



<http://dx.doi.org/10.11646/zootaxa.3630.2.11>

<http://zoobank.org/urn:lsid:zoobank.org:pub:70C11335-A5F6-4BCB-98E6-4D14EB1A4015>

Jubogaster towai, a new Neotropical genus and species of Trogastrini (Coleoptera: Staphylinidae: Pselaphinae) exhibiting myrmecophily and extreme body enlargement

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Abstract

Jubogaster towai **gen. et sp. nov.** is described from a colony of *Pheidole xanthogaster* Wilson (Hymenoptera: Formicidae) in the Peruvian Amazon. The new taxon is amongst the largest pselaphine species known. Its transverse head implies an affinity with Trogastrini (Pselaphinae: Euplectitae), but *J. towai* lacks typical characters diagnostic for trogastrines and possesses others, such as a Jubini-like pronotum and equally-sized tarsal claws, that obscure its systematic relationships. To place *J. towai* phylogenetically, we sequenced a fragment of 28s rDNA for the new species and a range of other pselaphines, including members of Trogastrini and other tribes of Euplectitae. The topology produced by this analysis supports the inclusion of *Jubogaster* in Trogastrini, thereby indicating that morphology within this tribe can be more malleable than previously thought. Many of the largest pselaphine taxa are guests of social insect colonies. We discuss whether an evolutionary correlation (or causal relationship) exists between body enlargement and an inquilinous lifestyle in Pselaphinae.

Key words: phylogeny, beetles, Peru, ant

Introduction

The pselaphine tribe Trogastrini is comprised of two dozen genera distributed in Australia, Europe, the Nearctic and the Neotropics (Newton and Chandler 1989), with the latter region holding the greatest diversity of genera and species (Park 1942; 1952). Trogastrini are currently placed in the supertribe Euplectitae, based on their possession of contiguous, projecting metacoxae and an absence of characters diagnostic of other supertribes. The tribe as a whole has a distinctive facies. They are distinguished from other euplectite taxa by the transverse head, which is received ventrally by a prosternal excavation when held deflexed. In addition, a dense beard of long setae commonly adorns the genae, and most genera possess reduced or hair-like posterior tarsal claws (Chandler, 2001). Trogastrini also tend to show distinct medial-longitudinal and antebasal sulci on the pronotum. Ecologically, little is known about their biology; most taxa have been recovered from forest litter samples and decaying wood, and like other pselaphines, trogastrines are probably predatory on microarthropods. However, a handful are known to be guests of social insects. The three known species of *Phategnomus* Raffray are thought to be termitophilous, while one species each of *Conoplectus* Brendel, *Eurhexius* Sharp and *Mesoplatus* Raffray have been collected from ant colonies (Lea 1912; Bruch 1929; Carlton 1983).

Here, we add a new and highly distinctive neotropical genus and species to the Trogastrini. The new taxon is remarkable for its greatly enlarged body size and putatively myrmecophilous lifestyle. Furthermore, although exhibiting apparent synapomorphies with the Trogastrini, the new genus lacks several characters normally exhibited by this tribe, and possesses others that suggest an affinity with another euplectite tribe, Jubini. Given its curious suite of morphological features, we have placed the genus into the current tribal classification using 28s rDNA, an informative molecular marker for higher-level pselaphine systematics (J. Parker and A. Vogler,

unpublished data). Finally, based on our personal observations, we note that many of the largest pselaphine species are myrmecophiles and termitophiles. We discuss a possible relationship between the inquilinous lifestyle that has evolved numerous times within the subfamily, and its apparent correlation with increased body size.

Material and methods

Morphological description: For the purposes of describing the new taxon, the specimen was observed with a Zeiss SteREO Discovery.V12 microscope. Specimen images were obtained using a Canon EOS 60D and Canon MP-E65 2.8 1–5x macro lens, and montage images were produced using CombineZM. The foveation pattern used to describe *J. towai* follows the nomenclature developed by Park (1942), as modified by Chandler (2001).

Taxon sampling for phylogenetic analysis: The following taxa were used for the molecular phylogenetic placement of the new taxon:

PSELAPHINAE Latreille, 1802

Faronitae Reitter, 1882

Sonoma sp. (USA)

Euplectitae Streubel, 1839

Trogastrini Jeannel, 1949

Conoplectus canaliculatus (USA)

Rhexius sp. (USA)

Platomesus sp. (Australia)

Oropus castaneus (USA)

Rhexidius cuspidatus (USA)

Jubini Raffray, 1904

Jubus sp. (close to *J. vulpinus*; Costa Rica)

Barrojuba sp. (Costa Rica)

Sebaga sp. (Costa Rica)

Euplectini Streubel, 1839

Leptoplectus pertenuis (USA)

Trichonychini Reitter, 1882: Trichonychina Reitter, 1882

Foveoscapha terracola (USA)

Trichonychini Reitter, 1882: Panaphantina Jeannel, 1950

Biblopectus integer (USA)

Piptoncus duplex sobrinus (Russia: Kuril Islands)

Trichonychini Reitter, 1882: Trimiina Bowman, 1934

Melba thoracica (USA)

Bythinoplectini Schaufuss, 1890

Zethopsus sp. (Thailand)

