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Taxonomy and Natural History of *Strumigenys thaxteri* Wheeler and *Strumigenys reticeps* (Kempf) (Hymenoptera: Formicidae)

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Abstract

We report finding *Strumigenys thaxteri* Wheeler in the Amazonian foothills of southeastern Ecuador, over 2000 km to the west of previously known records for the species in Trinidad and Guyana. Field observations suggest it is a sit and wait ambush predator that captures insects that alight on the vegetation upon which they position themselves. Once prey is subdued they descend with it to ground level, where they presumably nest. Their massive mandibles, robust claws, dense body cover of long silky hairs, and sting may all contribute to detecting, trapping, and subduing larger sized, flying prey. This type of predation is hitherto unreported for the genus. *Strumigenys reticeps* (Kempf), an apparently closely related species from southern Brazil, may share the same behavior but its key morphological traits are of a lesser degree of development than in *S. thaxteri*. Both species are redescribed and their morphological variability is discussed. High resolution images of both species are provided. The more frequent use of vegetation beating for ant-collecting is urged. *Strumigenys lojanensis* Lattke & Aguirre is synonymized as a junior synonym of *S. onorei* Baroni Urbani & De Andrade.

Key words: ambush predation, range extension, Ecuador, synonymy, functional morphology

Introduction

The genus *Strumigenys* Smith is one of the largest ant genera with over 830 described species (Bolton 2016). Even though the systematics of *Strumigenys* has been the subject of recent revisionary work (Bolton 2000) and subsequent regional faunistic studies that arguably makes it one of the taxonomically better known ant groups (Bolton 2016), undescribed species are still commonplace, particularly in the tropics, and we are very far from having information about the natural history of most members of the genus. They are found throughout the tropics, where most prefer to nest in mesic forested habitats at ground level in the litter or within cavities in decomposing wood or other types of relatively hard vegetable tissue, foraging in the same habitat. Nevertheless a few species, such as the *tococae* group members, are known to forage and nest in arboreal habitats (Lattke & Goitía 1997; Bolton 2000). They are all predators and are typically associated with the stalking of Collembola, though some evidence points to a greater breadth of prey selection in at least some species (Dejean 1982; Masuko 1984; Bolton 2000; Kaufmann *et al.* 2003; Masuko 2009).

Strumigenys thaxteri was originally described by W.M. Wheeler in 1916 from three workers taken in Trinidad. Since then the only other record is from Guyana (Sosa-Calvo *et al.* 2010). Nothing is known of its natural history except that it has been taken in humid forests, with the locality label from the Trinidad series including a suggestive "in beatings". Collecting activity in southern Ecuador in 2009 by Thibaut Delsinne and in 2014 by John Lattke captured significant numbers of workers, thus extending its known range by over 2000 km from northeastern South America to the Andean foothills of the Amazon drainage. These specimens have enabled a morphological reassessment of the species whilst the field work has shed some light on its natural history. Its striking morphology coupled with field observations and a comparison with the morphology of other *Strumigenys* species permits speculation regarding the relation between form and function in this species. Another poorly known species,

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Strumigenys reticeps (Kempf), with similar morphology and apparently closely related to *S. thaxteri* (Bolton 2000) is represented by scant specimens from the southern parts of the Brazilian Atlantic Forest. The finding of additional specimens of this species within the context of a review of the species of *Strumigenys* of the Atlantic Forest by Thiago SR da Silva also offers the opportunity to reassess this species and consider its natural history.

Methods and materials

The specimens of *S. thaxteri* were collected independently on different occasions in the same Ecuadorian locality during surveys of ant diversity. The specimens of *S. reticeps* were collected in several localities in the Atlantic Forest, mainly in Paraná and São Paulo states. For comparative purposes the images of several ants were examined, in particular those of *Strumigenys thaxteri*: a syntype worker from Trinidad, Port of Spain, specimen CASENT0900194, and a worker from Guyana, specimen USNMENT00441066. These images are available from www.antweb.org; these and other individual specimens mentioned in this text may be found by consulting their unique CASENT or USNMENT identifier. When observing the sculpturing of the polished and highly reflective integument of these ants is best to place a narrow strip of mylar plastic or thick tracing paper between the specimen and the light source. This eliminates highlights and brilliant reflections, rendering the sculpture more amenable to study. The technique works best with LED illumination and the paper as close as possible to the specimen. This technique was used on the Ecuadorian and Brazilian specimens.

Images of the aforementioned specimens were measured using Fiji (Schindelin *et al.* 2015). High resolution digital images of *Strumigenys thaxteri* were taken at the Royal Belgian Institute of Natural Sciences (RBINS) using a Leica DFC290 camera attached to a Leica Z6APO stereo-microscope. A series of images was taken by focusing the sharpness on different levels of the specimen, using the Leica Application Suite v38 (2003–2011) and combined with the stacking software Combine ZP (http://combinezp.software.informer.com/). Final editing of the images was done with Adobe Photoshop CS5. High resolution images of *Strumigenys reticeps* were taken by Júlio Chaul at the Laboratório de Ecologia de Comunidades of the Universidade Federal de Viçosa, Brazil, using a Canon 1100D camera attached to a Leica S8APO stereomicroscope. A series of images were manually taken by focusing the sharpness on different levels of the specimen and combining them with the stacking software Zerene Stacker Version 1.04, (www.zerenesystems.com). The resulting image was enhanced in Gimp 2.8.18 (www.gimp.org) and scale bars were added using ImageJ (Schindelin *et al.* 2015). For high-magnification images of microstructures, specimens were submitted to low vacuum scanning electron microscopy using a Tescan Vega3 LMU, after drying in a critical point dryer and mounting on a specimen stub using electrically conductive double-sided adhesive tape. SEM images were taken in the Centro de Microscopia Eletrônica da Universidade Federal do Paraná (CME-UFPR).

