0$. Elytron $1 / \mathrm{w}=1.3-1.7$. Venter slightly longer than 2 x lateral margin of metasternum; III centrally subplane; IV similar in length to V+VI; posterior margin of VII slightly emarginate to slightly rotundate, indistinct to projected (explanate), with short to long, fine setation. Pygidium transverse to trapezoidal, narrow, lateral margins posteriorly gradually converging, posterior margin slightly emarginate to slightly rotundate, explanate (see also below), parallel to orientation of tergum, without central impression.

Genital complex (Figs. 7A-7E). Tergum VIII (Fig. 7A) nearly $2 / 3$ as long as sternum VIII, transverse to trapezoidal, slightly convex, anterior margin slightly rotundate, anterolateral edges slightly projected, lateral margin slightly emarginate to rotundate, anteriorly with narrow emargination, posteriorly gradually converging, posterior margin projected (explanate), slightly emarginate to slightly rotundate, with short, broad, multifid setation (setae with 2-5 apices), absent along anterior and lateral margin, posterior margin glabrate, subposteriorly with fairly long, narrow, unifid setation. Tergum IX (Fig. 7B) sclerotized (although not distinctly), nearly $1 / 2$ as long as sternum VIII, transverse to triangular, anterior margin medially slightly to distinctly emarginate, anterolateral edges acutely projected, lateral margins slightly emarginate to slightly rotundate, posteriorly distinctly converging, posterior margin medially slightly to distinctly emarginate, with fairly short, narrow, unifid setation. Sternum VIII (Fig. 7C) narrow, basal $3 / 5$ stylate, slender, medially slightly flanged, apical $2 / 5$ bifurcate ( Y -shaped), fairly narrow, slightly arcuate, apically slightly broadened, subapically with or without sparse, short, narrow, unifid setation, porose, apically variously truncate, with 2-8 fairly long, broad, subrectate, unifid setae. Coxites (Fig. 7D) sclerotized (although not distinctly), nearly $1 / 3$ as long as sternum VIII, elongate, narrow, slightly arcuate,
posteriorly slightly converging, gradually narrowed, pyriform, sparsely porose throughout; styli fairly small, elongate, narrow, apically with 2-5 fairly short to fairly long, narrow, subrectate, unifid setae. Bursa copulatrix fairly small, elongate, slightly shorter than sternum VIII, with common oviduct. Spermatheca (Fig. 7E) with duct inserted near base (but see below); narrow to broad, variously abruptly deflexed ( $90-180^{\circ}$ ) near central region, basally slightly inflected, subrectate to slightly obliquely rotundate, apically gradually narrowed, apex acute to rotundate, with small membranous projection; reservoir inserted near base of spermatheca, fairly small, elongate.

Variation. Size variation is generally not exceptional yet appreciable in the larger species, e.g. Cyc. bipartita. Color variation can be considerable as it is common to collect recently emerged adults at the inflorescences. These homogeneously light-pigmented individuals lack several diagnostic features such as darker antennal segments. Furthermore, larger individuals tend to display slightly more exaggerated sculptural characteristics, e.g. elytral elevations. The shape of the rostrum is comparatively more distinctive as well, i.e. slightly more rectate or slightly more arcuate, depending on the species and gender. Intraspecific variation in the male and female genital complex has been observed but appears to be insignificant in comparison to the differences among species.

Type species. - Cyclanthura laticola, by present designation.

Etymology. - Named for its association with the inflorescences of the Anthurium (Araceae), Cyclanthus, and various other genera of Cyclanthaceae (see also below). The gender is feminine.

## Key to the species of Cyclanthura

Several species of Cyclanthura cannot be identified with confidence without examining the male and/or female genital complex. The subsequent key is therefore an attempt to provide unambiguous identification while focusing as much as possible on externally visible characters.

1. Color (dark) reddish-brown; rostrum in dorsal view fairly narrow, in lateral view ventrally subrectate to slightly arcuate (in both genders, e.g. Figs. 1B, 1D, 2A, 2B); median lobe in dorsal view apically fairly broad or gradually acutely narrowed (as opposed to abruptly), in lateral view deflexed (Figs. 6E.

6F, 7A-11B); association with Araceae
(Anthurium) ..... 2

- Color light to dark (reddish-) brown; rostrum in dorsal view fairly broad, in lateral view ventrally (slightly) arcuate (particularly in female, e.g. Figs. 2C, 3A, 3B \& 3C); median lobe in dorsal view apically abruptly acutely narrowed (cultrate), in lateral view sinuate (Figs. 12A-14B); association with Cyclanthaceae $\qquad$10

2(1). Eyes separated by distance smaller than or similar to breadth of apex of rostrum; median lobe either in dorsal view apically fairly broad (Figs. 6E \& 6F, 8A-9A) or in lateral view capitate at apex (Figs. 9B-10B) $\qquad$ 3

- Eyes separated by distance slightly greater than breadth of apex of rostrum; median lobe not as above (Figs. 11A, 11B)9

3(2). Median lobe in dorsal view apically fairly broad, in lateral view apically gradually narrowed, internally with 1 small, ampullate sclerite (Figs. 6E \& 6F, 8A-9A) $\qquad$4

- Median lobe in dorsal view apically distinctly narrowed, in lateral view apically (distinctly) capitate, internally without 1 small, ampullate sclerite (Figs. 9B-10B). $\qquad$ 7

4(3) Male profemur indistinct, without apicoventrally directed dens (e.g. Fig. 1B)....................

- $\quad \begin{aligned} & \text { Male profemur with distinct (although fairly } \\ & \text { small), apicoventrally directed dens (e.g. Fig. }\end{aligned}$ 2B)6

5(4). Antenna with club concolorous; median lobe in dorsal view apically rotundately narrowed, apicolaterally slightly emarginate, internally without denticulate region, with 1 elongate, slightly reflexed ampullate sclerite (Figs. 6E \& 6F); spermatheca J-shaped, with rotundate apex (Fig. 7E); association with Anthurium (Araceae) $\qquad$ Cyc. laticola sp. n.

- Antenna with I of club with slightly darker color; median lobe in dorsal view with apical 1/8 spatulate, apicolaterally slightly rotundate, internally with 1 small denticulate region, with 1 rhomboidal, deflexed ampullate sclerite (Fig. 8A); spermatheca V-shaped, apically narrowly projected (Fig. 8A); association with Sphaeradenia (Cyclanthaceae) ......

Cyc. sphaerata sp. n.
6(4). Median lobe in dorsal view with apical $1 / 10$ distinctly transversely broadened (cordatemalleate), internally with 1 elongate ampullate sclerite near central region, aedeagal apodemes fairly short (Fig. 8B); spermatheca basally indistinct, apically narrowly rotundate, reservoir inserted near basal $2 / 5$ (distad from orientation of apex, Fig. 8B); Ecuador. $\qquad$ Cyc. cordata sp. n.

- Median lobe in dorsal view with apical $1 / 8$ spatulate (only slightly broadened), internally with bifurcate ampullate sclerite basad of basal margin, aedeagal apodemes fairly long (Fig. 9A); spermatheca basally with 1 small lobulate projection (proximad to orientation of apex), apically (acutely) narrowed, reservoir basally inserted (Fig. 9A); Panama.

7(3). Male metasternum in posterocentral concave region with dense, posteriorly directed vestiture; median lobe in lateral view apically slightly (rotundately) broadened, internally without denticulate region (Fig. 9B); spermatheca V-shaped, apically acutely narrowed, insertion of duct + reservoir basal (Fig. 9B $\qquad$ .Cyc. pilosa sp. n.

- Male metasternum indistinct; median lobe in lateral view distinctly (transversely) broadened, internally with 1 subapical denticulate region (Figs. 10A \& 10B); spermatheca Jshaped, apically (narrowly) rotundate, insertion of duct + reservoir basilateral (Figs. 10A \& 10B
8(7). Median lobe in dorsal view elongate, in lateral view apically subrectate, aedeagal apodemes shorter than median lobe (Fig. 10A); female sternum VIII apically with 3-4 fairly long, broad setae (Fig. 10A)

Cyc. capitulata sp. n.

- Median lobe in dorsal view distinctly elongate, in lateral view apically slightly reflexed, aedeagal apodemes distinctly shorter than median lobe (Fig. 10B); female sternum VIII apically with 1 very long, broad seta (Fig. 10B) $\qquad$ . Cyc. tenuicola $\mathrm{sp} . \mathrm{n}$.
$9(2)$. Length $2.5-3.3 \mathrm{~mm}$; shape slightly depressed; antenna with club concolorous (or slightly darker); elytron with 2 distinct elongate tumescences (Fig. 2B); median lobe in lateral view with distinct ventral carina, apically very slightly reflexed (Fig. 11A); female sternum VIII apically with 10-12 fairly long, broad setae; spermatheca U-shaped, with rotundate apex (Fig. 11A)

Cyc. carinata sp. n.

- Length 2.2-2.5 mm; shape not depressed; antenna with I of club darker, II + III of club lighter; elytron without distinct elongate tumescences; median lobe in lateral view without carina, apically distinctly deflexed (Fig. 11B); female sternum VIII apically with 2 fairly long, narrow setae; spermatheca L-shaped, with acuminate apex (Fig. 11B)

Cyc. uncinata sp. n.
$10(1)$. Size fairly small, length $1.8-2.6 \mathrm{~mm}$; pronotum in dorsal view centrally slightly concave (or slightly impressed, e.g. Figs. 2C \& 3A); median lobe internally with 2 denticulate regions (Figs. 12A-13A); female tergum IX with posterior margin medially slightly emarginate

- $\quad$ Size fairly large, length $2.6-4.3 \mathrm{~mm}$; pronotum in dorsal view centrally slightly convex (e.g. Figs. 3B, 3C); median lobe internally with 1 denticulate (or finely granulate) region (Figs. 13B-14B); female tergum IX with posterior margin medially distinctly emarginate
11(10). Antenna with club concolorous; eyes large, distinctly protruded, separated by distance similar to breadth of club (Fig. 2C); pronotum subanteriorly with 2 small impressions;
median lobe in lateral view with apex ventrally slightly projected (Fig. 12A); female sternum VIII with inner subapical margin indistinct, apically with 3 fairly short setae; spermatheca fairly broad, with broadly rotundate apex (Fig. 12A); Ecuador ................................ Cyc. oculata sp. n.
- Antenna with I of club with slightly darker color; eyes fairly small, slightly protruded, separated by distance similar to breadth of apex of rostrum; pronotum centrally slightly concave; median lobe in lateral view with apex ventrally distinctly carinately projected (Figs. 12B \& 13A); female sternum VIII with inner subapical margin triangularly broadened, apically with 3 long setae; spermatheca fairly narrow, with slightly projected apex (Figs. 12B \& 13A); Costa Rica to Venezuela
12(11). Shape not depressed; elytron without distinct elongate tumescences; male pygidium with posterior margin medially shallowly narrowly emarginate; median lobe in lateral view with acute reflexed apex, internally with basal denticulate region contiguous (Fig. 12B); spermatheca C-shaped (Fig. 12B); Venezuela $\qquad$ Cyc. cultrata sp. n.
- $\quad$ Shape slightly depressed; elytron with 3 distinct elongate tumescences (Fig. 3A); male pygidium with posterior margin medially deeply narrowly emarginate; median lobe in lateral view with rotundate reflexed apex, internally with basal denticulate region separated (connected by membranes, Fig. 13A); spermatheca U-shaped (Fig. 13A); Costa Rica and Panama.

Cyc. striata sp. n.
13(10). Eyes separated by distance slightly smaller than breadth of apex of rostrum; elytron with anterior impression indistinct (but not absent, Fig. 3B); median lobe in lateral view with apex ventrally slightly projected, internally with 1 finely granulate region (Fig. 13B); female sternum VIII O-shaped; spermatheca U-shaped (Fig. 13B); association with Cyclanthus $\qquad$ Cyc. bipartita sp. n.

- Eyes separated by distance slightly greater than breadth of apex of rostrum; elytron with anterior impression distinct; median lobe in lateral view with apex ventrally (distinctly) carinately projected, internally with 1 densely denticulate region (Figs. 14A \& 14B); female sternum VIII Yshaped; spermatheca J-/L-shaped (Figs. 14A \& 14B); association with Asplundia or Carludovica.
14(13). Length 3.1-3.8 mm ; shape slightly depressed; color dark reddish-brown; antenna with I of club with slightly darker color; male profemur with distinct (although fairly small), apicoventrally directed dens; elytron with anterior elevation extending to stria V (Fig. 3C); median lobe in lateral view with apical 1/6 (slightly) reflexed (Fig. 14A); female sternum VIII with inner
margin subapically triangularly projected; spermatheca with small, deflexed, acuminate apex (Fig. 14A); association with Asplundia; Venezuela $\qquad$ Cyc. crepidula sp. n.
- Length 2.6-3.0 mm; shape not depressed; color light (reddish-) brown; antenna with club concolorous; male profemur indistinct, without apicoventrally directed dens; median lobe in lateral view with apical $1 / 3$ (distinctly) reflexed (Fig. 14B); female sternum VIII with inner margin subapically indistinct; spermatheca apically broadly rotundate (Fig. 14B); association with Carludovica; Costa Rica .... Cyc. palmata sp. n.


## Cyclanthura laticola Franz, sp. n.

(Figs. 1A-1D, 6A-6F \& 7A-7E)
Diagnosis. - Small, (dark) reddish-brown, rostrum fairly narrow, antennal segments concolorous, eyes separated by distance slightly smaller than breadth of apex of rostrum; median lobe in dorsal view apically rotundately narrowed, apicolaterally slightly emarginate, internally without denticulate region, with 1 elongate, slightly reflexed ampullate sclerite; female sternum VIII apically with 2 short +2 long setae, spermatheca J-shaped, with rotundate apex; association with Anthurium (Araceae). Cyclanthura laticola can be distinguished from the species of the pilosa-tenuicola clade (Fig. 17) by the apically fairly broad median lobe; from Cyc. cordata and Cyc. dentata by the ventrally indistinct profemur in males; and from Cyc. sphaerata by the concolorous antennal segments, the J-shaped and apically rotundate spermatheca, and the host plant association. There is considerable color variation among the specimens, ranging from light (yellowish-) brown in teneral individuals to the characteristic dark color in fully pigmented individuals. Apparently, this is the most widely distributed Cyclanthura species (Fig. 15).
Description. - Male. Small, length 1.8-2.2 mm, width $0.8-1.0 \mathrm{~mm}, 1 / \mathrm{w}=2.1-2.2$, (dark) reddishbrown (antenna + legs with slightly lighter coloration). Rostrum in lateral view fairly long, 0.60.8 mm , similar in length to pronotum, $\mathrm{r} / \mathrm{p}=1.0-$ 1.1, ventrally subrectate to slightly arcuate; antennal insertion near central region (towards apical $2 / 5$ ). Eyes separated by distance slightly smaller than breadth of apex of rostrum. Pronotum $1 / \mathrm{w}=0.9-1.0$, lateral margins slightly rotundate. Profemur slightly longer than pronotum, $\mathrm{f} / \mathrm{p}=1.0-$ 1.2 , ventrally slightly carinate; $\mathrm{t} / \mathrm{f}=0.9$. Elytron $\mathrm{l} / \mathrm{w}=1.3-1.5(\mathrm{~N}=10)$. Wing/body=1.3, wing $1 / \mathrm{w}=$


Figure 7. Cyclanthura laticola, female genital complex, scale bars 0.1 mm . (A) tergum VIII, ventral view (light shading indicates setose region, see magnified section); (B) tergum IX, ventral view; (C) sternum VIII, ventral view; (D) coxites + styli, ventral view; (E) spermatheca + reservoir, lateral view.
3.2-3.3 ( $\mathrm{N}=2$ ). Venter with VII slightly longer than V+VI, posterior margin slightly rotundate. Tergum VIII posteriorly slightly impressed, posterior margin broadly shallowly emarginate. Median lobe in dorsal view slightly elongate, $1 / \mathrm{w}=3.2-3.4 \quad(\mathrm{~N}=2)$, basal margin centrally distinctly rotundately emarginate, basilateral edges rotundate, lateral margins subrectate to slightly sinuate, subparallel along basal $3 / 4$, slightly emarginate, gradually converging along apical $1 / 4$, apex broad, rotundate; in lateral view deflexed, fairly narrow, greatest breadth
near apical $2 / 5$, dorsally gradually narrowed along apical $1 / 3$, apex fairly narrow; internally with 1 small, elongate, narrow, slightly reflexed, ampullate, moderately sclerotized sclerite near basal $2 / 5$, nearly $1 / 6$ as long as median lobe.
Female. Length 2.1-2.3 mm, width $1.0-1.1 \mathrm{~mm}$, $1 / \mathrm{w}=2.0-2.2$. Rostrum $0.8-1.0 \mathrm{~mm}$, slightly longer than pronotum, $\mathrm{r} / \mathrm{p}=1.2-1.3$; antennal insertion near central region. Pronotum $1 / \mathrm{w}=0.9-1.0$. Profemur ventrally not carinate, $\mathrm{f} / \mathrm{p}=1.0-1.1 ; \mathrm{t} / \mathrm{f}=0.9$. Elytron $1 / \mathrm{w}=1.3-1.5 \quad(\mathrm{~N}=10)$. Venter with VII
slightly longer than V+VI, posterior margin subrectate, with indistinct setation. Tergum VIII with lateral margins slightly sinuate, posterior margin subrectate to slightly emarginate; tergum IX with anterior margin medially distinctly emarginate, lateral margins slightly rotundate, posterior margin medially slightly emarginate; sternum VIII with furcae subcentrally slightly broadened, subapically with setation, apex slightly rotundate, with 2 short +2 long setae; styli with 2 short +1 fairly long setae; spermatheca fairly narrow, abruptly deflexed (by nearly $135^{\circ}$ ) near apical $2 / 5$ (J-shaped), basally obliquely subrectate, greatest breadth near basal $1 / 4$, apex rotundate.
Type material. - Male holotype, "PANAMA, Colon, C. Z., Ft. Sherman, Old Ft. San Lorenzo Rd, 7-31-1995, C. W. \& L. B. O'Brien/ on yellow flower Anthurium ochranthum C. Koch" (CWOB); female allotype, same label as male holotype (CWOB); male paratypes "COSTA RICA, P. Her., Est. Biol. La Selva (OTS), 40 m, 11-IV-1998, \# 4, leg. Nico Franz/ on Anthurium sp. (Araceae)" (CMNC, 4; CWOB, 4), same labels as male holotype (MIUP, 3; MUCR, 4), "Costa Rica, Heredia, La Selva, 40 m , on Anthurium (Araceae), leg. N. Franz, II-15-1998" (NMFC, 3); female paratypes "Costa Rica, Heredia, La Selva, 40 m , on Anthurium (Araceae), leg. N. Franz, II-15-1998" (CMNC, 5), "COSTA RICA, P. Her., Est. Biol. La Selva (OTS), 40 m, 11-IV-1998, \# 4, leg. Nico Franz/ on Anthurium sp. (Araceae)" (CWOB, 4), same labels as male holotype (MIUP, 5), "Costa Rica, Heredia, La Selva, 40 m , successional plots, leg. N. Franz, II-23-1998" (MUCR, 4).

