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A new species of *Gonatocerus* (Hymenoptera: Mymaridae) parasitic on proconiine sharpshooters (Hemiptera: Cicadellidae) in the New World

SERGUEI V. TRIAPITSYN[1], DANEL B. VICKERMAN[1], JOHN M. HERATY[1] & GUILLERMO A. LOGARZO[2]

[1]*Department of Entomology, University of California, Riverside, California, 92521, USA. E-mail: serguei.triapitsyn@ucr.edu; danel.vickerman@ucr.edu; john.heraty@ucr.edu*
[2]*USDA-ARS South American Biological Control Laboratory, 3130 Buenos Aires Place, Washington, D.C. 20521-3130, USA. E-mail: glogarzo@speedy.com.ar*

Abstract

A new species of *Gonatocerus* Nees (Mymaridae) is described from the states of San Luis Potosí and Tamaulipas in Mexico, with additional records from Argentina and Peru. Type specimens of *G. uat* S. Triapitsyn **sp. n.** were reared in Mexico from the eggs of proconiine sharpshooters (Cicadellidae: Cicadellinae: Proconiini) in the genera *Homalodisca* Stål and *Oncometopia* Stål. Taxonomic and molecular evidence from five gene regions (28S-D2, ITS1, ITS2, COI, COII) is provided to help differentiate the new species from the morphologically similar taxon, *G. ashmeadi* Girault, which also belongs to the *ater* species group of *Gonatocerus*.

Key words: Mymaridae, *Gonatocerus*, taxonomy, Proconiini, egg parasitoid, molecular, parsimony

Introduction

Gonatocerus Nees is a large, speciose, and common genus of Mymaridae (Hymenoptera). Huber (1988) provided an overview of the genus and revised two of its species groups in North America. Many members of the *ater* species group are known to be egg parasitoids of various proconiine sharpshooters (Cicadellidae: Cicadellinae: Proconiini) (Triapitsyn 2002a, 2002b; Triapitsyn *et al.* 2002). In the course of a "classical" biological control program against the glassy-winged sharpshooter, *Homalodisca coagulata* (Say) (Triapitsyn & Hoddle 2001, 2002), a new species of *Gonatocerus* was reared in Tamaulipas, Mexico, from eggs of at least two undetermined species of *Homalodisca* Stål and *Oncometopia* Stål, likely from some of those mentioned by Coronado-Blanco *et al.* (2000). The new species was first believed to be a mere color variant of the common and

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well-known Nearctic species *G. ashmeadi* Girault (Triapitsyn *et al.* 2002), but later examination of additional, better preserved specimens from Tamaulipas and San Luis Potosí revealed that they represent an undescribed species (Logarzo *et al.* 2003), which is described herein as *G. uat*. Molecular data further confirm its identity as a species distinct from *G. ashmeadi* and also its likely conspecificity with forms from Argentina and Peru, identified previously as *G.* sp. near *ashmeadi* (Logarzo *et al.* 2003). The Argentine form of the latter was shown to be genetically different from the North American *G. ashmeadi* (de León 2004).

Material and methods

Taxonomy

Gonatocerus is a well-known genus and its generic diagnosis is available elsewhere (Huber 1988). Terms for morphological features are those of Gibson (1997). Acronyms for depositories of specimens are as follows: CNCI, Canadian National Collection of Insects, Ottawa, Ontario, Canada; EMUT, Entomological Museum, Centro de Investigación, U.A.M. Agronomía y Ciencias, Universidad Autónoma de Tamaulipas, Ciudad Victoria, Tamaulipas, Mexico; UCRC, Entomology Research Museum, University of California, Riverside, California, USA; USNM, National Museum of Natural History, Washington, D.C., USA. An abbreviation used in the text is: F = antennal funicle segment (female) or antennal flagellar segment (male).

