

The Cleptoparasitic Bee Tribe Rhathymini (Hymenoptera: Apidae): Description of a New Genus and a Tribal Review

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Abstract.—The new genus *Rhathymodes* is proposed for *Rhathymus acutiventris* Friese [with its **new synonym**, *R. friesei* Ducke], and *R. bertonii* Schrottky; resulting in the **new combinations**: *Rhathymodes acutiventris* (Friese) and *R. bertonii* (Schrottky). A lectotype is newly designated for *R. friesei*. To accommodate the new genus, changes are suggested for a key to subfamilies and tribes of Apidae. The tribe Rhathymini and its two genera are characterized, as are the two species of *Rhathymodes*.

The neotropical cleptoparasitic apine tribe Rhathymini consists of moderate sized to large (13–28 mm body length) species superficially resembling vespid wasps, especially *Polistes*, or suggesting in form giant species of the bee genus *Nomada*. The impetus for the present paper was the discovery by Martin Cooper of Lyme Regis, U.K., and almost simultaneously by one of us (MSE), that some of the smaller species hitherto placed in *Rhathymus* do not run to the Rhathymini in the key to the subfamilies and tribes of Apinae by Michener (2000: 571–574). These smaller species represent a second genus of the, until now monogeneric, Rhathymini. It is a genus with some probable plesiomorphies relative to *Rhathymus* and therefore likely to provide some insight into relations between Rhathymini and other tribes of Apinae. We hope that recognition of the new genus, named below *Rhathymodes*, will encourage the discovery of its unknown hosts, and of its larval characteristics.

The morphological terminology used below follows that of Michener (2000) with some modifications as proposed by

Engel (2001); equivalents are indicated in brackets in keys and descriptions. The abbreviations T and S are for metasomal terga and sterna; T3, for example, is the third metasomal tergum. Antennal flagellar segment is abbreviated F. Photomicrography was done using a Microoptics ML-1000 Digital Imaging System.

Collections in which specimens are preserved are indicated by names of cities or towns in brackets, with names of relevant curators in parentheses, as below:

- [Berlin] = Museum für Naturkunde, Berlin, Germany (Frank Koch).
[Budapest] = Hungarian Natural History Museum, Budapest, Hungary (Lajos Zambon).
[Chamela] = Instituto de Biología, Universidad Nacional Autónoma de México, research station at Chamela, Jalisco, Mexico (Ricardo Ayala).
[Heredia] = Instituto Nacional de Biodiversidad (InBio), Heredia, Costa Rica (Carolina Godoy).



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Figs. 1-2. *Rhathymodes bertonii* (Schrottky). 1, Dorsal habitus. 2, Lateral view of head, mesosoma, and anterior metasoma (note absence of pleural tubercle).

[Lawrence] = Division of Entomology, University of Kansas Natural History Museum and Biodiversity Research Center, Lawrence, Kansas, USA.

[Lyme Regis]= Martin Cooper collection; Lyme Regis, UK (Martin Cooper).

[New York] = American Museum of Natural History, New York, New York, USA (Jerome G. Rozen, Jr.).

[San Lorenzo]= Museo Nacional de Historia Natural del Paraguay, San Lorenzo, Paraguay (Bolívar R. Garcete-Barrett).

SYSTEMATICS

Tribe RHATHYMINI Lepeletier

Rhathymites Lepeletier 1841: 539. Type genus: *Rhathymus* Lepeletier and Serville 1828. Combining stem: Rhathym-.

Description.—Body usually without areas of dense pale appressed pubescence; form elongate, pubescence short, so that habitus suggests *Polistes* wasps or giant *Nomada* (e.g., Fig. 1); coloration black to largely yellow, sometimes with metasoma red, or all red. Compound eyes slightly diverging below. Clypeus protuberant to less than width of compound eye in lateral view because lower part of compound eye quite broad. Mandible slender, simple. Labrum as long as or longer than median length of clypeus. Proboscis long, in repose reaching between or to apices of procoxae; labial palpus with first two segments subequal in length, last two segments minute, directed laterally; maxillary palpus absent. Antennal scape short, less than three times as long as wide; F1 about half as long as F2. Epistomal sulcus absent below anterior tentorial pits so that clypeus and lower paraocular areas are fused. Lateral ocellus separated from median ocellus by one-third ocellar diameter or less; preoccipital area rounded. Scutellum grading from somewhat elevated to form transverse shining ridge to distinctly bituberculate, posterior declivitous part longer, sometimes much longer, than anterior subhorizontal part; axilla small, rounded, not produced to form tooth. Propodeal triangle hairy. Procoxa tapering, mesal apical margin produced as flattened hairy process that looks like slender hairy spine in ventral view (Fig. 5). Protibia and mesotibia each with distinct outer apical spine; tibial spurs unmodified. Claws each with flattened basal tooth; arolia present. Scopa absent. Forewing with three submarginal cells; marginal cell large, longer