Goniaceritae Reitter, 1882 (1872)

Brachyglutini Raffray, 1904

Rybaxis longicornis (UK)

Reichenbachia juncorum (UK)

Proterini Jeannel, 1949

Mechanicus sp. (Malaysia)

Batrisitae Reitter, 1882

Batrisini Reitter, 1882

Cratna sp. (Malaysia)

Pselaphitae Latreille, 1802

Pselaphini Latreille, 1802

Pselaphaulax sp. (Australia)

Tyrini Reitter, 1882

Lasinus imperialis (Russia: Kuril Islands)

Ctenistini Blanchard, 1845

Ctenisodes sp. (USA)

OUTGROUPS: **Silphidae:** *Silpha obscura* Genbank AJ810772.1 **Staphylinidae:** *Proteinus brachypterus* (Proteininae), *Euconnus* sp. (Scydmaeninae), *Euaesthetus ruficapillus* (Euaesthetinae).

DNA Extraction and sequencing: Ethanol-preserved specimens were vacuum dried and immersed in 200ml of an SDS-based extraction buffer (Gilbert *et al.* 2007). Specimens were incubated for 2 days at 55°C without destruction, but with occasional agitation of the tube. Following incubation, specimens were removed from the solution and total genomic DNA was extracted once with phenol/chloroform/isoamyl alcohol. The organic phase was then back-extracted with an equal volume of 50mM Tris+15mM NaCl, and the aqueous samples were combined, extracted again with phenol/chloroform/isoamyl alcohol, and extracted once more with chloroform. DNA was precipitated with 100% ethanol+3M NaOAc+10ug glycogen. A ~700bp region of 28s rDNA was amplified with Advantage 2 Polymerase Mix (Clontech), using the forward primer 28sDD (5'-GGGACCCGTCTTGAACAC) and reverse primers 28sFF (5'-TTACACACTCCTTAGCGGAT) or Pselaphinae-specific 28sFFPsel (5'-ACCGTCCTGCTGTCTTTAGTT). Amplifications ran for 45 cycles with an annealing temperature of 50°C. Amplicons were ligated into PCR-XL-TOPO vector (Invitrogen) for sequencing with M13F and M13R primers. Due to the low yield of DNA from such small beetles, and the high number of PCR cycles, all extractions and PCR reactions were set up in a tissue culture hood washed with DNA-OFF (Clontech) to safeguard against contamination.

Phylogenetic analysis: Partial 28s rDNA sequences were aligned in both MUSCLE (Edgar 2004) and ClustalX (Larkin *et al.* 2007) with default parameters, and the resulting matrix was analysed by maximum parsimony (MP) with 1000 bootstrap replicates in MEGA 5.0 (Tamura *et al.* 2011). Due to length-variability of 28s, sensitivity of the results to alignment parameters was assessed by repeating the MP analysis on a set of alignments produced in ClustalX with a range of gap opening and gap extension costs. For Bayesian analysis, the default MUSCLE alignment was imported into jModeltest 2.1.1 (Darriba *et al.* 2012) for substitution model selection. An unpartitioned analysis was conducted in MrBayes 3.2 (Ronquist *et al.* 2012) with two runs of three heated chains and one cold chain. Chains were sampled every 100 generations, with the first 25% of trees discarded as burn-in. The analysis was stopped after 200,000 generations when the standard deviation of split frequencies dropped below 0.01. All trees were rooted using *Silpha obscura* (Silphidae) as the designated outgroup.

Jubogaster gen. nov.

Type species. *Jubogaster towai* sp. nov. here designated.

Diagnosis. Euplectite pselaphines with the following characters: transverse head articulating ventrally under pronotum when deflexed, typical of Trogastrini. Head with vertex excavate, lacking vertexal fovea; ventral head without the typical dense “genal beard” of setae common to most Trogastrini. Eleven-segmented moderately geniculate antennae, received by large excavations anterior to eyes. Pronotum jubine-like: broad and obcordate, constricted at basal quarter, with weakly-evident medial longitudinal sulcus and distinct antebasal sulcus. Pronotum afoveate, with margins smooth, devoid of crenulations or small spines found in other Trogastrini. Elytra lacking any stereotypical fovea. Legs with contiguous, projecting coxae, broad femora, basally flattened tibia, and three tarsal segments; segment 1 very small, 2 and 3 elongate and subequal in length. Tarsi with two equally-sized claws, unlike other Trogastrini which have unequally-sized claws. Bifid anterior protarsal claw in the type species *J. towai*.

Etymology. A combination of *Jubus* Schaufuss and *Trogaster* Sharp, the type genera of Jubini and Trogastrini, respectively. The name is chosen on account of the membership of the new genus in Trogastrini, despite apparent Jubini-like characters such as the shape of the pronotum and the presence of two equally-sized tarsal claws (a character state found in Jubini, but not other Euplectitae). The bifid anterior protarsal claw of the type species *J. towai* is also shared with *Phamismus myrmophilus* Silvestri of Jubini.

Description. Body large (5.1mm for the type species *J. towai* shown in Figure 1). Body shape approximately ovoid and strongly convex.