Most of the measurements and indices used here are the standard for ant taxonomy (Bolton 2000: 5) but the following are defined either because of infrequent use or conflicting definitions. PW—Pronotal width: greatest distance in dorsal view. PH—Petiolar height: greatest distance between two parallel lines, one tangent with the node apex and the other tangent with the ventral-most point of the petiole in lateral view. PL—Petiolar length: straight line distance between the posterior petiolar margin and its insertion in the propodeum in a lateral view. DPW—Dorsal petiolar width: greatest distance between the lateral margins of the petiolar node in dorsal view. OI—Ocular index: EL/HW. LPI—Lateral petiolar index: PH/PL. DPI—Dorsal petiolar index: DPW/PL.

The following collection acronyms are used:

ARCE	Ant Reference Collection Ecuador, Instituto de Ciencias Biológicas, Escuela Politécnica Nacional, Quito, Ecuador
DZUP	Coleção Entomológica Pe. Jesus Santiago Moure, Universidade Federal do Paraná, Curitiba, PR, Brazil
RBINS	Royal Belgian Institute of Natural Sciences, Brussels, Belgium
UFV	Laboratório de Ecologia de Comunidades, Universidade Federal de Viçosa, Viçosa, MG, Brazil

Results

Strumigenys thaxteri (Wheeler, 1916)
(Figs. 1A–D)

Codiomyrmex thaxteri Wheeler, 1916: 327, Fig. 1, w., Trinidad.
Pyramica thaxteri (Wheeler). Combination in *Pyramica*: Bolton, 1999:1672.
Strumigenys thaxteri (Wheeler). Combination in *Strumigenys*: Baroni Urbani & De Andrade, 2007: 129.

Worker measurements and indices. HL 0.63–0.65; HW 0.50–0.57; ML 0.10–0.18; EL 0.08–0.10; SL 0.32–0.33; PW 0.37–0.39; WL 0.67–0.76; PH 0.18–0.29; PL 0.33–0.39; DPW 0.18–0.20 mm. CI 0.79–0.90; MI 0.20–0.33; OI 0.14–0.19; SI 0.57–0.65; LPI 0.53–0.78; DPI 0.47–0.63. (n=5).

Worker description. Head in frontal view longer than broad; posterior cephalic margin laterally convex to straight, medially with shallow emargination framed by raised lamella; head widest posteriorly with broad concavity between posterolateral cephalic corner and frontal carina, cephalic lateral margins gradually converging anteriorly, each margin slightly sinuous; frontal carina projects laterally feebly as broad convexity. Frontal carina in cephalic dorsal view forms elongate surface with lateral margin higher than internal margin. Cephalic dorsum posteromedially markedly convex; most of cephalic surface rugose-reticulate except for clypeus and brief strip posteriorly of epistomal suture mostly smooth with scattered punctae. Clypeus longer than broad, posterior margin forms acute angle, margin broadly convex. Mandibles robust, mandibular lateral margin broadly convex, in lateral view mandibular median width is half its length. Mandibular dorsal surface smooth and shining, convex, with scattered piligeous punctulae, especially laterally; masticatory margin with series of 10–13 small interlocking teeth, apical tooth largest; ventral surface glabrous. Labrum slightly longer than broad in dorsal view (with mandibles open), wider basally than apicad, laterally broadly convex, apex bilobulate with fine incision. Width of labrum less than one-third that of clypeus in cephalic full-face view. Labrum in cross section at mid-length with convex dorsal margin and very concave ventral margin, in ventral view the lateral margin forms an elongate, column-like structure, apically bluntly rounded. Scattered fine hairs present along sides of labrum, apex with tuft of fine hairs shorter than half the basal labral width. Clypeal dorsum with appressed hairs directed meso-anteriorly; mandible with sparse fine, appressed hairs directed towards masticatory margin. In cephalic lateral view frontal carina extends posteriorly to posterolateral cephalic corner, lateral cephalic surface reticulose-punctate; eye protuberant, visible in cephalic frontal view, with 6–7 ommatidia across. Cephalic ventral surface posteriorly convex, coarsely rugose, distinct anteroventral tooth present close to mandibular insertion. Scape dorsal surface rugulose, ventral surface of scape mostly densely reticulate rugulose with smooth and shining elongate area that extends two-thirds along posterior margin of scape length, widest at apex and becoming progressively slender basally. Shining area light brown in contrast to surrounding darker sculpturing. Scapes do not reach posterior cephalic margin, in cross-section dorsal surface convex, ventral surface flat to concave.

Mesosoma in lateral view with sinuous dorsal margin, promesonotum broadly convex, posteriorly broadly concave with minor irregularities on propodeum; lateral mesosomal surface mostly smooth and shining, pronotum with broad rugae, mostly transverse to oblique on dorsolateral surface and longitudinal along ventrolateral surface. Propodeal spine elongate and acute, extending posteriorly as low keel. Mesopleuron and anterior metapleuron mostly smooth, with very broad undulations, and shining, anepisternum with reduced, irregular undulations; mesopleuron with lamella along anteroventral margin. Posterior metapleuron with series of depressions and punctae, densest close to metapleural gland. Lateral propodeal face mostly rugulose, spiracle directed posterolaterally, separated from posterior propodeal margin by approximately one diameter. In dorsal view mesosoma widest anteriorly, anterolaterally strongly angular, posteriorly converging. Most of pronotal dorsum smooth and shining with scattered punctae, lateral margins with shallow rugosities; mesonotum strongly rugulose with median longitudinal crest, propodeal dorsum rugose to areolate. Dorsal and declivitous propodeal faces separated by transverse fine carina, declivity anteriorly reticulate-areolate, posteriorly smooth and shining.

