

The First Gregarious Species of the Agathidinae (Hymenoptera: Braconidae)

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Abstract.—*Coccygidium gregarium* Sarmiento & Sharkey, the first known gregarious species of the subfamily Agathidinae (Braconidae), is described. This species was reared from a larva of *Euglyphis* sp. (Lasiocampidae). The SEM images of its last antennal flagellomere reveal that the characteristic acuminate shape is due to the presence of elongated, presumably sensory, structures. This type of flagellomere, together with its carinate hind trochantellus, are traits present in the genera *Coccygidium*, *Biroia*, *Dichelosus*, *Hemichoma* and in the Afrotropical genus *Hyrtanommadium*, suggesting a close phylogenetic relationship. The apex of the ovipositor sheath bears a small pointed process present in other *Coccygidium* species and also in *Biroia*, *Dichelosus*, and *Hemichoma* but not in *Hyrtanommadium*; this trait may suggest a close relationship among these genera. SEM images of this structure show that it is covered by ampulliform papillae, here reported for the first time. The pores on the inner apex of the ovipositor sheaths and the ampulliform papillae are either secretory or sensory.

The Agathidinae are comprised of approximately 52 genera worldwide, with 20 occurring in the New World. Nearly 1000 species have been described, mostly from tropical areas. The subfamily has been revised at the tribal level by Sharkey (1992), and there have been several faunal treatments and generic revisions (Muesebeck 1927, Marsh 1961, Nixon 1986, Sharkey 1983, 1986, 1988, 1990, Simbolotti and van Achterberg 1999, van Achterberg 1990, and Briceño 2003). The genus *Coccygidium* de Saussure, 1892 (in this paper we follow the generic concept of Chou and Sharkey 1989; including *Zelomorpha* Ashmead) is probably the most species-rich genus of the tribe Disophrini. This genus includes about 35 described species distributed worldwide but more than 100 Neotropical species are awaiting description. Although *Coccygidium* has never been revised, current studies (by C.S. and M.J.S.) suggest that the Neotropical genera *Biroia* Szépli-

geti, *Hemichoma* Enderlein and *Dichelosus* Szépligetii are derived clades within *Coccygidium*.

All agathidines for which there are reliable rearing records are reported as solitary koinobiont endoparasitoids of lepidopteran larvae. Members of *Bassus* and *Agathis* (Microdini and Agathidini respectively) oviposit in the host, placing the egg inside a ganglion of the ventral nervous system or attaching it to the lateral lobe of the protocerebrum; the larva remains as a first instar, floating in the haemocoel, during the feeding period of the host, and then quickly develops in the final larval and prepupal stage of the host; the final-instar parasitoid emerges after the host has spun its cocoon and completes its feeding externally (Shaw and Huddleston 1991, Sharkey 1997). *Coccygidium* species, as with all the members of the tribe Disophrini, possess short strong ovipositors and parasitize free-living caterpillars in

their late instars. Host records of *Coccygidium* include noctuids, arctiids, notodontids, and lasiocampids (<http://janzen.sas.upenn.edu>, Shenefelt 1970). Most species of Disophrini are diurnal and brightly colored, but some are nocturnal and have the characteristic pale coloration and enlarged ocelli of nocturnal hymenoptera (Sharkey 1997). In this paper we describe a new species of *Coccygidium* that represents the first record of agathidine larvae living gregariously within a single host individual.

Coccygidium gregarium n. sp. Sarmiento & Sharkey

Holotype Female (The variation observed in the paratypes is included in square brackets in italics)

Size. Mesosoma length 2.7 mm (Fig. 1). Forewing length 6.9 mm (Fig. 2).

Color. Mostly black except as follows: basal fourth of fore and mid-tarsi yellow with brown markings; wings infumate; metasoma orange.

Head. Medial ridge or convexity of face present (Fig. 3) [*or absent*]. Face convex medially, flat laterally, lacking striations, with small, sparse punctures laterally, and dense foveolate punctures medially (Fig. 3). Penultimate labial palpomere 25% shorter than apical palpomere. Eyes not emarginate; eyes not converging ventrally (Fig. 3). Posterior orbit not bordered by groove (Fig. 4). Lateral carina of frons incomplete posteriorly, composed of rugae and fovea. Frontal depression smooth. Distance between antennal insertions subequal to their diameter. Number of antennal flagellomeres 35 [36–37]. Apical flagellomere acuminate (Figs 5–6). Ratio of distance between inner margins of eyes to distance between lateral margins of lateral ocelli = 1.6. Depression laterad of lateral ocellus absent. Area of vertex posterior to ocelli smooth. Longitudinal depression posterior to ocelli weak, not indicated by distinct groove. Gena, at mid-height, posterior to eye, barely projecting posteriorly (Fig. 4). Posteroventral area of gena evenly

rounded, flanged and with a few irregular rugae basad of eye (Fig. 4). Ratio of length of malar space to eye height = 0.3.