than distance from apex to wing tip, apex rounded and separated from costal wing margin; pterostigma one-fourth to one-fifth as long as marginal cell, border of pterostigma in that cell straight or gently concave; wing hairy, alar papillae absent (Fig. 4). Hind wing with cu-a [cu-v] oblique, longer to slightly shorter than second abscissa of M+Cu; jugal lobe minute, rounded, about one-tenth as long as vannal lobe. Metasoma widest at T2 and T3; T1 markedly narrower than T2, lateral profile slanting, dorsal surface only weakly differentiated and less than half as long as slanting, more anterior, surface. T7 of male tapering to bidentate apex, without pygidial plate; S4, S5, and sometimes S3 of male strongly fringed; S7, S8, and male genitalia as illustrated (Figs. 6–13), genitalia with both upper and lower gonostylar processes well developed, upper rather slender with branched hairs, lower broad and translucent; penis valve heavily sclerotized, spatha largely membranous but with heavily sclerotized longitudinal bar at each side. Female without pseudopygidial area; pygidial plate present, tapering to apical narrowly rounded point, lateral margins weakly concave to weakly convex. Sting well developed; gonoplac [= gonostylus] long, slender, parallel-sided.

Comments.—Some of the characteristics used to identify the Rhathymini by Michener (2000) turn out to be generic characters of *Rhathymus* rather than tribal features. The key to subfamilies and tribes of Apidae (Michener 2000: 572) should be changed so that **couplet 17 omits the phrases about the mesepisternal tubercle**. Furthermore, because of probable confusion at couplet 16, Rhathymini should run out not only at couplet 17 but also through couplet 20. Change the outcome of the second alternative of couplet 20 to 20a and add a new couplet as follows:

- 20a (20). Maxillary palpus absent and axilla small, not at all produced; epistomal sulcus absent below anterior tentorial pit so that clypeus and lower paraocular areas are fused **Apinae, Rhathymini**
- Maxillary palpus present, or if absent, then axilla produced to point (*Odyneropsis* in Epeolini); epistomal sulcus usually complete **21**

KEY TO GENERA OF RHATHYMINI

1. Mesepisternum with large submedian tubercle; vein cu-a [cu-v] of hind wing strongly oblique and distinctly longer than second abscissa of M+Cu; supraclypeal area strongly elevated, crested medially, not continuing convexity of clypeus; ocellular area depressed below level of adjacent areas ***Rhathymus* Lepeletier and Serville**
- Mesepisternum without tubercle; vein cu-a [cu-v] of hind wing less strongly oblique and slightly shorter than or subequal to second abscissa of M+Cu; supraclypeal area with surface generally a continuation of convexity of clypeus although with small frontal tubercle at lower end of frontal line; ocellular area not depressed
..... ***Rhathymodes* Engel, Michener, and Rightmyer**

Genus *Rhathymus* Lepeletier and Serville

Figs. 6, 7, 10, 11

Colax Lepeletier and Serville 1825: 4, 213. *Nomen nudum*.

Rhathymus Lepeletier and Serville 1828: 448. Type species: *Rhathymus bicolor* Lepeletier and Serville 1828, monobasic. Lepeletier 1841: 539. Dalla Torre 1896: 323. Michener 2000: 739. Silveira *et al.* 2002: 129.

Colax Lepeletier and Serville 1828: 448. *Nomen praeoccupatum* [*nec* Hübner 1819 (Lepidoptera); Wiedemann 1824 (Diptera); *et* Stephens 1829 (Hymenoptera)]. Type species: *Rhathymus bicolor* Lepeletier and Serville 1828, monobasic. Established as a synonym of *Rhathymus* Lepeletier and Serville 1828 and therefore not available (ICZN 1999: Art. 11.6); see also Michener (1997).

Liogastra Perty 1833: 146. Type species: *Rhathymus bicolor* Lepeletier and Serville 1828, monobasic.