Etymology. - Named for the diagnostic apically broad median lobe in males - latus signifying "broad" and colis signifying "tail" (Brown 1956).

Distribution. - Cyclanthura laticola has been collected on the Atlantic slope of Costa Rica, Heredia, Estación Biológica La Selva (OET); in Mexico, Veracruz, Estación Biológica Los Tuxtlas (UNAM); and in Panama, (1) Bocas del Toro, Río Changuinola, (2) Colón, Fort Sherman, and (3) Zona del Canal, Isla de Barro Colorado (STRI) (Fig. 15).

Natural history. - At La Selva, Costa Rica, 2-5 individuals have been collected on the inflorescences of Anthurium sp. at daytime (10:00 a.m. to 04:00 p.m.) during various phases of the anthesis, i.e. the pistillate phase when the stigmata produce secretions, and the staminate phase when the pollen is released. No other insects could be observed, suggesting that Cyc. laticola is the primary pollinator of this arum species. Apparently, some individuals were feeding on the pollen, moving along the spadix at low velocity, and falling to
the ground when disturbed. Copulating pairs were present as well. On one occasion, an adult individual has been observed on an immature infructescence. At Isla de Barro Colorado, Panama, Cyc. laticola has been collected throughout the year at UV light traps (positioned at heights of 3 m and 26 m , respectively, the former trap yielded significantly more individuals). At Fort Sherman, Panama, over 20 individuals have been collected on an inflorescence of Anthurium ochranthum C. Koch.

## Cyclanthura sphaerata Franz, sp. n.

(Fig. 8A)
Diagnosis. - Small, dark reddish-brown, rostrum fairly narrow, antenna with I of club with slightly darker color, eyes separated by distance similar to breadth of apex of rostrum; median lobe in dorsal view with apical $1 / 8$ spatulate, apicolaterally slightly rotundate, internally with 1 small denticulate region, with 1 rhomboidal, deflexed ampullate sclerite; female sternum VIII apically with 4 long, broad setae, spermatheca V-shaped, apically narrowly projected; association with Sphaeradenia (Cyclanthaceae). Cyclanthura laticola can be distinguished from the species of the pilosa-tenuicola clade (Fig. 17) by the apically fairly broad median lobe; from Cyc. cordata and Cyc. dentata by the ventrally indistinct profemur in males; and from Cyc. laticola by the slightly darker first club segment; the V-shaped and apically narrowly projected spermatheca, and the host plant association. The leg coloration varies from light brown to dark brown.

Description. - Male. (Fairly) small, length 2.3 mm , width $1.1 \mathrm{~mm}, \mathrm{l} / \mathrm{w}=2.1$, dark reddish-brown (to black; rostrum, metasternum, venter, pygidium reddish-brown; legs light reddish-brown). Rostrum in lateral view fairly long, 0.8 mm , similar in length to pronotum, $\mathrm{r} / \mathrm{p}=1.0-1.1$, ventrally subrectate to slightly arcuate, dorsomedian impression indistinct, apically with lighter coloration; antennal insertion near apical $2 / 5$. Antenna with scape, funicle, II + III of club reddish-brown, I of club dark brown. Eyes separated by distance similar to breadth of apex of rostrum. Pronotum $1 / \mathrm{w}=1.0$. Profemur slightly longer than pronotum, $\mathrm{f} / \mathrm{p}=1.1$; $\mathrm{t} / \mathrm{f}=0.9$. Elytron $\mathrm{l} / \mathrm{w}=1.4-1.5 \quad(\mathrm{~N}=2)$. Venter with VII slightly longer than $\mathrm{V}+\mathrm{VI}$, posterior margin subrectate. Tergum VIII posteriorly slightly im-


Figure 8. The subsequent figures (i.e. Figs 8-14) display the male and female genitalia of 14 Cyclanthura species. For each species, the two drawings on the left depict the male aedeagus (1) in ventral view and (2) in lateral view, whereas the two drawings on the right depict (1) the apical region of the female sternum VIII in ventral view and (2) the female spermatheca + reservoir in lateral view. Scale bars 0.1 mm . (A) Cyclanthura sphaerata; (B) Cyclanthura cordata.
pressed, posterior margin broadly shallowly emarginate. Median lobe in dorsal view elongate, $1 / \mathrm{w}=$ 3.8-4.2 ( $\mathrm{N}=2$ ), basal margin centrally distinctly rotundately emarginate, basilateral edges acute to rotundate, lateral margins slightly sinuate along basal $3 / 4$ (narrowed near central region), apically slightly converging, narrow along apical $1 / 8$, moderately narrowly converging along apical $1 / 4$ (narrowed near apical $1 / 8$ ), apical $1 / 8$ spatulate, apex projected, fairly broad, rotundate; in lateral view deflexed (apex slightly deflexed), fairly nar-
row along basal $3 / 4$, greatest breadth near central region, dorsally gradually narrowed along apical $1 / 4$, apex narrow, acute (to rotundate); internally with 1 fairly small, elongate, fairly narrow, deflexed, ampullate, heavily sclerotized sclerite near basal $1 / 4$, apically gradually narrowed (rhomboidal), nearly $1 / 6$ as long as median lobe +1 fairly small, equilateral, fairly broad, sparsely denticulate region (membranous) near central region, nearly $1 / 8$ as long as median lobe.
Female. Length 2.3-2.5 mm, width 1.1-1.2 mm,
$1 / \mathrm{w}=2.0-2.1$. Rostrum $0.8-0.9 \mathrm{~mm}$, similar in length to pronotum, $\mathrm{r} / \mathrm{p}=1.1$; antennal insertion near apical $2 / 5$ (towards central region). Pronotum $1 / \mathrm{w}=1.0$. $\mathrm{F} / \mathrm{p}=1.1$; $\mathrm{t} / \mathrm{f}=0.9$. Elytron $1 / \mathrm{w}=1.4(\mathrm{~N}=2)$. Venter with VII slightly longer than IV+V, posterior margin subrectate, with indistinct setation. Tergum VIII with lateral margins sinuate, posterior margin projected, explanate, subrectate; tergum IX with anterior margin slightly to distinctly emarginate, lateral margins subrectate to slightly rotundate, posterior margin medially (broadly) emarginate; sternum VIII with furcae apically gradually broadened, subapically with setation, apex broadly rotundate, with 4 fairly long, (very) broad setae; styli with 2 fairly short setae; spermatheca fairly narrow, abruptly deflexed (by nearly $135^{\circ}$ ) near apical $2 / 5$ (V-shaped), basally obliquely subrectate, greatest breadth near base, apically gradually narrowed, apex slightly projected, acute.

Type material. - Male holotype "Costa Rica, Alajuela, Monteverde, E. B. Monteverde, $1800 \mathrm{~m}, 10^{\circ} 20^{\prime} \mathrm{N}$, $84^{\circ} 48^{\prime}$ W, on Sphaeradenia occidentalis, leg. N. Franz, VI-10-2001" (MUCR); female allotype, same label as male holotype (MUCR); male paratypes, same labels as male holotype (CMNC, 3; CWOB, 3; NMNH, 3; MIUP, 3, MUCR, 3), "COSTA RICA, Cart., 4 km NE Cañon, Genesis II, 2300 m, VIII-27-1998, Nico Franz/ on cone Sphaeradenia praetermissa" (CWOB, 1), "COSTA RICA, San José, Genesis II, 2300 m, 4-VII-1996, leg. Nico Franz/ from fruiting spadix Sphaeradenia cf. praetermissa R. Eriksson" (NMFC, 1); female paratypes, same labels as male holotype (CMNC, 3; CWOB, 3; NMNH, 3; MIUP, 3, MUCR, 3), "COSTA RICA, S. Jose, P. N. Braulio Carrillo, 9.5 km E Tunnel, 1000 m , III-IV-1990, P. Hanson, malaise trap" (CWOB, 1), "COSTA RICA, S. Jose, Zurquí de Moravia, 1600 m, malaise trap, V-1995, P. Hanson" (NMFC, 1).
Etymology. - Named for its association with the inflorescences of Sphaeradenia occidentalis R. Eriksson at Monteverde, Costa Rica (see also below).

Distribution. - Cyclanthura sphaerata has been collected in Costa Rica, Alajuela, Cordillera de Tilarán, Estación Biológica Monteverde and Estación Biológica Alberto Brenes (UCR), (2) San José, Cordillera Central, Parque Nacional Braulio Carillo and Zurquí de Moravia, and (3) San José, Cordillera de Talamanca, Genesis II (Fig. 15).

Natural history. - At Estación Biológica Monteverde, Costa Rica, nearly 50 individuals have been collected on the maturing reddish infructescences of Sphaeradenia occidentalis. Typically, no more than five adults could be observed on an infructescence, resting near the bases of the tepals (apparently without feeding), and moving
very slowly upon disturbance. Approximately 30 infructescences were dissected, half of which yielded larvae and pupae of Cyc. sphaerata. These immature stages are located in the interfloral, between the central axis and the peripheral berries. Very few seeds are consumed. As can be observed in Perelleschus and Systenotelus (Anderson \& Gómez 1997, Franz \& O’Brien 2001b), the adults remain inside until the exposure of the berries unless they eat their way from the periphery to the outside. At Genesis II, Costa Rica, several individuals have been collected in the infructescences of Sphaeradenia praetermissa R. Eriksson, however, they were absent from an inflorescence in its staminate phase at the same location. Both observations suggest that Cyc. sphaerata does not pollinate Sphaeradenia. Its biology is similar to that of other undescribed derelomines from La Selva, Costa Rica (Franz 1999). These species arrive at the inflorescences in low quantities, and their reproductive behavior is not closely synchronized with the anthesis of their host plant. They oviposit into the spaces between the pistillate flowers, and the larvae are herbivorous, feeding on the pulp of the maturing infructescence until pupation occurs. They do not appear to cause the abortion of infructescences.

Although there are previous reports of derelomines on Sphaeradenia hamata Harling (Eriksson 1994a, Anderson \& Gómez 1997), Cyc. sphaerata is the first identified species of Derelomini on Sphaeradenia.

## Cyclanthura cordata Franz, sp. n.

(Fig. 8B)
Diagnosis. - Fairly small, (dark) reddish-brown, rostrum fairly narrow, antenna with I of funicle + I of club with slightly darker color, eyes separated by distance similar to breadth of apex of rostrum, male profemur with distinct (although fairly small), apicoventrally directed dens; median lobe in dorsal view with apical $1 / 10$ distinctly transversely broadened (cordate-malleate), internally with 1 elongate ampullate sclerite near central region, aedeagal apodemes fairly short; spermatheca apically narrowly rotundate, reservoir inserted near basal $2 / 5$ (distad from orientation of apex, Fig. 8B); Ecuador. Cyclanthura cordata can be distinguished from most species of the laticolatenuicola clade (Fig. 17) by the ventrally dentate profemur in males; from Cyc. crepidula by the api-
cally fairly broad median lobe; and from Cyc. dentata by the apically cordate-malleate median lobe, its centrally positioned internal ampullate sclerite, the apically narrowly rotundate spermatheca with the laterally inserted reservoir, and the distribution.

Description. - Male. (Fairly) small, length 2.3-2.7 mm , width $1.1-1.5 \mathrm{~mm}, \mathrm{l} / \mathrm{w}=1.8-2.3$, (dark) red-dish-brown (pronotum with slightly darker coloration). Rostrum in lateral view fairly long, 0.91.0 mm , slightly longer than pronotum, $\mathrm{r} / \mathrm{p}=1.0-$ 1.3; antennal insertion near central region (towards apical 2/5). Antenna with I of funicle + I of club with slightly darker color. Eyes separated by distance similar to breadth of apex of rostrum. Pronotum $1 / \mathrm{w}=0.8-1.0$, convex (apparently positively allometric, globular in large individuals). $\mathrm{F} / \mathrm{p}=0.9-1.1$, profemur ventrally with 1 fairly small, triangular, acute, apicoventrally directed dens near apical $1 / 4 ; \mathrm{t} / \mathrm{f}=0.9-1.0$; mesofemur without apicoventrally directed dens. Elytron $1 / \mathrm{w}=1.2-$ $1.5(\mathrm{~N}=10)$. Wing/body=1.3-1.4, wing $1 / \mathrm{w}=3.2-3.4$ $(\mathrm{N}=2)$. Venter with VII slightly longer than $\mathrm{V}+\mathrm{VI}$, posterior margin subrectate. Tergum VIII posteriorly very slightly impressed, posterior margin broadly shallowly emarginate. Median lobe in dorsal view elongate, $1 / \mathrm{w}=5.4-5.8(\mathrm{~N}=2)$, basal margin centrally distinctly rotundately emarginate, basilateral edges acute to rotundate (triangular), lateral margins subrectate to slightly sinuate along basal $9 / 10$, subparallel to apically slightly converging, narrow near subapical $1 / 10$, apical $1 / 10$ distinctly transversely projected (nearly as broad as base of median lobe), cordate-malleate, semicircular to triangular, apex projected, broadly rotundate, medially slightly projected; in lateral view slightly deflexed (apex deflexed), fairly narrow along basal $3 / 4$, greatest breadth apical $1 / 4$, dorsally gradually narrowed along apical $1 / 4$, apex narrow, acute; internally with 1 fairly small, elongate, narrow, slightly deflexed to reflexed, ampullate, heavily sclerotized sclerite near central region, nearly $1 / 8$ as long as median lobe +1 fairly large, elongate, fairly broad, densely dentate region (membranous) near apical $2 / 5$, dentes apically directed, $1 / 6$ as long as median lobe; aedeagal apodemes shorter than median lobe.

Female. Length 2.1-2.7 mm, width 1.1-1.3 mm, $1 / \mathrm{w}=2.0-2.1$. Rostrum $0.9-1.1 \mathrm{~mm}$, slightly longer than pronotum, $\mathrm{r} / \mathrm{p}=1.1-1.3$; antennal insertion near central region (towards basal 2/5). Pronotum
$1 / \mathrm{w}=0.9-1.0$ (no apparent allometry). $\mathrm{F} / \mathrm{p}=1.0-1.1$, without apicoventrally directed dens; $\mathrm{t} / \mathrm{f}=0.9-1.0$. Elytron $1 / \mathrm{w}=1.3-1.5(\mathrm{~N}=10)$. Venter with VII similar in length to IV +V , posterior margin subrectate, with indistinct setation. Tergum VIII with lateral margins sinuate, posterior margin distinctly projected, explanate, subrectate to slightly emarginate; tergum IX with anterior margin medially distinctly emarginate (throughout entire structure), lateral margins subrectate to slightly rotundate, posterior margin medially (broadly) emarginate (medially weakly sclerotized); sternum VIII with furcae subcentrally slightly broadened, apically gradually narrowed, subapically with setation, apex narrow, obliquely rotundate, with 3 fairly long, narrow setae; styli with 2 short +1 fairly long setae; spermatheca fairly narrow, abruptly deflexed (by nearly $105^{\circ}$ ) near apical 2/5 (Jshaped), duct inserted near base, reservoir inserted near basal $2 / 5$ (distad from orientation of apex), greatest breadth near base, apically slightly narrowed, apex narrowly rotundate.

Type material. - Male holotype "ECUADOR, P. Napo, vic. Puerto Misahuallí, 1650-1900 ft., 6-19-IX-1998, J. E. Eger/ $1^{\circ} 2^{\prime} 2.4^{\prime \prime}$ S lat., $77^{\circ} 39^{\prime} 49.2^{\prime \prime}$ W lon." (QCAZ); female allotype, same label as male holotype (QCAZ); male paratypes, same labels as male holotype (CMNC, 3; CWOB, 3; QCAZ, 3); female paratypes, same labels as male holotype (CMNC, 5; CWOB, 5; QCAZ, 5).

Etymology. - Named for the diagnostic apically cordate median lobe in males - cordatus signifying "heartshaped" (Brown 1956).

Distribution. - Cyclanthura cordata has been collected on the Amazonian slope of Ecuador, Napo, Puerto Misahuallí (Fig. 16).

Natural history. - Unknown (but see discussion).

## Cyclanthura dentata Franz, sp. n.

(Figs. 2A \& 9A)
Diagnosis. - Small, (dark) reddish-brown, rostrum fairly narrow, antenna with I of club with slightly darker color, eyes separated by distance similar to breadth of apex of rostrum, male profemur with distinct (although fairly small), apicoventrally directed dens; median lobe in dorsal view with apical $1 / 8$ spatulate, internally with 1 elongate ampullate sclerite basad of basal margin, aedeagal apodemes fairly long; spermatheca basally with 1 small lobulate projection (proximad to orientation of apex), apically (acutely) narrowed; Panama.


Figure 9. (A) Cyclanthura dentata, male and female genitalia; (B) Cyclanthura pilosa, male and female genitalia.

Cyclanthura dentata can be distinguished from most species of the laticola-tenuicola clade (Fig. 17) by the ventrally dentate profemur in males; from Cyc. crepidula by the apically fairly broad median lobe; and from Cyc. dentata by the apically spatulate median lobe, its basally positioned internal ampullate sclerite, the apically acutely narrowed rotundate spermatheca with the basal lobulate projection, and the distribution.

