

A review of Central American *Centris* (*Heterocentris*) and evidence for male dimorphism in *C. labrosa* (Hymenoptera, Apidae)

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With 5 figures and 1 table

Abstract

In 1854 *Centris difformis* Smith was described from a female specimen, and in subsequent years only females of this species have been reported from different Central and South American countries. During a trap-nest study in northeastern Costa Rica, male and female bees were reared from nests of *C. difformis* females. In the present study the male of *C. difformis* is described for the first time and its characters compared to those of the other Central American species of the subgenus *Heterocentris*. The results of the analysis of male characters support the placement of *C. difformis* in the subgenus *Heterocentris*, in which it was previously included by different authors based on morphological characters of the female. A hitherto unrecorded male dimorphism in *C. labrosa* is described and the diagnostic characters of *C. analis* (Fabricius) and *C. labrosa* Friese are reviewed. An amended key for the Central American species of the subgenus *Heterocentris* is presented.

Key words: Apinae, Centridini, *Centris difformis*, taxonomy, Costa Rica.

Introduction

In 1854, Frederick Smith described *Centris difformis* (Smith 1854) from a female specimen from Rio Tapajos in Brazil. In his treatment of the taxonomy and distribution of centridine bees, Snelling (1984) wrote that “No males (of *C. difformis*) have been seen” and in the years following Snelling’s work no description or published records of the male of this species can be found. Since local abundance of the species is low (Thiele, unpubl. data) and sexual dimorphism pronounced, it is not surprising that no males have been described until now.

Females of *C. difformis* can be easily recognized by the large tooth-like process on the frontal, basal area of the mandible, combined with the characteristic shape and markings of the labrum. They seem to be rather uncommon in collections (Snelling 1984), but have been reported from various South and Central American countries since the original description (Crawford 1906, Moure 1945, Michener 1951, Vogel 1974, Snelling 1984).

Snelling (1984) predicted that the males of *C. difformis* should have bidentate mandibles, be considerably larger than those of *C. bicornuta*

(*C. bicornuta* is the only other *Heterocentris* species with bidentate mandibles), and that the hairs of the thoracic dorsum should have blackish apices. Snelling (1984) also provided a key to the Central American species of *Heterocentris*, in which the pregradular area of the second metasomal tergum was used as the sole character to distinguish between males of *C. analis* and *C. labrosa*. In the current study I describe the male of *C. difformis*. In addition I studied the distribution of diagnostic characters of *C. analis* and *C. labrosa* described or illustrated by Michener (1954) and the gradulus-character described by Snelling (1984) among a large set of specimens from both species. As a result the diagnostic value of the gradulus character is evaluated.

Methods

For compatibility reasons I adopt the terminology for anatomical structures of Snelling (1984) who provided an excellent treatment of the taxonomy and distribution of North and Central American centridine bees.

All bee specimens used in this study were collected between 1996 and 2000, at or in the vicinity of the forest of the La Selva Biological Station of the Organization of Tropical Studies (OTS). The 1550 ha reserve is located in the low-

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Received August 2002, accepted May 2003

lands of northeastern Costa Rica (10°26'N, 84°00'W), at 37–150 m above sea level. The forest is classified as tropical lowland wetforest in the Holdrige Life Zone System (Hartshorn and Hammel 1994). Mean annual rainfall is 3962 mm, and all months average at least 100 mm (Sanford et al. 1994).

For a short description of the trap-nests used to collect nests and bees of the species mentioned in this study see Thiele (2002).

In the following description, the first value represents the measurement of the specimen with the author's reference No. 5377. This specimen is deposited at the Natural History Museum, London, where the female holotype is also deposited. The values in parentheses give the range of each measurement across all six specimens measured, including the specimen mentioned above.

Centris difformis specimens used for the male description and deposited outside the author's collection can be found at the following Institutions: Natural History Museum, London (#5377); Museo de Insectos, Universidad de Costa Rica (#4223); University of Kansas Natural History Museum (#6846); Los Angeles County Museum of Natural History (#5928). The numbers in parenthesis again refer to the author's personal collection (RTHC) and not to the archiving system of the institution where the specimen is ultimately deposited.