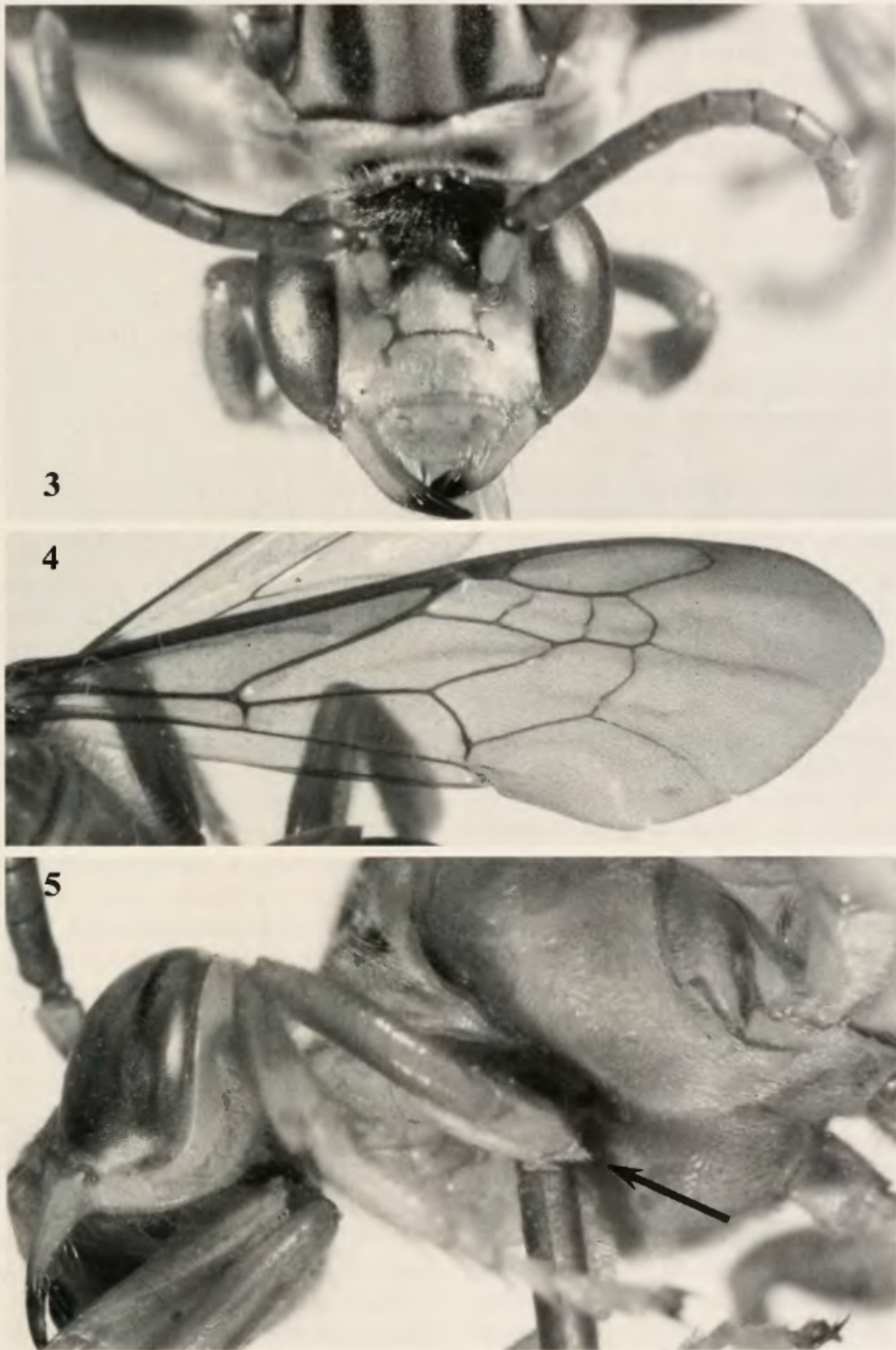
Rathymus Smith 1854: 278. *Lapsus calami et praeoccupatum* [*nec* Dejean 1831 (Coleoptera), *et* Gistel 1848 (Echinodermata)].

Bureauella Dominique 1898: 61. Type species: *Bureauella insignis* Dominique 1898, monobasic.

Diagnosis.—The principal characters of this genus are included as contrasting parenthetical notations in the description of *Rhathymodes*, below.

Comments.—The name *Bureauella* was synonymized by Michener (2000: 739). Its type species, briefly described by Dominique (1898), was very large, yellowish with dark metasomal bands. It is a possible senior synonym of *Rhathymus versicolor* Friese 1906. Friese (1912) gave a key to the species, including species now placed in *Rhathymodes* and in the genus *Odyneropsis* of the Epeolini. About 16 species-group names have been proposed for *Rhathymus* but the actual number of species is probably smaller; the genus is in need of revision and comprehensive cladistic study.

Biology.—So far as known, *Rhathymus* species are cleptoparasites of *Epicharis* (Apidae: Centridini), apparently depositing their eggs through a small opening in the host's brood-cell closure (Camargo *et al.* 1975; Hiller and Wittmann 1994; Rozen 1969, 1991, 2003). The hospicial, first instar dispatches the host larva before feeding on the provisions (Rozen 1969, 1991).



Figs. 3–5. *Rhathymodes bertonii* (Schrottky). 3, Frontal view of head. 4, Forewing. 5, Ventral-oblique view of head and mesosoma; arrow indicates short, setose extension of procoxa (note absence of pleural tubercle).

Larval stages were described by Rozen (1969, 1991), McGinley (1981), and Camargo *et al.* (1975) who also described the pupa. Rozen (2000, 2001) gave additional characters for distinguishing the mature larva and pupa of *Rhathymus* and Rozen (2003) described the eggs (as mature oöcytes) of two species. Raw (1991, 1992) gave an account of the post-emergence flight behavior of male *Rhathymus* as well as some host data.

***Rhathymodes* Engel, Michener, and
Rightmyer, new genus**
Figs. 1–5, 8, 9, 12, 13

Type species.—*Rhathymus acutiventris* Friese 1906.