Description. - Male. Small, length 2.1-2.4 mm, width $1.0-1.1 \mathrm{~mm}, 1 / \mathrm{w}=2.1-2.3$, (dark) reddishbrown (antenna + legs with slightly lighter coloration). Rostrum in lateral view fairly long, 0.7-
0.8 mm , similar in length to pronotum, $\mathrm{r} / \mathrm{p}=1.0-$ 1.1, ventrally subrectate; antennal insertion near central region (towards apical 2/5). Antenna with I of club with slightly darker color. Eyes separated by distance similar to breadth of apex of rostrum. Pronotum 1/w $=0.9-1.0$. $\mathrm{F} / \mathrm{p}=1.0-1.1$, profemur ventrally with 1 small, triangular, acute, apicoventrally directed dens near apical $1 / 4 ; \mathrm{t} / \mathrm{f}=0.9-1.0$; mesofemur without apicoventrally directed dens. Elytron $1 / \mathrm{w}=1.4-1.6 \quad(\mathrm{~N}=5)$. Wing/body=1.2-1.3, wing $1 / w=3.0-3.1(N=2)$. Venter with VII slightly longer than $\mathrm{V}+\mathrm{VI}$, posterior margin subrectate. Tergum VIII posteriorly slightly impressed, posterior margin broadly rotundately emarginate.

Spiculum gastrale fairly slender. Median lobe in dorsal view elongate, $1 / \mathrm{w}=4.0-4.5 \quad(\mathrm{~N}=2)$, basal margin centrally distinctly rotundately emarginate, basilateral edges acute, lateral margins slightly sinuate along basal $7 / 8$, apically slightly converging, fairly narrow near subapex, slightly rotundate along apical $1 / 8$, subparallel, apical $1 / 8$ spatulate, apex projected, fairly broad, rotundate; in lateral view deflexed (apex slightly deflexed), fairly broad along basal $3 / 4$, greatest breadth near central region, dorsally gradually narrowed along apical $1 / 4$, dorsally slightly projected near subapex, apex narrowly rotundate (spatulate), slightly angulate; internally with 1 fairly small, elongate, fairly narrow, ampullate, heavily sclerotized sclerite near base (beyond basal margin), apically gradually narrowed (rhomboidal), bifurcate (membranous), nearly $1 / 8$ as long as median lobe +1 fairly small, equilateral to elongate, fairly broad, distinctly irregularly undulate, finely sparsely granulate region (membranous), extending beyond apical orifice, nearly $1 / 6$ as long as median lobe.

Female. Length 2.2-2.4 mm, width $1.0-1.1 \mathrm{~mm}$, $1 / \mathrm{w}=2.1-2.2$. Rostrum 0.8-0.9 mm, slightly longer than pronotum, $\mathrm{r} / \mathrm{p}=1.2$; antennal insertion near central region (towards basal $2 / 5$ ). Pronotum $1 / w=0.9-1.0$. Profemur slightly longer than pronotum, $\mathrm{f} / \mathrm{p}=1.0-1.2$, without apicoventrally directed dens; $\mathrm{t} / \mathrm{f}=0.9$. Elytron $1 / \mathrm{w}=1.4-1.5(\mathrm{~N}=5)$. Venter with VII similar in length to IV +V , posterior margin slightly rotundate, with fairly long, fine setation. Tergum VIII with lateral margins slightly rotundate, posterior margin projected, explanate, subrectate; tergum IX with anterior margin medially slightly emarginate, lateral margins subrectate to slightly rotundate, posterior margin subrectate (medially weakly sclerotized); sternum VIII with furcae narrow, breadth similar throughout, subapically with setation, apex obliquely rotundate (truncate), with 1 fairly short +2 fairly long, fairly narrow setae; styli with 2 short +1 fairly long setae; spermatheca fairly narrow, abruptly deflexed (by nearly $105^{\circ}$ ) near apical $2 / 5$ (J-shaped), basally obliquely subrectate to irregular, with 1 small, lobulate, membranous projection (proximad to orientation of apex), greatest breadth near subbase, apically gradually narrowed, apex acute.
Type material. - Holotype male "PANAMA, Pan. 2700', Cerro Campana, May 23, 1978, CW \& LB O'Brien \& Marshall" (CWOB); female allotype, same label as male holotype (CWOB); male paratypes, same labels as male holotype (CMNC, 2; CWOB, 2), "PANAMA, Cerro Campana, VI-29-1974, C. W. \& L. O’Brien \& Marshall"
(MIUP, 1); female paratypes "PANAMA, Cerro Campana, VII-5-1974, C. W. \& L. O'Brien \& Marshall" (CMNC, 2), "PANAMA, Cerro Campana, VII-6-1974, C. W. \& L. O'Brien \& Marshall" (CWOB, 2), same label as male holotype (MIUP, 1).

Etymology. - Named for the diagnostic profemoral dens in males - dentatus signifying "toothed" (Brown 1956).
Distribution. - Cyclanthura dentata has been collected on the Atlantic slope of Panama, Chiriquí, Fortuna (Continental Divide Trail); on the Pacific slope of Panama, Panamá, Cerro Campana (Fig. 15).

Natural history. - Unknown (but see discussion).

## Cyclanthura pilosa Franz, sp. n.

(Fig. 9B)
Diagnosis. - Small, (dark) reddish-brown, rostrum fairly narrow; male metasternum in posterocentral concave region with dense, posteriorly directed vestiture, median lobe in dorsal view apically distinctly narrowed, in lateral view apically slightly capitate, internally without denticulate region, with 2 small semicircular sclerites; female sternum VIII apically with 1 short +2 long, narrow setae, spermatheca $V$-shaped, apically acutely narrowed, insertion of duct + reservoir basal. Cyclanthura pilosa can be distinguished from all Cyclanthura species by the ventrally densely setose male metasternum; from the species of the laticola-dentata clade (Fig. 17) by the apically distinctly narrowed median lobe; and from Cyc. capitulata and Cyc. tenuicola by the apically slightly capitate median lobe without an internal denticulate region, and the spermatheca.

Derscription. - Male. Small, length 2.1-2.2 mm, width 0.9-1.0 mm, $1 / \mathrm{w}=2.2-2.3$, (dark) reddishbrown (antenna + legs with slightly lighter coloration). Rostrum in lateral view fairly long, 0.7 mm , slightly longer than pronotum, $\mathrm{r} / \mathrm{p}=1.1-1.2$, ventrally subrectate to slightly arcuate, dorsomedian impression indistinct; antennal insertion near apical $2 / 5$ (towards central region). Eyes separated by distance similar to breadth of apex of rostrum. Pronotum $1 / w=1.0$, lateral margins slightly rotundate. Metasternum in posterocentral concave region with dense, posteriorly directed vestiture. Prothoracic leg similar in length to mesothoracic leg; profemur slightly longer than pronotum, $\mathrm{f} / \mathrm{p}=1.1 ; \mathrm{t} / \mathrm{f}=0.9$. Elytron $1 / \mathrm{w}=1.6$. Wing $/ \mathrm{body}=1.2$, wing $1 / w=3.3-3.4(\mathrm{~N}=2)$. Venter with VII similar in
length to IV+V, posterior margin subrectate. Tergum VIII posteriorly slightly impressed, posterior margin broadly shallowly emarginate. Median lobe in dorsal view elongate, $1 / \mathrm{w}=3.8-4.2 \quad(\mathrm{~N}=2)$, basal margin centrally distinctly (triangularly) emarginate, basilateral edges acute, lateral margins subrectate to slightly sinuate, apically slightly converging along basal $3 / 4$, emarginate, distinctly converging along apical $1 / 4$ (cultrate), apex narrow, apically distinctly projected, acute; in lateral view deflexed along basal $3 / 4$, subrectate along apical $1 / 4$, apex slightly reflexed, fairly narrow along basal $3 / 4$, greatest breadth near central region, narrow along apical $1 / 4$ (breadth similar throughout), apex slightly rotundately broadened (capitate), slightly angulate; internally with 2 small, equilateral to elongate, fairly narrow, reflexed, semicircular, apicoventrally rotundately emarginate, weakly sclerotized sclerites, extending along apical orifice, margins finely granulate, nearly $1 / 5$ as long as median lobe.

Female. Length 2.0-2.3 mm, width 0.9-1.0 mm, $1 / \mathrm{w}=2.2-2.4$. Rostrum 0.8 mm , slightly longer than pronotum, $\mathrm{r} / \mathrm{p}=1.2-1.4$; antennal insertion near central region. Pronotum 1/w=0.9-1.0. Metasternum without distinct posterocentral vestiture. $\mathrm{F} / \mathrm{p}=1.1 ; \mathrm{t} / \mathrm{f}=0.9$. Elytron 1/w=1.6-1.7 (N=2). Venter with VII similar in length to IV+V, slightly convex, posterior margin rotundate (projected), with indistinct setation. Tergum VIII with lateral margins slightly rotundate, posterior margin distinctly projected, explanate, subrectate to slightly emarginate; tergum IX with anterior margin medially distinctly emarginate, lateral margins subrectate to slightly rotundate, posterior margin medially broadly emarginate; sternum VIII with furcae narrow, subrectate to slightly arcuate, subapically slightly broadened, with setation, apex obliquely rotundate, with 1 fairly short +2 fairly long, narrow setae; styli with 2 fairly short setae; spermatheca fairly narrow, abruptly deflexed (by nearly $120^{\circ}$ ) near apical $2 / 5$ (V-shaped), basally obliquely rotundate, greatest breadth near base, apically acutely narrowed.
Type material. - Male holotype "Costa Rica, Heredia, La Selva, 40 m, on Anthurium (Araceae), leg. N. Franz, VI-07-1997" (MUCR); female allotype, same label as male holotype (MUCR); male paratype, same label as male holotype (CWOB, 1); female paratype, same label as male holotype (CWOB, 1).

Etymology. - Named for the diagnostic metasternal vestiture in males - pilosus signifying "hairy" (Brown 1956).

Distribution. - Cyclanthura pilosa has been collected on the Atlantic slope of Costa Rica, Heredia, Estación Biológica La Selva (OET) (Fig. 15).

Natural history. - At La Selva, Costa Rica, 5 individuals of Cyc. capitulata have been collected on an inflorescences of Anthurium sp., presumably another species of Anthurium that differs from those on which Cyc. laticola and Cyc. capitulata were observed.

## Cyclanthura capitulata Franz, sp. n.

(Fig. 10A)
Diagnosis. - Small, (dark) reddish-brown, rostrum fairly narrow; median lobe in dorsal view apically distinctly narrowed, in lateral view with apical region subrectate, apically distinctly capitate, internally with 1 subapical denticulate region; female sternum VIII sternum apically with 2-3 short + 3-4 long, broad setae, spermatheca Jshaped, apically (narrowly), insertion of duct + reservoir basilateral. Cyclanthura capitulata can be distinguished from the species of the laticoladentata clade (Fig. 17) by the apically distinctly narrowed median lobe; from Cyc. pilosa by the apically distinctly capitate median lobe with an internal denticulate region, and the spermatheca; and from Cyc. tenuicola by the moderately elongate median lobe which is apically subrectate in lateral view, the comparatively longer aedeagal apodemes, and the apical setation of the female sternum VIII.
Description. - Male. Small, length 1.9-2.3 mm, width $0.9-1.1 \mathrm{~mm}, \mathrm{l} / \mathrm{w}=2.1-2.2$, (dark) reddishbrown (antenna + legs with slightly lighter coloration). Rostrum in lateral view fairly short, 0.60.7 mm , similar in length to pronotum, $\mathrm{r} / \mathrm{p}=0.9-$ 1.0 , ventrally subrectate to slightly arcuate, dorsomedian impression indistinct; antennal insertion near apical $2 / 5$. Eyes separated by distance similar to breadth of apex of rostrum. Pronotum $1 / w=0.9-$ 1.1, convex (apparently positively allometric, globular in large individuals). $\mathrm{F} / \mathrm{p}=0.9-1.0 ; \mathrm{t} / \mathrm{f}=0.9$. Elytron $1 / \mathrm{w}=1.3-1.4 \quad(\mathrm{~N}=5)$. Wing/body=1.1-1.2, wing $1 / \mathrm{w}=2.9-3.1(\mathrm{~N}=2)$. Venter with VII slightly longer than $\mathrm{V}+\mathrm{VI}$, posterior margin subrectate. Tergum VIII posteriorly very slightly impressed, posterior margin broadly shallowly emarginate. Median lobe in dorsal view elongate, $1 / \mathrm{w}=5.1-5.3$ ( $\mathrm{N}=2$ ), basal margin centrally (broadly) emarginate, basilateral edges rotundate, lateral margins


Figure 10. (A) Cyclanthura capitulata, male and female genitalia; (B) Cyclanthura tenuicola, male and female genitalia.
subrectate to slightly emarginate, slightly converging along basal $1 / 3$, subparallel along apical $2 / 3$, gradually converging along apical $1 / 5$, apex narrow, apically slightly projected, acute to rotundate; in lateral view deflexed along basal $1 / 2$, subrectate along apical $1 / 2$, apex slightly reflexed, fairly narrow along basal $3 / 5$, greatest breath near apical $2 / 5$, dorsally gradually narrowed along apical $2 / 5$, subapically distinctly narrowed, apex rotundate, distinctly transversely broadened (capitate to malleate), slightly angulate, internally with 2 fairly large, elongate, fairly narrow, subparallel, sinuate, densely denticulate regions (membranous), ex-
tending beyond apical orifice, nearly $1 / 4$ as long as median lobe; aedeagal apodemes shorter than median lobe.
Female. Length $2.0-2.3 \mathrm{~mm}$, width $1.0-1.1 \mathrm{~mm}$, $1 / \mathrm{w}=2.0-2.2$. Rostrum 0.7 mm , similar in length to pronotum, $\mathrm{r} / \mathrm{p}=0.9-1.0$; antennal insertion near central region (towards apical 2/5). Pronotum $1 / w=1.0-1.1$ (no apparent allometry). $\mathrm{F} / \mathrm{p}=0.9-1.0$; $\mathrm{t} / \mathrm{f}=0.9$. Elytron $1 / \mathrm{w}=1.3-1.5 \quad(\mathrm{~N}=5)$. Venter with VII similar in length to IV +V , posterior margin subrectate to slightly rotundate (projected), with short setation. Tergum VIII with lateral margins sinuate, posterior margin distinctly projected,
explanate, medially broadly emarginate, posterolateral edges triangular; tergum IX with anterior margin medially slightly emarginate, lateral margins subrectate to slightly rotundate, posterior margin medially (broadly) emarginate; sternum VIII with furcae narrow, slightly arcuate, apically gradually broadened, with setation, apex slightly rotundate, with 2-3 fairly short + 3-4 (fairly) long, broad setae; styli with 2 short +1 fairly long setae; spermatheca fairly narrow, abruptly deflexed (by nearly $105^{\circ}$ ) near apical $2 / 5$ (J-shaped), basally obliquely rotundate, insertion of duct + reservoir basilateral (i.e. not at base, proximad to orientation of apex), greatest breadth near base, apically gradually narrowed, apex slightly deflexed, narrow, rotundate.
Type material. - Male holotype "Costa Rica, Heredia, La Selva, 40 m , understory, leg. N. Franz, II-18-1998" (MUCR); female allotype, same label as male holotype (MUCR); male paratypes, same label as male holotype (MUCR, 1), "COSTA RICA, P. Her., Est. Biol. La Selva (OTS), $40 \mathrm{~m}, 11-\mathrm{IV}-1998$, \#4, leg. Nico Franzl on Anthurium sp. (Araceae)" (CWOB, 2); female paratypes, same labels as male holotype (CWOB, 2; MUCR, 2), "COSTA RICA, P. Her., Puerto Viejo de Sarapiqui, Est. Biol. La Selva (OTS), $40 \mathrm{~m}, 16-8-1997 /$ leg. Nico Franz, feeding on pollen, mating on spadix Xanthosoma sp. (Araceae) [misidentification]" (CWOB, 1), "PANAMA, Bocas del Toro, Corriente Grande, Rio Changuinola/ $9^{\circ} 17^{\prime} 30^{\prime \prime} \mathrm{N}, 82^{\circ} 32^{\prime} 41^{\prime \prime}$ W, H. Wolda, Feb. 10, 1980 (CWOB, 1).
Etymology. - Named for the diagnostic apically capitate median lobe in males - capitulatus signifying "ending with small head" (Brown 1956).

Distribution. - Cyclanthura capitulata has been collected on the Atlantic slope of Costa Rica, Heredia, Estación Biológica La Selva (OET); and in Panama, Bocas del Toro, Río Changuinola (Fig. 15).

Natural history. - At La Selva, Costa Rica, 15 individuals of Cyc. capitulata have been collected on two inflorescences of Anthurium sp., presumably another species of Anthurium that differs from those on which Cyc. laticola and Cyc. pilosa were observed.

## Cyclanthura tenuicola Franz, sp. n.

(Fig. 10B)
Diagnosis. - Small, reddish-brown, rostrum fairly narrow; median lobe in dorsal view distinctly elongate, apically distinctly narrowed, in lateral view with apical region slightly reflexed, apically distinctly capitate, internally with 1 subapical den-
ticulate region, aedeagal apodemes distinctly shorter than median lobe; female sternum VIII sternum apically with 2 short +1 long, broad setae, spermatheca J-shaped, apically (narrowly), insertion of duct + reservoir basilateral. Cyclanthura tenuicola can be distinguished from the species of the laticola-dentata clade (Fig. 17) by the apically distinctly narrowed median lobe; from Cyc. pilosa by the apically distinctly capitate median lobe with an internal denticulate region and the spermatheca; and from Cyc. capitulata by the distinctly elongate median lobe which is apically slightly reflexed in lateral view, the comparatively shorter aedeagal apodemes, and the apical setation of the female sternum VIII.

