

JÚLIO CEZAR MÁRIO CHAUL

**ESTUDOS MORFOLÓGICOS E TAXONÔMICOS DO GÊNERO
STRUMIGENYS SMITH (HYMENOPTERA: FORMICIDAE:
MYRMICINAE)**

Dissertação apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Entomologia, para obtenção do título de *Magister Scientiae*.

VIÇOSA
MINAS GERAIS - BRASIL
2018

**Ficha catalográfica preparada pela Biblioteca Central da Universidade
Federal de Viçosa - Câmpus Viçosa**

T

C497e
2018 Chaul, Júlio Cezar Mário, 1989-
Estudos morfológicos e taxonômicos do gênero *S
trumigenys* Smith (Hymenoptera: Formicidae: Myrmicinae) /
Júlio Cezar Mário Chaul. – Viçosa, MG, 2018.
vi, 102 f. : il. ; 29 cm.

Texto em inglês.

Orientador: José Henrique Schoereder.

Dissertação (mestrado) - Universidade Federal de Viçosa.

Inclui bibliografia.

1. Formigas - Morfologia. 2. Formigas - Filogenia.
3. Biodiversidade. 4. Zoologia - Classificação. I. Universidade
Federal de Viçosa. Departamento de Entomologia. Programa de
Pós-Graduação em Entomologia. II. Título.

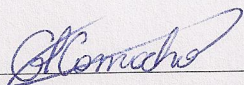
CDD 22. ed. 595.796

JÚLIO CEZAR MÁRIO CHAUL

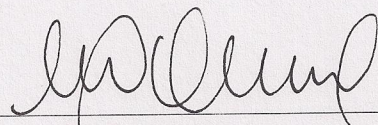
**ESTUDOS MORFOLÓGICOS E TAXONÔMICOS DO GÊNERO
STRUMIGENYS SMITH (HYMENOPTERA: FORMICIDAE: MYRMICINAE)**

Dissertação apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Entomologia, para obtenção do título de *Magister Scientiae*.

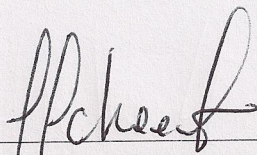
APROVADA: 5 de julho de 2018.



Gabriela Procópio Camacho



Mônica Antunes Ulysséa



José Henrique Schoereder
(Orientador)

AGRADECIMENTOS

Sou imensamente grato ao professor José Henrique Schoereder, o Zhé. A produção intelectual depende, antes de qualquer coisa, da liberdade em se discutir uma ideia boba, de poder propor ideias próprias, ou de se arriscar por em prática um projeto pouco convencional. Observei total apoio do Zhé a tudo isso durante os anos que passei no Laboratório de Ecologia de Comunidades, tanto para com alunos da pós quanto da graduação. Os que aproveitaram deste ambiente seguramente reconhecerão a importância desta postura do Zhé na sua formação. Além disso, mesmo tendo interesses bastante distintos da linha de pesquisa principal do laboratório, fui aceito e integrado ao grupo como qualquer outro aluno e, por isso, sou duplamente grato.

Agradeço aos membros do Labecol que conviveram comigo ao longo destes sete anos pela amizade. Em especial ao professor Ricardo Solar, Bob, que me "adotou" durante os primeiros anos como estagiário e depositou grande confiança. À Gabi Camacho, por perceber que eu tinha interesse na Taxonomia e ter me incentivado, junto com o Bob, a dar os primeiros passos em direção a esta área. Ao Francisko Rezende por dividir incontáveis ideias. Ao Rodrigo Jesus, por compartilhar da mesma obsessão que tenho com as formigas. Ao Gabriel Alves e à Gabi de Figueiredo, pela grande ajuda no projeto de inclusão da nossa coleção de formigas no site AntWeb, um trabalho ainda em andamento, mas do qual me orgulho dos resultados.

Grande parte desta tese consiste na organização de longos emails trocados com Thiago Sanches Ranzani da Silva sobre o gênero *Strumigenys* nos últimos cinco anos. Pelo entusiasmo, paciência e prontidão em discutir, sou grato.

Por último, mas não menos importante, agradeço à minha família: Thaís, Tereza, Vander, Valter, Vera, Toninho e "Mãe Velha". Também aos meus já falecidos avós "Pai Rolando", vó Maria e vô Beluca. À Nath e à nossa querida Polinha. A quantidade de apoio que recebi de vocês, seja na forma de afeto e carinho ou materializada em dinheiro, foi determinante para que eu pudesse desenvolver meus estudos e trata-se de um privilégio de poucos.

SUMÁRIO

RESUMO.....	v
ABSTRACT.....	vi
I. Introdução Geral	1
II. Referências Bibliográficas	3
III. CAPÍTULO I.....	6
MORPHOLOGICAL STUDIES ON THE GENUS <i>STRUMIGENYS</i> F. SMITH, 1860 (HYMENOPTERA: FORMICIDAE: MYRMICINAE) AND RELATED GENERA	6
ABSTRACT.....	6
1. Introduction.....	7
2. Material and Methods.....	11
2.1. Studied specimens and repositories	11
2.2. Disarticulation of specimens	12
2.3. Optical equipment and imaging	13
2.4. Terminology	14
3. Results.....	15
3.1. Defining characters of the <i>Strumigenys</i>	15
3.1.1. Ventral mesosoma	16
3.1.2. Metasoma	21
3.2. The labra of Neotropical <i>Strumigenys</i>.....	28
3.3. Glandular patches and bullae of <i>Strumigenys</i>	31
3.3.1. A census of the glands among Neotropical <i>Strumigenys</i>	33
3.3.2. The procoxal and propleural glandular patches	34
3.4. <i>Strumigenys</i> males.....	39
3.5. Defining characters of the SPB-clade	40
3.5.1. Opposable mandibles	42
3.5.2. Specialized labra.....	44
3.5.3. Basal process on mandibles	44
3.5.4. The phalacromyrmecine mandible	45
3.5.5. Labio-maxillary complex palpal formula	45
3.5.6. Basimandibular seta.....	45
3.5.7. Blister-like bullae on phalacromyrmecines	46
3.5.8. The antennal fossa, the scrobe, and the curved scape of the basicerotines.....	47
3.5.9. Eyes on dorsal margin of scrobe in the basicerotines.....	50
3.5.10. Expanded frontal lobes differ between <i>Strumigenys</i> and phalacromyrmecines	51
3.5.11. Clavate scapes.....	51
3.5.12. Ventral mesothoracic hair beds	51
3.5.13. The katapisternal grooves of the phalacromyrmecines.....	52
3.5.14. The carina on poststernite II (petiole) in phalacromyrmecines.....	54
3.5.15. The transversally carinated posttergites II, III and IV of <i>Strumigenys</i> and the basicerotines	55
3.5.16. Broad presclerites IV of the basicerotines	58
3.5.17. The basicerotine pilosity	61
3.5.18. The basicerotine cuticle sculpturing	63
Acknowledgements.....	64
References	64
IV. CAPÍTULO II	68

NEW SPECIES OF NEOTROPICAL <i>STRUMIGENYS</i> F. SMITH (HYMENOPTERA: FORMICIDAE: MYRMICINAE)	68
ABSTRACT	68
1. Introduction	69
2. Material and Methods	70
3. Results	74
3.1. Species accounts	75
3.1.1. <i>Strumigenys</i> ufv-20, Chaul sp. nov.	75
3.1.2. <i>Strumigenys</i> ufv-28, Chaul sp. nov.	79
3.1.3. <i>Strumigenys</i> ufv-27, Chaul sp. nov.	83
3.1.4. <i>Strumigenys</i> ufv-11 Chaul sp. nov.	87
3.1.5. <i>Strumigenys</i> ufv-64, Chaul sp. nov.	92
References	100
V. CONCLUSÕES GERAIS	102

RESUMO

CHAUL, Júlio Cezar Mário, M.Sc. Universidade Federal de Viçosa, julho de 2018. **Estudos morfológicos e taxonômicos do gênero *Strumigenys* Smith (Hymenoptera: Formicidae: Myrmicinae)**. Orientador: José Henrique Schoereder.

O gênero de formigas *Strumigenys*, membro da subfamília Myrmicinae, é composto por centenas de espécies de tamanho reduzido que habitam principalmente a serapilheira de florestas tropicais ao redor do planeta. O gênero compõe uma significativa parte da fauna de formigas destes ambientes, tanto em termos de riqueza quanto de abundância. A partir de 2000, quando o gênero foi revisado globalmente, trabalhos pontuais de taxonomia descreveram novas espécies e trabalhos de filogenia molecular revelaram relações de parentesco antes desconhecidas, tanto internas no gênero quanto entre *Strumigenys* e outros gêneros, e suportam a classificação atual da subfamília e do posicionamento do gênero. Uma caracterização morfológica destes clados recentemente recuperados não está disponível. Um capítulo desta tese consiste em um estudo de morfologia comparativa entre *Strumigenys* e gêneros relacionados que reexamina e reinterpreta caracteres já discutidos na literatura e apresenta novos caracteres como forma de diagnosticar os clados da classificação atual de Myrmicinae. O segundo capítulo descreve novas espécies Neotropicais do gênero.

ABSTRACT

CHAUL, Júlio Cezar Mário, M.Sc. Universidade Federal de Viçosa, July, 2018. **Morphological and taxonomic studies of the genus *Strumigenys* Smith (Hymenoptera: Formicidae: Myrmicinae)**. Adviser: José Henrique Schoederer.

The ant genus *Strumigenys* is a member of the subfamily Myrmicinae and is composed of very tiny, litter-dwelling species which inhabit the rainforests around the globe. The genus is an important part of the ant community in these environments, both in terms of abundance and species richness. After the year 2000, when the genus was revised globally, scattered taxonomic works described new species and molecular-based phylogenies revealed relationships not previously known, both between *Strumigenys* and other genera and internally, between the various lineages of *Strumigenys*. These works currently support the taxonomical classification of the subfamily and the positioning of the genus within it. Morphological characterization of the newly discovered clades are, however, lacking. The first chapter of this thesis consist of a comparative morphological study between *Strumigenys* and related genera. It reassess and reinterprets available morphological data and presents newly discovered characters as way of better diagnose the clades of the modern Myrmicinae classification. A second chapter describes new Neotropical species of *Strumigenys*.

I. Introdução Geral

As formigas são um dos mais conspícuos grupos de animais terrestres. A adaptação das mais de 13.000 espécies de formigas (Bolton, 2018) aos diversos ambientes terrestres tem sua explicação, dentre outros fatores, no seu modo de vida eussocial e na adaptação à exploração de uma grande quantidade de recursos (Hölldobler and Wilson, 1990; Lach et al., 2010). A origem da família Formicidae está no Mesozóico (Cretáceo), mas sua relevância como um grupo dominante de insetos se dá no Cenozóico (Lapolla et al., 2013; Barden, 2017). As formigas estão envolvidas em uma imensa rede de interações ecológicas com milhares de animais, plantas e microorganismos (Beattie and Hughes, 2002; Mehdiabadi and Schultz, 2009; Maderspacher and Stensmyr, 2011; Murray et al., 2013; Parker, 2016). Compreender as comunidades de formigas implica, em certa medida, na compreensão dos ecossistemas terrestres como um todo.

Estudos taxonômicos têm uma importância teórica por enriquecer a área da Taxonomia e da Sistemática em si e, ao mesmo tempo, uma importância prática por fornecer um modo de identificação das espécies para as outras áreas das Ciências Biológicas. Áreas como a Etologia, Biologia da Conservação, Ecologia de Comunidades, Controle Biológico, dentre muitas outras, dependem de uma classificação taxonômica confiável, compreensível e acessível para que se desenvolvam (Schlick-Steiner et al., 2010). Normalmente estas ferramentas são apresentadas na forma de chaves dicotômicas, mapas, pranchas de imagens (desenhos ou fotos) e descrições. As chaves dicotômicas são a principal forma usada para possibilitar o acesso à identidade de um *taxon*.

Nos últimos anos ocorreram grandes avanços na filogenia das formigas que foram acompanhados de profundas reclassificações taxonômicas. Estudos moleculares promoveram mudanças no nível de gêneros, tribos, subfamílias e do posicionamento da família Formicidae em relação aos demais Hymenoptera (Moreau et al., 2006; Brady et al., 2006; Ward et al., 2010; Schmidt, 2013; Brady et al., 2014; Ward et al., 2015; Ward et al., 2016a; Ward et al., 2016b; Branstetter et al., 2017; Peters et al., 2017) modificando substancialmente a compreensão da evolução das formigas e estabelecendo uma firme base teórica para o aprofundamento da sistemática nas diversas linhagens da família. Cada um destes trabalhos propõe hipóteses filogenéticas que estabelecem dezenas de clados que muitas vezes são compostos, cada um, por centenas ou até milhares de espécies. A tarefa de corretamente delimitar e organizar

estas espécies, responsabilidade dos alfa-taxonomistas, é imensa e normalmente não é tratada nos estudos moleculares como os citados acima, que são restritos a *rankings* supra-específicos. Pela natureza distinta dos dois tipos de estudo, aqueles sobre alfa-taxonomia não acompanham o ritmo dos trabalhos moleculares de classificação supra-específica, o que cria uma desproporção no conhecimento entre *rankings* supra-específicos (melhor resolução) e no nível de espécies (menor resolução). Um exemplo desta situação é o da subfamília Myrmicinae, que recentemente foi reinterpretada genericamente e tribalmente (Ward et al., 2015). Apesar das relações entre as linhagens desta subfamília estarem relativamente bem estabelecidas, a subfamília é tão vasta em número de espécies que muitas linhagens ainda permanecem pouco resolvidas alfa-taxonomicamente, a despeito das inúmeras contribuições (e.g. Brandão, 1990; Kugler, 1994; Lattke, 1997; De Andrade and Baroni Urbani, 1999; Bolton, 2000; Wilson, 2003; Longino, 2003; 2009 2010; 2013a; 2013b; Mayhé-Nunes and Brandão, 2007; Feitosa and Brandão, 2008; Longino and Boudinot, 2013; Ješovnik and Schultz, 2017).