Lateral face of procoxa transversely striate on basal half up to two-thirds, apically rugulose. Dorsal surface of meso and metacoxae rugulose. Tibiae and femora mostly smooth and shining with scattered punctulae. Femora basally densely reticulate-areolate, extension of reticulate area increasing from profemur to metafemur. Petiolar node in lateral view with abrupt, weakly convex anterior margin, anterodorsal margin convex; postpetiolar margin evenly convex. Peduncle of petiole with flattened dorsal surface, abruptly dropping laterally; lateral surface with

longitudinal carinae, swollen at spiracle; dorsal and lateral surface reticulate-areolate. Node of petiole rugose, postpetiolar dorsum rugulose with scattered longitudinal striae. Well-developed spongiform tissue present along length of petiolar ventrum, lateral margins of petiolar node, posterolateral margins of postpetiole, and lateral margins of abdominal sternite IV. Anteromedian region of abdominal sternite IV with thick tuft of hairs, resembling spongiform tissue. Basigastral costulae distinct, mostly along anterolateral margins, length under one-fourth of surface of abdominal tergite IV. Gaster dorsum smooth and shining except for scattered punctulae. Abundant long and silky hairs cover most of dorsum of cephalic capsule and mesosoma (except for propodeal dorsum), petiolar node, postpetiole and gastral tergum. Legs, including tarsi, also with abundant long hairs, hairs shortest on protarsi. Protarsal claws shorter and relatively more slender than meso- and metatarsal claws. Hairs on cephalic dorsum longest posteriorly, ventral cephalic surface also with abundant hairs but all relatively shorter. Scape and funiculus with abundant decumbent to appressed hairs, none standing. Body mostly black, legs dark brown to brown.

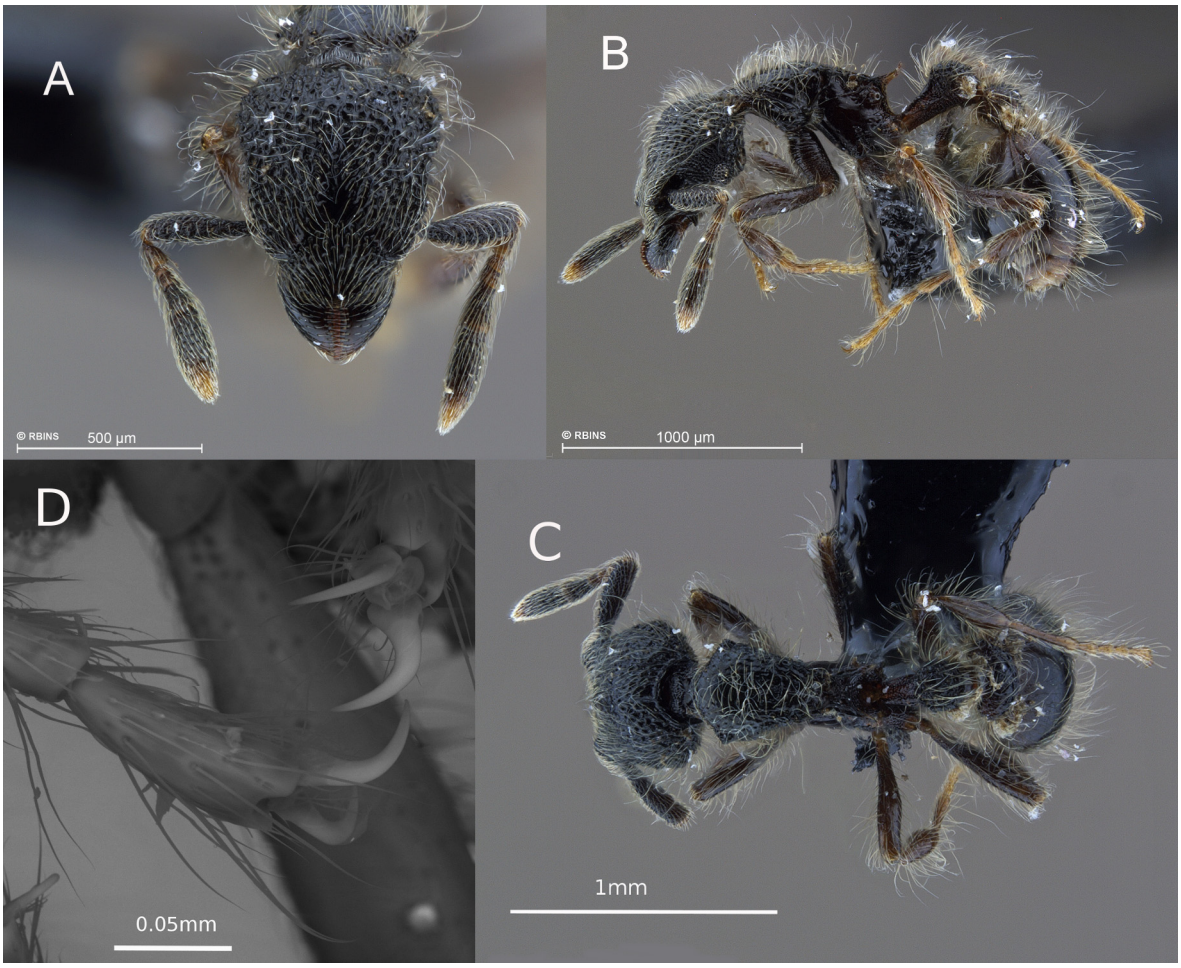

FIGURE 1. *Strumigenys thaxteri*, worker. Figs. (A–C) Specimen RBINS 3871503. (A) Dorsal view of head. (B) Lateral view of body. (C) Dorsal view of body. Fig (D) Specimen deposited in DZUP, SEM image of tarsal claw.