Head: Approximately triangular, strongly transverse (Fig 4). Vertex afoveate, concave, with moderately deep excavation extending from basal quarter to anterior margin of frons; excavation narrowing apically along midline as it passes between raised frontolateral margins. Frontolateral margins carinate, extending roughly arcuately from posterior of antennal insertion cavity to clypeus (Fig 5). Frontolateral face accommodating large circular cavity anterior to eyes to receive antennae (Fig 5). Eye flanked directly anteriorly by additional large excavation for retracted maxillary palpus (Fig 5). Ventral surface of head bisected by longitudinal gular carina situated within broader gular sulcus terminating in gular fovea. Gular sulcus widens basally, spanning the head-neck interface. Maxillary palpi apparently 4-segmented, with segment II long and curved at apex, III short and triangular, wider than II, IV oval, approximately 2x longer than wide (Fig 5). Antennae (Fig 3) with 11 antennomeres, moderately geniculate with enlarged segment I. Antennomeres IX–XI strongly elongate (XI longest).

Thorax: Pronotum (Fig 4) obcordate, 2x wider than head, almost as wide as elytra. Afoveate, with smooth margins. Anterior margin broadly arcuate, largely obscuring the deflexed head when viewed from above, and constricted sharply in basal quarter, so that pronotum is laterally expanded into broad, blunt spurs with curved edges. Medial longitudinal sulcus present on pronotal disc, weakly impressed, thin, terminating at deeper, bow-shaped antebasal sulcus that extends between bases of mediolateral spurs. Prosternum afoveate, with lateral longitudinal carinae extending from sides of neck to base. Mesosternum with median mesosternal foveae (MMSF), lateral mesosternal fovea (LMSF) and lateral mesocoxal fovea (LMCF) present. Other typical pselaphine mesosternal fovea listed in Chandler (2001) lacking. Metasternum strongly convex. Lateral metathoracic foveae (LMTF) present; median metathoracic fovea (MMTF) absent.

Abdomen: Abdomen with tergites strongly convex. Visible segments 1–3 (IV–VI) subequal in length (Fig 1), segment 4 (VII) longest (not apparent in Fig 1 due to curvature of abdomen). Tergites 1–3 (IV–VI) with pronounced paratergites, 4 (VII) with small tapering paratergites. Tergite 6 (IX) internalised. Six sternites visible (Fig 2), sternite 7 (IX) internalised. First visible sternite (III) with median process projecting between metacoxae. Sternites 2 and 3 (IV and V) subequal in length, 4 (VI) slightly shorter (Fig 2).

Elytra: Strongly convex, slightly broader than pronotum (Fig 1), approximately 0.3x total body length. At their longest, equal in length to visible abdominal segments 2+3 (V+VI) combined. Elytral humeri broadly rounded to almost half elytral length. Sutural stria entire; lacking sutural fovea and other stereotypical antebasal fovea. Lacking subhumeral fovea and subhumeral stria. One weakly defined, somewhat discal depression is evident halfway between suture and humerus; its homology to canonical pselaphine antebasal elytral fovea is unclear.

Legs: All coxae contiguous (Fig 2), procoxae conical, projecting ventrally, mesocoxae globose, metacoxae (Fig 7) transverse-conical, spanning from ventral midline to metasternal margin, and projecting posteriorly. Femora somewhat thickened, and excavated apically to receive retracted tibia. Tibia flattened basally. Femora and tibia lacking spines or processes. Tarsi elongate, 3-segmented, first segment extremely short, 0.2x the length of segment 2. Segment 2 and 3 subequal in length. All tarsi with 2 well-developed, equally-sized tarsal claws. Bifid anterior protarsal claw in type species *J. towai* (Fig 8).