Diagnosis.—The generic characters are listed below, each followed by the state of the same character in *Rhathymus*, in parentheses. Body length 13–18 mm (16–28 mm in *Rhathymus*). 1. Supraclypeal-frontal area convex, in profile continuing convexity of clypeus, frontal tubercle and carina above it rather weak, see figures 2–3 (this area strongly produced as crest, in profile elevated above imaginary continuation of clypeal convexity, sloping steeply at sides into depressions around antennal bases). 2. Ocellular area not depressed (strongly depressed below level of adjacent areas). 3. Scutellum bituberculate, the two convexities (sometimes weak) forming line between dorsal and posterior declivitous surfaces (with shining ridge, sometimes depressed medially to form weak bituberculation, on line between dorsal and declivitous surfaces). 4. Mesepisternum without anteromedian tubercle (with large, mostly impunctate and hairless, anteromedian tubercle). 5. Mesobasitarsus shorter than mesotibia (as long as mesotibia). 6. Forewing with second submarginal cell receiving 1m-cu [= first recurrent vein] near middle or distal third, see figure 4 (near apex of cell). 7. Hind wing with cu-a [c-v] subequal to or shorter than second abscissa of M+Cu (longer than). 8. Pygidial plate of female with lateral mar-

gins weakly concave, meeting apically to form translucent apex of T6 (margins straight or weakly convex, apex of T6 opaque and largely formed by extension of elevated discal part of pygidial plate). 9. Apical process of second valvifer of female forming slender hook above base of gonoplac [= gonostylus] (more robust and not hooked). 10. Male S4 and S5 simple, transverse, exposed surfaces as long as those of adjacent sterna (male S4 and S5 broadly emarginate, much shortened medially so that only narrow margins are exposed, thus exposed part of S6 large). 11. Lateral extremities of male S5 not produced (strongly produced posterolaterally and hairy, supporting hair tuft noticeable from above, see Michener 2000: fig. 102–2). 12. Male S3–S5 with apical fringes of erect, curved or sigmoid hairs (fringes appressed, not conspicuous, well developed only on S4 and S5). 13. Genitalia and hidden sterna as in figures 8–9, 12–13 (cf. Figs. 6–7, 10–11 for *Rhathymus*); lateral sclerotization of spatha arcuate and produced (not arcuate, not produced).

Included species.—Three names have been provided for species of *Rhathymodes*, as follows: *Rhathymodes acutiventris* (Friese), *R. friesei* (Ducke), and *R. bertonii* (Schrottky). All are new combinations and, as indicated below, the first two are subjective synonyms.

Etymology.—The new genus-group name is a combination of *Rhathymus* (Gr. *rhathymos*, meaning “carefree” or “lazy”) and the suffix *-odes* (Gr., an adjectival derivative of *eidos*, meaning “resembling”). The gender is masculine.

Distribution.—Jalisco, Mexico, to Paraguay, essentially the same as for *Rhathymus*.

Phylogenetic commentary.—Comparison with other tribes of Apinae suggests that characters 1, 2, 4, 10, and 11 are plesiomorphic relative to *Rhathymus*. Perhaps characters 3 and more certainly 9 and the spatha in 13 are derived (admittedly, the sting and male genitalia are unknown in *R. bertonii*).

KEY TO SPECIES OF *RHATHYMODES*
(based on females only)

- 1 Mandible longer than minimum distance between compound eyes; third submarginal cell as long as to longer than second submarginal cell; mesoscutal surface with four yellow stripes; propodeum yellow with black, median, longitudinal stripe on posterior surface (narrower and slightly fainter in specimens from Nicaragua); metasoma yellow or dusky yellow *R. acutiventris* (Friese)
- Mandible shorter than minimum distance between compound eyes (Fig. 3); third submarginal cell markedly shorter than other submarginal cells (Fig. 4); mesoscutal surface appearing yellow with two black stripes (Figs. 1, 3); propodeum yellow without black, median, longitudinal stripe (Fig. 1); metasoma mostly black (Figs. 1–2)
..... *R. bertonii* (Schrottky)