Description of the male of *C. difformis*

Diagnosis. Differs from males of other Central American *Heterocentris* by the strongly bicolored metasomal dorsum: Basal (pregradular) area of second metasomal tergum dark brown to black, apical (postgradular) half of second and entire third to seventh terga light brown to ferruginous; hairs on scutum greyish with brown tips, but not beige to ochreous, as in the other three species; mandible bidentate, as in males of *C. bicornuta* (tridentate in males of *C. labrosa* and *C. analis*); largest of the Central American *Heterocentris* species with a total body length of 11.8–15.2 mm.

Description. Measurements (mm): Head width 5.80 (4.20–5.80); head length 3.44 (2.56–3.44); forewing length 13.52 (9.95–13.52); total length 15.23 (11.81–15.23).

Head: 1.69 (1.62–1.80) times broader than long; occipital margin nearly flat and slightly below upper tangent of eyes; inner eye margins moderately convergent above; upper frontal width 0.77 (0.77–0.91) times lower frontal width. Mandible bidentate, inner tooth large, acute. Labrum 1.53 (1.49–1.61) times wider than long, apical margin weakly rounded to truncate, disc shiny between subcontiguous to close, fine to moderate punctures. Clypeus 1.80 (1.74–1.83) times wider than long; basal and apical ridge of elevated portion medially depressed; median area with dense, fine to moderate punctures. Interantennal distance 2.00 (1.95–2.11) times an-

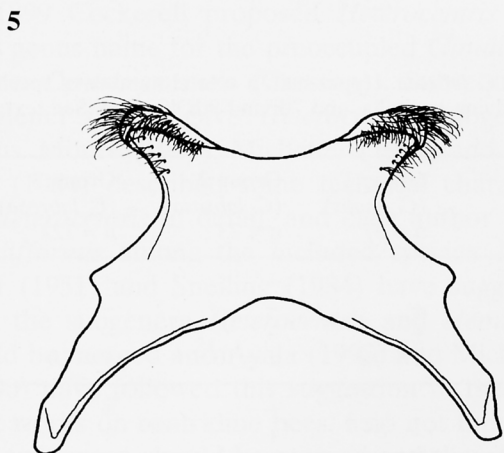
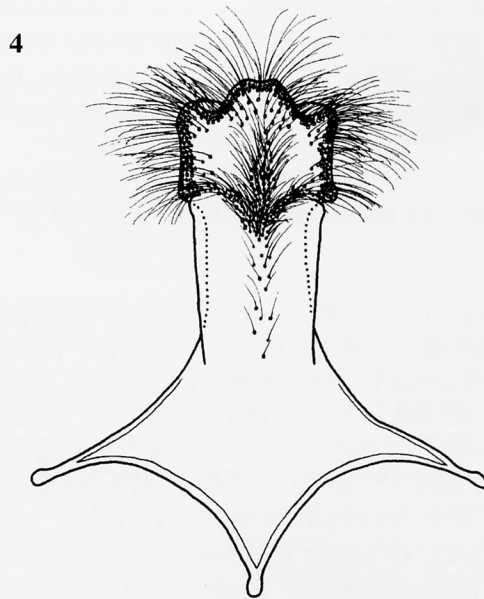
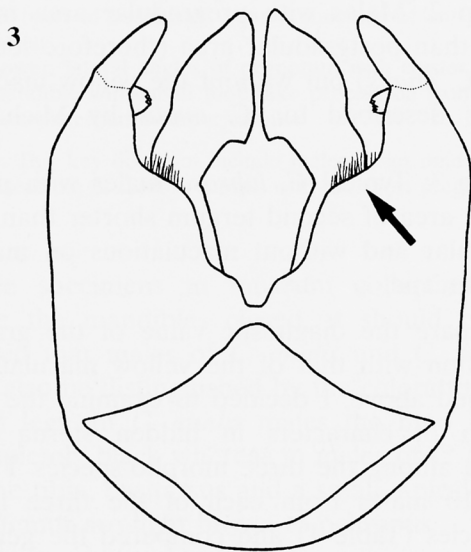
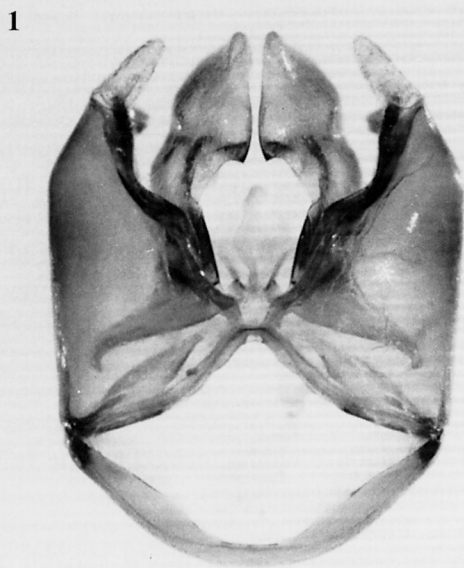
tennal socket diameter; antennocular distance 0.61 (0.59–0.76) times antennal socket diameter; scape stout, 1.64 (1.59–1.73) times longer than wide; scape length 0.55 (0.53–0.62) times length of first flagellar segment; first flagellar segment as long as following four segments combined, 5.00 (4.64–5.00) times length of second. Interocellar distance 1.79 (1.79–2.20) times diameter of anterior ocellus; ocellocular distance 1.29 (1.27–1.56) times diameter of anterior ocellus; ocelloccipital distance 2.18 (1.97–2.18) times diameter of anterior ocellus.