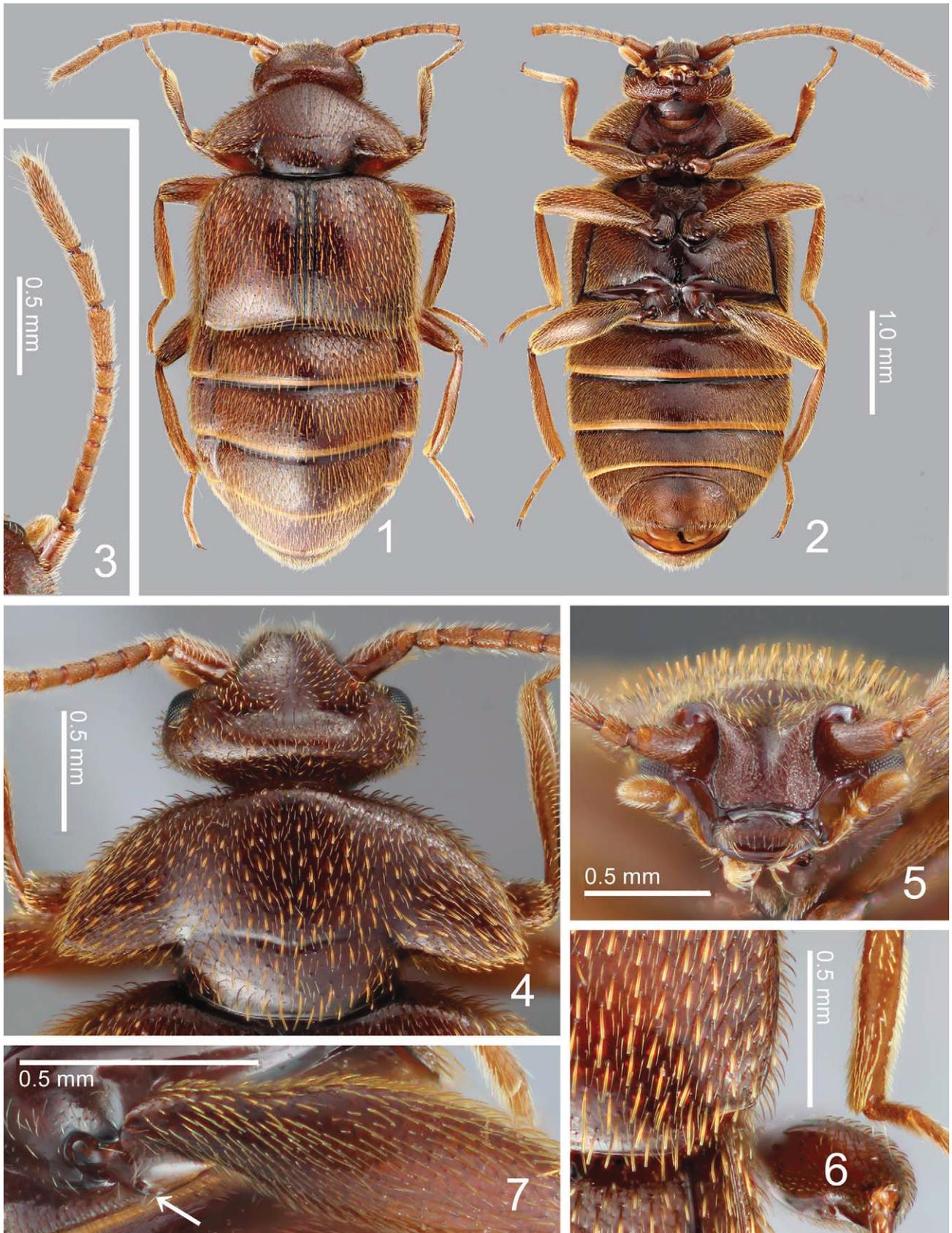
***Jubogaster towai* sp. nov.**

type material. Holotype, male, Peru, Satipo, Santa Ana, 25 I 2012, with *Pheidole xanthogaster* Wilson. Specimen deposited in Field Museum of Natural History, Chicago, IL, USA, with catalog number: FMNH-INS 0000 093 389.

Diagnosis. The sole known species of *Jubogaster* is highly distinctive among Trogastrini due to its greatly enlarged and robust body covered in thick, blunt golden setae, the unique concave head that lacks vertexal fovea, the large, circular excavations on the frons that receive the long, geniculate antennae, the absence of a genal beard, an afoveate pronotum and elytra, the two equally-sized tarsal claws, and the bifid anterior protarsal claw.

Etymology. The new species is named in honour of Towa Shimada, son of Taku Shimada, a remarkable collector of myrmecophiles.

Description. Body length 5.1mm (Fig 1). Colour dark reddish brown, antennae and legs somewhat lighter. Integument shiny. Most dorsal regions covered by conspicuous thick, erect, blunt golden setae, arranged at regularly spaced intervals and orientated posteriorly (depicted most clearly in figures 4–6). These are interspersed with shorter pubescence of the same colour, also orientated posteriorly. Ventral surfaces covered with fine, mostly aciculate golden pubescence (Fig 2).



FIGURES 1–7. *Jubogaster towai* Parker and Maruyama. 1) dorsal habitus 2) ventral habitus 3) left antenna, exterior face is to the left 4) vertex of head and pronotum 5) frontal of view of head, showing excavations for antennae and maxillary palpi 6) right elytron apical angle showing excision 7) left metacoxa, metatrochanter with arrow pointing to rhomboid-shaped tubercle.

Head: Eyes moderate in size. Transverse, triangular head (Fig 4) widest just behind eyes. Vertex and occiput uniformly setiferous with thick, blunt, erect golden setae, and shorter, sharper pubescence. Margins of large lateral cavities for antennal insertion and maxillary palp retraction carinate; interiors of cavities glabrous (Fig 5). Neck approximately 0.4x head width between eyes, shining and with sparse, very short dark setae on dorsal side; glabrous and with finger-print-like (“strigate”) microsculpturation on ventral side. Fourth segments of maxillary palpi (Fig 5) densely covered in short golden setae. Antennae (Fig 3) pigmented similarly to tibia and very elongate, approximately 2x pronotum length. Antennomere I conical, widest in basal half and equal in length to III+IV combined. Laterodorsal margin with short arcuate carina extending to one-quarter antennomere length. Lateral face glabrous in basal half. With circular apical notch to permit geniculation with II; II small and cylindrical, approximately 0.6x the length of III; III cylindrical-obconical, equal in length to IV; IV cylindrical, twice as long as wide; V slightly shorter and narrower than IV; V–VIII cylindrical-obconical, becoming gradually shorter apically, so that segment V is almost 2x longer than wide and VIII is as only slightly longer than wide; IX–X much larger, IX almost as long as VI–VIII combined; X slightly longer than VII+VIII combined. Both IX and X cylindrical-obconical, apical margins somewhat sloping interiorly due to slight lengthening of exterior antennomere face relative to interior face. Antennomere XI longest, twice the length of X; exterior face shallowly and evenly convex, interior face weakly concave before bending obtusely to form conical apex. Several long sensory setae on apical third (Fig 3).