O gênero de formigas *Strumigenys*, membro da tribo Attini da subfamília Myrmicinae, é composto por 837 espécies de tamanho reduzido que habitam principalmente a serapilheira de florestas tropicais ao redor do planeta (Bolton 1999, Bolton, 2018). O gênero compõe uma significativa parte da fauna de formigas destes ambientes, tanto em termos de riqueza quanto de abundância. *Strumigenys* foi globalmente revisado recentemente (Bolton, 2000) e sua diversidade quase dobrou naquele ano. Apesar de ter sua alfa-taxonomia bastante avançada desde o ano 2000, várias novas espécies continuaram a serem descritas desde então (Longino, 2006; Sosa-Calvo et al., 2006; Sosa-Calvo et al., 2010; Rigato and Scupola, 2008; Baroni Urbani and De Andrade, 2007; Lattke and Aguirre, 2015) e novas espécies continuam a se acumular em coleções mirmecológicas.

A presente tese, apresentada em dois capítulos, tem o intuito de desenvolver uma melhor caracterização morfológica do gênero *Strumigenys* e de suas linhagens relacionadas a fim de dar suporte a atual classificação baseada em dados moleculares, além de aumentar a diversidade do gênero para a região Neotropical através da descrição de novas espécies. Mais especificamente, o primeiro capítulo, além de apresentar novos caracteres morfológicos descobertos para o gênero *Strumigenys* e gêneros relacionados, também reinterpreta outros tantos caracteres já debatidos na literatura (Baroni Urbani and De Andrade, 1994; 2007; Bolton 1998; 1999; 2000), mas nunca antes discutidos à luz dos recentes trabalhos de filogenia molecular que

mudaram radicalmente a classificação da subfamília Myrmicinae. Apesar de também estudar o gênero *Strumigenys* internamente, o capítulo tem o principal foco de comparar *Strumigenys* com gêneros relacionados, principalmente as duas linhagens mais próximas, as phalacromyrmecíneas e as basicerotíneas. O segundo capítulo é composto de um compilado de descrições de espécies Neotropicais que não são proximamente aparentadas, pertencentes a diversos grupos Neotropicais, e tem o objetivo de expandir a diversidade do gênero.

II. Referências Bibliográficas

- Barden, P. Fossil ants (Hymenoptera: Formicidae): ancient diversity and the rise of modern lineages. *Myrmecological News*, 24: 1–30, 2017.
- Baroni Urbani, C.; De Andrade, M. L. First description of fossil Dacetini ants with a critical analysis of the current classification of the tribe (Amber Collection Stuttgart: Hymenoptera, Formicidae. VI: Dacetini). *Stuttg. Beitr. Naturkd. Ser. B (Geol. Palaontol.)*, 198: 1–65, 1994.
- Baroni Urbani, C.; De Andrade, M. L. The ant tribe Dacetini: limits and constituent genera, with descriptions of new species. *Annali del Museo Civico di Storia Naturale Giacomo Doria (Genova)*, 99: 1–191, 2007.
- Beattie, A.; Hughes, L. Ant-plant interactions. In: *Plant animal interactions: an evolutionary approach*. [s.l: s.n.]. p. 221–235, 2002.
- Bolton, B. Monophyly of the dacetone tribe-group and its component tribes (Hymenoptera: Formicidae). *Bulletin of the Natural History Museum*, 67: 65–78, 1998.
- Bolton, B. Ant genera of the tribe Dacetoniini (Hymenoptera: Formicidae). *Journal of Natural History*, 1999.
- Bolton, B. The ant tribe Dacetini. *Memoirs of the American Entomological Institute*, 65: 1–1028, 2000.
- Bolton, B. An online catalog of the ants of the world. Available from <http://antcat.org>. Accessed -- February 20-- 2018.
- Brady, S. G. et al., Evaluating alternative hypotheses for the early evolution and diversification of ants. *Proc. Natl. Acad. Sci. U.S.A.*, 103(48): 18172–18177, 2006.
- Brady, S. G. et al., The rise of army ants and their relatives: diversification of specialized predatory doryline ants. *BMC Evolutionary Biology*, 14(1): 93, 2014.
- Brandão, C. Systematic revision of the neotropical ant genus *Megalomyrmex* Forel (Hymenoptera: Formicidae: Myrmicinae), with the description of thirteen new species. *Arquivos de Zoologia*, 31(5): 411–481, 1990.
- Branstetter, M. G. et al., Phylogenomic Insights into the Evolution of Stinging Wasps and the Origins of Ants and Bees. *Current Biology*, 27(7): 1019–1025, 2017.

- De Andrade, M. L.; Baroni Urbani, C. Diversity and adaptation in the ant genus *Cephalotes*, past and present. *Stuttg. Beitr. Naturkd. Ser. B (Geol. Palaontol.)*, 271: 1–889, 1999.
- Feitosa, R. M.; Brandão, C. R. F. A taxonomic revision of the Neotropical myrmicine ant genus *Lachnomyrmex* Wheeler (Hymenoptera: Formicidae). *Zootaxa*, (1890): 1–49, 2008.
- Hölldobler, B.; Wilson, E. O. *The Ants*. [s.l.] Harvard University Press, v. N1, 1990.
- Ješovnik, A.; Schultz, T. R. Revision of the fungus-farming ant genus *Sericomyrmex* Mayr (Hymenoptera, Formicidae, Myrmicinae). *ZooKeys*, 670: 1–109, 2017.
- Kugler, C. Revision of the ant genus *Rogeria* (Hymenoptera: Formicidae) with descriptions of the sting apparatus. *Journal of Hymenoptera Research*, 1994.
- Lach, L.; Parr, C.; Abbott, K. (Eds.). *Ant Ecology*. 1st. ed. [s.l.] Oxford University Press, 2010.
- Lapolla, J. S.; Dlussky, G. M.; Perrichot, V. Ants and the fossil record. *Annual Review of Entomology*, 58: 609–30, 2013.
- Lattke, J. E. Revisión del género *Apterostigma* Mayr (Hymenoptera: Formicidae) *Arquivos de Zoologia - Museu de Zoologia da Universidade de São Paulo*, 1997.
- Lattke, J. E.; Aguirre, N. Two new *Strumigenys* F. Smith (Hymenoptera: Formicidae: Myrmicinae) from montane forests of Ecuador. *Sociobiology*, 62(2): 175–180, 2015.
- Longino, J. T. New species and nomenclatural changes for the Costa Rican ant fauna (Hymenoptera: Formicidae). *Myrmecologische Nachrichten*, 8: 131–143, 2006.
- Longino, J. T. The *Crematogaster* (Hymenoptera, Formicidae, Myrmicinae) of Costa Rica. *Zootaxa*, 151(February): 1–150, 2003.
- Longino, J. T. Additions to the taxonomy of New World Pheidole (hymenoptera: Formicidae). *Zootaxa*, (2181): 1–90, 2009.
- Longino, J. T. A revision of the ant genus *Octostruma* Forel 1912 (Hymenoptera, Formicidae). *Zootaxa*, 3699(1): 1–61, 2013a.
- Longino, J. T. A review of the Central American and Caribbean species of the ant genus *Eurhopalothrix* Brown and Kempf, 1961 (Hymenoptera, Formicidae), with a key to New World species. *Zootaxa*, 3693(2): 101–151, 2013b.
- Longino, J. T.; Boudinot, B. E. New species of Central American *Rhopalothrix* Mayr, 1870 (Hymenoptera, Formicidae). *Zootaxa*, 3616(4): 301–324, 2013.
- Maderspacher, F.; Stensmyr, M. Myrmecomorphomania. *Current Biology*, 21(9), 2011.
- Mayhé-Nunes, A. J.; Brandão, C. R. F. Revisionary studies on the attine ant genus *Trachymyrmex* Forel. Part 3: The Jamaicensis group (Hymenoptera: Formicidae). *Zootaxa*, (1444): 1–21, 2007.
- Mehdiabadi, N. J.; Schultz, T. R. Natural history and phylogeny of the fungus-farming ants (Hymenoptera: Formicidae: Myrmicinae: Attini). *Myrmecological News*, 13: 37–55, 2009.

- Moreau, C. S. et al., Phylogeny of the ants: Diversification in the age of angiosperms. *Science*, 312(5770): 101–104, 2006.
- Murray, E. A.; Carmichael, A. E.; Heraty, J. M. Ancient host shifts followed by host conservatism in a group of ant parasitoids. *Proceedings. Biological sciences / The Royal Society*, 280(1759): 20130495, 2013.
- Parker, J. Myrmecophily in beetles (Coleoptera): Evolutionary patterns and biological mechanisms. *Myrmecological News*, 22: 65–108, 2016.
- Peters, R. S. et al., Evolutionary History of the Hymenoptera. *Current Biology*, 27(7): 1013–1018, 2017.
- Rigato, F.; Scupola, A. Two new species of the *Pyramica gundlachi*-group from Ecuador (Hymenoptera Formicidae). *Biodivers. South America*, I. Mem. Biodiver., 1: 477–481, 2008.
- Schlick-Steiner, B. C. et al., Integrative Taxonomy: A Multisource Approach to Exploring Biodiversity. *Annual Review of Entomology*, 55(1): 421–438, 2010.
- Schmidt, C. Phylogenetics of Ponerine ants (Hymenoptera: Formicidae: Ponerinae). *Zootaxa*, 3647(2), 201–250, 2013.
- Sosa-Calvo, J.; Schultz, T. R.; Lapolla, J. S. A Review of the Dacetine Ants of Guyana (Formicidae: Myrmicinae). *Journal of Hymenoptera Research*, 19(1): 12–43, 2010.
- Sosa-Calvo, J.; Shattuck, S. O.; Schultz, T. R. Dacetine ants of Panama: new records and description of a new species (Hymenoptera: Formicidae: Myrmicinae: Dacetini). *Proc. Entomol. Soc. Washington*, 108(4): 814–821, 2006.
- Ward, P. S. et al., Phylogeny and biogeography of dolichoderine ants: Effects of data partitioning and relict taxa on historical inference. *Systematic Biology*, 59(3): 342–362, 2010.
- Ward, P. S. et al., The evolution of myrmicine ants: Phylogeny and biogeography of a hyperdiverse ant clade (Hymenoptera: Formicidae). *Systematic Entomology*, 40(1): 61–81, 2015.
- Ward, P. S.; Blaimer, B. B.; Fisher, B. L. A revised phylogenetic classification of the ant subfamily Formicinae (Hymenoptera: Formicidae), with resurrection of the genera *Colobopsis* and *Dinomyrmex*. *Zootaxa*, 4072(3): 343–357, 2016a.
- Ward, P. S.; Fisher, B. L. Tales of dracula ants: The evolutionary history of the ant subfamily Amblyoponinae (Hymenoptera: Formicidae). *Systematic Entomology*, 41(3): 683–693, 2016b.
- Wilson, E. O. 2003. *Pheidole* in the New World. A dominant, hyperdiverse ant genus. Cambridge, Mass.: Harvard University Press, [ix] + 794 pp.

III. CAPÍTULO I

MORPHOLOGICAL STUDIES ON THE GENUS *STRUMIGENYS* F. SMITH, 1860 (HYMENOPTERA: FORMICIDAE: MYRMICINAE) AND RELATED GENERA

ABSTRACT

Strumigenys is a genus of myrmicine ants with outstanding morphological variation. Some of these traits, like mandible shape and body pilosity, have been thoroughly studied, while others remain poorly explored or even neglected. We comparatively studied, among *Strumigenys* species and between *Strumigenys* and other myrmicine genera, some of these less studied characters, namely the ventral mesosoma, characters of the anterior metasoma (abdominal segments II, III and IV), labral shape, and the shape, position and distribution of glandular patches (bullae) on the sclerites. Four characters have been identified as important to set *Strumigenys* apart from closer genera: a hypertrophied metapleural seta, the notched ventral margin of the propodeal foramen, an anterior carina on poststernite II and tergosternal fusion of abdominal segment III. Additionally, the spongiform ventral pad on poststernite IV is showed to be composed of highly specialized setae. Its occurrence in conjunction with the cuticular spongiform outgrowths is not replicated in any other ant genus. Labral morphology and glands have been comparatively studied among Neotropical species. Labral morphology varies drastically in non-trap-jaw species and much less among trap-jaws. Glandular patches also varies a lot among species groups. Both labral morphology and "gland formula" can be useful in defining some groups of species and sometimes in supporting species level hypothesis. The glandular nature of the procoxal patches are corroborated and a propleural gland is described for the first time for some species in the genus. Finally, we discussed the importance of some characters previously disputed in the literature to define *Strumigenys* and its closest lineages, the phalacromyrmecines and the basicerotines.

Key-words: *Strumigenys*, morphology, Neotropics, synapomorphy

1. Introduction

Strumigenys is a cosmopolitan genus of ants composed of 841 species (Bolton, 2018). Despite having many species restricted to colder and drier environments, the genus peaks in diversity in the tropical rainforests around the world (Bolton, 1998). In the rainforests, *Strumigenys* is often an abundant component of the litter community (Ward, 2000). All species are thought to be predators of soft arthropods, especially of Entomobryomorpha (Collembola) (Dejean, 1985; Masuko, 1985, 2009), although the diet of the great majority of the species hasn't been documented yet and their unparalleled diversity in mandible morphology among ants implies they hunt a vast array of prey.

The *Strumigenys* have a set of exquisite morphological features, most of which have been vastly explored in previous taxonomic works (Brown, 1953, 1959, 1964; Bolton, 1983, 2000). Apart from the extreme variation in mandible shape pointed out above, examples of characters that have been intensively observed in the genus are head shape, pilosity, sculpturing, the presence of lamellate cuticle projections (mainly on head and propodeum), body proportions, and presence and quantity of "spongiform tissue" (Fig. 1). Other traits have been noticed, but not exhaustively scrutinized among species, like the presence of exocrine glands which form visible patches on the cuticle, the labrum shape among closely related species (labral morphology of larger groups inside the genus has been extensively studied), the variety of forms of the "spongiform tissue", especially the specificities of them on each sclerite they occur considered individually. Finally, characters of ventral mesosoma have been almost completely neglected, probably because the region is concealed by the coxae and/or by glue (due to the most common way of mounting ants by gluing a card triangle beneath the coxae).