Rhathymodes acutiventris (Friese),
new combination

Figs. 8–9, 12–13

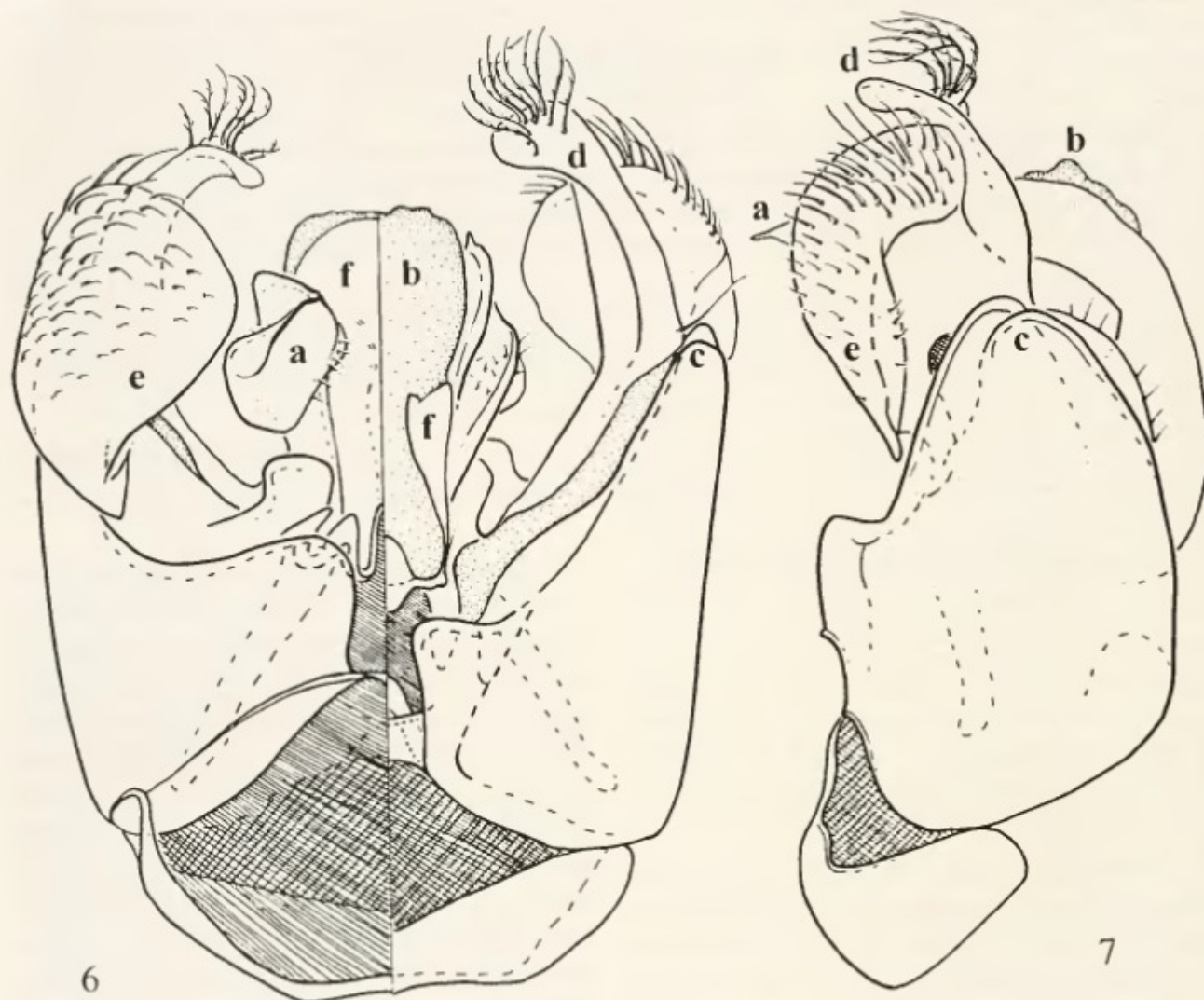
Rhathymus acutiventris Friese 1906: 120. Friese 1912: 226. Holotype [Budapest], examined.

Rhathymus friesei Ducke 1907: 458. Friese 1912: 225. Silveira *et al.* 2002: 129. Lectotype [Berlin], examined. **New synonym.**

Description.—Body length 13–18 mm. Mandible of female longer than minimum distance between eyes. Third submarginal cell measured on posterior margin nearly as long as to longer than second. Body and legs yellow (sometimes brownish yellow), the following areas black or blackish: apical half of mandible; labrum except for two brownish spots near base; subantennal sulci and epistomal sulcus between anterior tentorial pits; upper surface of antenna (sometimes brownish) except sometimes yellow or yellow-brown on base and apex of flagellum; ocellar area extending down on either side of supraclypeal elevation to antennal bases and usually extending laterally on occiput behind summit of compound eye; transverse spots on anterior surface of pronotum; spot at anterior base of pronotal lobe; mesoscutum except for lateral marginal yellow band, broadened anteriorly, and submedian longitudinal yellow band, thus four yellow bands on mesoscutum, none of them attaining anterior and posterior mesoscutal margins or lateral bands attaining poste-

rior mesoscutal margin, submedian bands sometimes partly fused; pretarsal claws; longitudinal median stripe on posterior surface of propodeum; apex of pygidial plate (sometimes brown rather than black). Ventral surface of flagellum yellow-brown except yellow F1. Tibial spurs dark brown. Metasomal terga sometimes dusky yellow with lighter yellow apical bands, although usually uniformly yellow. Wings transparent brownish, veins and pterostigma dark brown to blackish. Pubescence golden, short except on distal part of labrum (where it forms two tufts), genal area, sides of mesosoma and propodeum; pubescence of mesoscutum of rather uniform length, shorter than ocellar diameter, erect; pubescence of metasomal terga appressed, appearing dark against yellow background. Punctuation fine and dense so that most surfaces are dull but labrum, clypeus (especially impunctate lower margin), pronotal lobe and hypopimeral area shining because punctures less dense; metasomal terga especially uniformly dull because of fine punctuation and dense short hair. Male hidden sterna and genitalia as in Figs. 8–9, 12–13.