Mesosoma. Epicnemial carina complete and with distinct angle. Groove of epicnemial carina wide and flat, with about 10 robust transverse ridges, strongest at mid-length, absent in ventral third (Fig. 9). Mesopleuron uniformly punctured. Precoxal sulcus indicated ventrally by one crenula, otherwise barely depressed and smooth. Posterior margin of mesopleuron with 7–8 robust carinae. Suture between metaepisternum and metepimeron complete, smooth, transversed by carinae of subequal size (Fig. 10). Convex flange on posterodorsal border of mesopleuron absent. Dorsal apex of metaepisternum with two carinae. Flange at the anteroventral area of metepimeron (i.e., juxtacoxal flange) wide, with a transverse carina (Fig. 10). Area anterior to subpronope not modified into flange or disk. Posterolateral margin of pronotum smooth. Notaulus indicated by weak depression. Median longitudinal mesoscutal groove absent. Scutellar sulcus deep, subquadrate, with 1 [*or 3*] longitudinal carina[e]. Scuto-scutellar articulation absent. Posterior border of mesoscutal sulcus carinate. Scutellum rounded laterally, rugose. Transverse groove of scutellum deep, with crenulae extending anteriorly but not reaching midway to scutellar sulcus. Median areola of metanotum without median longitudinal carinae (Fig. 12). Posterior border of median areola of metanotum acute with acute longitudinal crest. Surface of propodeum with irregular striations (Fig. 12); median, lateral, and pleural areolae present; anteromedial and posteromedial areolae together forming spindle-shaped area with several transverse carinae; anterolateral areola divided by several ridges converging anterolaterally; posteromedial areola with a transverse carina; posteromedial keels weak, converging; transverse keel distinctly curved and complete to pleural carina, dividing propodeum into two distinct planes. Basal

tooth of fore-tarsal claw truncate. Tibial spur of fore-leg 0.58 times as long as basitarsomere. Longest tibial spur of mid-leg 0.68 times as long as basitarsomere. Hind femur rugoso-punctate dorsally and laterally, areolate-rugose ventrally. Longest spur of hind leg 0.53 times as long as basitarsomere. Carina of hind trochantellus weakly indicated (Fig. 11). Apex of hind tibia with 2 or 3 spines arising directly from apical margin. Basal tooth of hind tarsal claw truncate.

Wings. (Fig. 2) 3M vein of fore wing straight. 3RSa vein of fore wing shortly developed. RS2a vein of fore wing longer than r-m cross vein. RS2b vein of forewing absent. CUB vein of hind wing nebulous.

Metasoma. T1 weakly convex. Apex of ovipositor sheath lacking transparent lamella, curved dorsally with a small acute process (Fig. 13). Apex of the ovipositor sheath covered with ampulliform papillae (Figs 14–15).

Male. Does not differ from the female in non-sexual characters.

Etymology: The specific name refers to the gregarious behavior in the larval stage. This is the first known case of gregariousness for the genus *Coccygidium* and for the subfamily Agathidinae.

Distribution: Known from northwestern Costa Rica and from Fortín de las Flores, Veracruz, Mexico, but probably widespread in Central America and southern Mexico. Elevation range: 975–1150 meters.

C. gregarium can be distinguished from all other species of the genus by its unique color pattern and by the following combination of morphological characteristics: poorly developed lateral carina of frons; gena at mid-height, posterior to eye, without acute posterior projection; postero-ventral area of the gena round and evenly flanged; notauli weakly impressed; propodeum strongly carinate.