The genus belongs to the Myrmicinae and used to be placed in the old tribe Dacetini (Bolton, 2003), but has now been reclassified based on molecular results as a member of the tribe Attini. In the Attini, the *Strumigenys* clade is sister to the small "phalacromyrmecine" clade, the two being sisters to the "basicerotine" clade (Ward et al., 2015). *Strumigenys*, the phalacromyrmecines and the basicerotines are termed hereafter the *SPB-clade*. *Strumigenys* is not closely related to the "dacetine" clade (Ward et al., 2015), which is mostly formed by the genera that used to share the Dacetini tribe with it (terms in quotation marks in this paragraph will be used along the manuscript, see Material and Methods for a definition of their meaning). Prior to the molecular era, there have already been extensive and disputed morphological work

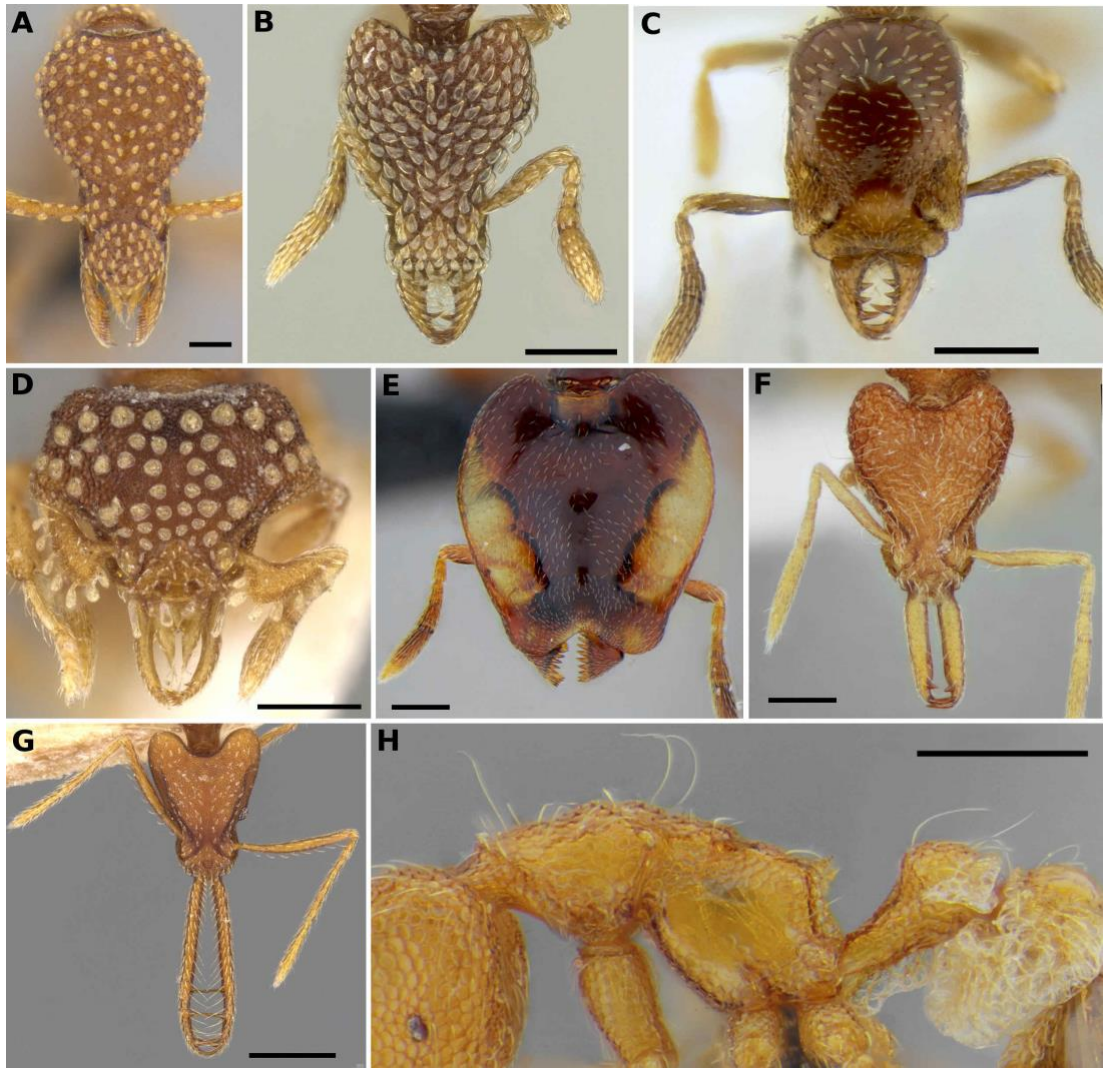


Fig. 1. Morphological diversity and general characters of *Strumigenys*. From A to G: diversity in head shape, pilosity, and mandible shape; H, zooming of profile view evidencing flagellate standing hairs, propodeal lamella and spongiform tissue on metasoma. **A**, *Strumigenys* n.sp (ANTWEB1032328, *disjuncta*-group); **B**, *S. undras* (CASENT0900855, *biroi*-group, photo by Ryan Perry, AntWeb); **C**, *S. nitens* (CASENT0106246, *nitens*-group, photo by Michael Branstetter, AntWeb); **D**, *S. laticeps* (CASENT0900046, *argiola*-group, photo by Will Ericson, AntWeb); **E**, *S. perissognatha* (ANTWEB1032467, *substricta*-group); **F**, *Strumigenys* ufv-14 (ANTWEB1032516, *hindenburgi*-group); **G**, *S. dolichognatha* (CASENT0900429, *mandibularis*-group, photo by Will Ericson), **H**. *S. tanymastax* (UFV-LABECOL-006722, *tanymastax*-group).

suggesting phylogenetic relations between *Strumigenys*, the phalacromyrmecines, and the basicerotines. However, these works also considered the dacetines as a related lineage (Brown, 1948, 1949; Baroni Urbani and De Andrade, 1994; Bolton, 1998; Baroni Urbani and De Andrade, 2007). The molecular results now show that at least part of the disagreements regarding the classification of those ants, termed in the latest morphology-based papers as the Dacetini tribe group (Bolton, 2003) or only Dacetini

(Baroni Urbani and De Andrade, 2007), can be at least partially explained by the fact that the dacetines were being considered as part of the group. In fact, the dacetines are only remotely related to the SPB-clade, having acquired a similar habitus by convergence, and being a sister clade to the fungus-growing ants, the "attines" (Branstetter et al., 2017). While some of the characters of the dacetines, now known to be convergent, were easily associated with those of SPB-clade members (e. g. mandibles, the labrum in some cases), others represented a morphological puzzle of difficult solution (e. g. scrobe, eyes, antennal count, the labrum in other cases). A large quantity of valuable morphological data was compiled by those authors and can now be reinterpreted in light of the molecular tree topology.

Strumigenys is one of the few examples, if not the only one, of a large, cosmopolitan genus of ants that have received a global alpha-taxonomic treatment (Bolton, 2000). In this monograph, a great number of new species were described and the genus has been organized in a system of groups of species, the majority of which are restricted to a particular biogeographic region. Long standing issues regarding the genus internal phylogeny were given at least incipient answers in Ward et al. (2015), due to the carefully selected OTUs of that work. First, whether *Pyramica* (currently a junior synonym of *Strumigenys*, Baroni Urbani and De Andrade, 2007) and *Strumigenys* were monophyletic in respect to each other or one genus were nested within the other. Second, whether the ancestral form of the genus was likely a trap-jaw species or a species with gripping mandibles. And third, how many times a type of mandibles, regardless of which one, gave rise to another type (Bolton, 1999; Baroni Urbani and De Andrade, 2007). Their results indicated that the synonymization of *Pyramica* into *Strumigenys* was correct, and that ancestrally the genus was probably an assemblage of species with gripping mandibles which gave rise, apparently three independent times, to trap-jaw lineages that irradiate in different continents (Ward et al., 2015, Fig. 2). Larger phylogenies might reveal yet new patterns of the evolution of this hyperdiverse, morphologically and biogeographically interesting genus.

In this contribution, we aimed to study specific morphological characters of *Strumigenys* which we believe could be further explored. More specifically, we focused on the study of the morphology of **(i)** the ventral mesosoma and **(ii)** the metasoma, focusing on abdominal segments II, III and IV. While examining (i) and (ii), we were in search of novelties, previously unnoticed characters setting *Strumigenys* apart from the other myrmicine genera. Therefore, we made a genus level

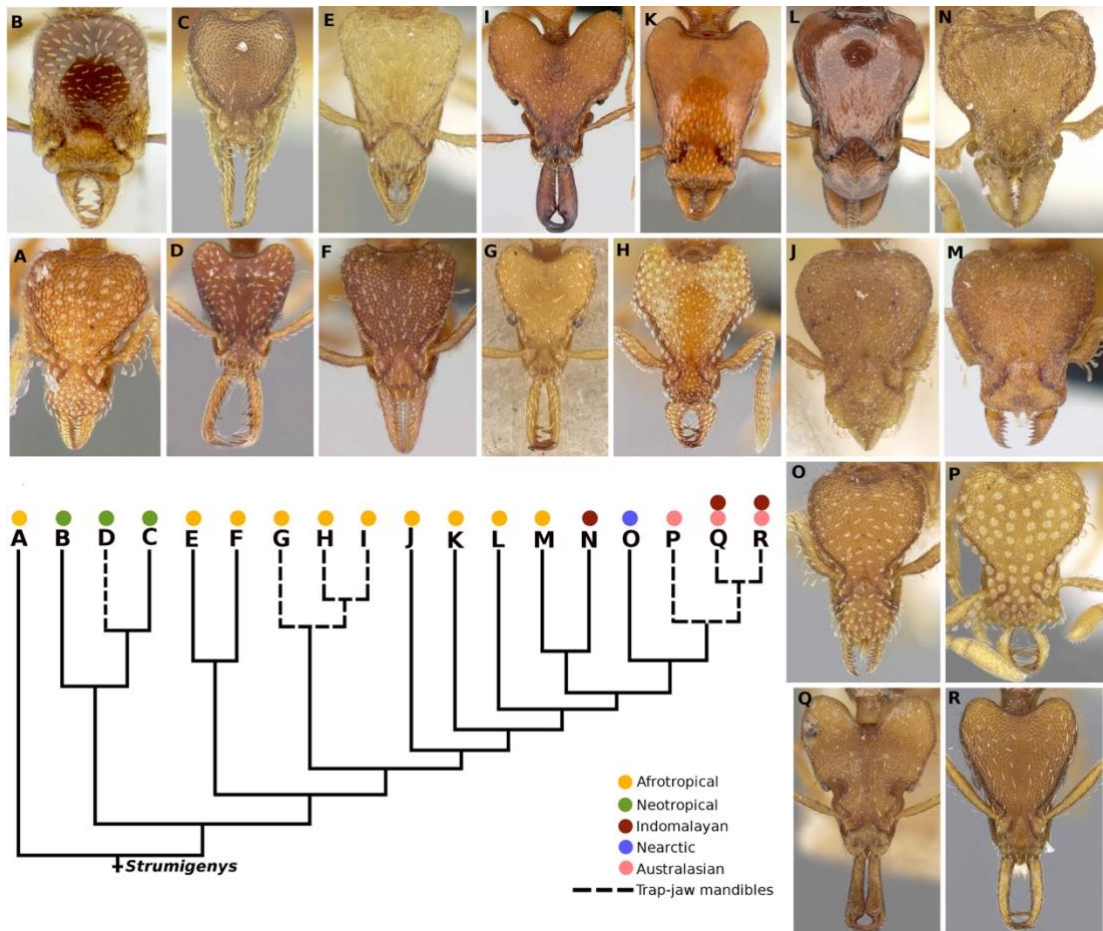


Fig. 2. The internal relations of the genus *Strumigenys* based on Ward et al., 2015 showing the repeated evolution of lineages with trap-jaw mandibles (traced lines) from lineages with gripping mandibles (solid lines). **A**, *S. ambatrix* (CASENT0005445, unknown image author); **B**, *S. nitens* (CASENT0106246, photo by Michael Branstetter); **C**, *S. gundlachi* (CASENT0915948, photo by Anna Pal); **D**, *S. biolleyi* (CASENT0106237, photo by Marek Borowiec); **E**, *S. erynnes* (CASENT0900034, photo by Will Ericson); **F**, *S. ludovici* (CASENT0056480, photo by April Nobile); **G**, *S. rogeri* (CASENT0900597 photo by Will Ericson); **H**, *S. coveri* (CASENT0153050, photo by Erin Prado); **I**, *S. dicomas* (CASENT0499800, photo by April Nobile); **J**, *S. maxillaris* (CASENT0922238, photo by Michelle Esposito); **K**, *S. olsoni* (CASENT0005455, unknown image author); **L**, *S. exiguavita* (CASENT0900036, photo by Will Ericson); **M**, *S. membranifera* (CASENT0133285, photo by Erin Prado); **N**, *S. ocypete* (CASENT0900141, photo by Will Ericson); **O**, *S. chircahua* (CASENT0914686, photo by Zach Lieberman); **P**, *S. emmae* (CASENT0914790, photo by Zach Lieberman); **Q**, *S. chyzeri* (CASENT0900867 Ryan Perry); **R**, *S. godeffroyi* (CASENT0914798, photo by Zach Lieberman). Branch size is meaningless, for correct branch size see Ward et al., (2015).

comparison between selected species of *Strumigenys* and a large set of myrmicine lineages, specially members of the tribe Attini. We also investigated **(iii)** the labrum shape and **(iv)** the occurrence, shape and position of glands that are visible by external examination (represented by blister-like bullae or modified patches on specific sclerites). While examining **(iii)** and **(iv)**, we focused on large numbers of Neotropical

species as our main goal was to determine if these traits have diagnosing value for species groups as well as in the species level. Labral shape has been thoroughly studied and used as a marker of "big trends" within the genus. However, it has never been comparatively studied among a large number of closely related species. The study of their glands is in a similar situation. Glands have been used in the identification keys for convenience, but a broad census, which could possibly define groups of species and species themselves, hasn't been made. Finally, we (v) reassessed the available characters (observed by us as well as those from the literature) in an attempt to identify which ones are good defining characters for the clades recovered in the molecular papers, the SPB-clade and its internal subdivisions (Ward et al., 2015; Branstetter et al., 2017). To do so, we commented individually some of the characters discussed in Baroni Urbani and De Andrade (2007), as these authors covered almost the entire amount of the morphological data presented before them, especially by Bolton (Bolton 1983, 1984, 1998, 1999, 2000, 2003) and themselves (Baroni Urbani and De Andrade, 1994). It is important to highlight that our goal was solely to discuss the diagnostic potential of each character and not their suitability for cladistic analysis, as was that of Baroni Urbani and De Andrade (2007).