Description. - Male. Small, length 2.0-2.2 mm, width $1.0-1.1 \mathrm{~mm}, 1 / \mathrm{w}=2.0-2.1$, reddish-brown (antenna + legs with slightly lighter coloration). Rostrum in lateral view fairly short, $0.6-0.7 \mathrm{~mm}$, similar in length to pronotum, $\mathrm{r} / \mathrm{p}=0.9-1.0$, ventrally slightly arcuate, dorsomedian impression indistinct; antennal insertion near central region (towards apical 2/5). Eyes separated by distance similar to breadth of apex of rostrum. Pronotum $1 / w=0.9-1.0$, lateral margins slightly rotundate. $\mathrm{F} / \mathrm{p}=0.9-1.1 ; \mathrm{t} / \mathrm{f}=0.9-1.0$. Elytron $1 / \mathrm{w}=1.3-1.4$ $(\mathrm{N}=5)$. Wing/body $=1.2-1.3$, wing $1 / \mathrm{w}=2.6-2.9$ ( $\mathrm{N}=2$ ). Venter with VII slightly longer than V+VI, posterior margin slightly rotundate. Tergum VIII posteriorly not impressed, posterior margin broadly shallowly emarginate. Tegmen nearly $1 / 4$ as long as median lobe; median lobe in dorsal view distinctly elongate, $1 / \mathrm{w}=7.5-7.8(\mathrm{~N}=2)$, basal margin centrally slightly emarginate, basilateral edges rotundate, lateral margins subrectate to slightly sinuate, subparallel to slightly converging along basal $7 / 8$, gradually converging along apical $1 / 8$, apex narrow, apically slightly projected, acute to rotundate; in lateral view deflexed along basal $1 / 2$, slightly reflexed along apical $1 / 2$ (apex slightly reflexed), narrow, dorsal + ventral margins basally + subapically slightly sinuate, dorsally gradually narrowed along apical $1 / 4$, narrow at subapex, apex rotundate, distinctly transversely broadened (capitate to malleate), slightly angulate; internally with 1 fairly large, elongate, fairly broad, densely denticulate region (membranous), extending along apical orifice, nearly $1 / 10$ as long as median lobe; aedeagal apodemes distinctly shorter than median lobe.

Female. Length 2.1-2.4 mm, width 1.0-1.1 mm,
$1 / \mathrm{w}=2.1-2.2$. Rostrum $0.7-0.8 \mathrm{~mm}$, similar in length to pronotum, $\mathrm{r} / \mathrm{p}=1.0-1.1$; antennal insertion near central region (towards apical 2/5). Pronotum $1 / \mathrm{w}=1.0$. $\mathrm{F} / \mathrm{p}=0.9-1.1 ; \mathrm{t} / \mathrm{f}=0.8-0.9$. Elytron $1 / \mathrm{w}=1.4-1.5(\mathrm{~N}=5)$. Venter with VII similar in length to $\mathrm{V}+\mathrm{VI}$, posterior margin subrectate, with indistinct setation. Tergum VIII with lateral margins sinuate, posterior margin distinctly projected, explanate, medially (broadly to deeply) emarginate, posterolateral edges triangular; tergum IX with anterior margin medially slightly emarginate, lateral margins slightly rotundate, posterior margin medially (narrowly) emarginate; sternum VIII with furcae narrow, slightly arcuate (breadth similar throughout), subapically with setation, apex slightly rotundate, with 2 fairly short + 1 (very) long, (very) broad setae; styli with 2 short +1 fairly long setae; spermatheca fairly narrow, abruptly deflexed (by nearly $105^{\circ}$ ) near apical 2/5 (L-shaped), basally obliquely rotundate, narrow, insertion of duct + reservoir basilateral (i.e. not at base, proximad to orientation of apex), greatest breadth near basal $1 / 3$, apically gradually narrowed, apex slightly deflexed, narrow, rotundate.

Type material. - Male holotype "C. R.: Puntarenas: P. N. Corcovado, 10-20.VIII.1980, on Anthurium fl., D. R. Whitehead" (NMNH); female allotype, same label as male holotype (NMNH); male paratypes, same labels as male holotype (NMNH, 3); female paratypes, same labels as male holotype (NMNH, 3).

Etymology. - Named for the diagnostic distinctly elongate median lobe in males - tenuis signifying "thin" and colis signifying "tail" (Brown 1956).

Distribution. - Cyclanthura tenuicola has been collected on the Pacific slope of Costa Rica, Puntarenas, Parque Nacional Corcovado (Fig. 15).

Natural history. - At Parque Nacional Corcovado, Costa Rica, 10 individuals of Cyc. tenuicola have been collected on an inflorescences of Anthurium sp.

## Cyclanthura carinata Franz, sp. n.

(Figs. 2B \& 11A)
Diagnosis. - Fairly small, slightly depressed, (dark) reddish-brown, rostrum fairly narrow, eyes separated by distance slightly greater than breadth of apex of rostrum, elytron with 2 distinct elongate tumescences; median lobe in lateral view with distinct ventral carina, apically slightly reflexed; female tergum IX with posterior margin medially
(distinctly) emarginate, sternum VIII apically with 10-12 long, broad setae, spermatheca U-shaped. Cyclanthura carinata can be distinguished from all Cyclanthura species by the 2 elytral tumescences (Cyc. striata has 3 elytral tumescences). Several other characteristics - e.g. as the ventrally carinate median lobe or the apically densely setose female sternum VIII - are diagnostic as well. There is considerable color variation among the specimens, ranging from light (yellowish-) brown in teneral individuals to the characteristic dark color in fully pigmented individuals.

Description. - Male. Fairly small, length 2.5-3.3 mm , width $1.1-1.5 \mathrm{~mm}, 1 / \mathrm{w}=2.1-2.2$, slightly depressed, (dark) reddish-brown (pronotum with slightly darker coloration). Rostrum in lateral view fairly long, $0.8-1.1 \mathrm{~mm}$, similar in length to pronotum, $\mathrm{r} / \mathrm{p}=1.0-1.1$, ventrally subrectate, dorsomedian impression indistinct; antennal insertion near central region (towards apical $2 / 5$ in small individuals). Antenna with scape reddish-brown, funicle + club brown. Eyes separated by distance slightly greater than breadth of apex of rostrum. Pronotum $1 / \mathrm{w}=0.9-1.0$ (apparently positively allometric). $\mathrm{F} / \mathrm{p}=0.9-1.1 ; \mathrm{t} / \mathrm{f}=0.9-1.0$. Elytron $1 / \mathrm{w}=1.4-1.5$ ( $\mathrm{N}=10$ ), with 2 distinct, elongate, convex, carinate tumescences (apparently positively allometric): (1) along anterior $1 / 6$ of II-III, (2) along central region of IV-V. Wing/body=1.2, wing $1 / w=3.1$ ( $\mathrm{N}=2$ ). Venter with VII similar in length to III, posterior margin subrectate. Tergum VIII posteriorly very slightly impressed, posterior margin broadly shallowly emarginate, medially narrowly emarginate. Spiculum gastrale fairly slender. Median lobe in dorsal view elongate, $1 / \mathrm{w}=4.6-5.0(\mathrm{~N}=2)$, basal margin centrally distinctly rotundately emarginate, basilateral edges acute (triangular), lateral margins subrectate to slightly sinuate, apically gradually converging along basal $3 / 4$, slightly emarginate, distinctly converging along apical $1 / 4$ (cultrate), apex narrow, apically distinctly projected, acute; in lateral view deflexed along basal 3/4, subrectate to slightly reflexed along apical $1 / 4$ (apex slightly reflexed); fairly narrow along basal $3 / 4$, greatest breadth near central region, ventrally with distinct, carinate, median elevation, extending along central region, dorsally gradually narrowed along apical $1 / 5$, narrow along subapex (breadth similar throughout), apex slightly broadened, dorsally slightly projected, rotundate; internally with 1 fairly large, elongate, fairly broad,


Figure 11. (A) Cyclanthura carinata, male and female genitalia; (B) Cyclanthura uncinata, male and female genitalia.
sparsely finely denticulate region (membranous) near basal $1 / 3$, nearly $1 / 4$ as long as median lobe.

Female. Length 2.7-3.2 mm, width 1.3-1.5 mm, $1 / \mathrm{w}=2.1-2.2$. Rostrum $0.8-1.0 \mathrm{~mm}$, similar in length to pronotum, $\mathrm{r} / \mathrm{p}=1.0-1.1$; antennal insertion near central region. Pronotum $1 / w=0.9-1.2$ (no apparent allometry). $\mathrm{F} / \mathrm{p}=0.9-1.1$; $\mathrm{t} / \mathrm{f}=0.9-1.0$. Elytron $1 / \mathrm{w}=1.4-1.6(\mathrm{~N}=10)$. Venter with VII similar in length to III +IV , triangular, convex, lateral margins posteriorly distinctly converging, posterior margin distinctly narrowly projected, explanate, rotundate, with short setation. Tergum VIII with lateral margins slightly sinuate, posterior margin
projected, explanate, rotundate; tergum IX with anterior margin distinctly emarginate (throughout entire structure), lateral margins slightly sinuate, posterior margin medially (distinctly) emarginate; sternum VIII with furcae subbasally slightly broadened, apically with breadth similar throughout, subapically with setation, apex obliquely truncate, with 10-12 fairly long, broad setae; styli with 2 fairly short setae; spermatheca fairly narrow, abruptly deflexed (by nearly $150^{\circ}$ ) near central region (U-shaped), basally subrectate, greatest breadth near base, apically gradually narrowed, apex slightly projected, rotundate.

Type material. - Male holotype "COSTA RICA: Punt., Las Cruces Biol. Sta., San Vito, Coto Brus, 1000 m, L. D. Gómez, VII.1996, on flowers Anthurium formosum" (CMNC); female allotype, same label as male holotype (CMNC); male paratypes, same labels as male holotype (CMNC, 10; CWOB, 5; MUCR, 3), "COSTA RICA: Puntarenas, Est. Biol. Las Cruces, 4 km S San Vito, 1150 $\mathrm{m}, 08^{\circ} 47^{\prime} 03^{\prime \prime} \mathrm{N}, 82^{\circ} 57^{\prime} 36^{\prime \prime} \mathrm{W}, 9 . V I I .1999$, R. Anderson, on flowers Anthurium sp., 99-124" (MIUP, 2; MUCR, 2), "COSTA RICA: Puntarenas, Est. Biol. Las Cruces, 4 km S San Vito, $1150 \mathrm{~m}, 08^{\circ} 47^{\prime} 03^{\prime \prime} \mathrm{N}$, 82 $57 ’ 36^{\prime \prime}$ W, VII.1997, L. D. Gomez, on flowers Anthurium formosum \# 971337" (MIUP, 3); male paratypes, same labels as male holotype (CMNC, 10; CWOB; 5, MIUP, 5; MUCR, 5).

Etymology. - Named for the diagnostic elytral tumescences - carinatus signifying "keeled" (Brown 1956).

Distribution. - Cyclanthura carinata has been collected in the Cordillera de Talamanca of Costa Rica, Puntarenas, Estación Biológica Las Cruces (OET); and on the Atlantic slope of Panama, Chiriquí, Fortuna (Fig. 15).

Natural history. - At Las Cruces, Costa Rica, over 50 individuals have been collected on the inflorescences of Anthurium formosum Schott. At Fortuna, Panama, Cyc. carinata has been collected at UV light traps.

## Cyclanthura uncinata Franz, sp. n.

(Fig. 11B)
Diagnosis. - (Fairly) small, dark reddish-brown, rostrum fairly narrow, antenna with I of club darker, II + III of club lighter, eyes separated by distance slightly greater than breadth of apex of rostrum; median lobe in lateral view apically distinctly deflexed, internally with subapical dentes region, aedeagal apodemes similar in length to median lobe; female sternum VIII with narrow, arcuate furcae, apically with 2 short +2 fairly long setae, spermatheca broad, L-shaped, apically acuminate. Cyclanthura laticola can be distinguished from the species of the laticola-tenuicola clade (Fig. 17) by the broadly separated eyes; from Cyc. carinata by the indistinct elytron; and in general by the diagnostic median lobe, female sternum VIII, and spermatheca.

Description. - Male. (Fairly) small, length 2.2-2.5 mm , width $1.0-1.1 \mathrm{~mm}, \mathrm{l} / \mathrm{w}=2.3-2.4$, dark reddishbrown (to black; tarsus, venter, pygidium reddishbrown). Rostrum in lateral view fairly long, 0.70.9 mm , slightly longer than pronotum, $\mathrm{r} / \mathrm{p}=1.1$,
dorsomedian impression indistinct, basal $2 / 3$ rugulose, apically with lighter coloration; antennal insertion near apical $1 / 3$. Antenna with scape red-dish-brown, funicle + I of club dark brown, II+III of club with lighter coloration. Eyes separated by distance slightly greater than breadth of apex of rostrum. Pronotum $1 / \mathrm{w}=1.1$. Prothoracic leg similar in length to mesothoracic leg; $\mathrm{f} / \mathrm{p}=0.9-1.0$; $\mathrm{t} / \mathrm{f}=0.9$. Elytron $1 / \mathrm{w}=1.6(\mathrm{~N}=2)$. Venter with VII similar in length to IV+V, posterior margin slightly rotundate. Tergum VIII posteriorly very slightly impressed, posterior margin broadly shallowly emarginate. Median lobe in dorsal view slightly elongate, $1 / \mathrm{w}=3.3-3.5(\mathrm{~N}=2)$, basal margin centrally rotundately emarginate, basilateral edges rotundate, lateral margins slightly emarginate along basal $3 / 4$, apically slightly converging, gradually to distinctly converging along apical $1 / 4$, apex narrow, projected, acuminate; in lateral view slightly deflexed along basal $2 / 3$, distinctly deflexed along apical $1 / 3$ (i.e. base + apex at an angle of $>90^{\circ}$ ), fairly narrow along basal $3 / 5$, greatest breadth near apical $1 / 3$, dorsally gradually narrowed along apical $1 / 4$, narrow at subapex, apex oblique to rotundate, slightly transversely projected, ventral margin acute, internally with 1 fairly small, equilateral to elongate, fairly broad, densely dentate region (membranous), dentes apicodorsally directed, extending along (distinctly inflected) apical orifice, nearly $1 / 6$ as long as median lobe; aedeagal apodemes similar in length to median lobe.

Female. Length 2.3-2.4 mm, width 0.9-1.0 mm, $1 / \mathrm{w}=2.3-2.4$. Rostrum 0.9 mm , slightly longer than pronotum, $\mathrm{r} / \mathrm{p}=1.3$; antennal insertion near apical $2 / 5$. Pronotum $1 / \mathrm{w}=1.0$. $\mathrm{F} / \mathrm{p}=1.0-1.1 ; \mathrm{t} / \mathrm{f}=0.9$. Elytron $1 / w=1.6-1.7(\mathrm{~N}=2)$. Venter with VII slightly longer than $\mathrm{V}+\mathrm{VI}$, posterior margin slightly rotundate, with indistinct setation. Tergum VIII with lateral margins slightly sinuate, posterior margin slightly projected, explanate, slightly rotundate; tergum IX with anterior margin medially distinctly emarginate (throughout entire structure), lateral margins slightly rotundate, posterior margin slightly rotundate (medially weakly sclerotized); sternum VIII with furcae (very) narrow, arcuate, apically slightly broadened, subapically with setation, apex broadly rotundate, with 2 short +2 fairly long setae; styli with 2 fairly short setae; spermatheca broad, abruptly deflexed (by nearly $90^{\circ}$ ) near central region (L-shaped), basally subrectate, breadth similar throughout, apex distinctly narrowed, acuminate.

Type material. - Male holotype "Costa Rica, Alajuela, Reserva Bosque Nuboso St. Elena, 1700 m, on Anthurium sp., leg. N. Franz, VI-14-2001" (MUCR); female allotype, same label as male holotype (MUCR); male paratype, same label as male holotype (CWOB, 1); female paratype, same label as male holotype (CWOB, 1).
Etymology. - Named for the diagnostic apically deflexed median lobe in males - uncinatus signifying "hooked" (Brown 1956).

Distribution. - Cyclanthura uncinata has been collected in the Cordillera de Tilarán of Costa Rica, Alajuela, Reserva Bosque Nuboso St. Elena (Fig. 15).

Natural history. - At Reserva Bosque Nuboso St. Elena, Costa Rica, several individuals of Cyc. uncinata have been collected on an inflorescence of Anthurium sp.

## Cyclanthura oculata Franz, sp. n.

(Figs. 2C \& 12A)
Diagnosis. - (Fairly) small, (light) reddish-brown, eyes large, distinctly protruded, separated by distance similar to breadth of club, pronotum subanteriorly with 2 small impressions; median lobe in dorsal view apically cultrate, in lateral view apically similar throughout (ventrally slightly projected), internally with 2 denticulate regions; female sternum VIII apically obliquely truncate, with 3 short, narrow setae, spermatheca apically broadly rotundate; Ecuador. Cyclanthura oculata can be distinguished from all Cyclanthura species by the large, distinctly protruded eyes. Several other characteristics - e.g. the comparatively light coloration, the small pronotal impressions, and the female sternum VIII - are diagnostic as well.

Description. - Male. (Fairly) small, length 2.2-2.4 mm , width $1.0-1.1 \mathrm{~mm}, 1 / \mathrm{w}=2.0-2.2$, (light) red-dish-brown (head + pronotum with slightly darker coloration; rostrum dark reddish-brown, light at apex), splendens, glabrate. Labial palpomere II without distinct apicolateral projection. Rostrum in lateral view fairly long, $0.7-0.8 \mathrm{~mm}$, slightly longer than pronotum, $\mathrm{r} / \mathrm{p}=1.0-1.3$, ventrally subrectate to slightly arcuate, dorsomedian impression indistinct, basally not rugulose; antennal insertion near central region (towards apical 2/5). Antenna extending beyond posterior margin of eye, light reddish-brown. Eyes large, distinctly protruded, distant from anterior margin of pronotum by nearly $1 / 3$ diameter of eye, separated by
distance similar to breadth of club (smaller than breadth of apex of rostrum). Head with frontal impression indistinct. Pronotum 1/w=0.8-1.0, anterior margin nearly as broad as posterior margin, lateral margins slightly rotundate, subanteriorly with 2 fairly small, shallow, subcircular, subcontiguous impressions. Prosternum with procoxal cavities inserted near central region. Prothoracic leg similar in length to mesothoracic leg; profemur slightly longer than pronotum, $\mathrm{f} / \mathrm{p}=1.0-1.2$; $\mathrm{t} / \mathrm{f}=0.9-1.0$. Elytron $1 / \mathrm{w}=1.4-1.6(\mathrm{~N}=5)$, with anterior impression slight to indistinct. Wing/body $=1 \cdot 2-1 \cdot 3$, wing $1 / w=3 \cdot 2-3 \cdot 4(\mathrm{~N}=2)$. Venter with VII slightly longer than V+VI, posterior margin subrectate. Tergum VIII posteriorly very slightly impressed, posterior margin broadly shallowly emarginate, medially narrowly emarginate. Median lobe in dorsal view elongate, $1 / w=3.8-4.0$ ( $\mathrm{N}=2$ ), basal margin centrally triangularly emarginate, basilateral edges acute to rotundate, lateral margins subrectate to slightly emarginate, subparallel to slightly converging along basal $4 / 5$, abruptly converging near apical $1 / 5$, narrow, cultrate along apical $1 / 5$, apex distinctly narrowly projected, acute; in lateral view sinuate: (distinctly) deflexed along basal 3/4, (slightly) reflexed along apical $1 / 4$ (apex slightly reflexed), fairly narrow along basal $2 / 3$, dorsally gradually narrowed along apical $1 / 3$, apical $1 / 5$ narrow, cultrate, breadth similar throughout, apex fairly narrow, obliquely rotundate (ventrally slightly projected, carinate); internally with 1 fairly large, elongate, fairly broad, very densely denticulate region (membranous), apically slightly broadened, extending beyond apical orifice, nearly $1 / 5$ as long as median lobe +1 fairly small, equilateral, fairly broad, moderately densely denticulate region near central region (both regions connected by membranes), nearly $1 / 8$ as long as median lobe; aedeagal apodemes similar in length to median lobe.