Thorax: Pronotum (Fig 4) obcordate, margins smooth, lacking crenulations or other protuberances. Uniformly setiferous and pubescent. Prosternum with lateral longitudinal carinae abruptly bending dorsally on reaching base (Fig 2). Region between carinae with reduced setation and pubescence relative to lateral regions, and with small transverse projection situated medially, anterior to procoxae. Region between carinae projecting sharply in basolateral portions to receive procoxae. Mesosternum with setiferous median mesosternal foveae (MMSF) and lateral mesocoxal fovea (LMCF). Region anterior to mesocoxae formed into a shield-shaped plate with carinate margins. Anterior margin of metasternum carinate around mesocoxae. Convex metasternum with median declivity adjacent to metacoxal projections. Metasternum uniformly covered with yellow pubescence of intermediate length. Median declivity somewhat less pubescent. Lateral metasternal fovea small and setiferous. Posterior margin of metasternum bow shaped (Fig 2); projection between metacoxae with small medial indentation.

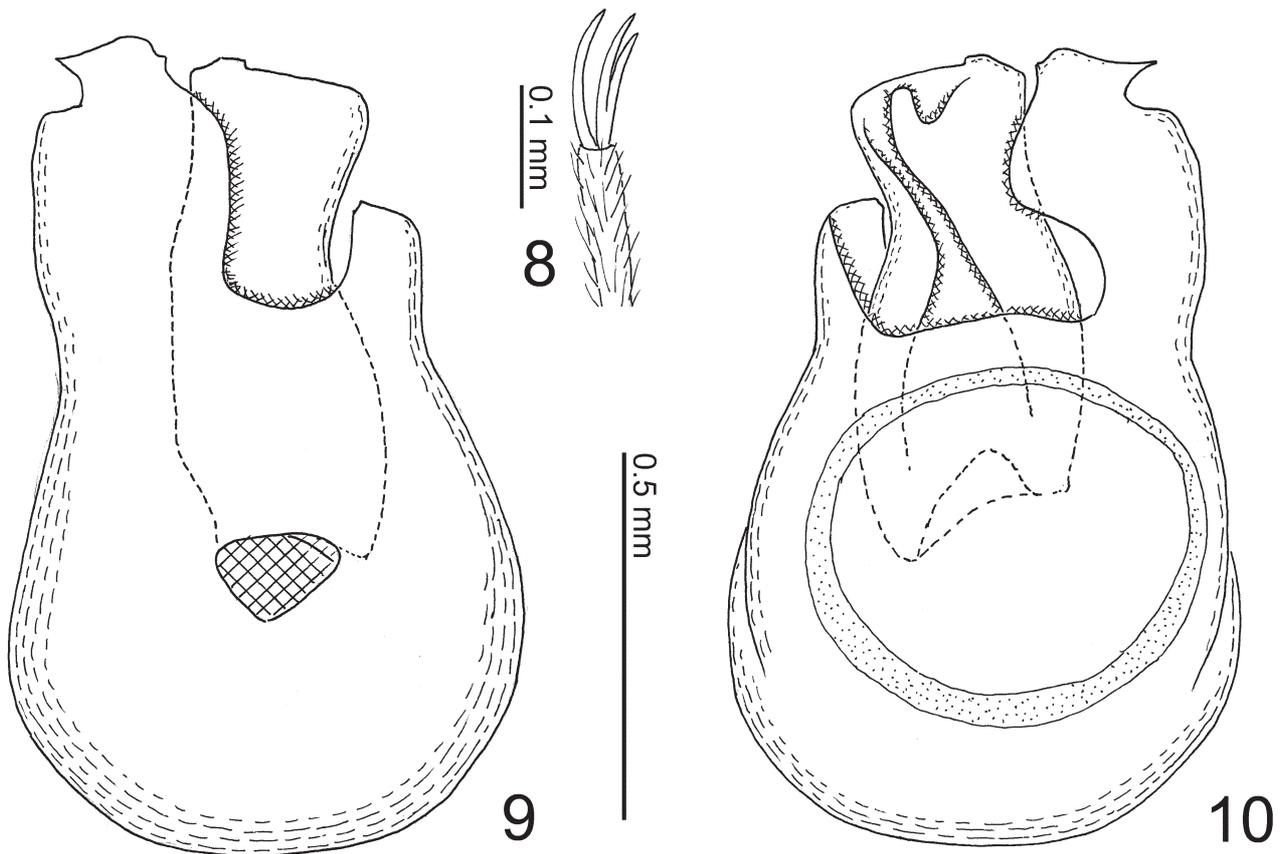
Abdomen: Tergites strongly convex with visible tergite 1 (IV) sloping to abdomen base. Visible tergite 2 (V) broadest, slightly broader than 1 (IV), with segments 3–5 (VI–VIII) evenly narrowing. Tergite 4 (VII) longest, approximately 1.5x tergite 3 (VI). Broad paratergites on segments 1–3 (IV–VI); paratergite margins of segment 4 converging apically to create a triangular paratergite. Anterior edges of abdominal tergites with narrow band of black pigment. Remainder of tergite reddish brown; intertergital membrane yellow with latticed microsculpture. Base of visible tergite 1 (IV) with short, blunt tubercles, situated halfway between midline and lateral margin. First visible sternite (IV) medially acuminate in anterior half, projecting ventrally between metacoxae. Last visible segment (6; VIII) with median declivity. Sternite 7 (XI) internalised. Pubescence on sternites 2–6 (IV–VIII) becoming finer and sparser toward midline (Fig 2).