2. Material and Methods

2.1. Studied specimens and repositories

We have examined specimens from the following institutions:

- Instituto Nacional de Pesquisas da Amazônia (INPA);
- Museu de Zoologia da Universidade de São Paulo (MZUSP);
- Laboratório de Ecologia de Comunidades (LABECOL) from the Universidade Federal de Viçosa (UFV);
- Coleção Entomológica Pe. Jesus Santiago Moure (DZUP) from the Universidade Federal do Paraná (UFPR);
- Laboratório de Evolução de Insetos de Dóssel e Sucessão Natural (LEEIDSN) from the Universidade Federal de Ouro Preto (UFOP);
- Images from AntWeb.org from specimens of various institutions (their unique specimen identifiers always cited along the text or Fig.s);

The specimens were identified by using available keys (Bolton, 2000), checking the original descriptions, and by comparing them to images of types available on AntWeb. When specimens couldn't be assigned to a described species by using one,

two, or all of the above procedures, they were assigned to a morphospecies starting with the code "ufv-" followed by a number, like *Strumigenys* ufv-14.

Apart from a small group of selected specimens from which we extracted most of the morphological data (mostly disarticulated specimens), we had hundreds of specimens available for general study and confirmation of the characters studied just mentioned and a complete list of them can be found at Antweb.org by applying the following filters at the Advanced Search tool: the field **Genus** filled as "Strumigenys", the field **Uploaded by** as Universidade Federal de Viçosa, the field **Statuses** as "All", the field **Images Only** as "Off", and the field **Group by** as "Specimen". For a complete list of *species* studied, mark the field **Group By** as "Species". Each of the links given in the result of this search represents a single pin (with one or more specimens) studied by us. Specificities of each pin, mainly the ones of disarticulated specimens, are described in *Specimens Notes* inside each link. Specimens with the field Specimens Notes empty are regular specimens, not disarticulated and without any specificity.

We didn't examine any physical specimens of phalacromyrmecines. There are 14 imaged specimens of them available at AntWeb, including species in the three genera. We made use of these images and were able to check several important characters. The specimen CASENT0179596, although determined as *Ph. fugax*, appears to be a sister undescribed species for having denser, longer, and flexuous pilosity, rather than the sparse, stiff and short setae which occur in the other specimens, including the type of *Ph. fugax*.

2.2. Disarticulation of specimens

Disarticulated specimens were either from fresh ethanol samples or dried pinned specimens. In the former case, they were pulled out of ethanol and readily disarticulated on an EVA foam piece soaked with ethanol (this material proved efficient to avoid damaging the specimen while dissecting). If the specimen was pinned and dry, then it was first put into hot water (if the specimen was dirty, a little bit of detergent was added too) for some minutes prior to disarticulation to hydrated and avoid damaging hairs or the sclerites which are brittle when specimens are dry. After that, procedure followed as that of fresh specimens. Most specimens were "completely disarticulated". A "complete" disarticulation was that in which the head was separated from mesosoma; the mesosoma from metasoma; in the head, the labio-maxillary complex, and labrum (and sometimes one mandible and/or one antenna) were removed

from the cephalic capsule by gently pushing these sclerites with an entomological pin; in the mesosoma the legs were removed from the coxae foramina; and in the metasoma, the petiole, postpetiole and gaster were separated. Other specimens were only partially disarticulated according to necessity (specific treatment is described in *Specimens Notes* field in each specimen's page at AntWeb.org, as explained above). Separated sclerites of a given specimen were then glued on several triangular cards and pinned together in the same entomological pin. Labio-maxillary complex, labrum and mandible were mounted in a drop of polyvinyl-lacto-phenol medium (Downs, 1943) placed in between a 10 mm and a 6 mm round cover glasses. A card was glued at the margin of the larger cover glass and then pinned together beneath the disarticulated sclerites.

All disarticulated specimens are deposited at the UFV-LABECOL ant collection, other specimens will each be sent back to their institutions (registered at *Owned by* field at the specimen's page at AntWeb.org) after the publication of this work.

2.3. Optical equipment and imaging

Specimens were studied either in a Leica S8 APO stereomicroscope coupled with a 2x auxiliary objective or in a Olympus SZ60 stereomicroscope coupled with a 2x auxiliary objective. When necessary, 20x eye pieces replaced the standard 10x. High magnification was crucial to confidently score bullae presence or absence in the specimens (we suggest at least 80x), as *Strumigenys* are often very tiny and the bullae can be only a minute patch on the surface of a specific sclerite. Bright LED lights were placed laterally and from above while studying the specimens. Specimens were placed in a specimen examination stage for easy changing of angles of visualization. Positioning the LEDs is very important, as the bullae sometimes are only revealed under specific light incidence. If not seeing the bulla straight away on a given sclerite, the specimen was tilted slightly or the direction of the light was slightly changed and then the sclerite reexamined. Only after "scanning" the sclerite in three or more different angles and not seeing anything we scored the bulla as not seen for that sclerite. It doesn't mean, however that it is not present, as some specimens appear to have the bullae with little or no contrast in relation to the surrounding integument. So, zeros in the bullae formula (proposed below) must be understood as *possibly absent* instead of *absent*. In our experience, specimens let to dry for half an hour or more in the incubator readily after pulled out from ethanol showed a more opaque cuticle and

with the bullae with greater contrast, so we recommend this procedure if possible (the same result can be achieved by placing the specimens on absorbent tissue and let them on a warm surface for some minutes). On the other hand, bullae were harder to observe in specimens that were washed with detergent.

Images were acquired either on the stereomicroscope, on the light microscope, or on the scanning electron microscope. The majority of the images were taken in a Leica S8APO stereomicroscope with a 2x auxiliary objective, coupled with a Canon 1100D, the latter with a T-mount 10x eye-piece adapter to link the camera to the stereomicroscope. "Final images" were the result of combining several "individual images" acquired in slightly different focus planes of a given angle and magnification of the specimen in the software Zerene Stacker, producing an image with artificially-created large depth of field. The resulting image was corrected for sharpness, rotation and light adjustments in the software GIMP (Kimball and Mattis, 1996) and scales bars were added in the software ImageJ (Schneider et al., 2012). A body measurement (e.g. head width, Weber's length, pronotal width) was taken in the specimen at the moment of acquiring the images and then used to calibrate the image in the software Image J to generate a scale bar of a preferable size. Images of the sclerites mounted on the rounded slides were taken in a ECEbi Olympus light microscope with the same camera and adapter mounted on it and following the same procedures described for the stereomicroscope images. Scanning electron microscope images were taken in the Centro de Microscopia Eletrônica at the Universidade Federal do Paraná (CME-UFPR), using a Tescan Vega Lmu under high vacuum. Images not made by us are credited to the corresponding authors in the legends of the plates they compose. They have all been taken from AntWeb, except images K-N in Fig. 20, which are prints from micro-CT scanning models made by the Arilab, from the Okinawa Institute of Science and Technology (OIST) and available at Sketchfab.com (<https://sketchfab.com/arilab/collections/strumigenys>).

2.4. Terminology

Most of the terms used here are the common terms used in ant literature (Bolton, 1995), but we made widely use of specific terms used in the bibliography of the SPB-clade (Bolton, 2000, 2003). For a greater precision, when referring to abdominal characters, we used the terms of each of its subdivisions. Therefore, we differentiated tergite from sternite and presclerite from postsclerite (Bolton, 2003; Keller, 2011),

ending up with four terms that were widely used across the text: pretergite, posttergite, presternite, and possternite. Also, presclerites and postsclerites were used when referring to both the tergite and the sternite at the same time (e. g. presclerites III instead of helcium). A number in front of these names indicates from which abdominal segment it belongs to. Adopting these terms allowed us to be more precise in the descriptions of the characters. For example, the poststernite II is commonly called in ant literature "the petiole sternite", when in fact it is only the posterior and larger part of the petiole sternite.

Across the text informal names were used to refer to clades inside the Attini. The term *attine* refers to all genera of fungus-growing ants (*sensu* Branstetter et al., 2017); the term "basicerotine" refers to the clade formed by *Basiceros*, *Octostruma*, *Rhopalothrix*, *Eurhopalothrix*, *Talaridris*, and *Protalaridris*; the term *dacetine* refers the clade formed by *Daceton*, *Acanthognathus*, *Lenomyrmex*, *Microdaceton*, *Epopostruma*, *Mesostruma*, *Colobostruma* and *Orectognathus*; and the term "phalacromyrmecine" refers to the clade formed by *Phalacromyrmex*, *Pilotrochus*, and possibly *Ishakidris*. *Ishakidris* hasn't been included in any molecular study yet, but a morphological study concluded it would be sister to *Phalacromyrmex*, both being sisters to *Pilotrochus* (Bolton, 1984). Apart from those clades, the tribe Attini have the other following lineages which weren't treated in detail here: the "pheidolines", the "cephalotines", "blepharidattines" and the "tranopeltines". Branstetter et al. (2017) called the fungus-growing ants the Attina, a subtribal rank. Although we agree that subtribal divisions will be appropriate to deal with the clades of Attini, we refrained to use subtribal names, like Attina, Basicerotina, Phalacromyrmecina, etc, because they haven't been officially proposed and to do such proposition is far from the scope of this contribution.

3. Results

3.1. Defining characters of the *Strumigenys*

In the following session, we discuss five newly discovered characters that are diagnostic for the *Strumigenys*. Later, we discuss the importance of other characters previously treated in the literature in the diagnose of the SPB-clade and/or the clades within it.

3.1.1. Ventral mesosoma

We studied the ventral morphology of 68 disarticulated specimens belonging to 36 different Myrmicinae genera. Among those specimens, there were 26 Attini genera represented, including 22 selected *Strumigenys* species (belonging to very distinct species groups and biogeographic regions) and at least one species of each basicerotine genera (Table 1). We detected two important mesosomal characters, one of them, a metapleural seta, occurs in the SPB-clade only; the other, the shape of the ventral margin of the propodeal foramen notched instead of evenly arched, is unique to *Strumigenys*.

The metapleural seta

All female *Strumigenys* (queens, ergatoids, and workers) possess a hypertrophied, posterodorsally curved seta originating just posterior to the metacoxal annulus (Fig. 3, D); in profile view it is seen at the posterior, lower corner of the metapleuron, beneath the metapleural gland bulla (Fig. 3, A-C). Although always present in this position in the female castes, the morphology of individual seta varies a lot among species, normally resembling the morphology of other standing setae elsewhere in the body. A minority of the examined males do possess the seta as well. Curiously, it is present only on one side in some of the few specimens of males that have the seta. Among the examined basicerotines, some, but not all, have a seta originating at the same position, but it is only gently curved and it is minute instead of hypertrophied, and it is not seen in profile view (better seen in ventral view of specimens with disarticulated legs, as in Fig. 4, posterior to the right metacoxal foramen of images A, B and E). At least the phalacromyrmecines *Ishakidris* and *Phalacromyrmex* seem to have the seta hypertrophied, just as in *Strumigenys*. Examination of all phalacromyrmecine images on AntWeb indicates that at least the morphospecies *Ishakidris* my01 (specimens CASENT0235145 and CASENT0235144) and *Phalacromyrmex fugax* (specimens CASENT0217029, CASENT0179596, and CASENT0103116) seem to possess the seta in a similar state as the *Strumigenys* (pink arrows in Fig. 19). *Pilotrochus besmerus* seems not to have it, but the seta is quite often not revealed in the photo stacked images and this species have very fine setae on the body, so confirmation is needed in actual specimens. No other examined myrmicine species possess a similar setae (Table 1). Many species (e.g. *Acromyrmex striatus*) have a series of dorsally oriented setae originating on a

carina at the corner of the lateral and ventral metapleuron, which stay in front of or very close to the metapleural opening. These setae don't correspond to the metapleural seta discussed here.