Specimens studied. Ecuador, Zamora-Chinchipe, 2.7km SSE Zamora, Posada Copalinga, Orange Trail, 1060m, -4.09106° -78.96210°, 26.X.2014, M. Tuza, M. Vélez, C. Gómez, G Piedra, J. Lattke 3697; point-mounted voucher specimens are deposited in ARCE and DZUP; thirteen ethanol preserved specimens are in DZUP. Same data except: Posada Copalinga, Blue Trail, 1030m, -4.09122° -78.96069°, 19.III.2009, Hand-collecting, T. Delsinne; 52 ethanol preserved specimens are deposited in RBINS (col-ID 35482 in Maurice Leponce's database). Same data as the previous one, except: 10.III.2010, 0.25m² Winkler sample extracted during 48h, J. Jacquemin; one point-mounted and photographed specimen, deposited in RBINS (col-ID 38715 in ML's database). Same data as the previous one, except: III.2010, vegetation beating; one specimen deposited in RBINS (col-ID 38823 in ML's database). Measurements and derived indices calculated from mounted specimens deposited in DZUP.

Morphology and identity. Wheeler's description is enough to satisfactorily determine the species, especially on account of several very distinctive characters such as the long silky, filiform hairs, relatively massive mandibles and the cephalic anteroventral tooth. Bolton (2000) offers a more thorough definition of the *thaxteri* group and *S. thaxteri* itself and the present specimens all agree with Bolton's defining traits. Nevertheless, prior to this study both species of the *thaxteri* group were known from a scant number of specimens and in the case of *S. thaxteri* only from the type series, all from the same locality and probably even from the same nest. The new specimens reported here permit a consideration of infraspecific morphological variation. Table 1 compares the metrics between these ants and it is evident that in most cases the values either overlap or form a continuum with the exception of a minor gap for LPI between the Ecuadorian and other specimens. Given the limited number of specimens and populations represented, it seems likely more overlap could be expected.

TABLE 1. Comparative metrics of *S. thaxteri* specimens. The acronyms in the Metrics column are defined in Materials and Methods. If a row in the Trinidad column has two values, they represent two syntype workers measured by Bolton (2000: 243), and if only one value is mentioned, it is from measuring specimen CASENT0900194. The Guyana column denotes values measured from the image of specimen USNMENT00441066. The Ecuador column denotes values from measuring 5 specimens from the series presently described. N/A means the image did not permit a view of the part for measuring.

Metrics (mm)	Trinidad	Guyana	Ecuador
HL	0.64–0.68	0.67	0.63–0.65
HW	0.58–0.60	0.55	0.50–0.57
ML	0.13–0.14	0.14	0.10–0.18
EL	0.06	0.10	0.08–0.10
SL	0.30–0.36	0.32	0.32–0.33
PW	0.38–0.40	0.37	0.37–0.39
WL	0.70–0.72	0.70	0.67–0.76
PH	0.18	0.17	0.18–0.29
PL	0.37	0.35	0.33–0.39
DPW	N/A	0.19	0.18–0.20
Indices			
CI	0.88–0.90	0.82	0.79–0.90
MI	0.19–0.22	0.21	0.20–0.33
OI	N/A	0.18	0.14–0.19
SI	0.55–0.60	0.58	0.57–0.65
LPI	0.49	0.49	0.53–0.78
DPI	N/A	0.54	0.47–0.63

Brown (1953: 21) studied the type series and generally agreed with Wheeler's description except for the higher values he obtained for TL, values corroborated by Bolton (2000: 243). Wheeler described the eyes as not visible in a cephalic dorsal view but the eyes are partially visible not only in the Ecuadorian series but also in the syntype image and Bolton (2000) considered the eye as prominent and bulging outwards. The clypeus was described as long as broad by Wheeler but calculating a clypeal index (clypeal width / clypeal length x 100) from the images and specimens reveals a continuity of values from 71 (Syntype) to 93 in an Ecuadorian worker. The posterior cephalic margin ranges from concave in the Guyanese specimen to slightly convex or straight in the other specimens. The mesosoma in the type series was described as mostly smooth and shining by Wheeler and study of the syntype image as well as the image of the worker from Guiana corroborate this. The Ecuadorian specimens are more sculptured: the anepisternum bears small irregular undulations vs. the smooth to broad undulations of the other specimens; the dorsal mesosomal surface is similar to the other ants in patterns of sculpture but these are more developed and deeper in the Ecuadorian ants; the lateral propodeal face is mostly smooth to broadly undulated in the Guiana and Trinidad ants but rugulose in the Ecuadorian samples. The Ecuador specimens are