Variation.—Because of variation in scutellar form we at first believed that the specimens here placed in *R. acutiventris* represented two or more species. Frequently the convexities are prominent so that the declivitous surface below their

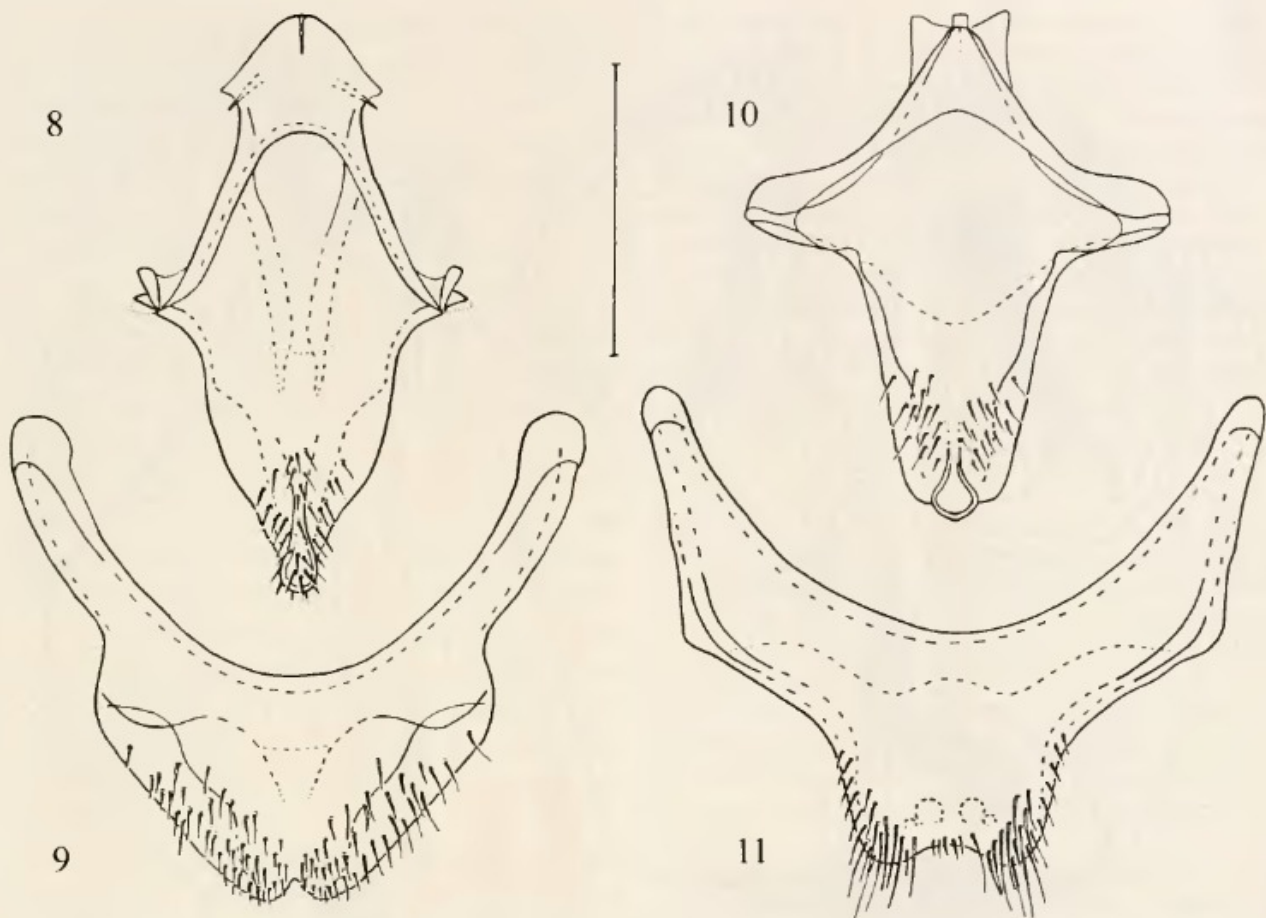


Figs. 6-7. *Rhathymus bicolor* Lepeletier and Serville, male genitalia. 6, Ventral (left) and dorsal (right) views. 7, Lateral view. Letters serve to indicate identical structures seen in different views (a = penis valve; b = aedeagus; c = upper gonocoxite; d = upper gonostylar process; e = lower gonostylar process; f = spatha).

summits is about one and one half times as long as the dorsal surface (seen in lateral view). Less commonly the convexities are smaller. Thus, in a specimen from Suriname the declivitous surface is more than twice as long as the dorsal surface and this condition is approached in a specimen from Cerro Campana, Panamá, although another collected on the same day had larger convexities. From the few specimens available we see no geographical significance in the scutellar variation. It would have been desirable to examine male terminalia from all parts of the range but males are available only from southern Mexico, Honduras, and Panamá; we have made dissections of specimens from

Mexico and Honduras and find no differences between them.