Female. Length 2.3-2.6 mm, width 1.1-1.2 mm, $1 / \mathrm{w}=2.0-2.2$. Rostrum 0.8 mm , slightly longer than pronotum, $\mathrm{r} / \mathrm{p}=1.0-1.3$; antennal insertion near central region (towards basal 2/5). Pronotum $1 / w=0.8-1.0$. Profemur similar in length to slightly longer than pronotum, $\mathrm{f} / \mathrm{p}=0.9-1.2 ; \mathrm{t} / \mathrm{f}=0.9-1.0$. Elytron $1 / \mathrm{w}=1.5-1.6(\mathrm{~N}=5)$. Venter with VII similar in length to IV +V , posterior margin subrectate (projected), with short setation. Tergum VIII with lateral margins slightly sinuate, posterior margin projected, explanate, subrectate to slightly rotundate; tergum IX with anterior margin medially dis-


Figure 12. (A) Cyclanthura oculata, male and female genitalia; (B) Cyclanthura cultrata, male and female genitalia.
tinctly emarginate (throughout entire structure), lateral margins subrectate to slightly rotundate, posterior margin medially (slightly) emarginate; sternum VIII with furcae narrow, breadth similar throughout, subapically with setation, apex slightly broadened, oblique, rotundate to truncate, with 3 fairly short, fairly narrow setae; styli with 3 short +1 fairly long setae; spermatheca fairly broad, abruptly deflexed (by nearly $135^{\circ}$ ) near central region (V-shaped), basally subrectate, breadth similar throughout, apex broadly rotundate.

Type material. - Male holotype "ECUADOR: Napo, Limoncocha, 6 June 1977, W. E. Steiner" (NMNH); female allotype, same label as male holotype (NMNH); male paratypes, same labels as male holotype (NMNH, 3); female paratypes, same labels as male holotype (NMNH, 3).
Etymology. - Named for the diagnostic large eyes - oculatus signifying "eyed" (Brown 1956).

Distribution. - Cyclanthura oculata has been collected in the Amazonian lowland of Ecuador, Napo, Limoncocha (Fig. 16).
Natural history. - Unknown (but see discussion).

## Cyclanthura cultrata Franz, sp. n.

(Fig. 12B)
Diagnosis. - Small, reddish-brown, rostrum dorsally and ventrally arcuate, fairly broad, antenna with I of with slightly darker color, pronotum centrally slightly concave; median lobe in dorsal view apically cultrate, in lateral view apicoventrally distinctly carinately projected, apically acutely reflexed, internally with 2 denticulate regions (basal region contiguous); female sternum VIII with inner margin subapically (distinctly) triangularly broadened, styli with 2 long setae, spermatheca Cshaped; Venezuela. Cyclanthura cultrata can be distinguished from the species of the laticolauncinata clade (Fig. 17) by the fairly broad rostrum and cultrate median lobe; from the species of the bipartita-palmata clade (Fig. 17) by, e.g., the small size, the pronotal concavity, and the apical region of the median lobe; from Cyc. oculata by the small eyes; and from Cyc. striata by the indistinct elytra. There is considerable color variation among the specimens, ranging from light (yellow-ish-) brown in teneral individuals to the characteristic darker color in fully pigmented individuals.

Description. - Male. Small, length 1.8-2.1 mm, width $0.9-1.0 \mathrm{~mm}, 1 / \mathrm{w}=2.0-2.1$, reddish-brown. Labial palpomere II without distinct apicolateral projection. Rostrum in lateral view fairly short, 0.6 mm , similar in length to pronotum, $\mathrm{r} / \mathrm{p}=0.9-1.0$,; antennal insertion near apical $2 / 5$. Antenna with I of club dark brown. Eyes separated by distance similar to breadth of apex of rostrum. Pronotum $1 / \mathrm{w}=1.0-1.1$, centrally slightly concave, lateral margins slightly rotundate. Profemur slightly shorter than pronotum, $\mathrm{f} / \mathrm{p}=0.9$; $\mathrm{t} / \mathrm{f}=0.9$. Elytron $1 / w=1.4(\mathrm{~N}=2)$. Venter with VII slightly longer than IV+V, posterior margin subrectate. Tergum VIII posteriorly very slightly impressed, posterior margin broadly shallowly emarginate, medially narrowly emarginate. Median lobe in dorsal view elongate, $1 / \mathrm{w}=4.2-4.4(\mathrm{~N}=2)$, basal margin centrally distinctly triangularly emarginate, basilateral edges acute, lateral margins subrectate to slightly sinuate along basal $3 / 4$, apically slightly converging, abruptly converging near apical $1 / 4$, very narrow, cultrate along apical $1 / 3$, apex distinctly narrowly projected, acute; in lateral view sinuate: (distinctly) deflexed along basal 3/4, (slightly) reflexed along apical $1 / 4$ (apex distinctly reflexed), fairly narrow along basal $3 / 4$, narrow
along apical $1 / 4$, apical $1 / 8$ cultrate: ventrally distinctly carinately projected (dorsally slightly broadened), apically gradually narrowed, slightly arcuate/reflexed, apex narrow, acute; internally with 1 fairly large, elongate, fairly broad, moderately densely denticulate region (membranous), extending beyond apical orifice, $1 / 6$ as long as median lobe +1 slightly smaller, less densely denticulate region near central region (both regions connected by membranes); aedeagal apodemes shorter than median lobe.
Female. Length $2.0-2.1 \mathrm{~mm}$, width $1.0-1.1 \mathrm{~mm}$, $1 / \mathrm{w}=1.9-2.0$, slightly depressed. Rostrum 0.7 mm , slightly longer than pronotum, $\mathrm{r} / \mathrm{p}=1.1$, dorsomedian impression present, basally slightly rugulose; antennal insertion near central region (towards apical $2 / 5$ ). Pronotum $1 / w=0.9-1.0$, centrally slightly convex. $\mathrm{F} / \mathrm{p}=0.9-1.0 ; \mathrm{t} / \mathrm{f}=0.9$. Elytron $\mathrm{l} / \mathrm{w}=1.3-1.4(\mathrm{~N}=2)$. Venter with VII slightly longer than IV+V, posterior margin subrectate (projected), with indistinct setation. Tergum VIII with lateral margins slightly rotundate, posterior margin distinctly projected, explanate, slightly rotundate; tergum IX with anterior margin medially distinctly emarginate (throughout entire structure), lateral margins slightly rotundate, posterior margin subrectate to slightly emarginate (medially weakly sclerotized); sternum VIII with furcae narrow along basal $1 / 2$, inner margin subapically distinctly triangularly broadened, subapically with setation, apex rotundate, with 2 (fairly) short +3 (fairly to very) long, fairly broad setae; styli with 2 fairly long setae; spermatheca fairly narrow, abruptly deflexed (by nearly $120^{\circ}$ ) near apical $2 / 5$ (Cshaped), basally subrectate, greatest breadth near base, apically gradually narrowed, apex slightly projected, slightly deflexed, narrowly rotundate.
Type material. - Male holotype "VENEZUELA, Aragua, P. N. Rancho Grande, La Cumbre, 1500 m, C. Bordon, 20.III.1987" (CWOB); female allotype "VENEZUELA: Aragua, Rancho Grande, 11 June 1983, Clark \& Clark" (CWOB).
Etymology. - Named for the diagnostic apically cultrate median lobe in males - cultratus signifying "knifelike" (Brown 1956).
Distribution. - Cyclanthura cultrata has been collected in Venezuela, Aragua, Estación Biológica Rancho Grande (UCV) (Fig. 16).
Natural history. - At Rancho Grande, Venezuela, Cyc. cultrata has been collected in flight intercept traps. The host plant association is unknown (but see discussion).


Figure 13. (A) Cyclanthura striata, male and female genitalia; (B) Cyclanthura bipartita, male and female genitalia.

## Cyclanthura striata Franz, sp. n.

(Figs. 3A \& 13A)
Diagnosis. - Small, slightly depressed, brown (but see below), rostrum dorsally and ventrally arcuate, fairly broad, antenna with I of with slightly darker color, pronotum centrally (slightly) concave, elytron with 3 distinct elongate tumescences; male pygidium with posterior margin medially deeply narrowly emarginate, median lobe in dorsal view apically cultrate, in lateral view apicoventrally distinctly carinately projected, apically rotundately reflexed, internally with 2 denticulate regions
(basal region separated, connected by membranes); female sternum VIII with inner margin subapically triangularly broadened, styli with 1 long seta, spermatheca U-shaped. Cyclanthura striata can be distinguished from all Cyclanthura species by the 3 elytral tumescences (Cyc. carina$t a$ has 2 elytral tumescences). There is considerable color variation among the specimens, ranging from light (greenish-) brown in teneral individuals to the characteristic darker color in fully pigmented individuals.

Description. - Male. Small, length 1.9-2.3 mm,
width $1.0-1.1 \mathrm{~mm}, 1 / \mathrm{w}=1.9-2.1$, slightly depressed, (light greenish- to dark reddish-) brown (rostrum, head, legs with slightly lighter coloration). Labial palpomere II without distinct apicolateral projection. Rostrum in lateral view fairly short, 0.7 mm , similar in length to pronotum, $\mathrm{r} / \mathrm{p}=0.9-1.1$, dorsally and ventrally arcuate, in dorsal view fairly broad, dorsomedian impression indistinct; antennal insertion near apical $2 / 5$ (towards apical $1 / 3$ ). Antenna with I of club with slightly darker color. Eyes separated by distance similar to breadth of apex of rostrum. Pronotum $1 / \mathrm{w}=1.0$, slightly concave, centrally with 1 large, shallow impression, laterally slightly elevated. Prothoracic leg similar in length to mesothoracic leg; $\mathrm{f} / \mathrm{p}=0.9-1.0 ; \mathrm{t} / \mathrm{f}=0.9-$ 1.0. Elytron $1 / w=1.3-1.4(\mathrm{~N}=8)$, with 3 distinct, elongate, convex, carinate tumescences (apparently positively allometric, with considerable individual variation): (1) near posterior $1 / 3$ of II-III, (2) near anterior $1 / 3$ of VI-VII, (3) near anterior $1 / 3$ of VIII-IX. Wing/body=1.4-1.5, wing $1 / w=3.2-3.3$ ( $\mathrm{N}=2$ ). Venter with VII slightly longer than IV+V, posterior margin subrectate. Tergum VIII posteriorly slightly impressed, posterior margin distinctly narrowly emarginate. Spiculum gastrale fairly slender. Median lobe in dorsal view elongate, $1 / \mathrm{w}=4.6-5.0(\mathrm{~N}=2)$, basal margin centrally distinctly (triangularly) emarginate, basilateral edges acute, lateral margins subrectate to slightly emarginate along basal $4 / 5$, subparallel to slightly converging, abruptly converging near apical $1 / 5$, very narrow, cultrate along apical $1 / 5$, apex distinctly narrowly projected, acute; in lateral view sinuate: (distinctly) deflexed along basal 3/4, reflexed along apical $1 / 4$ (apex slightly reflexed), fairly narrow along basal $2 / 3$, dorsally slightly narrowed along apical $1 / 3$, apical $1 / 6$ ventrally distinctly carinately projected, cultrate, margin slightly rotundate, apex fairly narrow, rotundate, dorsally slightly projected, rotundate; internally with 1 fairly large, elongate, fairly broad, very densely denticulate region (membranous), extending beyond apical orifice, nearly $1 / 5$ as long as median lobe +2 small, elongate, narrow, subparallel, moderately densely denticulate region (membranous, lateral), near central region (all regions connected by membranes), nearly $1 / 10$ as long as median lobe.

Female. Length 2.0-2.4 mm, width 1.0-1.2 mm, $1 / \mathrm{w}=1.9-2.1$. Rostrum $0.7-0.8 \mathrm{~mm}$, similar in length to slightly longer than pronotum, $\mathrm{r} / \mathrm{p}=0.9$ 1.2; antennal insertion near apical $2 / 5$. Pronotum $1 / \mathrm{w}=0.9-1.0$ (no apparent allometry). $\mathrm{F} / \mathrm{p}=0.8-1.1$;
$\mathrm{t} / \mathrm{f}=0.9$. Elytron $1 / \mathrm{w}=1.3-1.4(\mathrm{~N}=8)$. Venter with VII similar in length to slightly longer than IV+V, posterior margin narrow, slightly rotundate (projected), with short setation. Tergum VIII with lateral margins subrectate to slightly rotundate, posterior margin distinctly projected, explanate, rotundate; tergum IX with anterior margin medially distinctly emarginate (throughout entire structure), lateral margins slightly rotundate, posterior margin subrectate to slightly emarginate (medially weakly sclerotized); sternum VIII with furcae narrow, inner margin subapically triangularly broadened, subapically with setation, apex (narrowly) rotundate, with 1 fairly short + 3 long, fairly broad setae; styli with 1 fairly long seta; spermatheca fairly narrow, abruptly deflexed (by nearly $150^{\circ}$ ) near apical $2 / 5$ (U-shaped), basally (obliquely) subrectate, greatest breadth near base, apically slightly narrowed, apex slightly projected, slightly deflexed, narrowly rotundate.

Type material. - Male holotype "COSTA RICA: PUNT., Monteverde, 1520 m, 30.IV.1986, J. S. Ashe \& R. M. Timm, sifted forest litter" (CWOB); female allotype, same label as male holotype (CWOB); male paratypes "COSTA RICA: Puntarenas, Monte Verde, 1520-1570 m, 11 May 1989, J. Ashe, R. Brooks, R. Leschen, ex. pitfall trap/ Snow Entomol. Mus. Costa Rica Exp. \#. 117" (CMNC, 1), "COSTA RICA: Puntarenas, Monte Verde, 1550 m, 23 May 1989, J. Ashe, R. Brooks, R. Leschen, ex. flight intercept trap/ Snow Entomol. Mus. Costa Rica Exp. \#. 435" (CMNC, 1), same label as male holotype (CWOB, 1), "COSTA RICA, Punt., R. F. Golfo Dulce, 5 k. W Piedras Blancas, VII-1992, 100 m , malaise trap, P. Hanson" (MUCR, 2); female paratypes "PANAMA: Chiriqui, Hartmann's Finca, 27.7 km W Volcan, 17.18.VI.1996, 1600 m, J. Ashe \& R. Brooks, FIT, \# 180" (CMNC, 2), same label as male holotype (CWOB, 1), "COSTA RICA, Punt., Monteverde, 1500 m, 23.V.1979, H. \& A. Howden" (MUCR, 1), "COSTA RICA, Punt., Monteverde Reserve, 1500 m, 24.V.1979, H. \& A. Howden" (MUCR, 1).

Etymology. - Named for the diagnostic elytral tumescences - striatus signifying "furrowed" (Brown 1956).

Distribution. - Cyclanthura striata has been collected in Costa Rica, (1) Alajuela, Cordillera de Tilarán, Monteverde, (2) Puntarenas, Cordillera de Talamanca, Coto Brus, Estación Biológica Las Alturas, and (3) Puntarenas, Reserva Forestal Golfo Dulce (Piedras Blancas); and on the Atlantic slope of Panama, Chiriquí, (1) Alto Lino (Boquete), (2) Bambito (Volcán), (3) Cerro Punta (Audubon), (4) Finca Hartmann (Volcán), and (5) Fortuna (Fig. 15).

Natural history. - At various locations, several
individuals of Cyc. striata have been collected in flight intercept traps, Malaise traps, pitfall traps, sifted forest litter, and at UV light traps (for details see type information). The host plant association is unknown (but see discussion).