darker-colored than the other ants, with the syntype showing the lightest shade, a brown color. Color also exhibits a continuum of shades: the syntype is predominantly light brown; the Guyanese ant has a very dark, almost black, head with the rest of the body dark-brown; the Andean material is nearly black. It is possible that the syntype has experienced some loss of color since it was examined by Wheeler; he described the head as black and the body as castaneous brown. The syntype head is definitely not black. The definition of "castaneous brown" is problematic given the abundance of fanciful names given to colors and an individual's perception of color but an internet search for "castaneous brown" seems to side with a darker shade of brown, at least for human hair color. Brown (1953: 21) examined the syntypes and judged the dominant body color as deep ferruginous with a mahogany brown gaster. The density and length of the hairs also seem not to differ markedly amongst the samples. The syntype images are difficult to interpret as the specimen has evidently been subject to considerable wear, consisting of a disarticulated head and mesosoma, with the hairs apparently partially abraded and mostly in disarray. In general the pilosity is dense. The mesosomal dorsal hairs are densest on the promesonotum in all material, thinning out towards the propodeum. The hairs on the gastral tergum are of relatively uniform length, shorter than some of the hairs on the leg. We cannot totally discount the possibility the Ecuadorian series are not *S. thaxteri*, but a different, albeit very closely related species, using morphology as a guide. Even though this new material represents a great improvement towards a better understanding of what is *S. thaxteri*, it still is a very limited selection considering the considerable distance separating the Ecuadorian ants from the Trinidad—Guyanese ants. Since the characters that seem typical for the Ecuadorian samples are not starkly different from the other ants, we have chosen to consider this new material as a population of *S. thaxteri.*

Observed natural history. Here we narrate some predatory behavior as seen in the field. Our first observation was made on the afternoon of 19 March 2009 in an evergreen premontane rainforest at 1030m. The ants were observed on a single poorly-branched unidentified dicot about 1.4m high. Most ants were observed alone or in small groups (2–4 individuals) at the apex of almost every branch or exterior leaf, from the base to the top of the plant. Ants were motionless and remained impressively immobile when touched with forceps. No panic behavior was observed during the hand-collecting, even among ants closely located to a captured specimen. As a result, 52 specimens were easily collected (a few more specimens were present). Careful search did not reveal any other ants of this species on the vegetation nearby.

The next observation was made on the afternoon of 26 October 2014 and another the late morning of the following day. The ants were observed in small groups on the apex or close to the apex of a single shrub in secondary closed canopy forest, in a ravine with elevated humidity. The plant used by the ants was a single stem, understory, unidentified dicot about 1.4m high. Images taken in the field will be posted on www.antwiki.org. The ants were observed hunting on this plant only and a careful search of neighboring vegetation during each of the two field sessions failed to detect any specimens foraging elsewhere. A bromeliad on a neighboring tree had leaves crossing through the shrub, contacting its stem and leaves but no ants were found on it. Most ants were observed in the following stance: immobile, the body forming an angle with the substrate, lowest posteriorly with the head highest, pointing anterodorsally with the mandibles wide open (approximately 90°) and antennae fully extended. A few were observed walking slowly on the plant surface. Most of the immobile ants were in loose groups, some separated by more than a body length while others were distanced from each other by less than a body length.

One group of about 20 ants was observed along the apex of the apical leaf, another group of about 12 ants was observed on the dorsal surface of a leaf 2 levels down from the apex. This latter group was concentrated on or around the dead and moldy remains of a heteropteran. A few other ants were loosely congregated at the base of another leaf, close to the apex, either in the midst of or next to a group of scale insects. Initial efforts at collecting specimens using a pooter failed as the ants could not be sucked into the apparatus despite forceful efforts. They were then individually plucked from the plant surface using fine-tipped forceps. The effort required to separate each ant from the substrate was unexpectedly great, causing the apical leaves of the shrub to shake with each plucking, without, however, causing any panic behavior among the ants. On the second day of observation (27.X.2014) 10 ants were observed on the apex and 8 on a dead leaf that had fallen and lodged itself between the leaves of the plant (not there the previous day). After some time an apparent drosophilid fly approached the plant to land and it was seized by the ant on its head close to the rostrum and stung in the ventral thorax. The initial approach of the fly and reaction of the ant was not observed (the cost of a 2 second distraction). The ant lifted the fly and stayed mostly still, except for forward thrusts of its abdomen to sting the fly, until the dipteran ceased to move, whereupon it carried the fly down the stem of the plant into the leaf litter. The fly was about 25% larger than

the ant. No other ants were observed intervening during this episode. Interestingly, one specimen was collected in the same locality by vegetation beating and another one was found in a Winkler sample by our colleague Justine Jacquemin, both in March 2010.