Sequencing

Insects for molecular analysis were from the same collections as those obtained for morphological analysis described below. Chelex extraction of DNA, polymerase chain reaction (PCR) amplification and sequencing of the ITS1, ITS2, COI and COII gene regions were performed as described in Vickerman *et al.* (2004). The same protocols were followed for DNA extraction, PCR and sequencing of the 28S-D2 gene region except for the PCR cycling program, which was 3 min at 94° C, followed by 30 cycles of 45 sec at 94° C, 30 sec at 55° C, 1 min 30 sec at 72° C, and a final extension phase for 30 min at 72° C, using primers from Campbell *et al.* (2000). The 28S-D2 gene region was shown to be a good species marker in the Chalcidoidea and other Hymenoptera due to its slow rate of evolution (Campbell *et al.* 1993, Campbell *et al.* 2000, Babcock & Heraty 2000). For comparison, the 28S-D2 region was also sequenced for *G. ashmeadi* parasitoids from California, Florida, Hawaii, Louisiana, Texas, Georgia, and South Carolina (USA) and Tamaulipas (Mexico), collections described in Vickerman *et al.* (2004), as well as from Hawaii (Keehi Lagoon Beach Park, Honolulu, collected by R. Bautista 9.iii.2005, emerged 11.iii.2005, insect host *H. coagulata*, plant host *Bucida buceras*, Combretaceae). The 28S ribosomal region is considered to sustain a slow rate of mutation, and is more conserved than the ITS or Cytochrome Oxidase regions (Heraty 2004).

Three outgroup mymarid genera were included in the analysis for 28S-D2 only (*Ceratanaphes* sp., *Acmopolynema varium* (Girault), and *Borneomymar madagascar* Huber). Within *Gonatocerus*, four outgroup species were chosen (*G. fasciatus* Girault, *G. morrilli* (Howard), *G. novifasciatus* Girault and *G. triguttatus* Girault). Three populations of *G. uat* (Argentina, Mexico and Peru) and eight populations of *G. ashmeadi* (USA including Hawaii, and Mexico) were treated as the ingroup. All sequences are based on extractions from single individuals, except *G. triguttatus*, which was sequenced for a second individual for 28S-D2, which was identical for this region. ITS regions for outgroup taxa were not included in the analysis because of high sequence divergence and difficulty of alignment. Secondary vouchers (compared to specimens sequenced) are housed in UCRC. Nucleotide sequences for *G. uat* were deposited in Gen Bank under accession numbers: AY953522-AY953524, AY953536-AY953541 and AY956449-AY956462; sequences for 28S-D2 of *G. ashmeadi* and other outgroup taxa: AY953525-AY953535 and DQ167220; sequences of *G. ashmeadi* (Hawaii): DQ167222, DQ167224, DQ167226-DQ167227 and DQ167230-DQ167231. Nucleotide sequences for COI, COII, ITS1 and ITS2 of *G. ashmeadi* and other outgroup taxa can be found in GenBank under the following accession numbers: AY541069-AY541076; AY541080-AY541088, AY542705-AY542720 and AY542728-AY542740 from Vickerman *et al.* (2004).

Analysis

The 28S-D2 ribosomal sequences were aligned using a secondary structure model (Gillespie *et al.* 2005), with ambiguous regions, as defined by the model, aligned by eye. The nuclear internal spacer regions (ITS1 and ITS2) and mitochondrial cytochrome oxidase regions (COI and COII) were aligned in ClustalX and then optimized by eye. No gaps were present in the mitochondrial regions.

The dataset included 28S-D2 (935 aligned bases [AB], 107 parsimony uninformative [PU], 145 parsimony informative [PI]), ITS1 (705 AB, 17 PU, 36 PI), ITS2 (904 AB, 37 PU, 40 PI), COI (991 AB, 81 PU, 99 PI), and COII (608 AB, 45 PU, 32 PI). Using the χ^2 test implemented in PAUP*, there was a significant base composition bias (ACGT = 0.35, 0.10, 0.11, 0.45) for the mitochondrial regions, but none for the nuclear regions. The aligned matrix, including morphological data, is available online at http://www.treebase.org.