## Cyclanthura bipartita Franz, sp. n.

(Figs. 3B \& 13B)
Diagnosis. - Fairly large, (light) reddish-brown, rostrum fairly broad, eyes separated by distance slightly smaller than breadth of apex of rostrum, elytron with anterior impression indistinct (but not absent); median lobe in dorsal view apically cultrate, in lateral view apically similar throughout (ventrally slightly projected), internally with 1 finely granulate region; female tergum IX with posterior margin medially distinctly emarginate, sternum VIII O-shaped, spermatheca basally with 1 small lobulate projection (proximad to orientation of apex); association with Cyclanthus (Cyclanthaceae). Cyclanthura bipartita can be distinguished from the species of the laticola-uncinata clade by the fairly broad rostrum and comparatively lighter coloration; from the species of the ocu-lata-striata clade by the fairly large size; and from Cyc. crepidula and Cyc. palmata by the narrowly separated eyes, the female sternum VIII, and the host plant association.
Description. - Male. Fairly large, length 3.1-4.1 mm , width $1.4-1.8 \mathrm{~mm}, 1 / \mathrm{w}=2.2-2.3$, (light) red-dish-brown. Rostrum in lateral view fairly short, $0.8-1.1 \mathrm{~mm}$, slightly shorter than pronotum, $\mathrm{r} / \mathrm{p}=0.8-0.9$, in dorsal view fairly broad, basally not rugulose; antennal insertion near apical $2 / 5$. Eyes separated by distance slightly smaller than breadth of apex of rostrum. Head with frontal impression indistinct. Pronotum $1 / \mathrm{w}=0 .-1.0$, lateral margins slightly rotundate. Prothoracic leg similar in length to mesothoracic leg; profemur slightly shorter than pronotum, $\mathrm{f} / \mathrm{p}=0.8-0.9 ; \mathrm{t} / \mathrm{f}=0.9-1.0$. Elytron $1 / \mathrm{w}=1.5-1.6(\mathrm{~N}=10)$, with anterior impression slight to indistinct. Wing/body=1.1-1.2, wing $1 / w=3.1-3.2 \quad(\mathrm{~N}=2)$. Venter with VII similar in length to IV+V, posterior margin subrectate. Tergum VIII posteriorly very slightly impressed, posterior margin broadly shallowly emarginate, medially narrowly emarginate. Median lobe in dorsal view elongate, $1 / \mathrm{w}=4.8-5.0 \quad(\mathrm{~N}=2)$, basal margin centrally triangularly emarginate, basilateral edges rotundate, lateral margins subrectate, broadly heavily sclerotized, subparallel along
basal $2 / 3$, abruptly converging near apical $1 / 3$, narrow, cultrate along apical $1 / 3$, apex distinctly narrowly projected, acute; in lateral view slightly sinuate: deflexed along basal $2 / 3$, slightly reflexed along apical $1 / 3$ (apex slightly reflexed), fairly narrow along basal $2 / 3$, dorsally gradually narrowed along apical $1 / 3$, apex narrow, slightly obliquely rotundate (dorsally slightly projected); internally with 1 fairly large, elongate, fairly broad, plicate (irregular), densely finely granulate region (membranous), apically slightly broadened, extending beyond apical orifice, nearly $1 / 4$ as long as median lobe, apical rami dorsally slightly projected beyond apical orifice.

Female. Length 3.4-4.3 mm, width $1.5-1.9 \mathrm{~mm}$, $1 / \mathrm{w}=2.2-2.4$. Rostrum $0.9-1.0 \mathrm{~mm}$, slightly shorter than pronotum, $\mathrm{r} / \mathrm{p}=0.8-0.9$, dorsally and ventrally arcuate; antennal insertion near central region (towards apical 2/5). Pronotum 1/w=0.9-1.0. Profemur slightly shorter than pronotum, $\mathrm{f} / \mathrm{p}=0.8$ 0.9 ; $\mathrm{t} / \mathrm{f}=0.8-1.0$. Elytron $1 / \mathrm{w}=1.6-1.7 \quad(\mathrm{~N}=10)$. Venter with VII slightly longer than IV, centrally slightly depressed, posterior margin subrectate to slightly rotundate, with indistinct setation. Tergum VIII with lateral margins anteriorly slightly emarginate, posteriorly slightly rotundate, posterior margin projected, explanate, subrectate to slightly rotundate; tergum IX with anterior margin medially distinctly emarginate (throughout entire structure), lateral margins slightly rotundate, posterior margin medially distinctly emarginate (triangular, medially weakly sclerotized), posterolateral edges rotundate; sternum VIII with furcae fused at apex, elliptical (O-shaped), broad, arcuate, apically gradually broadened, canaliculate-striate, subapically with setation, apex slightly rotundate (medially slightly emarginate, sulcate), with $2 \times 3$ short, fairly broad setae; styli with 3 short +1 fairly long setae; spermatheca fairly broad, abruptly deflexed (by nearly $150^{\circ}$ ) near central region (U-shaped), basally subrectate to slightly rotundate, with small, lobulate, membranous projection (proximad to orientation of apex), breadth similar throughout, apex slightly narrowed, rotundate.

Type material. - Male holotype "Costa Rica, Puntarenas, Golfito, La Gamba, 50 m , on Cyclanthus bipartitus, leg. N. Franz, VI-22-2001" (MUCR); female allotype, same label as male holotype (MUCR); male paratypes, same labels as male holotype (CWOB, 2; MUCR, 1), "COSTA RICA: Punt., Las Cruces Biol. Stn., Coto Brus, 1100 m, II.1994, L. D. Gomez, on inflor. Cyclanthus bipartitus L." (CMNC, 3), "PANAMA, Chiriqui, Fortuna ( $8^{\circ} 44^{\prime} \mathrm{N}, 82^{\circ} 15^{\prime} \mathrm{W}$ ), 1050 m , UV trap June 16 ,

1979/ H. Wolda, collector" (MIUP, 1); female paratypes, same labels as male holotype (CWOB, 2; MUCR, 1), "COSTA RICA: Punt., Las Cruces Biol. Stn., Coto Brus, 1100 m, II.1994, L. D. Gomez, on inflor. Cyclanthus bipartitus L." (CMNC, 3), "PANAMA, Bocas del Toro, Corriente Grande, Rio Changuinola/ $9^{\circ} 17^{\prime} 30^{\prime \prime} \mathrm{N}$, $82^{\circ} 32^{\prime} 41^{\prime \prime}$ W, H. Wolda, Apr. 26, 1980" (MIUP, 1).

Etymology. - Named for its association with the inflorescences of Cyclanthus bipartitus at Golfito, Costa Rica (see also below).

Distribution. - Cyclanthura bipartita has been collected in the Cordillera de Talamanca of Costa Rica, Puntarenas, (1) Estación Biológica La Gamba (FN), and (2) Estación Biológica Las Cruces (OET); on the Atlantic slope of Panama, Chiriquí, Fortuna, and Bocas del Toro, Río Changuinola (Fig. 15).

Natural history. - At La Gamba, Costa Rica, over 50 individuals have been collected on various inflorescences of Cyclanthus bipartitus during all phases of the anthesis. No other insects were present, and mature infructescences were present as well, suggesting that Cyc. bipartita is the primary local pollinator. No immature stages could be located in over 10 infructescences. The previous observations are in conflict with two previous and personally confirmed reports on the floral biology of Cyclanthus bipartitus at La Selva, Costa Rica (Beach 1982), and at Estación Biológica Rancho Grande (Parque Nacional Henri Pittier, UCV), Venezuela (Seres \& Ramírez 1995). Both reports mention dynastine scarab beetles (Coleoptera: Scarabaeidae: Dynastinae: Cyclocephalini: Cyclocephala spp.) as the primary pollinators. On the contrary, Anderson \& Gómez (1997: 887) state that scarabs were infrequent on the inflorescences of Cyclanthus bipartitus throughout the Southwestern region of Costa Rica.

From an ecological perspective, thus, it appears that Cyclanthus bipartitus can be pollinated by either derelomines or dynastines. From an evolutionary perspective, however, the following aspects should be considered when addressing the question of how the current pollinating condition in Cyclanthus bipartitus could have evolved. Initially, there are three plausible scenarios: (1) dynastine pollination is the original condition, (2) derelomine pollination is the original condition, and (3) both are original. Potential evidence in support of the first scenario is the widespread occurrence of dynastine pollination throughout the distributional range of Cyclanthus bipartitus, and,
perhaps more importantly, an array of convergent characteristics common to this species and other dynastine-pollinated plants, particularly arums like Dieffenbachia longispatha Engler \& K. Krause (Young 1986). Cyclanthus bipartitus is the single representative of the Cyclanthoideae and sister to all remaining derelomine-pollinated cyclanths which are placed in the Carludovicoideae (Eriksson 1994a, 1994b). To complicate the situation, the original pollinating agent of the Pandanaceae, the Paleotropical sister taxon to cyclanths, is presently not known. Freycinetia Gaudich. is vertebrate-pollinated, Pandanus Linnaeus f. is wind-pollinated, and Sararanga Hemsl. is insect-pollinated (Cox 1990). This signifies that five different pollinating agents could be optimized at the basal node of the clade that consists of Cyclanthaceae and Pandanaceae (i.e. derelomines, "insects", scarabs, vertebrates, and wind). Velloziaceae, presumably the next most closely related taxon, is pollinated by bees and birds ( R . de Mello-Silva, personal communication). Interestingly, Cox (1990: 836) has observed "small beetle-like flying insects" on the pistillate flowers of Sararanga sinuosa Hemsl. in the Solomon Islands, but was unable to collect them for identification. It would be informative to study the pollination biology of Sararanga in more detail to determine whether the pollinators are derelomines. Although Cox (1990: 837) hypothesizes that the earliest Pandanaceae species were pollinated by wind, he contends that only few transformations in inflorescence morphology are necessary to account for the different pollination agents.
The preceding comments indicate that there is research to be done on the phylogenetic relationships of Cyclanthaceae and Pandanaceae and their pollination biologies. Of particular interest is the original pollinating condition of the Cyclantha-ceae-Pandanaceae clade. Apparently, derelomines and dynastines are of sufficient age to have been associated with the oldest cyclanths in the Paleocene (Kuschel 1992, C. J. Marshall, personal communication). It is conceivable that similarities in the inflorescence morphologies of Carludovicoideae and Pandanaceae are indicative of pollination by wind and/or relatively small beetles (see Henderson 1986 for convergent evolution in Arecaceae). If so then the pollination by dynastines in the highly autapomorphic Cyclanthus bipartitus would be secondary, along with considerable transformations in its floral biology (Beach 1982).




Figure 14. (A) Cyclanthura crepidula, male and female genitalia; (B) Cyclanthura palmata, male and female genitalia.

However, this is not to say that Cyc. bipartita has been associated with Cyclanthus bipartitus since its origin. According to the present cladogram (Fig. 17), this species is far too young.

## Cyclanthura crepidula Franz, sp. n.

(Figs. 3C \& 14A)
Diagnosis. - Fairly large, slightly depressed, dark reddish-brown, rostrum fairly broad, antenna with I of funicle $+I$ of club with slightly darker color, eyes separated by distance slightly greater than breadth of apex of rostrum, male profemur with
distinct (although fairly small), apicoventrally directed dens, elytron with anterior elevation extending to V ; median lobe in dorsal view apically cultrate, in lateral view with apical 1/6 (slightly) reflexed, apicoventrally distinctly carinately projected; female tergum IX with posterior margin medially distinctly emarginate, sternum VIII with inner margin subapically triangularly projected, spermatheca fairly narrow, apically acuminately deflexed; association with Asplundia (Cyclanthaceae); Venezuela. Cyclanthura crepidula can be distinguished from the species of the laticolauncinata clade by the fairly broad rostrum and the
cultrate median lobe; from the species of the ocu-lata-striata clade by the fairly large size; from Cyc. bipartita by the darker color, the broadly separated eyes, and the elytral elevations; and from Cyc. palmata by the male profemoral dens, the female sternum VIII and spermatheca, and the distribution. There is appreciable color variation among the specimens, ranging from (light) red-dish-brown in teneral individuals to the characteristic dark color in fully pigmented individuals.

Description. - Male. Fairly large, length 3.2-3.8 mm , width $1.4-1.6 \mathrm{~mm}, 1 / \mathrm{w}=2.2-2.4$, slightly depressed, dark reddish-brown (rostrum, antenna, legs with slightly lighter coloration). Rostrum in lateral view fairly short, $0.9-1.0 \mathrm{~mm}$, slightly shorter than pronotum, $\mathrm{r} / \mathrm{p}=0.8$, in dorsal view fairly broad; antennal insertion near central region (towards apical 2/5). Antenna with I of funicle + I of club with slightly darker color. Eyes separated by distance slightly greater than breadth of apex of rostrum. Pronotum 1/w=1.0 (apparently positively allometric, darker in incompletely pigmented individuals), finely densely punctulate. Prothoracic leg similar in length to mesothoracic leg; profemur slightly shorter than pronotum, $\mathrm{f} / \mathrm{p}=0.8-0.9$, fairly stout, distinctly depressed, ventrally with 1 fairly small, triangular, acute to rotundate, apicoventrally directed dens near apical $1 / 4 ; \mathrm{t} / \mathrm{f}=0.9-1.0$; mesofemur slender, without apicoventrally directed dens. Elytron $1 / \mathrm{w}=1.5-1.6(\mathrm{~N}=2)$, with anterior elevation extending to V (in large individuals, apparently positively allometric). Wing/body=1.21.3 , wing $1 / \mathrm{w}=3.3(\mathrm{~N}=2)$. Venter with VII slightly longer than IV+V, lateral margins posteriorly distinctly converging, posterior margin subrectate. Tergum VIII posteriorly very slightly impressed, posterior margin broadly shallowly emarginate, medially narrowly emarginate. Spiculum gastrale fairly slender. Median lobe in dorsal view (distinctly) elongate, $1 / \mathrm{w}=5.6-6.0(\mathrm{~N}=2)$, basal margin centrally distinctly rotundately emarginate, basilateral edges acute, lateral margins subrectate along basal $5 / 6$, apically slightly converging, emarginate, distinctly converging along apical $1 / 6$ (cultrate), apex distinctly narrowly projected, acute; in lateral view sinuate: deflexed along basal 5/6, reflexed along apical $1 / 6$ (apex slightly reflexed), fairly narrow, greatest breadth near central region, dorsally slightly narrowed along apical $1 / 2$, apical $1 / 8$ ventrally distinctly carinately projected, cultrate, margin slightly rotundate, apex
fairly broad, rotundate; internally with 1 fairly small, elongate, fairly broad, moderately densely denticulate region (membranous), extending along apical orifice, nearly $1 / 8$ as long as median lobe + 2 small, elongate, narrow, subparallel, moderately densely denticulate region (membranous, lateral), near central region (all regions connected by membranes), nearly $1 / 10$ as long as median lobe, apical rami weakly sclerotized, dorsally slightly projected; aedeagal apodemes shorter than median lobe.

Female. Length 3.1-3.7 mm, width 1.4-1.6 mm, $1 / \mathrm{w}=2.3$. Rostrum $0.9-1.0 \mathrm{~mm}$, slightly shorter than pronotum, $\mathrm{r} / \mathrm{p}=0.9$; antennal insertion near central region. Pronotum 1/w=1.0-1.1 (no apparent allometry). Profemur slightly shorter than pronotum, $\mathrm{f} / \mathrm{p}=0.8-0.9$, fairly slender, compressed, without apicoventrally directed dens; $t / f=0.8-0.9$. Elytron 1/w=1.5-1.6 ( $\mathrm{N}=3$ ). Venter with VII similar in length to IV+V, subposteriorly with distinct, deep, semicircular impression, posterior margin subrectate to slightly emarginate (projected), with long setation. Tergum VIII with lateral margins subrectate slightly rotundate, posterior margin distinctly projected, explanate, rotundate; tergum IX with anterior margin medially slightly emarginate, lateral margins subrectate to slightly rotundate, posterior margin medially distinctly emarginate (triangular, medially weakly sclerotized); sternum VIII with furcae with breadth similar throughout, inner margin subapically with small, triangular, centrobasally directed projection, subapically with setation, apex fairly narrow, rotundate, with 1 fairly short +2 fairly long, broad setae; styli with 3 fairly long setae; spermatheca fairly narrow, abruptly deflexed (by nearly $120^{\circ}$ ) near apical $2 / 5$ (J-/L-shaped), basally subrectate, greatest breadth near base, apically slightly narrowed, apex slightly very narrowly projected, deflexed, acuminate to rotundate.

Type material. - Male holotype "VENEZUELA: Aragua, P. N. Henri Pittier, E. B. Rancho Grande, $10^{\circ} 21^{\prime} 15^{\prime \prime} \mathrm{N}, 67^{\circ} 41^{\prime} 11^{\prime \prime}$ W, 6.VI.1999, H. Escalona, on flowers Asplundia caput-medusae" (IZAV); female allotype, same label as male holotype (IZAV); male paratypes "VENEZUELA, Aragua, Rancho Grande, $\pm$ $1100 \mathrm{~m}, 13-\mathrm{V}-1999$, Bordón leg., en flor de Asplundia caput-теdиsae" (CMNC, 2), "VENEZUELA, Aragua, Rancho Grande vía Guacamaya, 1400 m, 6-VI-1999, Escalona leg., en flor de Asplundia caput-medusae" (CWOB, 2), same label as male holotype (IZAV, 1); female paratypes "VENEZUELA, Aragua, Rancho Grande, $\pm 1100 \mathrm{~m}, 13-\mathrm{V}-1999$, Bordón leg., en flor de Asplundia caput-medusae" (CMNC, 2), "VENEZUELA, Aragua, Rancho Grande vía Guacamaya, 1400 m,


Figure 15. Distribution of the species of Cyclanthura in Southern Central America, Costa Rica and Panama. ■ Cyc. laticola (with one additional locality in Los Tuxtlas, Mexico); $\square$ Cyc. sphaerata; - Cyc. dentata; $\bigcirc$ Cyc. pilosa; $\boldsymbol{\nabla}$ Cyc. capitulata; $\nabla$ Cyc. tenuicola; $\boldsymbol{\Delta}$ Cyc. carinata; $\triangle$ Cyc. uncinata; $\rightarrow$ Cyc. striata; $\diamond$ Cyc. bipartita; and $\square C y c$. palmata.

6-VI-1999, Escalona leg., en flor de Asplundia caputmedusae" (CWOB, 2), same label as male holotype (IZAV, 1).

Etymology. - Named for the diagnostic apically explanate median lobe in males - crepidula signifying "little shoe" (Brown 1956).
Distribution. - Cyclanthura crepidula has been collected in Venezuela, Aragua, Estación Biológica Rancho Grande (UCV) (Fig. 16).

Natural history. - At Rancho Grande, Venezuela, several individuals have been collected on the inflorescences of Asplundia caput-medusae (Hooker fil.) Harling, where they arrive in low quantities. No immature stages could be observed in over 25 infructescences of this species, suggesting that Cyc. crepidula develops either in the staminate flowers or in the staminodes (although it is conceivable that the sample size was insufficient).