Thorax: Scutum moderately shiny between subcontiguous to dense, fine to moderate punctures; scutellum simple, without prominent depressions or elevations, punctured like scutum except for smooth, narrow anterior area; metanotum weakly shiny, tessellate and with scattered oval to round, shallow punctures; mes- and metepisternum with subcontiguous to dense, fine punctures, interspaces partly dull; basal area of propodeum with contiguous minute to fine punctures.

Abdomen: Dorsum of first metasomal tergum moderately shiny, weakly tessellate between close, fine punctures; second metasomal tergum dull, strongly tessellate between dense to close, fine punctures; remaining terga only weakly tessellate; third and following terga moderately shiny and apical margins with weak transverse striae.

Terminalia: Apical margin of seventh sternum broadly emarginate and distinctly bent ventrad at angle of about 70 degrees, two lateral lobes of apical part covered with medium to long, mostly branched hairs, densely to closely spaced (Fig. 5). Eighth sternum with distal process apically enlarged, rectangular, margins ventrally covered with branched hairs and with large tuft at basal, median border of process; process with conspicuous median elevation at apical, ventral margin (Fig. 4). Genitalia ventrally with median parts of interior margin of gonocoxite forming moderate angle of about 135 degrees, apical portion of angle with row of simple hairs (Fig. 3); ventral gonostylar processes not reaching level of penis valves (Fig. 1), with minute hairs only; ventral processes of penis valves with edge terminating in a sharp point at proximal end (Fig. 1); dorsal gonostylar processes, not elongate, rather rimlike, small, inconspicuous (Fig 2).

Pilosity: Dense, white, plumose hairs on supra-clypeal area, genal area and sparse on second and third sternum. Some blackish hairs along in-



Figs 1–5. *Centris difformis*. 1, Genitalia, ventral view. 2, Genitalia, dorsal view. 3, Sketch of genitalia in ventral view showing row of hairs (arrow). 4, 8th sternum ventrally. 5, 7th sternum ventrally. Scale bar in Fig. 1 equals 0.5 mm. All figures are reproduced at same scale.

ner and upper margin of eyes and on meta-, mesotibia and meta-, mesobasitarsus. Disc of second tergum with blackish, simple hairs; hairs on third tergum reddish and partly black tipped, remaining terga only with yellowish, partly long and plumose hairs. Mesosoma covered with grey-brown to sand-colored hairs, those on mesosomal dorsum mostly with darker tips.

Color: Head and thorax blackish brown. Front of second to ninth flagellar segments light brown, sharply separated from dark brown distal part. Pregradular area of second metasomal tergum black to dark brown, postgradular area and discs of third to seventh terga light brown to ferruginous. Sterna light ochreous. Legs, except for metatibiae and basitarsi, blackish brown. Metatibiae and outer surface of metabasitarsi ferruginous.

Following structures yellow: Entire frontal part of protuberant clypeus and lower, lateral area, entire labrum except for a narrow dark band on apical margin, triangular spots on frontal part of scape, three fifths of length of mandible from basal part to insertion of lower, basal tooth.