Natural history and morphology. The morphological analysis and scant field observations suggest *S. thaxteri* preys upon flying insects that alight on the surface of the shrub it is positioned upon. The immobile stance practiced by these ants on exposed leaf surfaces is interpreted as ambush behavior. The presence of sensory hairs that detect air currents has been studied for several insects other than ants (Taylor *et al.* 2007) and filiform hairs in particular are regarded as being quite sensitive to air currents (Pflüger & Wolf 2013). The extraordinarily long filiform body hairs of these ants would constitute ideal detectors of air currents and could enable the ant to detect the approach of flying insects. The meso- and metatarsal claws of the species (Fig. 1D) have a relatively robust appearance that would conceivably be of great utility preventing the ant being dislodged from its perch by flying prey before it has been immobilized. The effort needed to manually collect specimens attests to the effectiveness of its grip. We speculate that a *Strumigenys* on the ground that has just latched onto a large Springtail not yet paralyzed by the ant's sting may have to ride out one or two thumps of the furcula, but it will probably not be cast so far from its hunting route as to lose its way back to the nest. The situation is different for a *S. thaxteri* worker, as large flying prey could carry it a distance far beyond the possibilities of returning to its nest. A brief qualitative survey of relative claw size in about 22 assorted species of long- and short-mandibulate *Strumigenys* from 11 different species groups, as defined by Bolton (2000), gives us the impression that *S. thaxteri* has a greater claw width / claw length ratio than the others. Only in *S. beebei* (Wheeler) did the claws seem to appear similarly robust. The minute size of their claws made it quite difficult to measure them with the optics at hand but it was possible to discern they were relatively more elongate than in *S. thaxteri*. *Daceton armigerum* (Latreille) is another arboreal ambushing ant that will take prey much larger than its size and it bears very robust claws that contribute to the ant's stability when struggling with prey, and ultimately preventing prey loss (Dejean *et al*. 2012; Billen *et al*. 2017). Dejean *et al.* (2010) report on enlarged claws and other morphological modifications such as specialized arolia are known in other arboreal ambushing ants such as *Azteca andreae* Guerrero, Delabie & Dejean. Ideally a comparison of claw morphology and its relation with function should be performed by measuring the claws, their curvature, modeling force vectors, behavior, and controlling for phylogeny. Additionally, claw size is not necessarily equal in the same individual as the foretarsal claws may be quite reduced compared with the metatarsal claws, such as in *S. xenochelyna* Bolton. Such a study goes beyond the intentions of this publication.

The mandibles of *S. thaxteri* are quite massive if compared with other short-mandibulate *Strumigenys*. If measured in lateral view and in the same plane, the maximum mandibular width divided by the mandible's length from base to apex should give a qualitative index of how massive the jaw is, with values close to 1.0 characterizing a massive, block-like jaw. In *S. thaxteri* this value is about 0.88–0.92 (n=4) and in *S. reticeps* it is about 0.64–0.70 (n=4). The mandible in *S. thaxteri*, when seen laterally, is triangular with a broad and wide base, gradually tapering to the apex with its dorsal margin forming a broad convexity and its ventral margin is almost straight. Massive mandibles with a broad dorsal area or masticatory margin would conceivably help this ant secure a firm grip on prey approaching it from above. Other short-mandibulate species may have very robust mandibles as indicated by the aforementioned index, but their shape will be quite different, complicating comparisons. *Strumigenys* of the *excisa* group (Bolton 2000: 169) are similarly robust but the masticatory margin of their mandibles is not just dorsal but extends slightly ventrad (two examples: *S. turpis* Bolton, specimen CASENT0281950; *S. dontopagis* Bolton, specimen CASENT0900212). *Strumigenys* of the *leptothrix* group (Bolton 2000: 427) also bear powerful appearing mandibles with a similar shape to the mandibles of the *excisa* group (two examples: *S. leptothrix* (Wheeler), specimen CASENT0280704; *S. assamensis* De Andrade, specimen CASENT0900133). A study of mandibular structure and function should take into account a variety of factors such as shape, size, mass, dentition, ant and prey behavior, to say the least. Ants that forage in open spaces tend to have relatively larger eyes than those that forage in the leaf litter or underground (Weiser & Kaspari 2006). Most *Strumigenys* forage either in the litter or soil so a tendency towards smaller eyes would be expected for most. As a predator on foliage, *S. thaxteri* would be expected to have relatively larger eyes than usual and its eyes do project laterad, and are visible in a cephalic full-face view. The *tococae* species group of *Strumigenys* includes several species associated with trees (Bolton 2000: 563) and their relatively larger eyes are characteristic for the group. The two species of *Daceton* are also arboreal and have very prominent eyes dorsally positioned on the head (Azorsa & Sosa-Calvo 2008). This condition can be explained by the fact that larger eyes provide higher sampling resolution (Narendra *et al*. 2016), meaning that individuals presenting this condition can optimize tracking for potential prey, or threats, in a wider area.

Ambush behavior is thus known for other arboreal foraging ants that nest in trees or shrubs (Dejean *et al.* 2009; Dejean *et al.* 2010; Rodríguez-Gironés *et al.* 2013), but the present record is the first report of ambush hunting on shrubs for a ground nesting ant (A. Dejean, pers. comm.). The few observations narrated here open many more questions and make for a wonderful study of natural history. What is the relation between the ant nest and the "host" plant? Is it always a single plant? How is the plant chosen? How high do the ants forage into the understory? What is the breadth of prey diversity and size? Will more than one ant subdue the same prey item? What is the impact or relation of other ants foraging in the same plant? The apparent rarity of this species is undoubtedly the main obstacle towards garnering biological information about it.

Strumigenys reticeps **(Kempf, 1969)**
(Figs. 2A–D)

Codiomyrmex reticeps Kempf, 1969: 286, figs. 7–9 (w.) Brazil.
Glamyromyrmex reticeps (Kempf). Combination in *Glamyromyrmex*: Bolton, 1995: 208.
Pyramica reticeps (Kempf). Combination in *Pyramica*: Bolton, 1999: 1672.
Strumigenys reticeps (Kempf). Combination in *Strumigenys*: Baroni Urbani & De Andrade, 2007: 126.