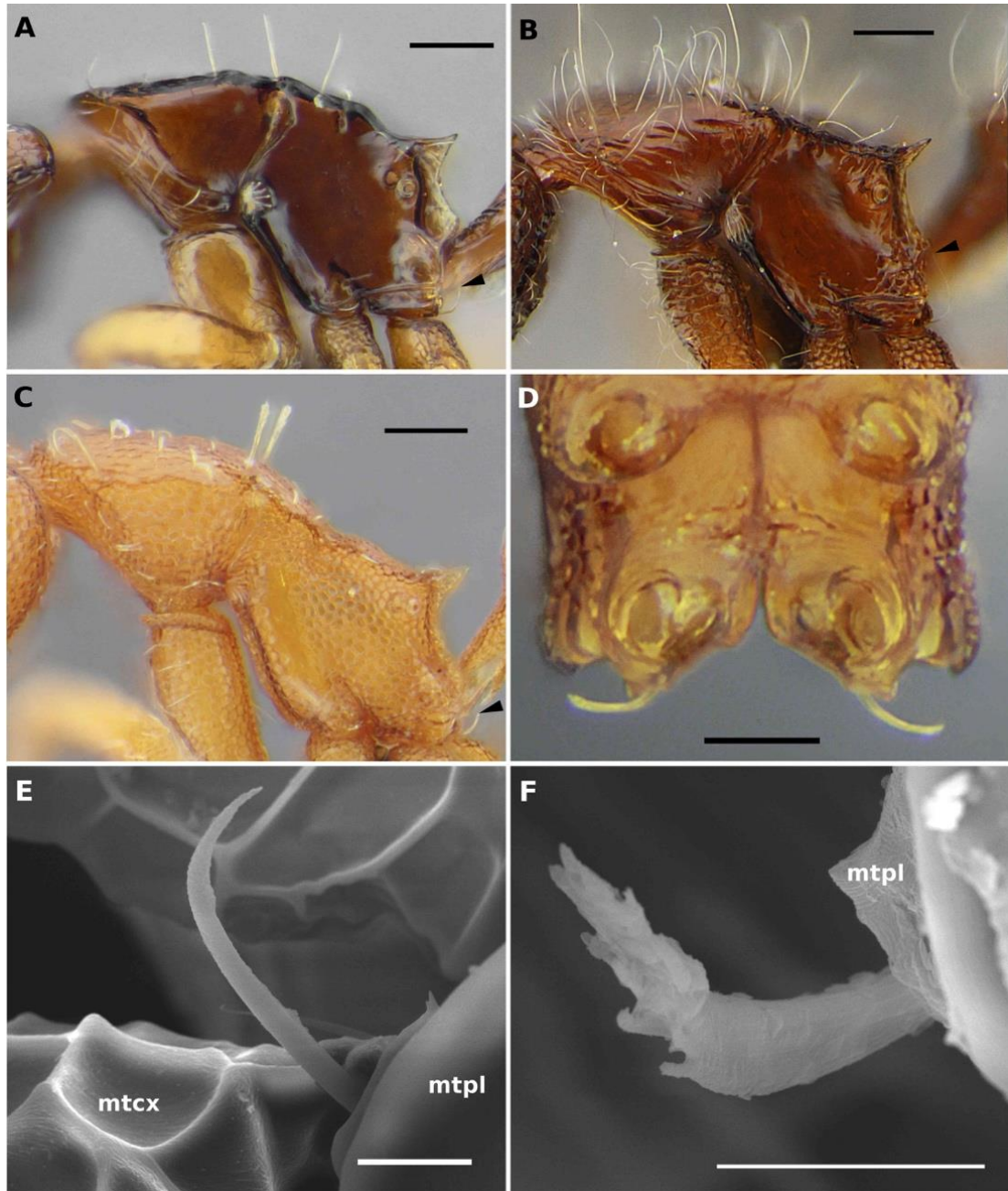


Fig. 3. Metapleural seta in various *Strumigenys* species. **A, B** and **C**, Lateral mesosoma view of *S. lilloana*, *S. reticeps* and *Strumigenys* ufv-06 (*louisianae*-group), respectively. **D**, ventral view of *Strumigenys* ufv-06 (legs removed). **E** and **F**, metapleural setae in great magnification. Black arrows in **A - C** are pointing to the apex of the metapleural setae. Scale bars in **A - D** are 0.1 mm, in **E - F** are 0.01 mm. In **E** and **F**, mtcx stands for metacoxa and mtpl, for metapleuron.

The notched ventral margin of the propodeal foramen

Among the studied species of *Strumigenys*, all of them possessed a modified ventral margin of the propodeal foramen. The dorsal (upper) margin of the propodeal foramen among ants is complex, wavy, with two large lateral arches which accommodates the petiole presclerites dorsolateral expansions and a small medial arch that accommodates the basal process of the petiole. On the other hand, the ventral margin which articulates with presternite II, is often simpler, commonly an even arch-shaped margin (Fig. 4). It is normally hidden by the metacoxae, but can be seen in pinned specimens in ventral view if the metacoxae are moved anteriorly and if the petiole is inclined upwards. It can be much better seen in a "full ventral view", in specimens that had their legs removed (Fig. 4 and 5). In most ants, the arched margin passes close to the metacoxal foramina annuli, although in some lineages it fuses with the metacoxal foramina ("open metacoxal foramina" *sensu* Bolton, 2003). In *Strumigenys*, differing from all Myrmicinae studied, the margin indents in between the metacoxal foramina as a thin medial, deeply incised notch (Fig. 5). The notch and the arch around it sometimes resembles a baby bottle nipple (Fig. 5, G and J). The tip of the notch normally reaches or surpasses the anteriormost points of metacoxal foramina. We will commonly refer to this trait as the "notched propodeal foramen" for ease of communication. Among the species examined for this trait most were Neotropical, but there were also Afrotropical, Indomalayan, Australasian, and Oceanian specimens, which probably represents a significant phylogenetic coverage of the genus, assuming the incipient topology recovered in Ward et al. (2015) holds true. Moreover, the notched propodeal foramen was observed in all male morphospecies examined. If confirmed absent in phalacromyrmecines, this is possibly the strongest synapomorphy of *Strumigenys*.

Curiously, the state of this character in the Pogonomyrmecini stands out for being very distinct as well, although differing strikingly from the *Strumigenys*. In their case, the ventral margin of the foramen is also indented in between the metacoxal foramina, however as a very broad finger-like incision (see specimen UFV-LABECOL-009002 on AntWeb).

Table 1. Diversity of four important characters for defining *Strumigenys* among the Myrmicinae. For the metacoxal seta and the carina on poststernite II columns, 0 means absent, 1 means present. In the tergosternal fusion column, 0 means not fused, 1 is partially fused and 2 is entirely fused. See text for details about the shape of the ventral margin of the propodeum foramen.

Tribe	Genus	Number of species examined	Metacoxal setae	Propodeal foramen ventrally	Carina on poststernite II	Tergosternal fusion of A3
Attini	<i>Strumigenys</i>	22	1	notched	1	2
Attini	<i>Basiceros</i>	2	1	arched	0	0 or 1
Attini	<i>Octostruma</i>	3	1	arched	0	1 or 2
Attini	<i>Eurhopalothrix</i>	2	1	arched	0	1
Attini	<i>Talaridris</i>	1	1	arched	0	1
Attini	<i>Protalaridris</i>	1	0	arched	0	0
Attini	<i>Rhopalothrix</i>	3	1 or 0	arched	0	1 or 2
Attini	<i>Daceton</i>	1	0	arched	0	0
Attini	<i>Acanthognathus</i>	1	0	arched	0	0
Attini	<i>Mycocepurus</i>	1	0	arched	0	0
Attini	<i>Myrmicocrypta</i>	1	0	arched	0	0
Attini	<i>Apterostigma</i>	1	0	arched	0	0
Attini	<i>Cyatta</i>	1	0	arched	0	0
Attini	<i>Kalathomyrmex</i>	1	0	arched	0	0
Attini	<i>Cyphomyrmex</i>	2	0	arched	0	0
Attini	<i>Mycetophylax</i>	2	0	arched	0	0
Attini	<i>Atta</i>	1	0	arched	0	0
Attini	<i>Acromyrmex</i>	1	0	arched	0	0
Attini	<i>Trachymyrmex</i>	1	0	arched	0	0
Attini	<i>Pheidole</i>	3	0	arched	0	0
Attini	<i>Procryptocerus</i>	1	0	arched	0	0
Attini	<i>Cephalotes</i>	1	0	arched	0	2
Attini	<i>Lachnomyrmex</i>	1	0	arched	0	0
Attini	<i>Blepharidatta</i>	1	0	arched	0	0
Attini	<i>Wasmannia</i>	1	0	arched	0	0
Crematogastrini	<i>Crematogaster</i>	1	0	arched	0	0
Crematogastrini	<i>Meranoplus</i>	2	0	arched	0	2
Crematogastrini	<i>Tetramorium</i>	1	0	arched	0	0
Pogonomyrmecini	<i>Hylomyrma</i>	1	0	finger-like	0	0
Pogonomyrmecini	<i>Pogonomyrmex</i>	1	0	finger-like	0	0
Solenopsidini	<i>Megalomyrmex</i>	1	0	arched	0	0
Solenopsidini	<i>Monomorium</i>	1	0	arched	0	0
Solenopsidini	<i>Rogeria</i>	1	0	arched	0	0
Solenopsidini	<i>Solenopsis</i>	1	0	arched	0	0
Stenammini	<i>Aphaenogaster</i>	1	0	arched	0	0
Stenammini	<i>Messor</i>	1	0	arched	0	0

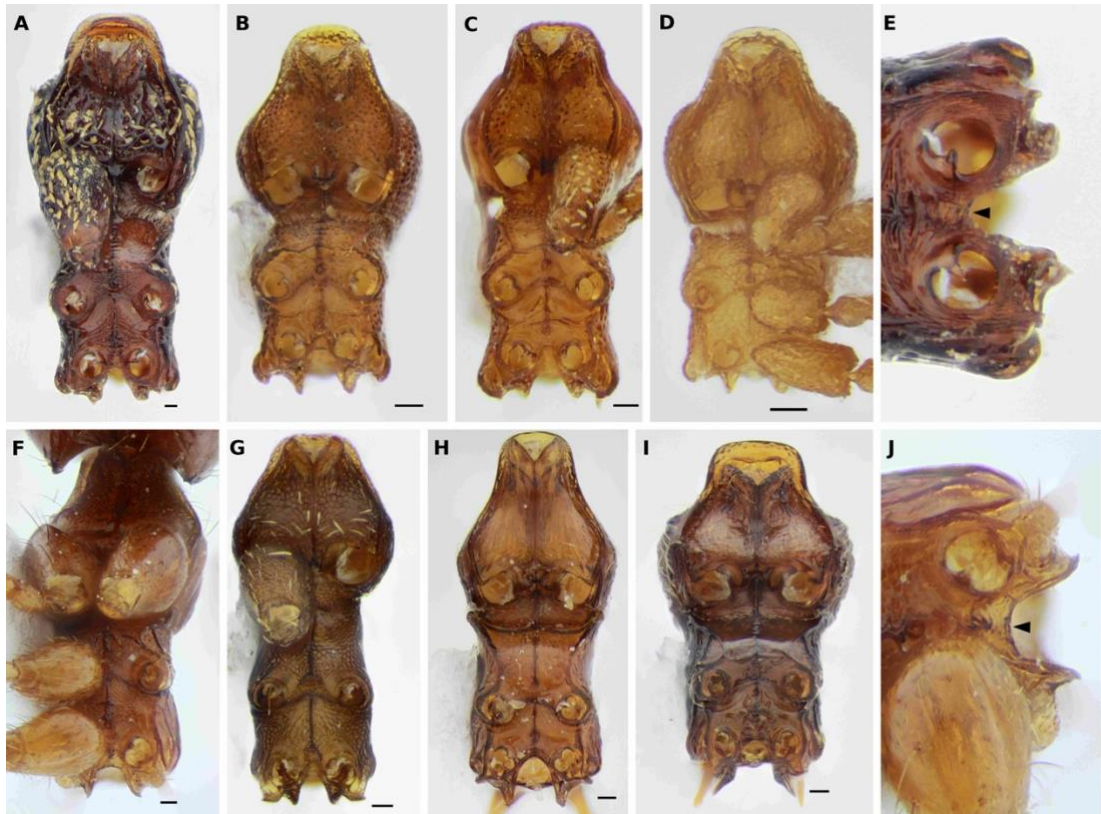


Fig. 4. Ventral view of mesosoma of various Attini genera. **A**, *Basiceros disciger* (UFV-LABECOL-008926); **B**, *Octostruma rugifera* (UFV-LABECOL-008981); **C**, *Eurhopalothrix spectabilis* (UFV-LABECOL-008988); **D**, *Rhopalothrix ufv_sp1* (UFV-LABECOL-008560); **E**, zooming of *B. disciger* ventral propodeal foramen (from A); **F**, *Pheidole fimbriata* (UFV-LABECOL-008930); **G**, *Kalathomyrmex emeryi* (UFV-LABECOL-008529); **H**, *Acanthognathus rudis* (UFV-LABECOL-008983); **I**, *Lachnomyrmex victori* (UFV-LABECOL-008994); **J**, zooming of *Pheidole fimbriata* ventral propodeal foramen (from F). Legs removed from at least from one side of the body. Scale bars are 0.1 mm.