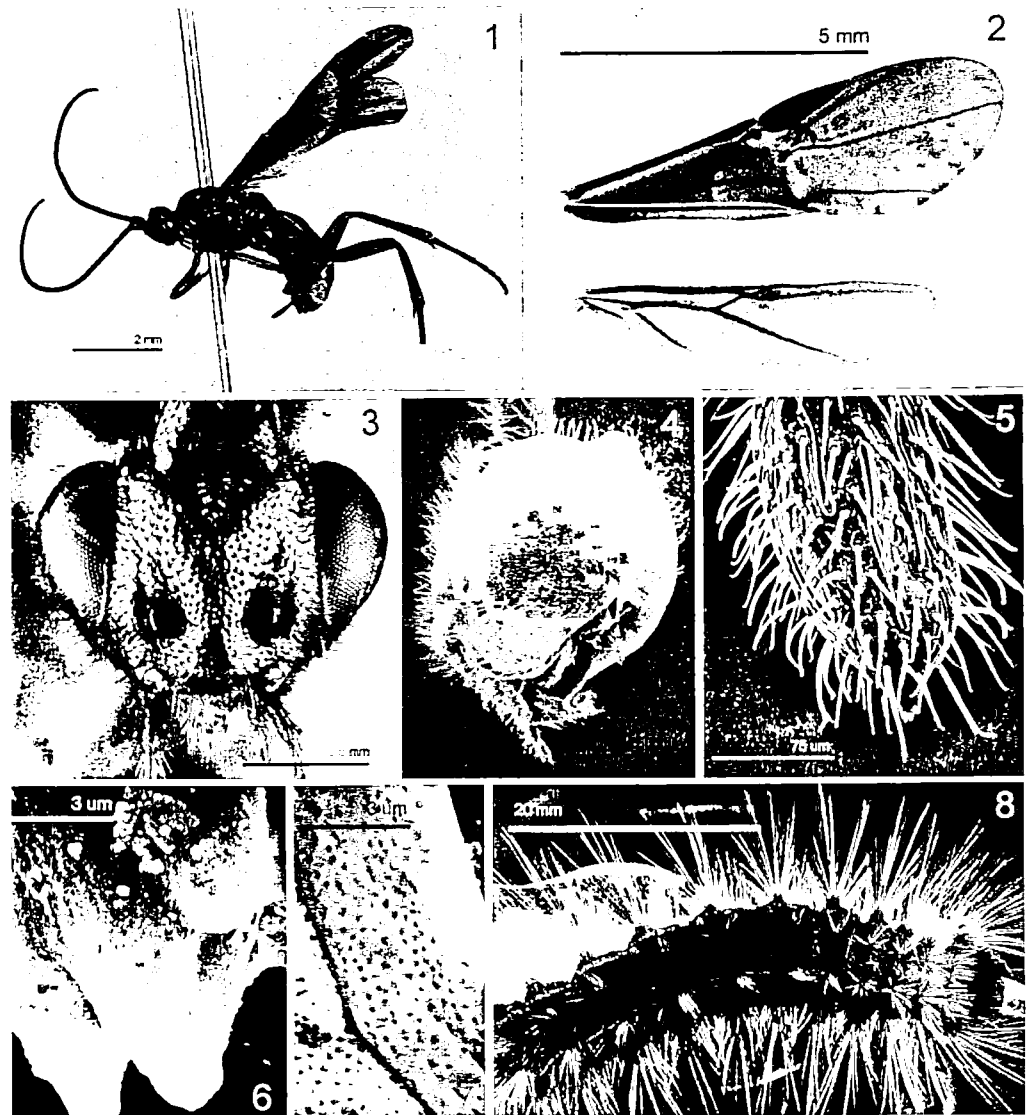
Material examined

Holotype female: 1 ♀, (label 1) COSTA RICA, Guanacaste, Area de Conservación

Guanacaste, Sector Cacao, Estación Cacao, 1150 meters, Lambert coordinates: North 323104 East 375725, (Lat 10.92691, Long -85.46822), jul/15/1999, Mariano Pereira collector, voucher 99-SRNP-1161 <http://janzen.sas.upenn.edu> (label 2) Ex *Euglyphis* sp Janzen14, (Lasiocampidae), feeding on *Beilschmiedia costaricensis* (Lauraceae), (D. Janzen's database 99-SRNP-1161 <http://janzen.sas.upenn.edu>). Caterpillar prepupal date 3 August 1999, 19 tightly packed, elongate, large, white/gray cocoons completely filling the host cocoon, not silked together. Eclosed on 22 August 1999. Deposited in the Instituto Nacional de Biodiversidad, Costa Rica (INBIO). **Paratypes:** 4 ♂♂, 14 ♀♀, same data as holotype and from same brood; 1 ♀, MEX: Veracruz, Fortín de las Flores, XII-22-63/Blacklight L. R. O'Brien collector, Insect Collection Los Angeles County Museum of Natural History. Paratypes deposited at INBIO, Instituto de Ciencias Naturales of the Universidad Nacional de Colombia, American Entomological Institute, Hymenoptera Institute, University of Kentucky Insect Collection, and Los Angeles County Museum of Natural History.