Elytra: Blunt setae on elytra somewhat longer and slightly thicker than on other parts of body. Apicolateral angles of elytra with margins weakly excised (Fig 6).

Legs: Coxae contiguous. Mesocoxae with proximodistal carina along posterior face. Metacoxae glabrous except for pubescence on internal face and around projection to trochanter. Apices of metacoxae produced into flat, blunt spines that extend posteriorly to half trochanter length (Fig 7). Metatrochanters with small rhomboid-shaped tubercles on exterior face (Fig 7). Femora brownish red, covered with thick, blunt golden setae. Tibia somewhat flattened in proximal half, carinate along anterior edge to half-tibia length. Tibia lighter in colour than femora, yellowish brown, with similar but shorter setae. Tarsi narrow and longer than half tibial length; also yellowish brown, with fine, sharp, aciculate setae. Protarsus with bifid anterior claw (Fig 8).

Aedeagus: Asymmetric, broad, lacking parameres (Fig 9 and 10). Wide, globose basal bulb with asymmetric left and right apical projections. An asymmetric, apically-truncate sclerotised stylus emerges from within the basal bulb.

Biological and collection information. The single specimen of *J. towai* was collected in a colony of *Pheidole xanthogaster* Wilson under a log. The ants were apparently unaware of the beetle, which was found deep inside the nest. This suggests that *J. towai* is a true myrmecophile, but information about its biology and behaviour are unavailable at this time. It has no clear myrmecophilous adaptations, so may belong to the “obligate synoekete” class.



FIGURES 8–10. 8) apical protarsus showing bifid anterior protarsal claw 9) aedeagus, ventral view 10) aedeagus, dorsal view.

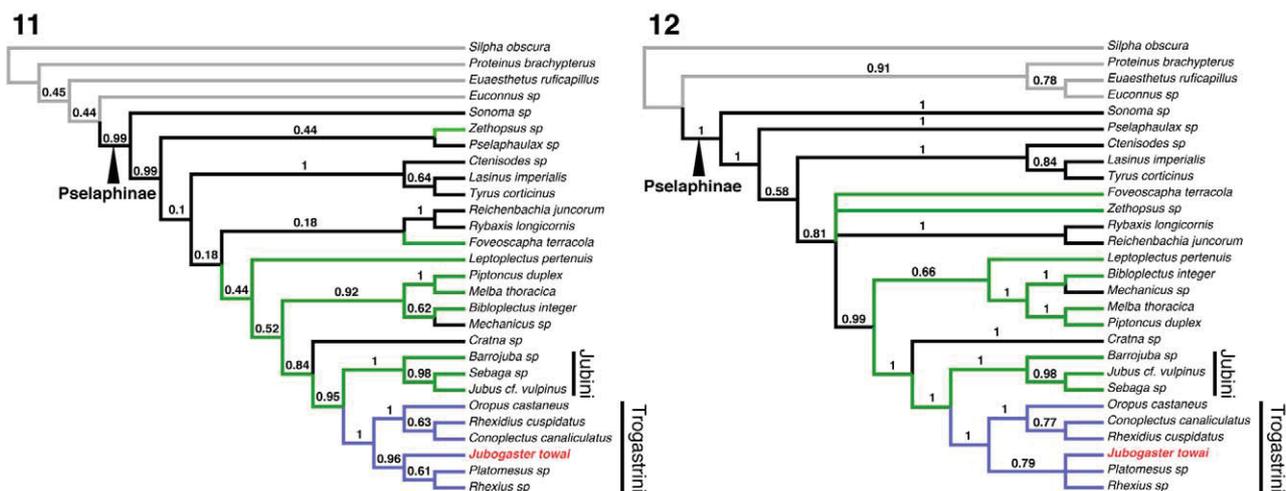
Comments. *J. towai* has distinctly internalised terminal tergites and sternites. The plesiomorphic condition in Pselaphinae is for visible sternite 7 (IX) to form a penial plate, flanked by left and right sclerites formed from visible tergite 6 (which is also segment IX). However, in *J. towai*, segment IX is internalized; in figure 2 the internal sclerites can be seen enclosed within the genital aperture. This arrangement makes segment VIII (visible sternite 6 and visible tergite 5) the posterior-most external segment. Don Chandler (University of New Hampshire) has kindly surveyed the character state of segment 7 (XI) and found internalisation to be relatively common in Trogastrini: in many genera the segment is not externally visible (*Rhexinia* Raffray, *Xerhius* Raffray, *Aporhexius* Raffray, *Rhexius* LeConte, *Eurhexius* Sharp, *Platomesus* Chandler, *Austrorhexius* Chandler) while in others it is clearly present (*Conoplectus* Brendel, *Fletcherhexius* Park, *Adrogaster* Raffray). In still others, the segment is visible but thin (*Anarmodius* Raffray, *Rhexidius* Casey). Two genera, *Oropus* and *Mesoplatus*, are polymorphic, with species falling into two or all of the three classes. Furthermore, in most Jubini and some Goniaceritae, segment 7 is not externally apparent (D. S. Chandler, *pers comm.*). Hence, a recurring trend is for internalization of the terminal segment, as exemplified by *J. towai*.