Parsimony analyses were done using PAUP*4.0ß10 (Swofford 2000) using the Branch and Bound search algorithm. Two analyses were performed using 28S-D2 alone, and another with all gene regions combined. The three genera of Mymaridae were used as the outgroup. Constant sites were included in all analyses, and gaps were treated as missing. Successive approximation character weighting was applied to the resulting trees using the maximum value of the rescaled consistency index and a base weight of 1000, with the resulting tree rescaled to unity character weights and compared in length to the most parsimonious tree (Carpenter 1988, Heraty 2002). Bootstrap support was evaluated with

1000 replicates, with each replicate starting from a random tree. A likelihood analysis was performed using PAUP with all parameters estimated from a Neighbor-Joining start tree. Character state changes were optimized on the parsimony tree topologies using MacClade 4.0 (Maddison & Maddison 2000).

Results and discussion

Taxonomy

***Gonatocerus uat* S. Triapitsyn, sp. n.**
(Figs 1–5)

Type material

Holotype female on slide [UCRC], labeled: 1."MEXICO, San Luis Potosí, Ciudad Valles, 28.iii.2001, D. Morgan, C. Pickett, S. Myartseva, A. Ríos. Ex. *Homalodisca* sp. egg mass on hibiscus leaf. S & R 01-05-10-A. Mounted by V. Berezovskiy 2001 Canada balsam"; 2. (red) "*Gonatocerus uat* S. Triapitsyn HOLOTYPE female". Paratypes: MEXICO. San Luis Potosí, Ciudad Valles, same data as holotype [1 female on slide, CNCI]. Tamaulipas: Gómez Farías, 23°02’56’’N, 99°09’24’’W, 26.iii.2001, D. J. W. Morgan, C. Pickett, S. N. Myartseva, A. Ríos (ex. *Oncometopia* sp. egg mass) [1 female in ethanol, kept in a freezer, UCRC]; 28.iii.2001, D. J. W. Morgan, C. Pickett, S. N. Myartseva, A. Ríos (ex. *Oncometopia* sp. egg mass) [1 female on slide, UCRC]; 13.iii.2003, S. V. Triapitsyn, E. Ya. Shouvakhina, S. N. Myartseva (ex. *Homalodisca* sp. or *Oncometopia* sp. egg masses on orange leaves; emerged 15.iii.2003 in Ciudad Victoria, Tamaulipas) [2 females on slides (except mesosoma of one of them on stub for SEM), E MUT, UCRC; 2 females on points, UCRC, USNM; and 1 male on slide, UCRC].

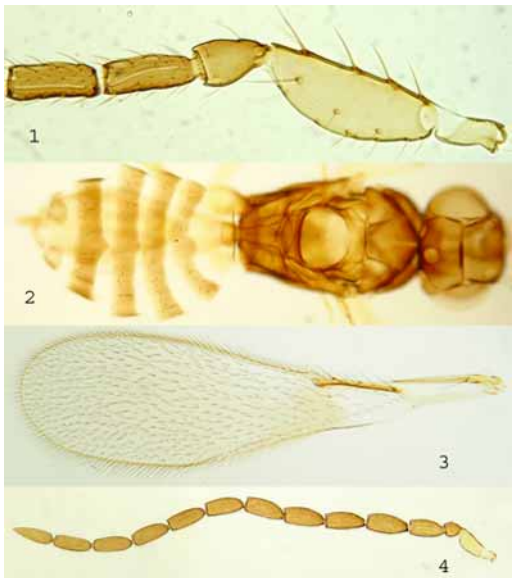
Additional material examined [all in UCRC]