Morphology. The acuminate apex of the last antennal flagellomere is composed of six tubular projections (Fig. 5) and, although their shape strongly suggests a sensorial function, high resolution images (Figs. 6) indicate that these processes are devoid of any appreciable sensory structure for chemical reception such as the placoid sensillae or the pores present in other parts of the antenna (Figs. 5, 7). The surface of these tubular projections instead is completely smooth and solid (Fig. 6). These structures may be sensory organs to test physical characteristics such as surface vibrations.

This shape of the last antennal flagellomere is characteristic of all species of the genus, and of the nominal Neotropical genera *Biroia* Szépliget, *Hemichoma* Enderlein, and *Dichelosus* Szépliget. We have also observed this trait in the Afrotropical

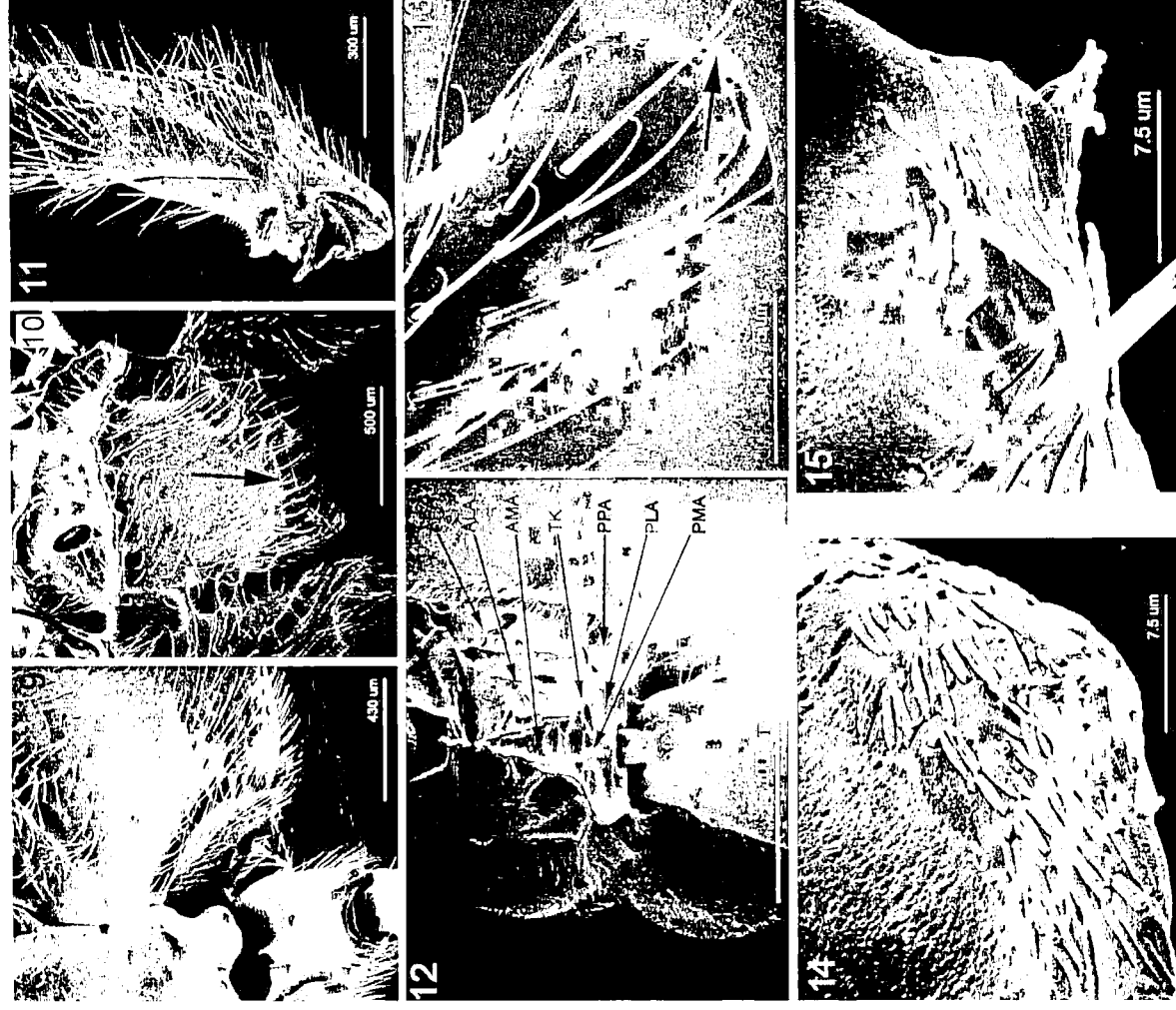


Figs. 1-8. *Coccygidium gregarium* n. sp.: 1, habitus; 2, wings; 3, head in anterior view; 4, head in lateral view; 5, terminal or last antennal flagellomere; 6, close up of the apex of the last flagellomere; 7, detail of the surface of the antenna far from the apex, note the evenly distributed multiple pores; 8, Habitus of *Euglyphis* Janzen 14, host larva of *C. gregarium* n. sp.

genus *Hyrtanommatus* Enderlein. This character, in conjunction with the carinate hind trochantellus, suggests a monophyletic clade comprised of these genera (Sarmiento & Sharkey, in prep).