Molecular phylogenetic placement of *Jubogaster*

While the head of *Jubogaster* is suggestive of Trogastrini, other characters typical of this tribe are absent. There is no dense genal beard of setae, the tarsal claws are both well-developed and equally-sized, rather than being unequal in size or consisting of one well-developed and one setiferous claw. A strongly-impressed median longitudinal sulcus on the pronotal disc is also lacking; although the sulcus is present, it is barely evident and only weakly-defined. Furthermore, the obcordate form of the pronotum, sharply constricted at the base, is far more similar to members of Jubini, another euplectite tribe.

Jubogaster's curious suite of features confounds a definitive assignment of the new taxon to tribe using morphology alone. To reliably place *Jubogaster* phylogenetically, we employed a non-destructive procedure to extract DNA from the type specimen, without damaging or altering its external morphology (Gilbert *et al.* 2007). Using this approach, we successfully amplified a fragment of 28s rDNA from *J. towai*. This region is particularly informative for higher-level pselaphine systematics, resolving many relationships at the supertribal, tribal and subtribal levels (J. Parker and A. Vogler, unpublished data). We also sequenced this gene region from a range of other Pselaphinae including 5 genera of Trogastrini, 3 Jubini genera, and representatives of all other euplectite tribes except Metopiasini, Dimerini and Mayetiini. A variety of non-euplectite pselaphines from different supertribes were included, totalling 24 ingroup taxa. Three other staphylinids (from the subfamilies Proteininae, Euaesthetinae and Scydmaeninae) and the silphid *Silpha obscura* were used as outgroups.

Both MP (Fig 11) and Bayesian (Fig 12) analyses placed *Jubogaster* within the Trogastrini with maximum support, forming a clade with *Platomesus* and *Rhexius*. This placement was recovered across all alignment parameter combinations tested with consistently high support. Although the taxonomic coverage is limited, *Jubogaster* emerges in the same position in a far more comprehensive analysis of >150 ingroup taxa, with extensive taxon sampling from almost all pselaphine tribes and subtribes (data not shown; J. Parker and A. Vogler, unpublished data). Hence, we conclude with a high degree of certainty that *Jubogaster* is indeed a member of Trogastrini.



FIGURES 11–12. Phylogenetic position of *Jubogaster towai*. Trees were rooted using *Silpha obscura* (Silphidae) as the designated outgroup. Grey branches denote outgroup taxa, black branches non-euplectite Pselaphinae, green branches Euplectitae, and purple branches Trogastrini. **11)** Single most parsimonious tree of 2236 steps (CI = 0.50, RI = 0.56) found from an MP search on the default MUSCLE alignment. Values above branches are bootstrap proportions from 1000 replicates. ClustalX alignments made with a range of gap opening and extension costs produced highly similar topologies that differ only outside the Jubini+Trogastrini clade. **12)** Bayesian consensus tree made from an unpartitioned analysis with the GTR+I+G model. Posterior probabilities for each node are shown above branches.

Discussion

***Jubogaster* and its phylogenetic relationships.** The phylogenetic analysis presented here confidently places *Jubogaster* within the Trogastrini. It is notable that in both MP and Bayesian analyses, Jubini and Trogastrini emerge as sister groups with strong support, to the exclusion of the other euplectite ingroup taxa. However, while these tribes may indeed be phylogenetically close, *Jubogaster*'s emergence from within Trogastrini indicates its jubine-like characters are derived, and convergent with Jubini, rather than evidence of a genuine affinity of this genus with Jubini. *Jubogaster*'s placement in Trogastrini allows assessment of some of the character states of the new genus. The trend in Pselaphinae is for the two tarsal claws to first become asymmetric, followed by loss of the secondary claw (Chandler, 2001). In Trogastrini, the secondary (posterior) claw is clearly smaller than the primary (anterior) claw, and in some it is present simply as a seta-like structure. In *Jubogaster*, both claws are well-

developed, suggesting that a reversion to the ancestral condition may have occurred. The split anterior protarsal claw is also a novelty (seen occasionally in a number of different groups), as is the shape of the pronotum. Elsewhere, *Jubogaster* shows derived features: all dorsal fovea and many ventral ones have been lost, and only a thin, weakly-evident median sulcus is present on the pronotum. Furthermore, internalisation of both the sternite (penial plate) and tergite of abdominal segment 7 (IX) has occurred. Hence, *Jubogaster* has departed substantially from the typical trogastrine form. Future collecting efforts targeting the poorly known Neotropical trogastrine fauna may expand the range of this tribe's morphology still further.