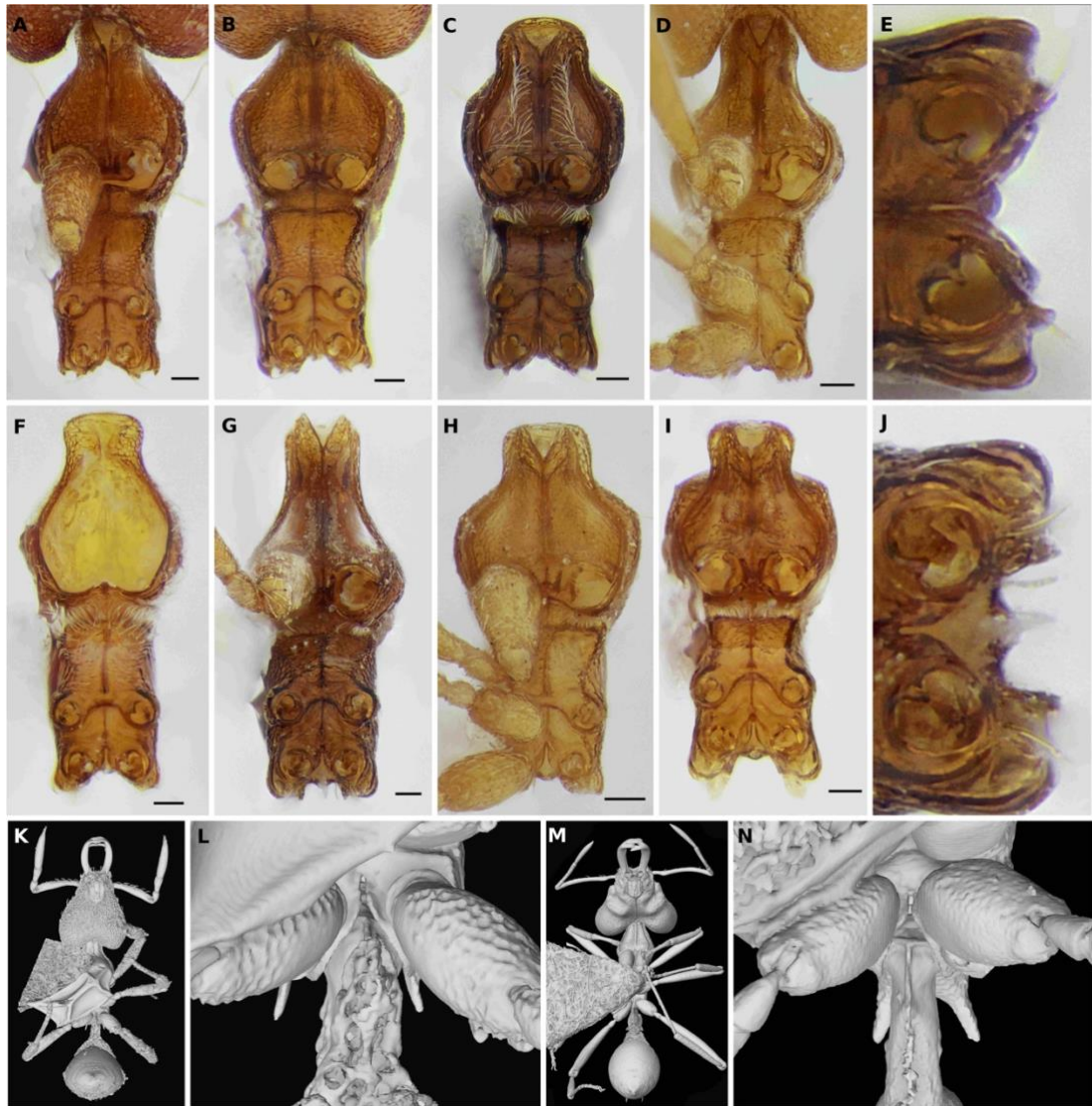


Fig. 5. Ventral view of mesosoma of *Strumigenys* with the legs removed (at least from one side). **A**, *Strumigenys* ufv-06 (UFV-LABECOL-008990, *louisianae*-group); **B**, *S.* aff. *zeteki* (UFV-LABECOL-008984, *gundlachi*-group); **C**, *Strumigenys* ufv-10 (UFV-LABECOL-001929, *appretiata*-group); **D**, *S. rogeri* (ANTWEB1032294, *rogeri*-group); **E**, zooming of *Strumigenys* ufv-10 ventral propodeal foramen (from C); **F**, *S. goddefroyi* (UFV-LABECOL-001908, *goddefroyi*-group); **G**, *S. chyzeri* (ANTWEB1038254, *loriae*-group); **H**, *S. emmae* morph2 (ANTWEB1032299, *emmae*-group); **I**, *S. membranifera* (ANTWEB1038347, *membranifera*-group); **J**, zooming of *S. chyzeri* ventral propodeal foramen (from G); **K** and **L**, *Strumigenys* FJ13 (CASENT0186982); **M** and **N**, *Strumigenys* FJ01 (CASENT0185902). Scale bars are 0.1 mm.

3.1.2. Metasoma

The following three metasomal characters are important in diagnosing the *Strumigenys*. The first two, a longitudinal carina anteriorly on the petiole poststernite, and the tergosternal fusion of the postpetiole, are present in all species examined in the

genus, females and males. To better understand their occurrence across the SPB-clade, the first must be confirmed in the phalacromyrmecines and the second must be confirmed in phalacromyrmecines and in more basicerotines, as it varied among the basicerotine species studied. The third character, the ventral basigastral hairs, when considered together with the petiole and postpetiole cuticular spongiform appendages, also represent a combination of structures not seen elsewhere in ants.

Poststernite II longitudinal carina (translucent patch of petiole)

As in all Myrmicinae, the petiole of *Strumigenys* has complete tergosternal fusion (Bolton, 2003). Therefore, the limits of tergite and sternite can only be vaguely set, with the petiole spiracle being an important marker in doing so. Presclerites and postsclerites are also not that easy to distinguish, but at least presternite appears to be in most species a slightly elevated crescent-shaped area on the anteriormost portion of ventral petiole. All *Strumigenys*, male and female, possess a longitudinal carina on the anteriormost portion of the petiole poststernite that meets the presternite posteromedially, sometimes forming a roughly T-shaped carina (Fig. 6, C and Fig. 5, N, black arrows indicating the longitudinal carina and white arrow indicating the posterior limit of presternite). Posteriorly along the poststernite II, the carina either fades (Fig. 6, B); or develops into the spongiform curtain (Fig. 6, A); or continues as a low carina or, more rarely, as a well-developed lamella across some or all the extent of the poststernite. It can also in some species bifurcates posteriorly at a certain length of the petiole. In profile view, the longitudinal carina often appears as a translucent thin patch that is better seen with a white background (Fig. 6, A and B). The transversal carina posteriorly on the presternite II is developed in some but not all males (Fig. 15 B white arrow) and it is only rarely absent in females *Strumigenys*.

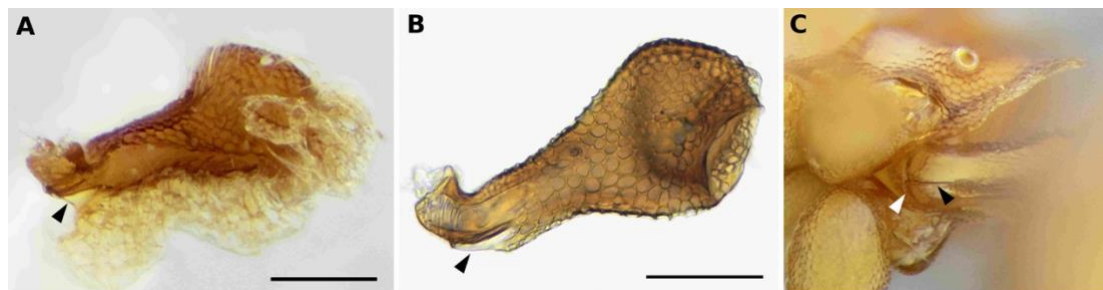


Fig. 6. Petiole of *Strumigenys* species, black arrows indicate anterior poststernite II longitudinal carina, white arrow indicates presternite II posterior margin. **A**, *S. goddefroyi* (*goddefroyi*-group); **B** and **C**, *S. aff. zeteki* (UFV-LABECOL-002480 and ANTWEB1041071, respectively, *gundlachi*-group).

It hasn't escaped our attention the fact that the notched ventral margin of the propodeum and the longitudinal carina of the poststernite II seem to fit tightly during full contraction of the metasoma (Fig. 7). It is possible that the ventral margin acts adjusting the orientation of the metasoma and restraining its movement to the sagittal line of the body during movement. In other words, if during the beginning of the contraction the metasoma is offset from the sagittal axis, it will be channeled and, at the end of the contraction, it will necessarily be aligned to it. A mechanism like this, if existent, would help in delivering the venom to only one spot, somewhere close to the tip of the mandible, consistently and precisely where the prey is right after the mandible strike. The idea remains to be tested and must be treated as speculative for the time being.



Fig. 7. Ventral view of the petiole and posterior mesosoma of a queen of *Strumigenys precava* (ANTWEB1038963) showing three putative synapomorphies of *Strumigenys* in one image: the notched ventral margin of the propodeal foramen, the metapleura setae, and the carinated anterior poststernite II.

Tergosternal fusion of abdominal segment III (postpetiole)

Tergosternal fusion of A3 is universal in the Dorylinae females and almost universal among poneroids (Ward, 1994; Bolton, 2003; Keller, 2011). In the Myrmicinae, however, it has only been documented for *Cataulacus*, *Myrmicaria*, and

Cephalotes (Bolton, 2003), three independent fusion events as they are unrelated lineages within the subfamily (Ward et al., 2015). We observed tergosternal fusion of abdominal segment III (postpetiole) in all examined species of *Strumigenys*, females (Table 1) and males. The segment is fused all along its length, pre- and postsclerites. Moderate pressure, enough to separate tergite from sternite in the species that do not have fusion, was never enough to do so in *Strumigenys*. Further pressure resulted in tearing of either the tergite or the sclerite, most commonly the tergite, somewhere across the “postpetiole disc” (Fig. 8, C). The tergosternal suture markings are present (Fig. 8, B, left gray arrow), but visualization is often hard as spongiform tissue covers them in many species.

We have observed partial or complete fusion in several basicerotine genera: *Octostruma* (complete), *Eurhopalothrix* (complete and partial), *Talaridris* (complete), *Rhopalothrix* (partial), and *Basiceros* (partial). The genus *Protalaridris* was the only exception among basicerotines for having no fusion whatsoever (Table 1). It remains inconclusive whether the fusion has evolved independently in *Strumigenys* and in the basicerotines or if it was present in their ancestor and have been reversed to a partially fused or unfused state in some basicerotine lineages. Confirming the state of this character in the phalacromyrmecines as well as knowing better the phylogeny of the basicerotines is necessary to understand this character state in the SPB-clade.

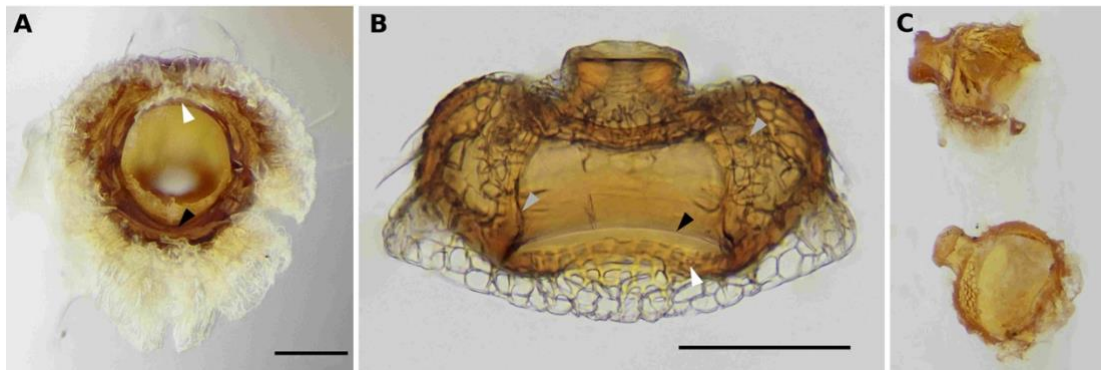


Fig. 8. Details of postpetiole of *Strumigenys* species. **A**, posterior view of disarticulated postpetiole of *S. saliens* (*mandibularis* group); **B**, ventral view of mounted postpetiole of *S. aff. zeteki* (UFV-LABECOL-002480, *gundlachi*-group); **C**, postpetiole of *S. saliens*, torn after attempt to separate tergite from sternite. Black arrows indicate sternite posterior margin, white arrows the tergite posterior margin; lower gray arrow in B indicate tergosternal suture marking and upper gray arrow indicate postpetiole spiracle, partially hidden beneath spongiform tissue.

The Crematogastrini genus *Meranoplus* also has tergosternal fusion. We dissected only two, but rather different species: *M. snellingi* and *Meranoplus* sp.

(*hirsutus*-group, same morphospecies as that of specimen CASENT0906547). We observed two, or maybe three (considering the *Strumigenys* fusion may be independent from that of the basicerotines) additional abdominal III tergosternal fusion events in the Myrmicinae, which now totals 5 or 6 events for the subfamily. The number might be much higher as we have extensively covered only the Attini tribe.

Specialized setae on poststernite IV (ventral basigastral hairs)

The spongiform tissue which grows in various degrees of development in almost all species of *Strumigenys* was examined in detail. It generally occurs as sponge-like cuticle outgrowths at specific portions of the first metasomal sclerites. They occur commonly on the petiole, postpetiole, and first gaster segment, and only extremely rarely on the mesosoma as well (e. g. *S. kempfi*). The way these outgrowths occur on sclerites have been detailed by Bolton (1999) but are briefly summarized ahead: a transverse outgrowth posteriorly on posttergite II, sometimes continued anterolaterally (Fig. 9, *a* in image A); a longitudinal, medial "curtain" on poststernite II (Fig. 9, *b* in A); a transversal outgrowth anteriorly on posttergite III, the anterior margin of "postpetiole disc" (Fig. 9, *c* in A); an outgrowth posteriorly on posttergite III, the posterior margin of postpetiole disc, often continued anterolaterally and even fused with the anterior posttergite outgrowth (Fig. 9, *d* in A); an outgrowth on poststernite III (Fig. 9, *e* in A); an anterior projection on posttergite IV (called *limbus* by Bolton, 1999) (Fig. 9, *f* in A); and a "felt-like pad" or "the basigastral ventral pad" of spongiform tissue anteriorly on poststernite IV, (Fig. 9, *g* in A).

During our examinations, we found that the spongiform tissue forming the *basigastral ventral spongiform pad* were in fact always composed of setae, often highly specialized, and not having cuticular origin as is the case of the spongiform tissue elsewhere. Bolton call the structure felt-like pad (1984) and mention it as being a pad or strip, as if differentiating it somehow from the lobes of the petiole and postpetiole (Bolton, 1999). MacGown and Brown (2012) studied the ultrastructure of the spongiform tissue, but discussed only the outgrowths of the petiole and postpetiole. We were unable to find in the literature any reference to the spongiform pad of the first gaster sternite of *Strumigenys* as being made of modified setae. The setae, often arranged as an arched band anteriorly on poststernite IV, have variable morphology among the species. In some species the setae have thickened bases and expanded and branched apexes (Fig. 9, E and I), with the ramifications of individual seta

superimposed and interspersed, giving the structure a spongiform look. In higher magnifications, however, a texture difference becomes apparent between the setae on A4 and the spongiform lobes on A2 and A3 (Fig. 9, g in A) and in sclerites mounted on slides or imaged by scanning electron microscopy the setae are clearly revealed (Fig. 9, E, G, H and I). In some species the pad is more easily identified as being made of setae (Fig. 9, B and C), while others are composed by setae with a clear spongiform appearance and harder to discern from the cuticular outgrowths of the posttergite above it (Fig. 9, F, compare f to g). We suggest the informal term *ventral basigastral hairs* to be used in place of the commonly used *basigastral ventral pad*, although to call the structure "specialized setae of anterior poststernite IV" is more accurate. The terms can be complemented with the adjective *spongiform*, if applicable. Many species of *Strumigenys* have the ventral basigastral hairs reduced or even absent. However, giving how widespread it is found in the genus, we attribute that to secondary reductions or losses.