The process on the ovipositor sheath is present on most species of *Coccygidium* and in the nominal Neotropical genera

listed above, but not in the Afrotropical genus *Hyrtanommatus*. SEM images reveal that this process and most of the sheath apex are covered by ampulliform papillae (Figs. 14-15). In addition, the internal side of the sheath is covered with pores which may indicate the presence of a secretory system. Previous studies have



Figs. 9–15. *Coccysidium gregarium* n. sp.: 9, epicnemial carina; 10, meta-epimeron (the arrow points to the juxtacoxal carina); 11, carina of hind trochantellus; 12, dorsal view of metanotum and propodeum (APA = anteropleural areola, ALA = anterolateral areola, AMA = anteromedial areola, TK = transverse keel, PPA = posteropleural areola, PLA = posterolateral areola, PMA = posteromedial areola); 13, ovipositor sheath (the arrow points to the apical process); 14, apex of ovipositor sheath, medial (internal) view showing the ampulliform papillae (see text); 15, apex of ovipositor sheath, lateral (external) view.

reported the presence of several types of sensory organs on both the ovipositor and the ovipositor sheath of the Hymenoptera (Quicke et al. 1999, Vilhelmsen 2003), but this is the first report of ampulliform pa-

pillae. Their function is unknown but possibly they are used to mark hosts with chemical secretions, or they may be sensory structures to test host suitability.

Biology: This is the first gregarious spe-

cies reported for the subfamily Agathidinae. Nineteen adult wasps emerged on 19 August 1999 from a cocoon of *Euglyphis* sp. Janzen14 (Lasiocampidae) (Fig. 8). The lasiocampid cocoon was filled with 19 elongate tightly packed large white/gray silk cocoons that were, however, not silked, glued, or otherwise attached to each other. The wasp larvae emerged from the prepupa of the host as is typical for all known species of Agathidinae. The lepidopteran larva (Fig. 8, and also images at <http://janzen.sas.upenn.edu>, voucher code 99-SRNP-1161) was collected as a penultimate instar on 15 July 1999, and spun on 3 August 1999, in the full rainy season. Its food plant, *Beilschmiedia costaricensis* Mez & Pittier, is among the many lauraceous trees fed on by at least 10 species of *Euglyphis* Huebner in this rainforest—cloud forest intergrade located on the western slope of Volcán Cacao, Area de Conservación Guanacaste (ACG), northwestern Costa Rica. The two localities where specimens of *C. gregarium* have been collected, Estación Cacao and Fortín de las Flores (Mexico), are extremely similar in their climate and in their original vegetation/ecosystem (personal observation, D.H.J.), despite being respectively on the Pacific and Atlantic coasts of Central America and being separated by several thousand kilometers.

Through 2002, the 24-year-old ongoing lepidopteran larvae inventory of the ACG (e.g., Burns and Janzen 2001, Janzen 2003, Janzen et al. 1998, 2003, Schauuff and Janzen 2001, Sharkey and Janzen 1995) has reared 1,452 wild-caught lasiocampid larvae, 98% of which are members of 20+ species of *Euglyphis*, without any other rearings of *C. gregarium*. Indeed, these larvae only produced 21 other hymenopterous parasitoids, all of which are representatives of a single undescribed species of Microgastrinae (*Parapanteles* "par22", Braconidae, det. Alejandro Valerio). Since this species of *Euglyphis* (Janzen14) has not been found either previously or subse-

quently by the inventory, it is either a very rare species or one that normally lives in the crowns of tall trees. These traits may apply to *Coccygidium gregarium* as well.

ACKNOWLEDGMENTS

We thank P. Southgate (U. of Kentucky) for the SEM images. Debra Murray (U. of Kentucky) and the two reviewers for their insightful comments. This research was supported by NSF grants DEB 9972024 and 0205982 to M. Sharkey and B. Brown (L. A. County Natural History Museum), and by NSF grants 8307887, 8610149, 9024700, 9306296, 9400829, 9705072, and 0072730 to D.H.J. We thank the parataxonomists in the ACG for collecting, rearing, and by entering the information about these larvae and their parasitoids in the data base. This is paper 04-08-059 of the Kentucky Agricultural Experiment Station.

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