ARGENTINA. Jujuy, Santa Clara: 24.i.2001, G. Logarzo, 4 females, 3 males (ex. sentinel eggs of *Tapajosa rubromarginata* (Signoret) on citrus); 12–21.ii.2002, G. Logarzo, 4 females, 1 male (ex. sentinel eggs of *T. rubromarginata*, died on route to USDA-APHIS Mission quarantine laboratory in Edinburg, Texas, USA); 13.iv.2003, G. Logarzo, 1 female (ex. egg mass of an unidentified proconiine sharpshooter on mandarin). Originally from: Tucumán, Tafí Viejo, 1–18.iii.2002, E. Virla (ex. sentinel eggs of *T. rubromarginata* on lemon), first generation progeny of an unfertilized female (23 males, emerged 17.iv.2002) in USDA-APHIS Mission quarantine laboratory in Edinburg, Texas, on eggs of *H. coagulata*. MEXICO. Tamaulipas, Llera de Canales, 23°18’58’’N, 99°01’30’’W, 8.iii.2000, L. G. Bezark, S. V. Triapitsyn, 1 female, 1 male (ex. proconiine sharpshooter (*Homalodisca* sp. or *Oncometopia* sp.) egg mass on hibiscus leaf, emerged 23.iii.2000 in University of California, Riverside quarantine laboratory). PERU. Junín,

Chanchamayo, Genova (near La Merced), Fundo farm, G. Logarzo, L. Varone, 8 females, 1 male (ex. eggs of *Oncometopia* n. sp., *Pseudometopia amblardii* (Signoret) and *P. phalaesia* (Distant), caged 9–10.v.2002 on Satsuma mandarin (*Citrus reticulata* var. *satsuma*), emerged 17.v–3.vi.2002 in University of California, Riverside quarantine laboratory).

Description

FEMALE (holotype and paratypes)**.** Body length 1.6–2.0 mm. Head and mesosoma (Fig. 2) mostly dark brown except for face (light brown) and occiput (pale); mesosomal sternum with distinct, well-defined yellow streak between fore- and middle coxae, very similar to those in *G. ashmeadi*, as described by Huber (1988). Scape light brown, other antennal segments brown to dark brown. Legs mostly pale yellow, hind femur (distally only) and hind tibia notably darker (brown). Petiole light brown; gaster (Fig. 2) mostly pale, with 4 transverse brown bands on terga IV–VII and 2 brown spots on tergum VIII, tergum IX light brown; inner and outer ovipositor plates and cercal plates brown.

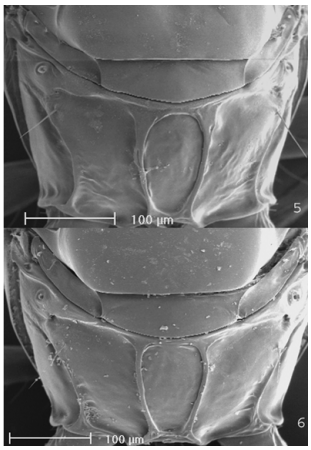


FIGURES 1–4. *Gonatocerus uat* (paratypes). (1) Scape, pedicel, and first two funicle segments of antenna (female); (2) Body (female); (3) Forewing (female); (4) Antenna (male).

Antenna with radicle about 2.3x as long as wide, scape (Fig. 1) about 2.7x as long as wide, almost smooth, with several rows of strong setae; pedicel (Fig. 1) shorter than F1 and almost smooth; F1-F4 usually subequal in length but F1 and/or F3 sometimes a little shorter than F2, F5-F8 each progressively shorter than preceding funicle segment; F1 (Fig. 1) almost always with 2 longitudinal sensilla, rarely with 1 sensillum, F2-F8 each with 2 longitudinal sensilla; all funicle segments densely setose; clava with 8 longitudinal sensilla, about 2.8x as long as wide, a little wider than scape (in lateral view), and nearly as

long as combined length of F1-F3; its ventral surface covered with numerous minute, short setae and placoid sensilla, its dorsal surface densely covered with longer setae.