The Crematogastrini genera *Theteamyрма* and *Dacatinops* as well as the dacetine *Colobostruma cerornata* also possess spongiform tissue on the anterior metasoma. We haven't studied any specimen of those species and relied only on the descriptions and available images to conclude that the spongiform material on their metasoma is structurally different from that found in *Strumigenys*. Bolton (1991) states that in *Tetheamyрма* the ventral petiole, ventral postpetiole and first gaster sternite are covered on "spongiform material that appears to be composed of densely interwoven or fused pilosity". Taylor (1985) described the structures present in *Dacatinops* as "masses of spongiform material" but gives no detail if they are originated from the cuticle or composed of setae. However, by analyzing Taylor's SEM images we suspect the masses on postsclerites II, III and IV are all composed of dense highly modified thin setae instead of cuticular outgrowths. In *C. cerornata*, the spongiform tissues are treated as "spongiform cuticle" (Shattuck, 2000). Images of specimen ANIC32-003939 of *C. cerornata* (available at the Australian National Insect Collection website) confirm the structure as clearly having cuticular origin, derived from the edges of spongiform striae, including the outgrowths on poststernite IV. *Strumigenys* is the only genus to combine in the body cuticular spongiform outgrowths and highly modified ventral basigastral hairs.

The term *limbus*, used to describe the transversal outgrowth anteriorly on posttergite IV (Bolton, 1999), is not used here and we detail why in the topic "The

transversally carinated posttergites II, III and IV of *Strumigenys* and the basicerotines" below.

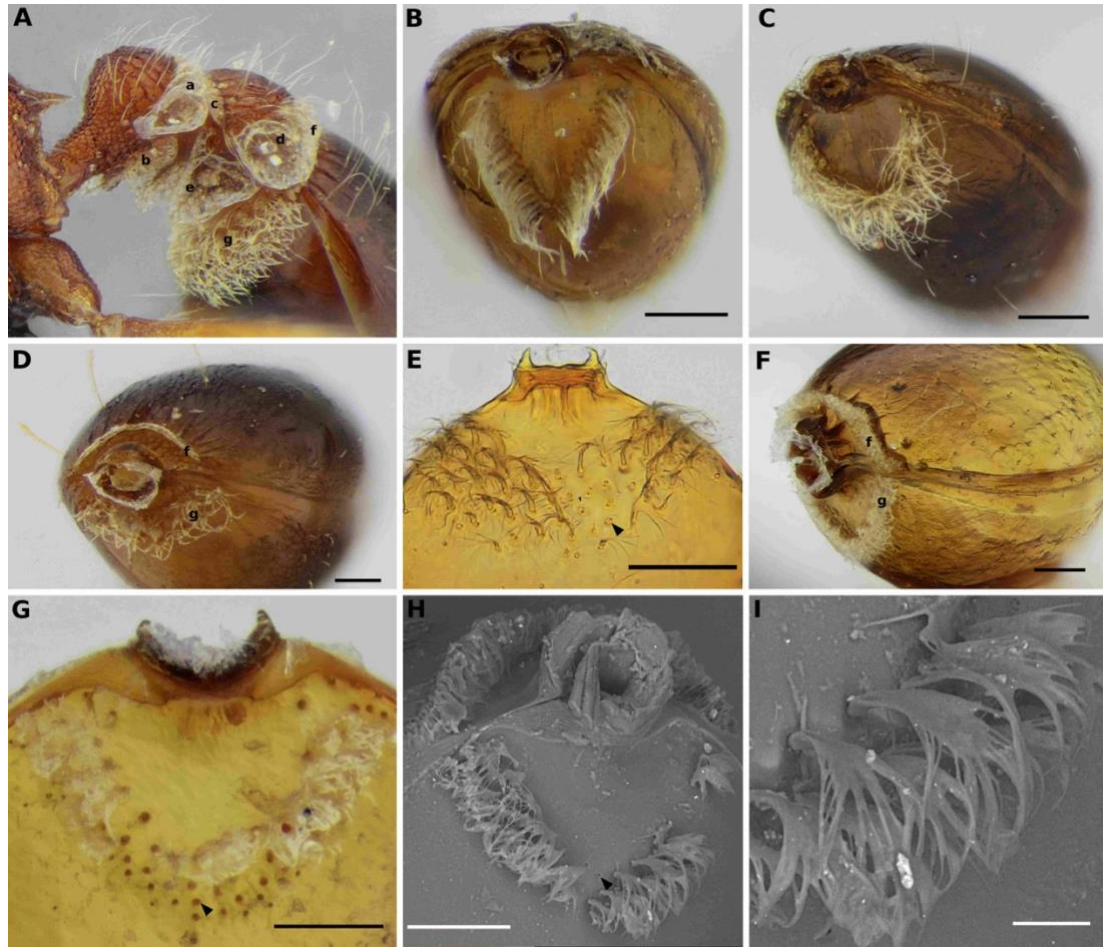


Fig. 9. Abdominal segment IV of various *Strumigenys* evidencing modified setae anteriorly on the poststernite. **A**, *Strumigenys* ufv-14 (ANTWEB1032535, *hindenburgi*-group), a-f indicating spongiform tissue of cuticular origin on abdominal segments II, III and IV (detailed above in text) and g representing modified setae anteriorly on poststernite IV; **B**, **C**, **D** and **F**, oblique anterior view of abdominal segment IV of *S. membranifera* (ANTWEB1038347, *membranifera*-group), *Strumigenys* ufv-10 (UFV-LABECOL-001929, *appretiata*-group), *Strumigenys* ufv-06 (UFV-LABECOL-008990, *louisinae*-group), *S. saliens* (*mandibularis*-group), respectively, f and g in D and F are the same as in A; **E**, zooming of mounted presternite and anterior portion of poststernite IV of *Strumigenys* ufv-14 (UFV-LABECOL-008904, *hindenburgi*-group); **G**, zooming of mounted presternite and anterior portion of poststernite IV of *S. saliens*; **H** and **I**, SEM images evidencing morphology of specialized setar in *S. saliens*. Scale bars are 0.1 in all images, except H and I in which scale bars are 0.01 mm. Black arrows in E, G and H pointing at seta socket, where seta has been abraded.

3.2. The labra of Neotropical *Strumigenys*

The shape and pilosity of the labra of Neotropical species of *Strumigenys* vary drastically (Fig. 10 and 11). However, the trap-jaw species (treated as *Strumigenys in Bolton, 2000*) have a relatively conserved morphology (Fig. 10). Their labra are always formed by a main body, which is roughly quadrate to trapezoidal, from which two digitiform lobes arise distally. The majority of the species, with few exceptions, have apart from smaller setae a pair of very long trigger hairs arising at the tip of the lobes. The lobes vary from very thin (*S. precava*, Fig. 10, H) to extremely thick (*S. smilax*, Fig. 10, I). Lateral margins of main body vary from being slightly sinuous to strongly diverging distally, forming the labral "arms". Reduction of trigger hairs occur in species with extremely long mandibles of the *mandibularis*-group (*S. cordovens*, Fig. 10, F) and in the *trudifera*-group (*S. trudifera*, Fig. 10, G), suggesting there is maximum limit of length for the setae to be functional and that there must be alternative ways to sense prey in those species (maybe this morphological difference can reflect in their behavior as well).

Non-trap-jaw species (treated as *Pyramica in Bolton, 2000*) show an enormous variety of labral shapes and labral setae (Fig. 11). Among them, long trigger hairs are only present in a subset of the *gundlachi*-group, the *gundlachi*-complex (Fig. 11, W and X), as previously noted by Bolton (1999, 2000) and in the *tanymastax*-group (Fig. 11, P). Setae, morphology vary from simple, to ribbon-like (Fig. 11, H, K, R and S), droplet-shaped (Fig. 11, G), golf-club-shaped (Fig. 11, D), hand-held-fan-shaped (Fig. 11, B), stout spiniform (Fig. 11, U and V). Labral lobes can be extremely reduced (Fig. 11, C and H) or extremely long (Fig. 11, P and V), with a lot of variation in between the extremes. Main body varying from narrow (Fig. 11, U and V) to broad (Fig. 11, A and C), with diverging but most of the times converging lateral margins, the latter rarely with a middle constriction (Fig. 11, L and M).

There is diversity in labral morphology within groups of species. For example, in the *mandibularis*-group the species with very long mandibles have reduced trigger hairs. In the *louisianae*-group, among six species studied (described and undescribed), variations of shape were considerable, more or less within the amount seen between images A and B of Fig. 10. Two described species, *S. louisianae* (from a particular locality) and *S. infidelis*, have more similar labra than *S. louisianae* itself when the various morphospecies within *S. louisianae* complex of species are compared (Chaul, J., *in prep.*). Other example of species with very similar, but distinguishable labrum

shape is between the two closely related *S. denticulata* (Fig. 10, X) and *S. eggersi*. The *appretiata*-group also have a typical labral morphology that varies slightly among its species. Curiously, the labrum of *S. beebei*, a species similar in habitus to those of the *appretiata*-group, have a relatively similar shape but radically different setae. The *schulzi*-group also has a relatively uniform shape shared among its species, except for the odd species *S. depressiceps*. However, for lack of dissected material, we weren't able to conclude if it helps to discern very close species within that group.

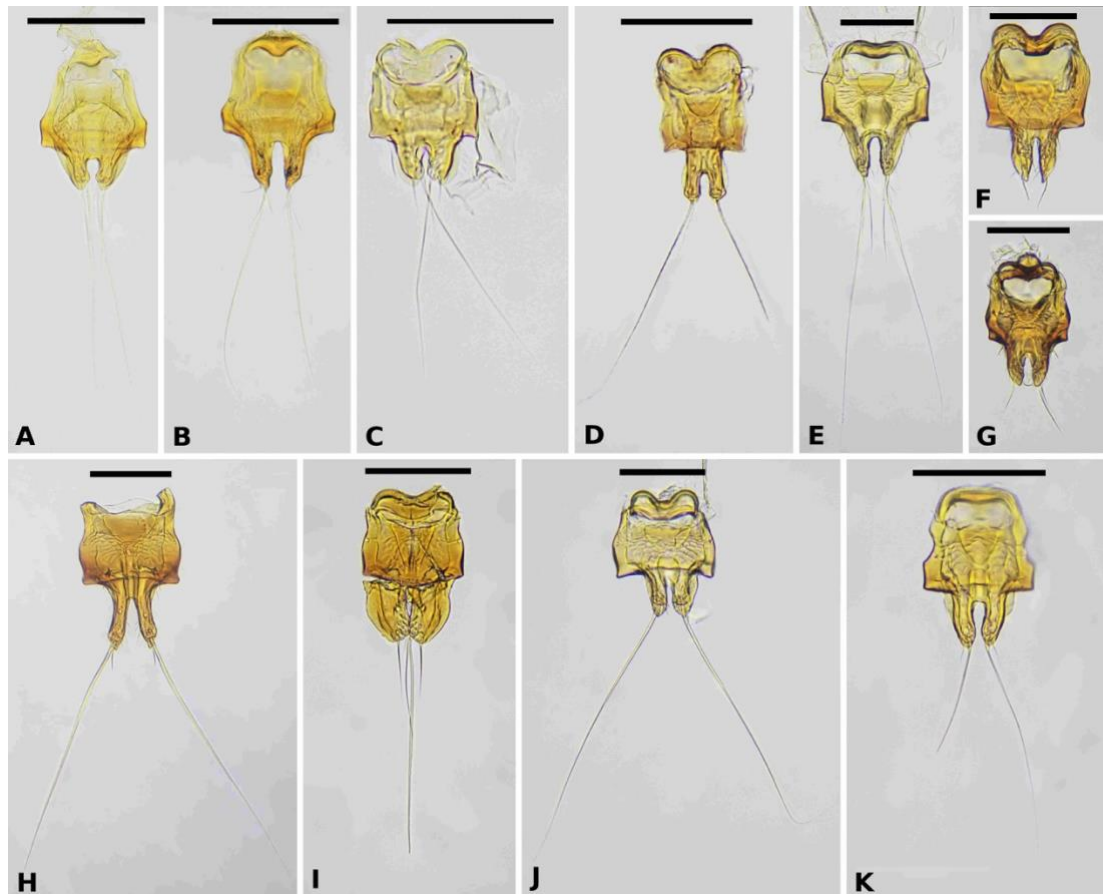


Fig. 10. Labra of various Neotropical species of *Strumigenys* with kinetic mandible action (trap-jaws). **A**, *Strumigenys* ufv-05 (UFV-LABECOL-001552, *louisianae*-group); **B**, *Strumigenys* ufv-06 (*louisianae*-group); **C**, *S. carinithorax* (UFV-LABECOL-001490, *silvestrii*-group); **D**, *S. elongata* (*elongata*-group); **E**, *S. saliens* (*mandibularis*-group); **F**, *S. cordovens* (ANTWEB1032478, *mandibularis*-group); **G**, *S. trudifera* (ANTWEB1032479, *trudifera*-group); **H**, *S. precava* (ANTWEB1032471, *precava*-group); **I**, *S. smilax* (ANTWEB1032491, *smilax*-group); **J**, *S. trinidadensis* (ANTWEB1032480, *trinidadensis*-group); **K**, *Strumigenys* sp. (ANTWEB1032473, *hindenburgi*-group). Scale bars are 0.1 mm.