## Cyclanthura palmata Franz, sp. n.

(Fig. 14B)
Diagnosis. - Fairly small, light (reddish-) brown, rostrum fairly broad, eyes separated by distance
slightly greater than breadth of apex of rostrum; male pygidium with posterior margin medially deeply narrowly emarginate, median lobe in dorsal view apically cultrate, in lateral view with apical $1 / 3$ (distinctly) reflexed, apicoventrally distinctly carinately projected, aedeagal apodemes shorter than median lobe; female tergum IX with posterior margin medially distinctly emarginate, spermatheca broad, apically broadly rotundate; association with Carludovica (Cyclanthaceae). Cyclanthura palmata can be distinguished from the species of the laticola-uncinata clade by the fairly broad rostrum and the cultrate median lobe; from the species of the oculata-striata clade by the broadly separated eyes; from Cyc. bipartita by the median lobe and female sternum VIII; and from Cyc. crepidula by the smaller size, the lighter color, the by absent profemoral dens in males, and the distribution. There is appreciable color variation among the specimens, ranging from pale yellow-ish-brown in teneral individuals to the characteristic reddish color in fully pigmented individuals.

Description. - Male. Fairly small, length 2.7-2.9 mm , width $1.3 \mathrm{~mm}, 1 / \mathrm{w}=2.2-2.3$, light (reddish-)


Figure 16. Distribution of the species of Cyclanthura in Northern South America, Ecuador and Venezuela. $\square$ Cyc. cordata; © Cyc. oculata; © Cyc. cultrata; and Cyc. crepidula.
brown (rostrum, head, pronotum with slightly darker coloration). Labial palpomere II without distinct apicolateral projection. Rostrum in lateral view fairly short, $0.8-0.9 \mathrm{~mm}$, slightly shorter than pronotum, $\mathrm{r} / \mathrm{p}=0.9$, in dorsal view fairly broad, basally not rugulose; antennal insertion near apical $1 / 3$. Eyes separated by distance slightly greater than breadth of apex of rostrum, dorsally with fairly short setation. Head with frontal impression indistinct. Pronotum 1/w=1.0. Prothoracic leg similar in length to mesothoracic leg; profemur slightly shorter than pronotum, $\mathrm{f} / \mathrm{p}=0.8-0.9 ; \mathrm{t} / \mathrm{f}=0.9$. Elytron $1 / \mathrm{w}=1.4-1.6(\mathrm{~N}=5)$. Wing/body=1.3, wing $1 / \mathrm{w}=3.0-3.2(\mathrm{~N}=2)$. Venter with VII slightly longer than IV+V, posterior margin slightly rotundate. Tergum VIII posteriorly very slightly impressed, posterior margin distinctly narrowly emarginate. Spiculum gastrale fairly slender. Median lobe in dorsal view elongate, $1 / \mathrm{w}=4.8-5.2(\mathrm{~N}=2)$, basal margin centrally (broadly to deeply) emarginate,
basilateral edges acute to rotundate, lateral margins subrectate to slightly sinuate along basal $2 / 3$, subparallel to slightly converging, distinctly converging near apical $1 / 3$, narrow, cultrate along apical $1 / 3$, apex distinctly narrowly projected, acute; in lateral view sinuate: deflexed along basal $2 / 3$, reflexed along apical $1 / 3$ (apex distinctly reflexed), fairly narrow along basal $2 / 3$, dorsally slightly narrowed along apical $1 / 3$, subapical $1 / 10$ ventrally carinately projected, apex narrow, arcuate, rotundate; internally with 2 small, elongate, narrow, sublinear, subparallel, moderately sclerotized sclerites, extending along central region of apical orifice (nearly $1 / 10$ as long as median lobe) +2 fairly large, elongate, fairly narrow, subparallel, finely denticulate regions (membranous), extending beyond apical orifice, nearly $1 / 5$ as long as median lobe; aedeagal apodemes shorter than median lobe.

Female. Length 2.6-3.0 mm, width 1.2-1.3 mm,
$1 / \mathrm{w}=2.1-2.3$. Rostrum $0.8-0.9 \mathrm{~mm}$, similar in length to pronotum, $\mathrm{r} / \mathrm{p}=1.0$; antennal insertion near apical $2 / 5$. Pronotum $1 / w=0.9-1.1 .0$. Profemur slightly shorter than pronotum, $\mathrm{f} / \mathrm{p}=0.8-0.9$; $\mathrm{t} / \mathrm{f}=0.9$. Elytron $\mathrm{l} / \mathrm{w}=1.5-1.6$ ( $\mathrm{N}=5$ ). Venter with VII slightly longer than IV+V, posterior margin slightly rotundate (projected), with long setation. Tergum VIII with lateral margins subrectate to slightly rotundate, posterior margin posterior margin distinctly projected, explanate, subrectate to slightly rotundate; tergum IX with anterior margin medially distinctly emarginate (throughout entire structure), lateral margins subrectate to slightly rotundate, posterior margin medially distinctly emarginate (triangular, medially weakly sclerotized), posterolateral edges triangular; sternum VIII with furcae apically gradually broadened, subapically with setation, apex obliquely rotundate, with 1 fairly short +1 fairly long +1 long, broad setae; styli with 2 short setae; spermatheca broad, abruptly deflexed (by nearly $105^{\circ}$ ) near apical $2 / 5$ (J-shaped), basally broadly rotundate, greatest breadth near base, apically slightly narrowed, apex broad, rotundate.

Type material. - Male holotype "Costa Rica, Puntarenas, Coto Brus, Las Cruces, 1100 m , on Carludovica palma$t a$ leg. L. Gómez, XII-1994" (MUCR); female allotype, same label as male holotype (MUCR); male paratypes, same labels as male holotype (CWOB, 2; MUCR, 1); "COSTA RICA: Punt., San Vito, 1200 m, V.1993, L. D. Gomez, on inflor. Carludovica palmata \& C. drudei" (CMNC, 2); female paratypes, same labels as male holotype (CWOB, 2; MUCR, 1), "Costa Rica, Puntarenas, Coto Brus, Fila de Cal, $560 \mathrm{~m}, 08^{\circ} 43^{\prime} 16^{\prime \prime} \mathrm{N}, 82^{\circ} 57^{\prime} 25^{\prime \prime}$ W, on Cyclanthaceae (\# 941310), leg. L. Gómez, XII1993" (CMNC, 1), ); "COSTA RICA: Punt., San Vito, 1200 m, V.1993, L. D. Gomez, on inflor. Carludovica palmata \& C. drudei" (CMNC, 1).

Etymology. - Named for its association with the inflorescences of Carludovica palmata Ruíz \& Pavón at Las Cruces, Costa Rica (see also below).

Distribution. - Cyclanthura palmata has been collected in the Cordillera de Talamanca of Costa Rica, Puntarenas, Estación Biológica Las Cruces (OET), and Fila de Cal (Fig. 15).

Natural history. - At Las Cruces, Costa Rica, several individuals of Cyc. palmata have been collected on the inflorescences of Carludovica drudei Masters and Carludovica palmata. It is unknown whether they oviposit into the pistillate flowers, staminate flowers, or staminodes of these species.

## Cladistic analysis

Characters. - The following characters and character states were used to construct the data matrix (Table 1). The character polarity was determined during the analysis (i.e. not a priori) by rooting the cladogram with the outgroup taxa (Nixon \& Carpenter 1993, see also above). The characters were coded as additive unless noted otherwise.

1. Maxillary palp: (0) 3-segmented; (1) 2-segmented. The (0) condition appears to be plesiomorphic for Curculioninae (but without the fusion of the palpiger with the galea + lacinia, Ting 1936).
2. Labial palp: (0) 3-segmented; (1) 2-segmented.
3. Labial palpomere II: (0) indistinct (i.e. subrectate to slightly rotundate); (1) with distinct apicolateral projection. Perelleschus has an apically obliquely narrowed labial palpomere II (Franz \& O'Brien 2001b).
4. Rostrum in dorsal view: (0) fairly broad; (1) fairly narrow. This character is difficult to code for those taxa that do not have the apomorphic (1) condition, particularly the outgroup taxa Der. chamaeropsis, Not. basalis, and Sta. vectoris which are coded as inapplicable. Presumably, the plesiomorphic ( 0 ) condition is homologous among the respective outgroup and ingroup taxa, although the coding for Cyc. oculata is ambiguous and coded as inapplicable as well. The exclusion of this character results in one additional topology which is discussed below.
5. Antenna with $I$ of club (as well as I of funicle): (0) indistinct (i.e. concolorous with as antenna); (1) with slightly darker color.
6. Eyes: (0) separated by distance smaller than or similar to breadth of apex of rostrum; (1) separated by distance slightly greater than breadth of apex of rostrum.
7. Pronotum in dorsal view: (0) indistinct (i.e. centrally slightly convex); (1) centrally slightly concave.
8. Prosternum in ventral view: (0) indistinct (i.e. glabrate); (1) with dense, short vestiture.
9. Procoxal cavities: (0) separated; (1) contiguous.
10. Profemur: (0) indistinct (i.e. without dens); (1) with small, apicoventrally directed dens near apical $1 / 4$.
11. Apex of protibia: (0) with row of 20-40 narrow setae along both antero- and posteroventral

Table 1. Character matrix for the cladistic analysis of the species of Cyclanthura and selected outgroup taxa. The three multistate characters 21,27 , and 32 were coded as nonadditive, "-" denotes inapplicable character states, and "?" denotes missing character states (as detailed in the text).

| Taxon / character | 5 | $\begin{aligned} & 1 \\ & 0 \end{aligned}$ | 1 5 | 2 0 | 2 5 | 3 0 |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Der. chamaeropsis | 000-0 | 00000 | 00000 | 000-0 | 01000 | - 0000 | 00 |
| Not. basalis | 000-0 | 00000 | 00000 | 000-0 | 00-00 | - 0000 | 00 |
| Sta. vectoris | 010-0 | 00010 | 00000 | 000-0 | 01000 | - 0000 | 01 |
| Per. carludovicae | 10000 | 00110 | 10010 | 000-0 | 00-00 | - 01-0 | 11 |
| Sys. carludovicae | 11000 | 00110 | 10010 | 000-0 | 00-00 | - 0000 | 11 |
| Phy. semirufus | 10100 | 00110 | 00010 | 000-0 | 01000 | - 0000 | 0 - |
| Gan. undulatus | 10100 | 00110 | 10010 | 110-0 | 01000 | -01-0 | 01 |
| Cyc. laticola | 10110 | 00110 | 01010 | 100-0 | 00-11 | $0100-$ | 02 |
| Cyc. sphaerata | 10111 | 00110 | 01010 | 101-0 | 01011 | 01000 | 11 |
| Cyc. cordata | 10111 | 00111 | 01010 | 101-0 | 01011 | 01000 | ?? |
| Cyc. dentata | 10111 | 00111 | 01010 | 101-0 | 01011 | 01000 | ? ? |
| Cyc. pilosa | 10110 | 00110 | 01010 | 11-00 | 10-01 | 00000 | 02 |
| Cyc. capitulata | 10110 | 00110 | 01010 | 11-00 | 11001 | 01001 | 02 |
| Cyc. tenuicola | 10110 | 00110 | 01010 | 11-00 | 11001 | - 1001 | 02 |
| Cyc. carinata | 10110 | 10110 | 01111 | 11-00 | - 1001 | 11000 | 02 |
| Cyc. uncinata | 10111 | 10110 | 01010 | 11-00 | -1001 | 10000 | 02 |
| Cyc. oculata | 100-0 | 01110 | 01011 | 11-11 | 21101 | 11000 | ?? |
| Cyc. cultrata | 10001 | 01110 | 01011 | 11-11 | 21101 | 11010 | ?? |
| Cyc. striata | 10001 | 01110 | 01111 | 11-11 | 21101 | 11010 | ?? |
| Cyc. bipartita | 10100 | 00110 | 01011 | 11-11 | -1001 | 121-0 | 01 |
| Cyc. crepidula | 10101 | 10111 | 01011 | 11-11 | 21001 | 12000 | 01 |
| Cyc. palmata | 10000 | 10110 | 01011 | 11-11 | 21001 | 12000 | 01 |

margin; (1) with row 8-12 broad spines (which are homologous to setae) along either anteroor posteroventral margin.
12. Elytron: (0) indistinct (i.e. without elevations and/or impressions); (1) with slight convex elevation near anterior $1 / 8$ of striae I-III, posteriorly slightly impressed.
13. Elytron: (0) indistinct (i.e. without distinct carinate tumescences); (1) with 2-3 distinct carinate tumescences (see details above).
14. Orientation of pygidium in male: (0) parallel to orientation of tergum; (1) perpendicular to orientation of venter.
15. Posterior margin of pygidium in male: (0) with broad medioventral emargination; (1) with narrow medioventral emargination.
16. Basal margin of median lobe in male: (0) irregular to subrectate; (1) centrally distinctly emarginate. The (very) slightly emarginate basal margin of the median lobe in Perelleschus (Franz \& O'Brien 2001b) may be homologous to the (1) condition, however, such a coding does not affect the topology of the cladogram.
17. Apical region of median lobe in male in dorsal view: (0) apically slightly narrowed (but relatively broad), rotundate; (1) apically distinctly
narrowed, acute. Reductive coding was used for characters 17-19 (Strong \& Lipscomb 1999, see also below).
18. Apical region of median lobe in male in dorsal view: (0) apically gradually narrowed; (1) apically variously broadened (i.e. cordate-malleate to spatulate). Character 18 was coded for those taxa that have the ( 0 ) condition for character 17. All other taxa were coded as inapplicable. The coding for Cyc. laticola (i.e. [0] condition) does not reflect its distinctive characteristics (Figs. 6E \& 6F) which are different from those of the outgroup taxa.
19. Apical region of median lobe in male in dorsal view: (0) gradually acutely narrowed, lateral margins emarginate; (1) abruptly acutely narrowed, cultrate (lateral margins subrectate). Character 19 was coded for those taxa that have the (1) condition for character 17. All other taxa were coded as inapplicable. The characteristics of Cyc. pilosa (Fig. 9B) and Cyc. carinata (Fig. 11A) appear to be homologous to the ( 0 ) condition.
20. Median lobe in male in lateral view: (0) deflexed; (1) sinuate.
21. Apical region of median lobe in male in later-
al view: (0) apically gradually narrowed (indistinct); (1) apically transversely broadened, capitate; (2) ventrally carinately projected. Coded as nonadditive (since no further homology could be proposed). Inapplicable in Cyc. carinata, Cyc. uncinata, and Cyc. bipartita.
22. Internal sac of median lobe in male: (0) indistinct (i.e. without denticulate region); (1) with denticulate region(s).
23. Internal sac of median lobe in male: (0) with 1 denticulate region; (1) with 2 denticulate regions. Inapplicable in those taxa that have the ( 0 ) condition for character 22.
24. Internal sac of median lobe: indistinct (i.e. without ampullate sclerite); with ampullate sclerite.
25. Posterior margin of tergum VIII in female: (0) indistinct (i.e. slightly emarginate to slightly rotundate, but not projected); (1) posteriorly (distinctly) projected, explanate.
26. Explanate region of posterior margin of tergum VIII in female: (0) subrectate to slightly emarginate; (1) slightly rotundate. Inapplicable in the outgroup taxa (region not present) and in Cyc. tenuicola (region deeply emarginate).
27. Posterior margin of tergum IX in female: (0) medially slightly rotundate; (1) medially slightly emarginate; (2) medially distinctly emarginate. Coded as nonadditive (reductive coding does not affect the topology of the cladogram).
28. Apical region of sternum VIII in female: (0) bifurcate, Y-shaped; (1) elliptical, O-shaped.
29. Inner margin of furcae of sternum VIII in female: (0) indistinct (i.e. breadth similar throughout); (1) subapically triangularly broadened. Inapplicable in Gan. undulatus, Per. carludovicae, and Cyc. bipartita (furcae not present).
30. Insertion of duct + reservoir on spermatheca in female: (0) basal; (1) basilateral. Inapplicable in Cyc. laticola (insertion of duct + reservoir separated).
31. Larval habit: (0) detritivorous, pupation in the ground (oviposition into caducous floral organs); (1) herbivorous, pupation in the infructescence (oviposition into noncaducous floral organs). Missing for Cyc. cordata, Cyc. dentata, Cyc. oculata, Cyc. cultrata, and Cyc. striata (see also discussion).
32. Host plant association: (0) Arecaceae; (1) Cyclanthaceae; (2) Araceae. Coded as nonad-
ditive (since no further homology could be proposed). Inapplicable in Phy. semirufus (associated with Rosaceae). Missing for Cyc. cordata, Cyc. dentata, Cyc. oculata, Cyc. cultrata, and Cyc. striata (see also discussion).

Analysis. - The data matrix included 22 taxa (i.e. 7 outgroup species +15 ingroup species) and 32 characters (i.e. 29 binary +3 multistate). Using the parsimony ratchet, the cladistic analysis yielded one most parsimonious cladogram with $\mathrm{L}=56$, $\mathrm{CI}=62$, and $\mathrm{RI}=83$ (Fig. 17). In spite of considerable homoplasy, Bremer values indicate good support for the monophyly of Cyclanthura, as well as that of the laticola-uncinata clade and the oculatapalmata clade (including the oculata-striata clade). All characters had unambiguous optimizations except for characters 31 and 32 (larval habit and host plant association, respectively) which are displayed under slow (DELTRAN) optimization. In the course of generating the character matrix, several preliminary analyses placed Cyc. uncinata as the sister taxon to all remaining species of Cyclanthura, and Cyc. carinata as the sister taxon to the oculata-palmata clade. This alternative cladogram would be obtained if character 4 (breadth of rostrum) is excluded from the data matrix. However, the current topology, although it includes the weakly supported carinata-uncinata clade, is preferred for the following attributes: (1) it conserves the primary homologies of the latico-la-uncinata clade (Fig. 17), i.e. the narrow, subrectate rostrum (e.g., compare Figs. 2A \& 2B versus Figs. 3A \& 3B) and the association with Araceae (Anthurium), and (2) it does not "isolate" Cyc. uncinata from the remaining Cyclanthura species for its evidently autapomorphic male genitalic characters. Future studies on Cyclanthura will hopefully resolve these issues. The presumable evolution of host plant associations indicates that an association with Cyclanthaceae is the plesiomorphic condition for Cyclanthura, whereas an association with Araceae (Anthurium) is synapomorphic for the laticola-uncinata clade (Fig. 18). More specific patterns of host plant association are apparent but difficult to homologize.