Material examined.—**MEXICO:** *Jalisco:* 1♀, Chamela, 13 July 1990 (R. Ayala) [Chamela]. *Chiapas:* 1♂, Agua Azul, N of Ocosingo, 23 April 1993 (F. Noguera) [Lawrence]; 1♀, Parque Laguna Belgica, 19.3 km N of Ocozocoautla, 1560 m, 12 June 1991 (J. Ashe) [Lawrence]. **GUATEMALA:** 1♀, Zarapa, 3.5 km SE of La Union, 1500 m, 23 Jun. 1993 (J. Ashe, R. Brooks) [Lawrence]. **HONDURAS:** *Atlántida:* 1♀, Lancetilla Botanical Garden, Tela, 10 m, 15°46'N, 87°27'W, 22 June 1994 (J. Ashe, R. Brooks, methyl salicylate and eucalyptus oil attractants) [Lawrence]. *Cortez:* 3♂, 3♀, Parque Nacional Cerro

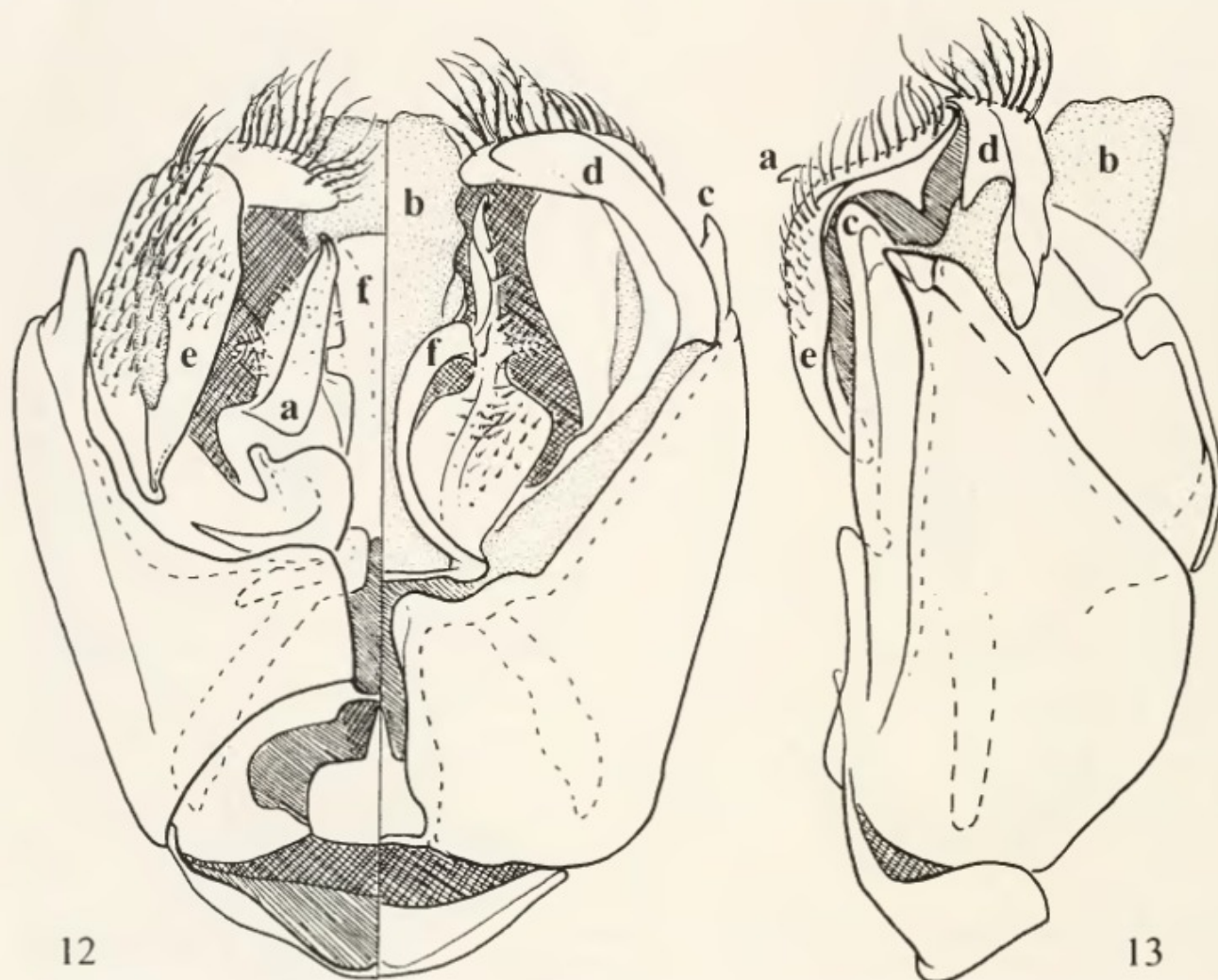


Figs. 8–11. Male internal sterna. 8–9, *Rhathymodes acutiventris* (Fries): 8, Eighth sternum. 9, Seventh sternum. 10–11, *Rhathymus bicolor* Lepeletier and Serville: 10, Eighth sternum. 11, Seventh sternum.