Pronotum divided medially, each lobe with 2 dorsal and 1 lateral setae. Mesoscutum much wider than long, a little shorter than scutellum; midlobe of mesoscutum with a pair of strong setae. Dorsellum of metanotum (Fig. 5) with posterior margin slightly angulate medially. Propodeum (Fig. 5) with well-developed lateral carinae and slightly curved submedial carinae (meeting near anterior and posterior margins of propodeum, notably wider anteriorly); propodeum almost smooth between submedial carinae but slightly wrinkled (posteriorly only) between submedial and lateral carinae. Foretibia with 3–7 conical sensilla. Forewing (Fig. 3) 3.4–3.7x as long as wide; marginal setae short, the longest marginal seta about 1/5 maximum wing width. Forewing disc notably infuscated beyond venation, bare behind submarginal vein, with several scattered setae behind marginal and stigmal veins, cubital row of setae complete, remainder of blade densely setose. Submarginal vein with 1 macrochaeta, marginal vein with 5 or 6 microchaetae between proximal and distal macrochaetae. Hind wing 16–17x as long as wide, the blade bare except for the usual two complete rows of setae along margins and several scattered setae at apex and behind tip of venation.



FIGURES 5, 6. Scutellum (posterior part only), metanotum, and propodeum (female, scanning electron micrographs, magnification 200x). (5) *Gonatocerus uat* (San Luis Potosí, Mexico); (6) *Gonatocerus ashmeadi* (Tamaulipas, Mexico).

Petiole almost as long as wide, subquadrate. Ovipositor about 3/4 length of gaster, barely exserted beyond its apex. Ovipositor:mesotibia ratio 1.0–1.1. Outer plates of ovipositor each with 1 distal seta.

Measurements of the holotype (in µm, as length, or length:width ratios). Body 2005; head 283; mesosoma 695; petiole 76; gaster 1027; ovipositor 558. Antenna: radicle 78; scape 191; pedicel 76; F1 97; F2 107; F3 95; F4 100; F5 92; F6 82; F7 76; F8 68; clava 276. Forewing 1596:474; longest marginal seta 97. Hind wing 1107:49; longest marginal seta 102.

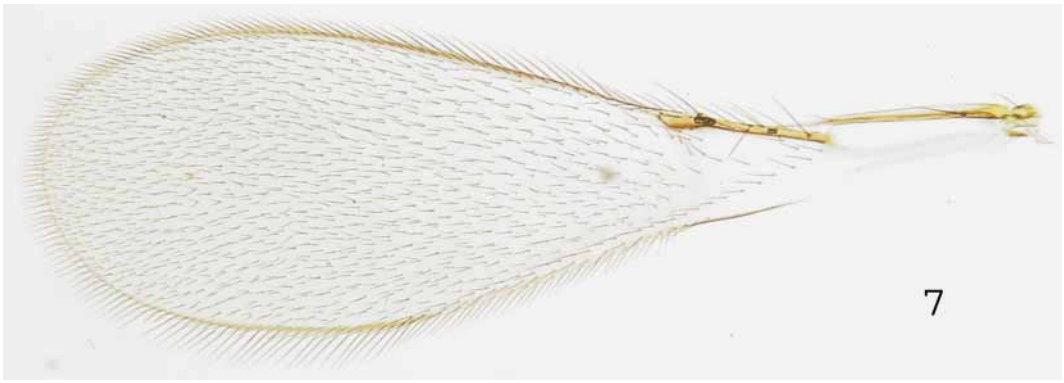


FIGURE 7. Forewing of *Gonatocerus ashmeadi* (California, USA).

MALE (paratype on slide)**.** Body length (before slide-mounting) 1.4 mm. Similar to female in coloration. Antenna (Fig. 4) with scape and radicle fused, scape (excluding radicle) about 2x as long as wide; pedicel very small, basal flagellomeres a little wider than distal ones, all flagellomeres with numerous longitudinal sensilla. Forewing about 3.6x as long as wide; infuscation of its disc perhaps slightly less conspicuous than in female. Genitalia very similar to those in *G. ashmeadi*.

Etymology

This species is named after the Universidad Autónoma de Tamaulipas in Ciudad Victoria, Tamaulipas, Mexico, which is commonly abbreviated there as U.A.T.