Worker measurements and indices. HL (0.45–0.52); HW (0.35–0.40); ML (0.05–0.07); EL (0.04–0.07); SL (0.19–0.24); PW (0.25–0.27); WL (0.48–0.53); PH (0.12–0.13); PL (0.22–0.28); DPW (0.11–0.14) mm. CI (0.75–0.78); MI (0.10–0.15); OI (0.11–0.18); SI (0.51–0.66); LPI (0.46–0.54); DPI (0.46–0.50). (n=4).

Specimens studied. Brazil, Paraná, Irati, Fazenda Água Quente, 25°35'36.11S 50°49'12.06"W, 09.X.2014, Marques, C. G. P., Falbot, L. col. and Brazil, São Paulo, Ribeirão Grande, Fazenda Intermontes, VII–VIII. 2008; XI.2008; IV.2009. Nine point-mounted voucher specimens deposited in DZUP. Brazil, Minas Gerais, Viçosa, Mata da Biologia, 20º45'30.44"S 42º51'49.65" W, 731m, 5.V.2013, J. Chaul & N. Safar, Specimen UFV-LABECOL-000005. Epigeic Winkler E-13. Deposited in UFV.

Morphology. The original description made by Kempf (1969) is complete and provides most of the characteristics found in this species. There are only a small number of features that appears to vary among specimens. The size of the spiniform projection on the anterior margin of the clypeus is smaller in some specimens collected in the eastern region of São Paulo state, in the Peripheral Depression, although this variation is discrete. The promesonotal sculpture varies in intensity and size, being well-marked and prolonged almost to the propodeal dorsum in some specimens, and less marked and restricted to the promesonotal disc in others. The dorsum of the petiole node is normally as long as wide, but is wider than long in some specimens. Similar to *S. thaxteri*, the scape ventral surface is mostly densely reticulate rugulose with a smooth and shining elongate area extending up to halfway along the posterior margin, and the width is relatively uniform throughout the length. However, the sculpture is less marked when compared to *S. thaxteri*. Bolton (2000) was uncertain about the orientation of the pilosity along the leading edge of the scape due to the possible loss of hairs in the specimens he observed. On the specimens studied in the present work, the hairs found in this region are filiform, with a few flagellate hairs, all of them oriented towards the apex of the scape. They are extremely fine and probably easily lost through abrasion. Most measurements obtained from the studied specimens are similar to those obtained by Kempf (1969) and Bolton (2000). However, they have lower values of DPW (Dorsal Petiolar Width) compared to those obtained by Brown (1969). This discrepancy could be a reflection of shape variation of the petiole node. However, the original description and illustration are similar to some specimens observed in this study, more precisely with those with lower values of DPW. A thorough study of shape variation using analytical tools would better describe these structural nuances in the available specimens.

Morphology and natural history. *Strumigenys thaxteri* and *S. reticeps* are the only members of the informal *thaxteri* group proposed by Bolton (2000: 241). They both share a similar mandibular shape, with serially dentate mandibles and a convex dorsal margin when seen laterally; an acute triangular tooth on the cephalic dorsum, prominent humeral angles in dorsal view; spongiform appendages on the petiole and postpetiole, and the body clothed with abundant long and standing, flexuous hairs. *Strumigenys reticeps* has the smaller range of the two and is presently known from a few specimens taken in the southern Atlantic Forests of Brazil in the states of Minas Gerais, Rio de Janeiro, São Paulo, and Santa Catarina (Bolton 2000; Silva 2014, in thesis). The few known specimens suggest the species may be rare and not prone to being collected in litter samples. Even though *S.*

reticeps bears long silky hairs similar to *S. thaxteri*, it lacks robust mandibles and claws, thus its foraging may not necessarily be the same, perhaps taking smaller prey items from the understory. The peculiar posteriorly oriented filiform pilosity in the clypeal dorsum might be related to a distinctive method of perceiving prey or facilitating compound volatilization from a possible clypeal gland. In addition, the long flagellate hairs distributed on the cephalic surface could contribute to perception of hovering prey. The eye length is relatively smaller compared to *S. thaxteri* (EL<0.07), but both possess rather similar Ocular Index (OI) values. The similar proportion of eye length/head width found in both species possibly indicates a shared prey preference, with the smaller values of eye length in *S. reticeps* simply reflecting an isometric scaling of the eye size with the overall size of this species. Relatively smaller eyes, to a certain extent, may not necessarily imply a greatly reduced perception of potential prey or threats as the perception of environmental light patterns in insects is an interplay of various factors, not just eye size, that enable visually challenging tasks for even relatively small insects (Gonzalez-Bellido *et al*. 2011).