Distinguishing characters of *C. analis* and *C. labrosa*

In his key to the Central American species of *Heterocentris*, Snelling (1984) used the position of the gradulus of the second metasomal tergum as the sole character to distinguish the males of *C. analis* and *C. labrosa*. After studying 60 male *C. analis* and 122 male *C. labrosa* I observed an extreme size dimorphism in the *C. analis* males. The 60 male *C. analis* had been identified based on the position of the gradulus of the second metasomal tergum as described by Snelling (1984). In the 23 large males, then identified as

C. analis (Group 2 in Table 1), the postgradular area of the second tergum was about four times as long as the pregradular area, typical for specimens of *C. analis* according to Snelling (1984). However, these 23 large males did not show the yellow maculations on the scape and mandibles described by Michener (1954) as being typical for *C. analis* and which were present in the 37 smaller males of *C. analis* (Group 1 in Table 1). In other words: when both, the yellow maculations described above and the gradulus character were considered as diagnostic characters for identifying tridentate specimens of the subgenus *Heterocentris*, three morpho-species could be distinguished which are characterized by the following combination of characters:

Group 1: Typical *C. analis* males with pregradular area of second tergum much shorter than postgradular area and with yellow maculations on mandible and scape as described for *C. analis* by Michener (1954).

Group 2: Males with pregradular area much shorter than postgradular area (therefore identified as *C. analis*) but without the yellow maculations as described for *C. analis* by Michener (1954).

Group 3: Typical *C. labrosa* males with postgradular area of second tergum shorter than the pregradular and without maculations on mandible and scape.

To compare the diagnostic value of the gradulus-position with that of the yellow maculations mentioned above, I decided to examine the distribution of characters in hidden sterna and genitalia among the three morpho-species. I dissected 10 males from each of the three morpho-species (Table 1) and compared the genitalia and hidden sterna from each group with Michener's (1954) drawings of those structures for *C. labrosa* and *C. analis* (listed under its

Table 1

Distribution of diagnostic characters among males of *Centris analis* and *C. labrosa*. Upper half: n = total number of specimens examined. Lower half: 10 specimens from each group, dissected for studying genitalia, and 7th and 8th sternum. See text for a detailed description of the three groups.

	Group 1 (<i>C. analis</i>) n = 37	Group 2 (<i>C. labrosa</i>) n = 23	Group 3 (<i>C. labrosa</i>) n = 122
Postgradular area shorter than pregradular area (T2)	–	–	+
Yellow area on mandible	+	–	–
Yellow spot on scape	+	–	–
	n = 10	n = 10	n = 10
S7 apically only about half as wide as basally	–	+	+
Apical process of S8 with pronounced apical indentation	–	+	+
Gonostyli clearly exceeding apical level of penis valves	+	–	–

synonym *C. totonaca*). All males of group two and three showed no differences in genitalia and hidden sterna and agreed with Michener's drawings for *C. labrosa*. The genitalia and hidden sterna of all males of group 1 were consistent with Michener's drawings for *C. analis*. In

other words, males of group 2 and 3 differed only in the position of the gradulus of the second tergum but shared all other diagnostic characters of *C. labrosa* (Table 1). The following key was therefore modified from that of Snelling (1984).

Key to the Central American species of *Heterocentris*

1a. Male, antenna 13-segmented, basitibial plate absent	2
b. Female, antenna 12-segmented, basitibial plate present	5
2a. Mandible bidentate (on apical half)	3
b. Mandible tridentate (on apical half)	4
3a. Metasomal terga uniformly black	<i>bicornuta</i> Mocsáry
b. Pregradular area of second metasomal tergum blackish, following terga reddish, ferruginous	<i>difformis</i> F. Smith
4a. Mandible and scape uniformly brown to blackish	<i>labrosa</i> Friese
b. Mandible and scape with yellow areas	<i>analis</i> (Fabricius)
5a. Clypeus without lateral horn-like processes	6
b. Clypeus with pair of long, slender horn-like processes	<i>bicornuta</i> Mocsáry
6a. Clypeal maculation a pair of apical, yellow triangles; mandible without or with inconspicuous tooth-like process on basal third; clypeus less than 1.8 times wider than long	7
b. Clypeal maculation an apical yellow band; mandible with large, elongate tooth-like process on basal third; clypeus more than twice wider than long	<i>difformis</i> F. Smith
7a. Lower lateral angle of pronotum with long, plumose hairs only; mandible with elevated ridge (not resembling a tooth) on front of basal half; ventral juncture of anterior and posterior surfaces of mesepisternum with short, lamelliform carina	<i>labrosa</i> Friese
b. Lower, lateral angles of pronotum with cluster of long yellowish or reddish, simple setae as well as plumose hairs; mandible with small tooth-like process on front of basal half; ventral juncture of anterior and posterior surfaces of mesepisternum without carina	<i>analis</i> (Fabricius)

Note: This key does not include males of an unidentified species from Panama mentioned by Snelling (1984). Possibly they represent the *C. labrosa* morph with the short pregradular area (see text for details).