Diagnosis

In Huber's (1988) key to the North American species of the *ater* group, *G. uat* would key to *G. ashmeadi*. The known distribution of *G. ashmeadi* is strictly within the Nearctic region (S. V. Triapitsyn, unpublished) whereas *G. uat* is mainly a Neotropical species; these two taxa might be sympatric only in the Ciudad Victoria area of Tamaulipas, Mexico. Although presently *G. ashmeadi* is not known South of Ciudad Victoria and *G. uat* is not known North of Llera de Canales; both locations are formally placed within the Nearctic region but have many Neotropical elements. The specimens of *G. ashmeadi* from Venezuela, mentioned by Huber (1988) but not examined by us (material is not available), thus probably belong to *G. uat.*

The following morphological features distinguish this new species from *G. ashmeadi*: F1 of female antenna (Fig. 1) almost always (in specimens from Mexico and Peru) with 2 longitudinal sensilla, rarely with 1 sensillum (always none in *G. ashmeadi*); the propodeum (Fig. 5) is slightly wrinkled (distal half only) between submedial and lateral carinae and the submedial carinae meet near anterior margin of propodeum, whereas in *G. ashmeadi* the propodeum (Fig. 6) is almost smooth between submedial and lateral carinae and the submedial carinae do not meet near anterior margin of propodeum; the submedial

carinae on the propodeum are notably wider anteriorly in *G. uat* than in *G. ashmeadi* (Figs 5, 6, respectively); the forewing disc is notably infuscated beyond the venation (Fig. 3), and more conspicuously so behind the tip of the marginal vein (hyaline or at most with a faint, uniform brownish tinge in *G. ashmeadi*, Fig. 7). Also, the female forewing of *G. uat* from Mexico (length:width ratio 3.4–3.7, 3.5–3.6 in most specimens) is somewhat narrower than that of *G. ashmeadi* (length:width ratio 3.0–3.4, 3.2–3.3 in most specimens). *Gonatocerus uat* is morphologically very similar to and, as we conclude from the molecular evidence presented below, conspecific with the forms from Argentina and Peru, which were tentatively identified previously as *G.* sp. near *ashmeadi* by Logarzo *et al.* (2003). Neither the Mexican nor Argentine nor Peruvian specimens of *G. uat* match the descriptions and available types of any of the numerous species of *Gonatocerus* from Argentina and elsewhere in South America described by A. A. Ogloblin and others.

Variation. The forewings of *G. uat* from Argentina and Peru are somewhat wider (length:width ratio about 3.1) than from Mexico (length:width ratio 3.4–3.7). As reported by Logarzo *et al.* (2003), the Peruvian specimens of *G. uat* displayed a dramatic body size variability, which was apparently host-induced; body length of dry-mounted females reared from the very large eggs of *Oncometopia* n. sp. was 1.9–2.1 mm whereas for individuals reared from the notably smaller eggs of *Pseudometopia amblardii* (Signoret) and *P. phalaesia* (Distant) it was 1.4–1.5 mm (also very similar to the body size of females reared at the University of California, Riverside quarantine laboratory on a factitious host, *H. coagulata*). The body length of dry-mounted females from Argentina, reared from the even smaller eggs of *Tapajosa rubromarginata* (Signoret), was also significantly less (1.0–1.2 mm) than of those reared from all of the larger, aforementioned hosts. In the smaller specimens from Argentina, often F1 and sometimes F2 of the female antenna lack one or both longitudinal sensilla.

DNA Sequences

Although *G. ashmeadi* and *G. uat* may be sympatric (possibly in the Ciudad Victoria area of Tamaulipas, Mexico), molecular evidence demonstrates a clear distinction between the two species. A single most parsimonious (MP) tree resulted from both the analysis of 28S-D2 alone (Fig. 8) and for all of the gene regions combined (Fig. 9). Both analyses were stable to successive weighting (same MP tree retrieved). The 28S-D2 tree (length 396, c.i. 0.75, r.i. 0.77) showed no difference between populations of *G. ashmeadi*, and demonstrated only a single base difference between the Argentina, Peru and Mexico populations of *G. uat*. The single 28S substitution supporting a relationship between the Mexican *G. uat* and *G. ashmeadi* is homoplasious, with the same state (cytosine) also found in *G. fasciatus* and *G. novifasciatus* (thymine in all other taxa). Outgroup relationships generally had high bootstrap support, although less so between *G. ashmeadi* and *G. uat* (Fig. 8). Relationships among the outgroup genera and species of *Gonatocerus*