At this time, an attempt to place the new genus within Trogastrini is premature due to limited taxon sampling, although in the trees in figures 10 and 11, *Jubogaster* emerges with *Platomesus* and *Rhexius*, to the exclusion of *Oropus*, *Rhexidius* and *Conoplectus*. The weakly geniculate antennae of *Jubogaster* suggest the genus may be close to other Trogastrini that share this character; indeed, *Platomesus* and *Rhexius* both have strongly geniculate antennae, while *Oropus*, *Rhexidius* and *Conoplectus* do not. The phylogenetic utility of geniculate antennae is presently unknown.

Body size and social insect associations in Pselaphinae. In Pselaphinae, body size generally varies from <1 to 3mm in length (with about 2mm being “average” and 3mm qualifying as a “large” species). The upper limit of this range is surpassed in a few tribes such as Jubini, Tyrini, Tmesiphorini and Goniacerini, the latter containing several exceptionally large-bodied genera such as *Ogmocerodes* Jeannel (reaching 5.5mm) and the longest pselaphine species known, the 7.1mm *Kistneriella termitobia* Leleup. The single specimen of *J. towai* measures 5.1mm in length, but must nonetheless rank among the largest and most robust species on account of its particularly broad and convex body form. Trogastrini also contains another relatively large species, *Eurhexius muticus* (Raffray) at 4.25mm.

Too little is known about the biology of pselaphines to confidently propose reasons for these expansions in scale. However, we note that a possible relationship between body size and inquilinous behaviour may exist in this subfamily. As stated above, *J. towai* was found in a nest of *Pheidole xanthogaster* Wilson. In Goniacerini, *Kistneriella termitobia* Leleup is a termitophile, as are several of the other larger African members of this tribe (Jeannel 1959; Leleup 1971). In the Neotropical tribe Metopiasini, the small-bodied Rhinoscepsina are thought to be free-living, but their relatives, the Metopiasina, contain many larger-bodied species that are myrmecophiles and termitophiles (Park, 1942). Likewise, among Tmesiphorini, many large-bodied genera (*Tmesiphorus* LeConte, *Eudranes* Sharp, *Jardine* Chandler) are facultative or obligate inquilines, while the smaller-bodied *Raphitreus* Sharp, at least in Japan, is believed to be free-living. In New World Tyrini, several of the genera with larger species such as *Cedius* LeConte, *Ceophyllus* LeConte and *Hamotus* Aubé include myrmecophiles and termitophiles. Amongst Australian Tyrini, the average maximum size of genera recorded from ant or termite colonies is 3.13 (n=7), as opposed to 2.84 (n=14) for genera that to date have not been recorded from these habitats (measurements from Chandler, 2001; note that phylogeny potentially confounds these averages). *Attapsenius* Bruch, a symbiont of the *Atta* leaf-cutter ant colonies of South America, and the sole genus in Attapseniini, is also above average size. In Pselaphini, the large *Margaris* Schaufuss is known from ant nests and thought to be myrmecophilous (Chandler, 2001), whereas other genera in this tribe are smaller and tend not to frequent nests. Both genera of the East Asian tribe Arnylliini, *Awais* Löbl and *Harmophorus* Motschulsky, are significantly above average size, and although the lifestyles of these genera are unclear, some members of each genus have been recovered from ant colonies (M. Maruyama and T. Shimada, unpublished observations). Within the Euplectini, body size is generally under 2mm and most species are free-living, but the trend is broken by an undescribed genus and species from New Zealand that inhabits *Pachycondyla* nests and measures ~3mm (S. Thorpe, *pers comm*; see <http://species.wikimedia.org/wiki/File:Euplectitae.jpg>).

All this is not to say that all large taxa are inquilines and all small taxa free living; many exceptions exist—indeed, the most derived and highly integrated of myrmecophilous Pselaphinae, the Clavigeritae, are generally about average size, and often smaller (the >3mm Madagascan *Microclaviger* Raffray being exceptional). Likewise, many Ctenistini are myrmecophiles and not above average in size. Yet, there may be grounds for making a case for a *general* evolutionary correlation between inquilinous behaviour and increased body size. A large body size could predispose pselaphines to become inquilines; conversely, it could be that the inquilinous lifestyle—which often leads to bizarre changes in morphology—may also commonly permit selection for a larger body. One might imagine that the potential nutritional resources offered by ant and termite colonies, or the greater room for maneuverability afforded by nest galleries compared to small soil/litter interstices, could allow a larger body size to evolve. Defensive strategies to withstand attacks from the host, or mechanisms of host deception or mimicry, may likewise be assisted by body enlargement.

Acknowledgements

We thank Alfred Newton and Margaret Thayer (Field Museum, Chicago), Shuhei Nomura (National Science Museum, Tokyo), and Sergei Kurbatov (Moscow) for providing several specimens for the molecular phylogenetic analysis. Don Chandler (University of New Hampshire) surveyed the penial plate character in Trogastrini, and Stephen Thorpe (University of Auckland) provided information about the large, undescribed myrmecophilous member of Euplectini. Stefan Cover (MCZ, Harvard) kindly identified the host ant. We are extremely grateful to Chris Carlton (Louisiana State University), Don Chandler, Taro Eldredge (University of Kansas) and Darren Mann (Oxford University Museum of Natural History) for providing critical feedback on the manuscript.

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