Since specimens in museum collections often have the mandibles closed, it should be mentioned that males of *C. analis* and *C. bicornuta* can also be distinguished by the coloration of the hind legs. In *C. analis* males the hind legs are completely black whereas in males of *C. bicornuta* the tibia, basitarsus and a small, apical area of the femur are light brown to ochreous.

Discussion

In 1899 Cockerell proposed *Heterocentris* as a new genus name for the preoccupied *Gundlachia* (Type: *Centris cornuta* (Cresson)). Subsequently Michener (1951) gave *Heterocentris* subgeneric status. Moure (1945), Michener (1951) and Snelling (1984) described some technical characters of *Heterocentris* in detail, and each author listed *C. difformis* among the included species. Michener (1951) and Snelling (1984) have suggested that the subgenera *Heterocentris* and *Hemisiella* could be merged and Ayala (1998) and Michener (2000) have followed this suggestion in their recent works on centridine bees. I do not think the two subgenera should be merged and therefore I

have applied the older classification (as in Snelling 1984) in the current study; however, a systematic review is beyond the scope of this paper.

All *C. difformis* males studied by me showed the strongly extended lateral portion of the first metasomal tergum and erect, plumose setae with bent and flattened apices at the extreme side of the segment. These characters, applied by Snelling (1984), readily differentiate *Heterocentris* males from those of the subgenera *Hemisiella* and *Trachina*. The presence of these characters clearly assigns *C. difformis* to the subgenus *Heterocentris*.

When only externally visible characters are taken into account, one could argue that the *C. labrosa* morph with the *C. analis*-like gradulus could represent an undescribed species. This possibility has to be rejected, considering that no differences in the morphology of genitalia and hidden sterna could be found between the two *C. labrosa* morphs despite the complexity and abundance of fine structures in *Heterocentris* genitalia and hidden sterna. The complete lack of group-specific characters in genitalia and hidden sterna in the two *C. labrosa* morphs, combined with the distribution pattern of the three external charac-

ters among the examined specimens of *C. analis* and *C. labrosa* (Table 1), leaves no doubt about the dimorphic nature of the gradulus character in males of *C. labrosa*, at least for the La Selva population. Future studies need to examine whether the gradulus of the second tergum is dimorphic in other populations of *C. labrosa* throughout its range. Male dimorphism has been described for several *Centris* species of various subgenera (Michener 2000) mostly referring to males that are much larger than the usual form, and commonly have more extensive yellow markings, more enlarged hind legs and other distinctive features. However, dimorphism in *C. labrosa* males is only evident in the structure of the second metasomal tergum and not in body size, color, or shape of the hind femur as in the so-called “metanders” or “beta males” described in other studies.

In addition to the dimorphism in *C. labrosa* males from La Selva, the application of the gradulus position as a key-character is now less appropriate since in males of *C. difformis* the pregradular area is longer than the postgradular, as it is in the majority of *C. labrosa* males.

I have not seen the *Heterocentris* males from Panama, which Snelling (1984) lists as “*Centris* (*Heterocentris*) species”, a possibly undescribed species. However, the described characters of this “species”, including the dull and roughened spaces between clypeal punctures, agree with the *C. labrosa* morph with the short pregradular area. Therefore it seems likely that the specimens Snelling (1984) described as “*Centris* (*Heterocentris*) species” could represent individuals of the *C. labrosa* morph with the short pregradular area described in the current study.

Acknowledgements

For financial support I am indebted to Wolf Engels and the “Tropenökologisches Begleitprogramm” of the GTZ (Gesellschaft für Technische Zusammenarbeit).

I am especially grateful to Ralf Britz for his help with the illustrations and valuable comments on the manuscript; to Roy Snelling for his hospitality and help during my visits at the Los Angeles County Museum of Natural History. I thank Michael S. Engel and an anonymous reviewer for helpful comments on the manuscript. Further I want to express my thanks to all the people at the La Selva Biological Station in Costa Rica, Javier Guevara of MINAE for his help with permits and Martina Hohloch for the photo lab work.

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