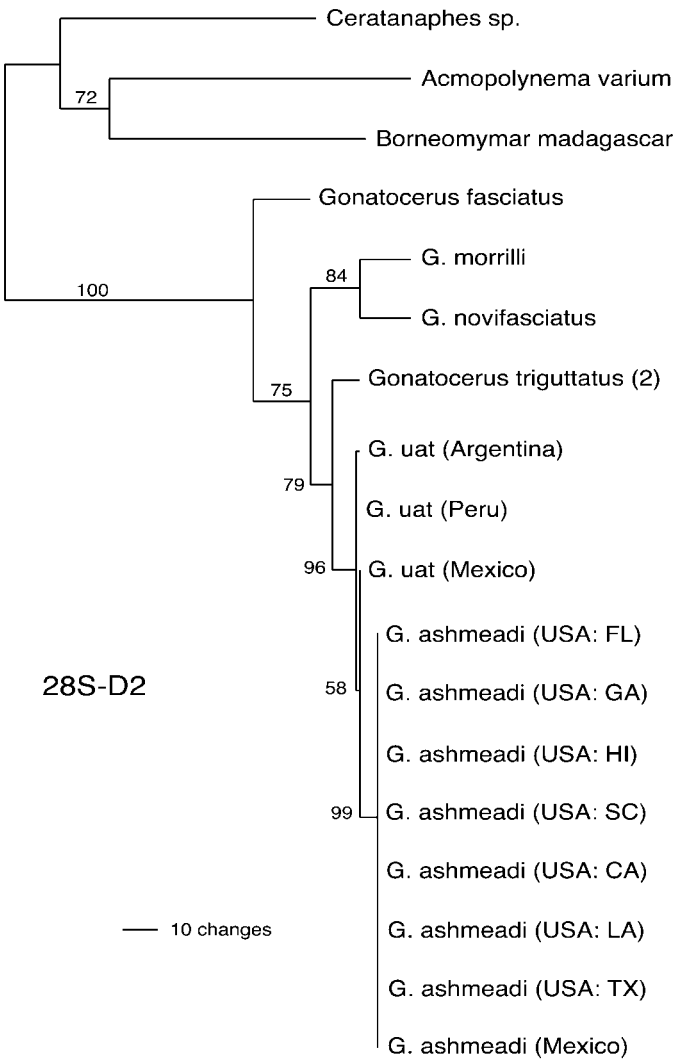
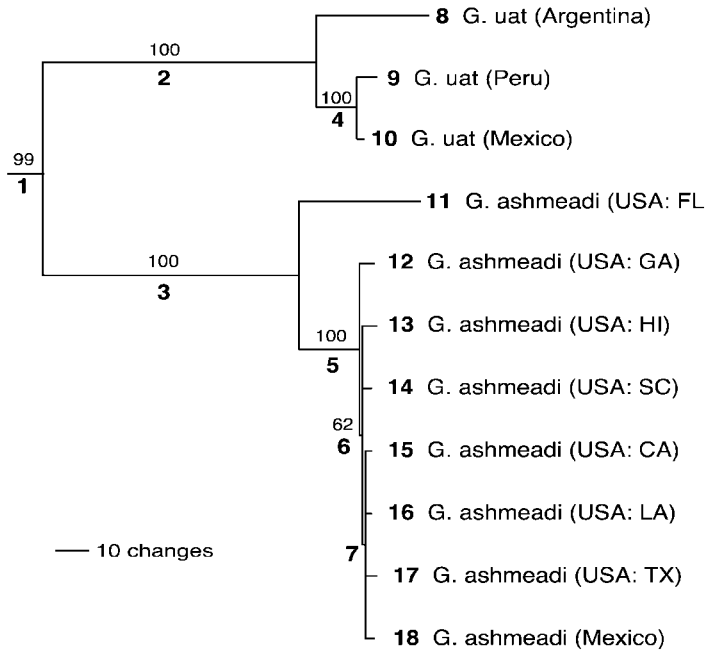