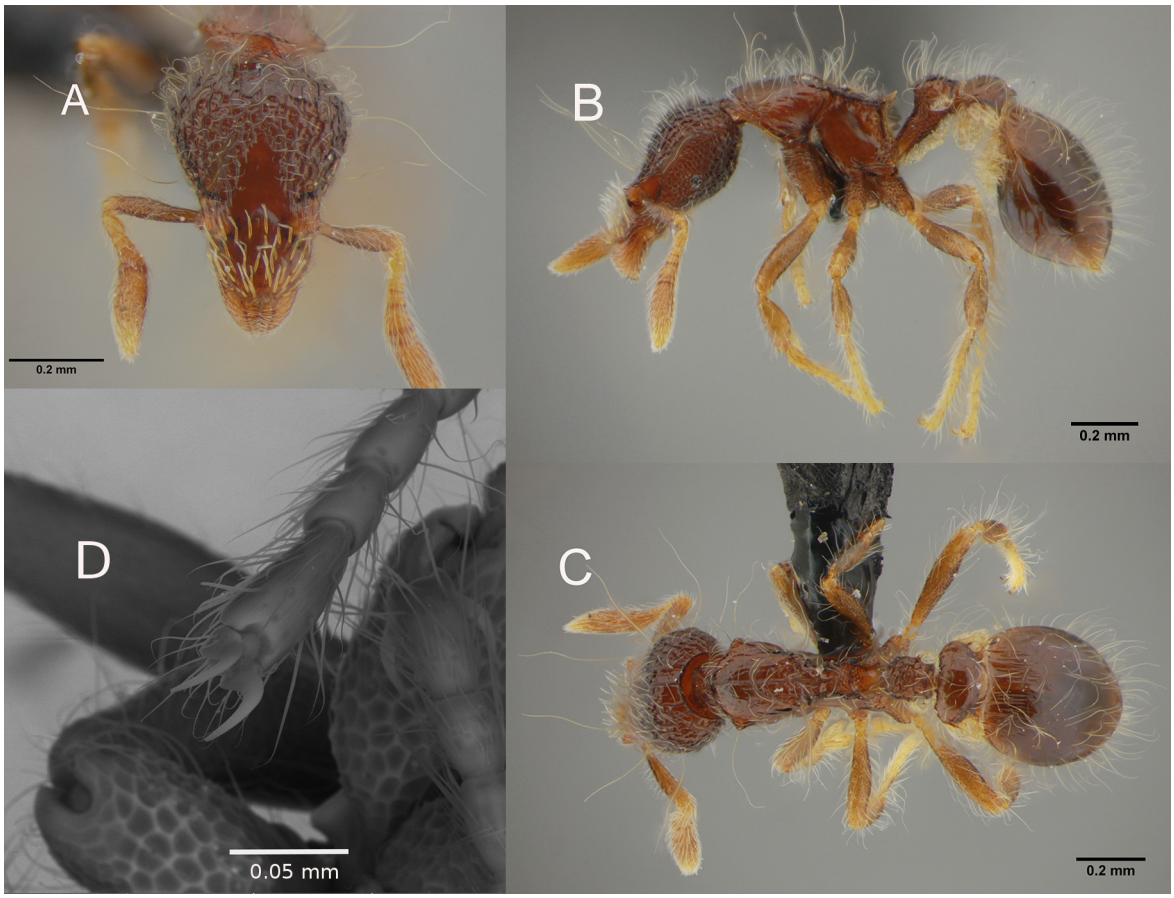

FIGURE 2. *Strumigenys reticeps*, worker. Figs (A–C) Specimen UFV-LABECOL-000005: (A) Dorsal view of head. (B) Lateral view of body. (C) Dorsal view of body. Fig (D) Specimen deposited in DZUP, SEM image of tarsal claw.

Other morphologically similar species are found in the Malaysian *leptothrix* group, which also possesses robust, serially dentate mandibles with convex dorsal margin seen laterally, and well-developed spongiform appendages on the petiole and postpetiole. Although most species do not have elongate and flexuous hairs, some have elongate simple hairs on entire dorsal head or restricted to the area behind the highest point of vertex. According to Bolton (2000), some species of the *leptothrix* group (*S. elegantula* (Terayama & Kubota), *S. jacobsoni* Menozzi and *S. stheno* Bolton) have particular dentition that increases the gripping/holding ability of the mandible, in which larger teeth intercalate with smaller teeth, with all of them slightly out of alignment and the longer teeth strongly inclined medioventrally. However, this arrangement differs from *S. thaxteri* and *S. reticeps*, which have the basal 8–9 teeth larger than those situated more distally, with the apical tooth larger than those immediately preceding it. In any case, given such a diverse genus it is expected that similar problems will be met with different solutions.

Sampling arboreal Strumigenys. The sparse records for both species and the huge gap in the distribution for *S.*

thaxteri imply both are relatively scarce. If their foraging is mostly upon understory vegetation and not in the leaf litter then this apparent scarcity can be partially considered as a sampling artifact since leaf litter sifting is poorly suited for retrieving arboreal foraging ants. The locality label of the imaged syntype states "from beatings", implying the collecting method used to capture the material studied by Wheeler (1916). The widespread use of leaf-litter sifters coupled with processing the litter using Winkler type extractors has been a milestone for ant collecting, changing our concept of ant diversity, especially that of ground ants. Our knowledge of the diversity of the genus *Strumigenys* has especially been broadened and deepened, but this very diversity obliges us to try novel collecting methods and explore habitats not usually probed by myrmecologists. A classical insect collecting method, the beating tray, has been used by generations of entomologists for general collecting or collecting insects associated with vegetation. Perhaps now is the time to incorporate this contraption into the ant collector's toolkit and collect the specimens that should fill in the distribution of *S. thaxteri* within the Amazon-Orinoco Basin. Jacquemin's use of this technique permitted the collection of an additional specimen of *S. thaxteri* and in Central America some myrmecologists are fully embracing vegetation beating (ADMAC 2016).

Synonymy of *S. lojanensis.*

Strumigenys onorei Baroni Urbani & De Andrade, 2007: 143, fig. 50 (w.) Ecuador
Strumigenys lojanensis Lattke & Aguirre, 2014: 176, figs. 1–3 (w., q.) Ecuador. **n. syn.**

A new evaluation of the characters used to define *S. lojanensis* leave little doubt it is the same species as *S. onorei*. All characters supposedly diagnostic for *S. lojanensis* agree with the description of *S. onorei* and since we could not find any other that may support its distinctness we regard it as a junior synonym of *S. onorei*.

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