Azul-Meambar, Los Pinos, 800 m, 14°42.4'N, 87°54.7'W, 10–16 May 2002 (S. Peck) [Lawrence]. **NICARAGUA:** *Granada*: 3♀, Volcan Mombacho, Santa Ana 2, 15 May 1998, malaise trap (J. M. Maes) [Lawrence]. 1♀, Volcan Mombacho, Santa Ana 2, 21 June 1998, malaise trap (J. M. Maes) [Lawrence]. **COSTA RICA:** *Alajuela*: 1♀, Caño Negro, 20 m, 10–19 March 1993 (K. Martinez) [Heredia]. *Guanacaste*: 1♀, Maritza Biological Station, 550 m, 22 May 1993 (J. & A. Ashe) [Lawrence]. 1♀, Parque Nacional Guanacaste, Est. Pitilla, 9 km S of Est. Cecilia, 700 m, 19 May–3 June 1993 (P. Ríos) [Heredia]. *Puntarenas*: 1♀, Fila Moras, Buenos Aires, A. C. Amistad, 1000m, 19 May 1993 (M. A. Zumbado, S. Rojas) [Heredia]. **PANAMA:** *Chiriquí*: 1♀ [type of *R. acutiventris*, in Budapest, examined]. *Panamá*: 2♀, Cerro Campana (Capira), 825 m, 8°44'N, 79°57'W, 1–5 June

1995 (J. Ashe, R. Brooks) [Lawrence]. **Colón**: 3♀, 14 km N of junction of Escobal and Pina roads, 30 m, 2 June 1996 (J. Ashe, R. Brooks) [Lawrence]; 2♂, Barro Colorado Island, 29 May 1977 (R. B. & L. S. Kimsey) [Lawrence]. **SURINAME:** *Brokopondo*: 1♀, Brownsberg Nature Preserve, Witi Creek Trail, 80 m, 4°56'55"N, 55°10'53"W, 23–25 June 1999 (Z. Falin, A. Gandadin, H. Hiwat) [Lawrence]. **BRAZIL:** *Para*: 1♂, Estado do Para, Vbidos (Rio Branco), VIII.1912, Ducke [Berlin]. *Pernambuco*: 1♀, Caruaru, 900 m, April 1972 (M. Alvarenga) [New York]. *Minas Gerais*: 1♂, Barbacena, 14.12.1905, Ducke [lectotype of *R. friesei*, Berlin, see below]. *São Paulo or Paraná*: 1♂, Rio Paraná, Süd-Brasil, 1904 [description and photograph, Fries 1912: 225, examined, Berlin].

Lectotype designation.—Several specimens of *R. friesei* are located in the Fries



Figs. 12-13. *Rhathymodes acutiventris* (Friese), male genitalia. 12, Ventral (left) and dorsal (right) views. 13, Lateral view. Lettering as in Figs. 6-7.

collection [Berlin] and many bear his characteristic "typus" labels. As is unfortunately not rare for specimens bearing such labels, many are not part of the original type series (e.g., several were collected at localities not mentioned in Ducke's original account or, worse yet, were collected years after the publication of the species!). However, among the material is at least the specimen collected by Ducke at Barbacena in Minas Gerais (the other specimens mentioned by Ducke are not in Berlin), and this is assuredly one upon which he based his description. For the express purpose of nomenclatural stability we hereby designate and label this individual as lectotype. LECTOTYPE: 1♂, Brazil, Estado de Minas Ger., Barbacena, 14.12.1905, Ducke [Berlin].

Comments.—Just over half of the specimens were collected by flight intercept traps set up in forests. Frequently used by coleopterists, such traps prove to be useful in collecting forest bees rarely seen by bee collectors.

Rhathymodes bertonii (Schrottky),
new combination
Figs. 1-5

Rhathymus bertonii Schrottky 1920: 217. Holotype [San Lorenzo], compared.

Diagnosis.—Similar to *R. acutiventris* except as follows: Mandible shorter than minimum distance between compound eyes (Fig. 3), suggesting mandible of male of *R. acutiventris*. Third submarginal cell markedly shorter than others (Fig. 4). Me-

soscutum with mesal yellow stripes fused so that surface appears yellow with two black stripes (as in the male) and very narrow black anterior margin (Figs. 1, 3) (male also with minute black triangle at posterior margin). Propodeum entirely yellow, without black median stripe (Fig. 1). T3–T6 black (with black bands in male), T3 and T4 with apical margins brownish translucent (Fig. 1); preapical part of pygidial plate reddish yellow, otherwise plate black.

The inner metatibial spurs appear broken apically, alike on the two sides, the truncate apices slightly darkened suggesting that the truncation is normal or that breaking occurred during the life of the insect. The spurs of the male holotype are not truncated, having typical, pointed apices, furthering the suggestion that the truncation of the female is the result of breakage.

Variation.—The following feature is variable within *R. acutiventris* but is recorded here for our specimen of *R. bertonii*: scutellum strongly bituberculate with ascending dorsal surface measured to apices of tubercles about two-thirds as long as declivitous surface.

Material examined.—Aside from the male holotype from Puerto Bertoni, Paraguay [San Lorenzo], this species is known from one female as follows: **PARAGUAY:** Paraguari, Parque Nacional de Ybycui [ca. 26°S, 57°W], 300 m elevation, December 13–18, 1989 (M. Cooper) [Lyme Regis].

Comments.—This species was described from a male from Paraguay, preserved in the Museo Nacional de Historia Natural del Paraguay. In the Martin Cooper collection is one female that agrees in several respects with the male and that we regard as *R. bertonii*. The above diagnostic remarks are based on the female with some parenthetical notes derived from the original description of the male.

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