FIGURE 8. Single most parsimonious tree for 28S-D2 (length 396, c.i. 0.75, r.i. 0.77). Bootstrap values indicated above or beside branches.

were the same in the 28S and combined gene analyses. There was no bootstrap support for the relationships between *G. morrilli*, *G. novifasciatus* and *G. triguttatus* in the combined analysis, which may be due to the exclusion of ITS1 and ITS2 data for these species. The results of the combined analysis (length 885, c.i. 0.76, r.i. 0.83) are presented in Fig. 9, but with the outgroup taxa pruned from the figure. The Florida population of *G. ashmeadi* is very divergent from the other populations from the USA and Mexico, based largely on ITS2 and COI (branches 11 and 5, Fig. 9). The Georgia population differs by 5 base substitutions only in ITS1 (branches 12 and 6, Fig. 9). The remaining USA, including Hawaii, and Mexico populations differ by only a few substitutions, most of which occur in ITS1 or ITS2. The divergence between *G. ashmeadi* and *G. uat* are strongly supported by bootstrap analysis and by the concordant base changes in the mitochondrial regions (Fig.

9). The likelihood analysis produced the same resulting trees for both analyses as from parsimony and are not discussed further.



node	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
D2	5	0	5	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0
ITS1	-	-	-	1	0	1	0	8	1	0	1	4	3	2	0	0	0	0
ITS2	-	-	-	3	3	0	0	7	1	0	19	0	1	0	0	1	2	3
COI	18	18	14	6	10	0	0	9	4	1	9	0	0	0	1	0	0	0
COII	4	14	6	0	1	0	1	5	0	0	1	0	0	0	0	0	0	0

FIGURE 9. Single most parsimonious tree for 28S-D2, ITS1, ITS2, COI and COII (length 885, c.i. 0.76, r.i. 0.83); outgroups pruned from tree. Bootstrap values indicated above branches. Table presents unambiguous base substitutions (minimum number) for branches numbered on tree in boldface.

Molecular evidence supports the separation of *G. uat* from *G. ashmeadi* and also its generic similarity with the specimens previously identified as *G.* sp. near *ashmeadi* from Argentina and Peru (Logarzo *et al.* 2003). For the conserved ribosomal gene 28S-D2, all 8 geographically defined populations of *G. ashmeadi* were identical, but *G. ashmeadi* differed from *G. uat* from Mexico by 6 bp (Fig. 9), and from Argentina and Peru populations by 6 and 5 bp respectively (Fig. 9). The cumulative differences for all of the gene regions were much higher, with the Argentina and Mexico populations of *G. uat* differing by 40 bases (nodes 4, 8 and 9, Fig. 9) and between *G. uat* from Argentina and *G. ashmeadi* by 77 bases (nodes 2, 3 and 8, Fig. 9). The maximum divergence within *G. ashmeadi* was 34 base substitutions (nodes 11 and 12, Fig. 9). There was no distinct

morphological difference between the specimens from Peru and Argentina, which differed from *G. uat* by substitutions of 1 and 2 bp respectively.

In a previous study, an isofemale line (regional standard) of the *G. ashmeadi* population from California was crossed with isofemale lines from Texas, Louisiana and Florida using reciprocal crosses; all were found to be reproductively compatible despite the genetic divergence found between the California and Forida populations (Vickerman *et al.* 2004). All of the *G. ashmeadi* populations are identical for 28S-D2. The three individuals of *G. uat* differed by a single base for 28S-D2, which given the geographical range is extremely minor (Fig. 8). Live specimens of *G. uat* from Argentina, Mexico, and Peru were unavailable and therefore reproductive compatibility assays were not possible for these groups. However, overall the molecular divergence for the other gene regions is far less than for *G. ashmeadi* (Fig. 9), and this may lend credence to the notion that the three populations of *G. uat* are reproductively compatible and isolated from *G. ashmeadi*.

Acknowledgments

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