## Discussion

Systematics. - The monophyly of Cyclanthura is indicated by the putatively synapomorphic elytral elevations and impressions, the posteriorly


Figure 17. Phylogeny of the species of Cyclanthura and selected outgroup taxa, according to the most parsimonious cladogram ( $\mathrm{L}=56, \mathrm{CI}=62$, RI 83). Characters 31 and 32 is displayed under slow optimization, all other characters have unambiguous optimizations. The black rectangles indicate (single) nonhomoplasious character state transformations, whereas the white rectangles indicate (multiple) homoplasious character state transformations. The numbers above and below each rectangle correspond to the characters and states, respectively. Bremer support values are provided at the right end of each node (see text for details).
explanate female tergum VIII, and the posteriorly emarginate female tergum IX (characters 12, 25, and 27, respectively, Fig. 17). The latter two synapomorphies are correlated with transformations in the male genital complex (most distinctly so in the bipartita-palmata clade). None of these characteristics are present in the outgroup taxa, and in particular the elytral transformations appear to be unique among all derelomine taxa. Several additional characteristics are congruent with this
pattern, i.e. the slightly impressed frons, the distinctive sulcus along the posterior margin of the eye, the comparatively deep striae, and the association with Araceae and Cyclanthaceae (Fig. 18). However, these characteristics vary in grades among the species of Cyclanthura, and can be observed in certain undescribed species of Derelomini as well. This is why they were excluded from the data matrix. The same is true for various other characteristics, e.g. the mouthparts, the ven-


Figure 18. Phylogeny of the species of Cyclanthura and selected outgroup taxa, according to Fig. 17 but with emphasis on host plant associations (i.e. character 32 in part, all other characters are omitted, for details see discussion). Host plant transitions are indicated by transformations in color and/or texture. The solid lines imply homology, whereas the dashed lines represent additional biological information which was excluded from the character matrix (see discussion for details).
tral segments, and the internal structures along the apical orifice of the median lobe. Some of these character systems will become available for cladistic analysis after the description of other new taxa which are already at hand in collections. This research represents only a step in a cycle on the complex relationships of the species that have been assigned to Phyllotrox, and is expected to continue in the future (Kluge 1998). Furthermore, it is possible to make the circumscription of Cyclanthura narrower, e.g. by delimiting the lati-cola-uncinata from the oculata-palmata clade (or even further). Such an approach would be pre-
ferred under traditional conceptions that emphasize similarities in the Gestalt of higher taxa. But in the case of Cyclanthura it would be difficult to reproduce and in conflict with many internal (and often homoplastic) characters. Considering the relatively high number of host plant transitions among the species of Cyclanthura (e.g. Cyc. bipartita and Cyc. sphaerata), it is also not favorable for the communication of their respective biologies. The current classification is conservative because it takes into account that many new species are yet to be discovered in the Neotropics. Finally, it is in my opinion preferable to be able to
recognize higher taxa (such as genera) without having to refer to exclusively internal characteristics.

Homoplasy is abundant in the cladogram, especially in the more apical clades (Fig. 17). The phylogenetic position of Ganglionus with respect to Perelleschus and Systenotelus versus Phyllotrox is conflicting but irrelevant for this project. Neither Ganglionus nor Phyllotrox are considered to be the sister taxon of Cyclanthura. Within the genus several clades can be identified with confidence. Among them are the laticola-uncinata clade which is characterized by the fairly narrow rostrum and the association with Araceae (characters 4 and 32, respectively). The descriptive phrase "rostrum fairly narrow" is intended to align with unique evolutionary transformations in the shape of the rostrum which are difficult to capture with words but easy to observe in comparison with other derelomine taxa. This condition is present in Cyc. carinata and Cyc. uncinata which comprise, nevertheless, one of the most weakly supported clades in the present topology. Stronger support can be assigned to the laticola-dentata clade which is characterized by the presence of an ampullate sclerite in the median lobe (character 24) and the pilosa-tenuicola clade which has an apically capitate median lobe (character 21). The dentate male profemur has evidently evolved twice in the cordata-dentata clade and in Cyc. crepidula (character 10). The oculata-palmata clade is supported by the apically cultrate, sinuate, apicoventrally carinately projected medial lobe (characters 19,20 , and 21 , respectively), to which the medially distinctly emarginate female tergum IX in the bipartita-palmata clade appears to correspond (character 27). The oculata-striata clade is characterized by the centrally slightly impressed pronotum and two separated denticulate regions in the internal sac of the median lobe (characters 7 and 23, respectively). The topology within the biparti-ta-palmata clade is conflicting since all three species have various unique characteristics, e.g. the O-shaped female sternum VIII in Cyc. biparti$t a$ (character 28) or the absence of an apicolateral projection in the labial palpomere II in Cyc. palmata (character 3, both are reversals). The broadly separated eyes in the carinata-uncinata clade and in the crepidula-palmata clade are evidently convergent transformations (character 6). The carinate elytral tumescences in Cyc. carinata and Cyc. striata (character 13) are not homologous
either. As emphasized above, many of these conflicting characteristics have to be addressed in future analyses.

Biology. - Cyclanthura - and in particular the lati-cola-uncinata clade (Fig. 18) - is the first derelomine taxon for which an association with Araceae (Anthurium) has been reported. Anthurium is an exclusively Neotropical and diverse genus of Araceae (Mayo et al. 1997). Its biogeographic distribution and occurrence in wet forest habitats are similar to Cyclanthaceae (Harling 1958). However, there are significant differences in inflorescence morphology and pollination biology. Cyclanth inflorescences have pistillate flowers that are inserted into the spadix and surpassed by densely arranged staminate flowers which leave small entrances through which the pollinators have to penetrate. Their crepuscular anthesis is synchronized with the reproductive behaviors of the associated derelomine species which constitute the only efficient pollinators (for details see Gottsberger 1991, Eriksson 1994a, Seres \& Ramírez 1995, Franz 1999, Franz \& O'Brien 2001a, 2001b). Typically, they mate on the inflorescences and oviposit into caducous floral organs, e.g. the staminate flowers or the pistillate filiform staminodes (Franz 2003). Subsequently, the larvae complete their development while feeding on detritus in the leaf litter. Perelleschus, Systenotelus, and the apparently highly unique Cyc. sphaerata are notable exceptions to this pattern because the adults oviposit into the pistillate flowers and the larvae are herbivorous, feeding on the pulp and seeds of the maturing infructescences (Anderson \& Gómez 1997). Although the pollination biology of Anthurium is very incompletely known, it is evident that its inflorescences are protogynous as well and display various mode of staminal emergence and pollen presentation (Croat 1980). Generally, various kinds of insect pollinators have access to the stigmata, including bees (e.g. Euglossini), flies, and small "flower" beetles (e.g. Aleocharinae). Based on detailed observations on the antheses of over 25 species of Anthurium, Croat (1980) suggests that there have to be relatively high levels of pollinator specificity. The herein presented information cannot be used against this suggestion. At La Selva, three Cyclanthura species have been collected at three different (although not identified) species of Anthurium. These species do not appear to be the
host plants of different species at different localities. But this is as far as our fragmentary knowledge of this association extends at the moment. It can be assumed that the species of the laticolauncinata clade are relatively specific pollinators of Anthurium, that they are attracted to the inflorescences by olfactory stimuli, and that they mate on them. It is questionable whether they oviposit into the pistillate flowers since no immature stages have been observed in several (possibly over 20) dissected infructescences at La Selva. Many species of Anthurium retract their stamina after pollen presentation (Croat 1980), which limits the substrate for larval development in comparison with Cyclanthaceae. However, detritivorous larvae are the plesiomorphic condition for Derelomini and most likely present in Cyclanthura. The present contribution is intended to facilitate field research on the reproductive behavior of these species in the future.

The evolutionary pattern of host plant associations within Cyclanthura indicates various significant transitions (Fig. 18), i.e. in the laticola-uncinata clade from Cyclanthaceae to Anthurium (Araceae), in Cyc. sphaerata from Araceae to Sphaeradenia (Cyclanthaceae), in Cyc. bipartita from Carludovicoideae to Cyclanthoideae. It should be noted here that these transitions represent very imprecise propositions of homology. Eventually it might become feasible to refine the descriptive phrase "association with Anthurium" into something like "oviposition into the stamens of the Anthurium subclade X " versus "development in the pistillate tepals of the Anthurium species $Y$ ", etc. To select the "generic level" (Fig. 18) for the communication of the patterns of host plant associations is merely a simplification: this is neither how the patterns have been observed in the field (i.e. at the level of species) nor how they are likely to be significant to the taxa (i.e. at the level of evolutionarily relevant character state transformations). Nevertheless, the patterns suggest the occurrence of considerable (unobserved) physiological and behavioral adaptations to different host plants within Cyclanthura, in addition to the (observed) morphological transformations. With the knowledge of the phenology of the hosts comes the possibility for behavioral observations in the field (Franz 2003). Furthermore, the patterns generate testable predictions for the host plant associations of (1) the cordata-dentata clade (i.e. Anthurium, if the transitions in Cyc. sphaerata are
unique), and (2) the oculata-striata clade (i.e. Cyclanthaceae, although one individual record on Araceae alters the optimization for the entire clade). Considering the incomplete distributional information on Cyclanthura (Figs. 15 \& 16) - e.g. without any specimen records from Colombia high numbers of new species of Cyclanthura are expected to result from future field work on arums and cyclanths. These taxa will be used to test the information presented herein.

## Acknowledgments

I thank Robert Anderson, Hermes Escalona, Steven Lingafelter, Kelly Miller, Charles O'Brien, and Quentin Wheeler for field assistance, specimen loans, and valuable comments, and Huyen Do for general support in the course of this project. David Grimaldi and Tam Nguyen facilitated the use of the SEM at the American Museum of Natural History. Funding was provided in part through the National Science Foundation Doctoral Dissertation Improvement Grant DEB-0206093.

## References

Alonso-Zarazaga, M. A. \& Lyal, C. H. C. (1999) A world catalogue of families and genera of Curculionoidea (Insecta: Coleoptera) (excepting Scolytidae and Platypodidae). 315 pp. Entomopraxis, Barcelona.
Anderson, R. S. \& Gómez-P., L. D. (1997) Systenotelus, a remarkable new genus of weevil (Coleoptera: Curculionidae) associated with Carludovica (Cyclanthaceae) in Costa Rica and Panamá. Revista de Biología Tropical 45: 887-904.
Anstett, M. C. (1999) An experimental study of the interaction between the dwarf palm (Chamaerops humilis) and its floral visitor Derelomus chamaeropsis throughout the life cycle of the weevil. Acta Oecologica 20: 551-558.
Arnett, R. H. Jr., Samuelson G. A. \& Nishida, G. M. (1993) The insect and spider collections of the worlds, second edition, Fauna \& Flora Handbook no. 11. 310 pp. Sandhill Crane Press, Gainesville.
Beach, J. H. (1982) Beetle pollination of Cyclanthus bipartitus (Cyclanthaceae). American Journal of Botany 69: 1074-1081.
Bremer, K. (1994) Branch support and tree stability. Cladistics 10: 295-304.
Brown, K. E. (1976) Ecological studies on the cabbage palm, Sabal palmetto. Principes 20: 3-10.
Brown, R. W. (1956) Composition of scientific words, revised edition. 882 pp . Smithsonian Institution Press, Washington, D. C.
Burke, H. R. (1959) Morphology of the reproductive systems of the cotton boll weevil (Coleoptera, Curculionidae). Annals of the Entomological Society of America 52: 287-294.
Cox, P. A. (1990) Pollination and the evolution of breeding systems in Pandanaceae. Annals of the Missouri Botanical Garden 77: 816-840.
Croat, T. B. (1980) Flowering behavior of the Neotropi-
cal genus Anthurium (Araceae). American Journal of Botany 67: 888-904.
Eriksson, R. (1994a) The remarkable weevil pollination of the Neotropical Carludovicoideae (Cyclanthaceae). Plant Systematics and Evolution 189: 75-81.
Eriksson, R. (1994b) Phylogeny of the Cyclanthaceae. Plant Systematics and Evolution 190: 31-47.
Franz, N. M. (1999) Biología reproductiva de algunas ciclantáceas (Cyclanthaceae) y de los picudos asociados (Coleoptera: Curculionidae). 97 pp. M. Sc. thesis, University of Costa Rica.
Franz, N. M. (2001) Description and phylogeny of Staminodeus, a new genus of Derelomini (Coleoptera: Curculionidae) associated with Cyclanthaceae. Coleopterists Bulletin 55: 397-418.
Franz, N. M. (2003) Mating behaviour of Staminodeus vectoris (Coleoptera: Curculionidae), and the utility of systematics in behavioural studies. Journal of Natural History 37. (in press)
Franz, N. M. \& O'Brien, C. W. (2001a) Ganglionus, a new genus of Derelomini (Coleoptera: Curculionidae) associated with Carludovica (Cyclanthaceae). Annals of the Entomological Society of America 74: 835-850.
Franz, N. M. \& O'Brien, C. W. (2001b) Revision and phylogeny of Perelleschus (Coleoptera: Curculionidae), with notes on its association with Carludovica (Cyclanthaceae). Transactions of the American Entomological Society 127: 255-287.
Goloboff, P. (1999) NONA (NO NAME), version 2.0 (for Windows). Published by the author, Tucumán, Argentina. Program and manual available at http://www. cladistics.com.
Gottsberger, G. (1991) Pollination of some species of Carludovicoideae, and remarks on the origin and evolution of the Cyclanthaceae. Botanisches Jahrbuch der Systematik 113: 221-235.
Grandcolas, P., Deleporte, P., Desutter-Grandcolas, L. \& Daugeron, C. (2001) Phylogenetics and ecology: as many characters as possible should be included in the cladistic analysis. Cladistics 17: 104-110.
Harling, G. (1958) Monograph of the Cyclanthaceae. Acta Horti Bergiani 18: 1-428, 110 plates.
Henderson, A. (1986) A review of pollination studies in the Palmae. Botanical Review 52: 221-259.
Kirsch, T. (1874) Beiträge zur Kenntnis der Peruanischen Käferfauna, auf Dr. Abendroth's Sammlungen basirt (Drittes Stück). Berliner entomologische Zeitschrift 18: 385-432.
Kluge, A. G. (1998) Sophisticated falsification and research cycles: consequences for differential character weighting in phylogenetic systematics. Zoologica Scripta 26: 349-360.
Kuschel, G. (1952) Los Curculionidae de la Cordillera Chileno-Argentina (1. ${ }^{\mathrm{a}}$ parte). Revista Chilena de Entomología 2: 229-279.
Kuschel, G. (1992) Reappraisal of the Baltic Amber Curculionoidea described by E. Voss. Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg 73: 191-215.
Madison, M. (1979) Protection of developing seeds in Neotropical Araceae. Aroideana 2: 52-61.
Mayo, S. J., Bogner, J. \& Boyce, P.C. (1997) The genera of Araceae; with contributions from J.C. French and R. Hegnauer; illustrations by E. Catherine. 370 pp. Royal Botanical Gardens, Kew.

Nichols, S. W. (1989) The Torre-Bueno glossary of entomology, including supplement A by George S. Tulloch. 840 pp. New York Entomological Society, New York.
Nixon, K. C. (1999) The parsimony ratchet, a new method for rapid parsimony analysis. Cladistics 15 : 407-414.
Nixon, K. C. (2002) WinClada, version 1.00.08. Published by the author, Ithaca, NY. Program and manual available at http://www.cladistics.com.
Nixon, K. C. \& Carpenter, J. M. (1993) On outgroups. Cladistics 9: 413-426.
Seres, A. \& Ramírez, N. (1995) Biología floral y polinización de algunas monocotiledóneas de un bosque nublado Venezolano. Annals of the Missouri Botanical Garden 82: 61-81.
Strong, E. E. \& Lipscomb, D. (1999) Character coding and inapplicable data. Cladistics 15: 363-371.
Syed, R. A. (1979) Studies on oil palm pollination by insects. Bulletin of Entomological Research 69: 213224.

Thompson, R. T. (1992) Observations on the morphology and classification of weevils (Coleoptera, Curculionoidea) with a key to major groups. Journal of Natural History 26: 835-891.
Ting, P. (1936) The mouth parts of the coleopterous group Rhynchophora. Microentomology 1: 93-114.
Velázquez de Castro, A. J. (1998) Morphology and taxonomy of the genus Sitona Germar, 1817. (I): the Metendosternite (Coleoptera: Curculionidae). Pp. 109-123, in Colonnelli, E., Louw, S. \& Osella, G.: Taxonomy, ecology and distribution of Curculionoidea (Coleoptera: Polyphaga), proceedings of a symposium (28 August, 1996, Florence, Italy), XX International Congress of Entomology. 294 pp. Museo Regionale di Scienze Naturali, Torino.
Voss, E. (1954) Curculionidae. Pp. 193-376, in Titschack, E.: Beiträge zur Fauna Perus, Band IV, Wissenschaftliche Bearbeitungen. 386 pp. VEB Gustav Fischer Verlag, Jena.
Warner, R. E. (1976) Descriptions of a new species of Phyllotrox infesting seeds of Acer grandidentatum, with new synonomy and a note on Euclyptus (Coleoptera: Curculionidae: Erirhininae). Great Basin Naturalist 36: 463-466.
Wheeler, Q. D. \& Platnick, N. I. (2000) The phylogenetic species concept (sensu Wheeler and Platnick). Pp. $55-69$, in Wheeler, Q. D. \& Meier, R.: Species concepts and phylogenetic theory: a debate. 230 pp . Columbia University Press, New York.
Yeates, D. K. (1992) Why remove autapomorphies? Cladistics 8: 387-389.
Young, H. J. (1986) Beetle pollination of Dieffenbachia longispatha (Araceae). American Journal of Botany 73: 931-944.
Zherikhin, V. V. \& Gratshev, V. G. (1995) A comparative study of the hind wing venation of the superfamily Curculionoidea, with phylogenetic implications. Pp. 633-777, in Pakaluk, J. \& Slipiński, S. A.: Biology, phylogeny, and classification of Coleoptera: papers celebrating the 80th birthday of Roy A. Crowson, volume 2. 533 pp . Muzeum i Instytut Zoologii PAN, Warszawa.

Revised manuscript accepted March 2003.