Fig. 11. Labra of various Neotropical species of *Strumigenys* with static pressure (gripping) mandibles. **A**, *S. xenochelyna* (UFV-LABECOL-000091, *appretiata*-group); **B**, *Strumigenys* sp., detail of handheld fan-like setae on labrum distal margin (ANTWEB1032007, *appretiata*-group); **C** and **D**, *S. beebei*, labrum and detail of golf club-like setae on its distal margin (UFV-LABECOL-000092, *beebei*-group); **E**, *S. browni* (ANTWEB1032477, *browni*-group); **F** and **G**, *S. perissognatha*, labrum and detail of droplet-shaped setae on its distal margin (ANTWEB1032467, *substricta*-group); **H**, *S. reticeps* (*thaxteri*-group); **I**, *S. lilloana* (ANTWEB1038989, *lilloana*-group); **J**, *S. inusitata* (ANTWEB1032493, *splendens*-group); **K**, *S. splendens* (UFV-LABECOL-000096, *splendens*-group); **L**, *S. hyphata* (UFV-LABECOL-000095, *hyphata*-group); **M**, *S. cincinnata* (ANTWEB1032490, *hyphata*-group); **N**, *Strumigenys* ufv-11 (ANTWEB1032422 *probatix*-group); **O**, *Strumigenys* ufv-22 (ANTWEB1038183, *alberti*-group); **P**, *S. tanymastax* (ANTWEB1032475, *tanymastax*-group); **Q**, *S. urrhobia* (UFV-LABECOL-001861, *schulzi*-group); **R**, *Strumigenys* ufv-20 (ANTWEB1032003, *schulzi*-group); **S**, *S. depressiceps* (ANTWEB1041088, *schulzi*-group); **T**, *S. grytava* (UFV-LABECOL-001719, *schulzi*-group); **U**, *S. crassicornis* (ANTWEB1032002, *gundlachi*-group); **V**, *S. aff. zeteki* (UFV-LABECOL-001492, *gundlachi*-group); **W**, *S. subdentata* (UFV-LABECOL-007326, *gundlachi*-group); **X**, *S. denticulata* (*gundlachi*-group).

3.3. Glandular patches and bullae of *Strumigenys*

We investigated the presence of the exocrine glands that can be visualized by external examination under the stereomicroscope among Neotropical species of *Strumigenys*. These glands are manifested on the cuticle either as (i) pale, smooth, and normally rounded to ovoid (blister-like) and small patches (Fig. 12) or as (ii) differentiated, flat or excavated, regions surrounded by hairs and normally large (Fig. 14). The first type occurs basally and ventrally on mandibles (Fig. 12, A-F), ventrally and apically on scapes (Fig. 12, G and H), distally and dorsally on the leg segments (femora, tibiae and tarsi) (Fig. 12, I to N). All of them have been previously reported (Bolton, 1999, 2000). Tarsal bullae (Fig. 12, M and N) are not discussed in Bolton (1999) neither at the introduction of Bolton (2000), but they are mentioned in the Malagasy *Strumigenys* section (Fisher, 2000).

The second type are the flat procoxal glandular patches positioned anteriorly and basally on the procoxae of species of the Neotropical *hindenburgi*-group (Bolton, 2000) and the propleural excavated putative glandular patches, described below for the first time for the *Strumigenys*.

Femoral and tibial blister-like bullae have been demonstrated to be truly glandular. The cuticle composing the patches has numerous irregular channels transversing it (seen externally and in very high magnification as a porous surface) and is thinner than the surrounding cuticle. The epithelium beneath the patches is composed of secretory cells and is relatively thicker than the epithelium elsewhere (Billen et al., 2000). It is plausible to assume based on the morphologically very similar bullae on scapes, mandibles, and tarsi are glandular as well. In fact, we were able to observe a porous surface on the mandible bulla of one species (Fig. 12, F). As for the propleural and procoxal patches, we demonstrate here that they are either porous or have even more complex structures, strongly suggesting both are external portions of gland systems.

The intramandibular glands described for the species *S. membranifera*, positioned on the inner distal surface of the cuticle (Billen and Espadaler, 2002), appear not to be externally visible and not the same as the basimandibular gland.

We have observed calcar bullae (Fisher, 2000) in some species, including some basicerotines. We were in doubt whether it represents the external impression of a glandular region. In many specimens it was pale as the blister-like bullae (Fig. 13, A)

and in many others it was translucent. This type of putative gland is not shown in Table 2.



Fig. 12. Bullae on different sclerites of various species of *Strumigenys*. A - F, ventral basimandibular bullae; G and H, ventral bullae on scapes; I - N, bullae on legs. **A**, *Strumigenys* ufv-14 (UFV-LABECOL-007515, *hindenburgi*-group); **B**, *S. borgmeieri* (ANTWEB1032494, *mandibularis*-group, note the bullae are not symmetrical and that there is a distal patch in the right mandible, indicated by the lower black arrow); **C**, *S. alberti* (UFV-LABECOL-001577, *alberti*-group); **D** *S. beebei* (UFV-LABECOL-000092, *beebei*-group); **E**, *S. aff. zeteki* (UFV-LABECOL-008640, *gundlachi*-group); **F**, detail of E, evidencing micropores on the bullae patch; **G**, *S. louisianae* (CASENT0633459, *louisianae*-group); **H**, *Strumigenys* ufv-03 (UFV-LABECOL-000119, *louisianae*-group); **I**, hypertrophied femoral bullae of *S. aff. borgmeieri* (ANTWEB1032465, *mandibularis*-group); **J**, minute hind femoral bulla (black arrow) of *S. mixta* (JTLC000009687, *louisianae*-group); **K**, femoral bullae of *Strumigenys* sp.J (ANIC32-002182-1, *emmae*-group); **L**, protibial bullae of *Strumigenys* **sp.n.** (ANTWEB1032248, *emmae*-group); **M**, probasitarsal bulla of *S. infidelis* (ANTWEB1041097, *louisianae*-group); **N**, metatibial bulla and bullae on second and third metatarsomeres of the same specimen of *S. infidelis*. Black arrows indicate exact position of bullae.

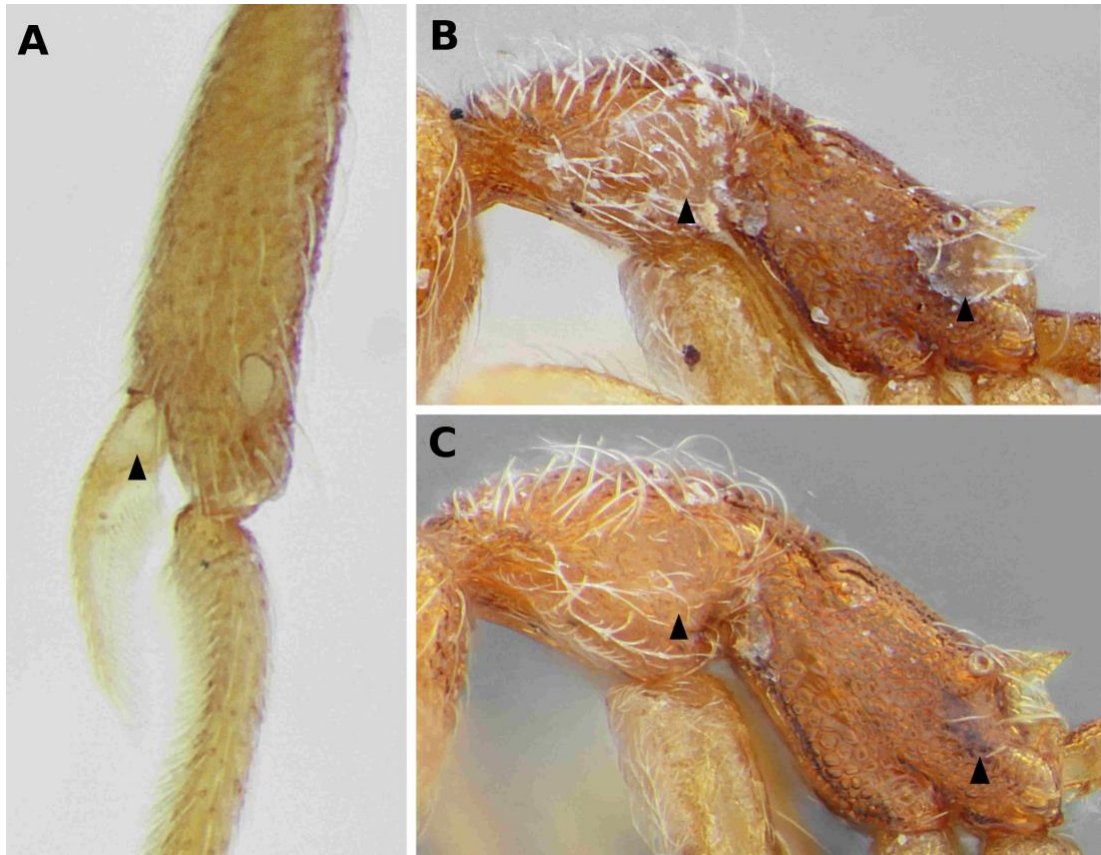


Fig. 13. Putative glandular areas which needs verification, the calcar bullae seen in many species and the pronotal and propodeal smooth patches of the *hindenburgi*-group. **A**, calcar bulla of *S. chyzeri* (ANTWEB1038333, black arrow showing calcar bulla, protibial bulla also evident in the image). **B**, lateral pronotal and lateral propodeal "plaques of debris" (black arrows) in *S. lanuginosa* (ANTWEB1032495) and **C**, the revealed smoother areas (black arrows) in the same worker after cleaned.

3.3.1. A census of the glands among Neotropical *Strumigenys*

We propose a gland formula to facilitate cataloging the existing variation of glands among the species of *Strumigenys*. The formula should be written substituting the names of the following sclerites in the sentence ahead for zeros (gland not seen) or ones (gland observed), without the commas and adding a space where indicated: mandible, scape, *space*, propleura, procoxa, *space*, profemur, mesofemur, metafemur, *space*, protibial, mesotibial, metatibial, *space*, protarsomere I, protarsomere II, protarsomere III, protarsomere IV, protarsomere V, *space*, mesotarsomere I, mesotarsomere II, mesotarsomere III, mesotarsomere IV, mesotarsomere V, *space*, metatarsomere I, metatarsomere II, metatarsomere III, metatarsomere IV, metatarsomere V. Therefore, in a worker of *S. louisianae*, for example, that only possess bullae on scapes, on the protarsomere I, and on each of the first three

mesotarsomeres and metatarsomeres, the glandular formula would be: 01 00 000 000 10000 11100 11100.

3.3.2. The procoxal and propleural glandular patches

The Neotropical *hindenburgi*-group has anterior flat surfaces on the procoxae surrounded by dense patches of setae. These patches are present on all species of the group but are more developed in the species *S. hindenburgi*. We confirmed that the flat surface is porous for two species, *S. hindenburgi* and *Strumigenys* ufv-14 (Fig. 14, H), strongly suggesting the structure is indeed glandular.

The propleural glands are described here for the first time. Their general structure consists of relatively large, paired, longitudinally oriented, excavated, elliptical cavities, one on each side of the propleura. Their morphology varies a lot among the species. They were first seen by us in the Neotropical *mandibularis*-group, where conspicuous cavities covered on spongiform tissue with a slit-shaped longitudinal opening can be seen. A thick spongiform tissue borders the inside of the outer margins (Fig. 14, B, black arrow) of the cavities and a very thin strip borders the inside of the inner margins, with a medially offset slit-shaped opening between these two spongiform masses (Fig. 14, B white arrow).

The structures were observed in 30 species, most of them belonging to the *mandibularis*-group, but also many other from rather different groups, like the *appretiata*, *beebei*, *splendens*, *thaxteri*, *substricta*, *probatrice*, *tococae*, *precava*, *trinidadensis*, *goddeffroyi*, and possibly *emmae* groups. In the *mandibularis*-group, 14 species (out of the 18 described species in the group) were examined, all except *S. borgmeieri* have the cavities. They were *S. borgmeieri*, *S. aff. borgmeieri*, *S. cordovensis*, *S. cultridgera*, *S. diabola*, *S. dolichognatha*, *S. godmanni*, *S. aff. rehi*, *S. monstra*, *S. planeti*, *S. prospiciens*, *S. saliens*, *S. smithii*, *S. sublonga*. In other groups, the propleural cavities were either shallower or without spongiform tissues or both. Species with shallow cavities, for example, were *S. tococae*, *S. precava*, *S. princeps* and *S. thomae*. The species *S. perissognatha* of the *substricta*-group has "lung-shaped" cavities with fine hairs on their inner borders (Fig. 14, C). Other species with the cavities were *S. probatrice*, *S. thaxteri*, *S. beebei*, *S. glenognatha* (and related undescribed species *Strumigenys* ufv-10, Fig. 5, C), *S. kompsomala*, *S. emmae*, *S. goddeffroyi*.

In *S. godeffroyi* we had the first evidence that the cavities were glandular. Some specimens from a series studied by us preserved whitish masses on the cavities (Fig. 14, D). Callow workers from that series didn't possess as much or anything of the whitish substance. Dissected and mounted propleura of *S. godeffroyi* show the cavity is porous (Fig. 14, E and F). Pores could be seen in the mounted propleura of *S. emmae* as well, however no sign of cavities can be seen externally in this species.

Relatively similar propleural glands have been described for *Cyphomyrmex muelleri* and *C. costatus*. They, together with body fovea, maintain symbiont bacteria (Currie et al., 2006). The simple techniques of light microscopy we used didn't allow us to determine if there were any crypts harboring bacteria in the *Strumigenys*. In overall shape, the propleural glands of *C. muelleri* are similar to the propleural cavities observed in *S. perissognatha* and *S. godeffroyi*. Interestingly, the shape of the porous plates and hairs around the cavities (Currie et al., 2006, their Fig. 1, c) resembles better the procoxal gland of *S. hindenburgi* (Fig. 14, H) than any propleural gland found in *Strumigenys*.

All species examined by us had at least one type of blister-like bulla on the body (Table 2). Our results show that some species groups do have a "bullae pattern". Some examples are the *hindenburgi*-group, the only group with a procoxal gland and without variation of the formula among its species, except for differences in the tarsomere bullae (something expected for all groups of species and even between specimens of a species since presence and absence are hard to score in the minute tarsomeres). A different case is that of the *louisianae*-group, in which the Central America species *S. dubitata* and *S. mixta* have basimandibular and femoral glands, while the remaining of the species in the group never have such bullae and have a fairly similar pattern. Among the latter, part of the morphospecies belonging to the *louisianae* complex have tarsomere bullae on the third segment of the middle and hind legs, while others in the complex and *S. infidelis* have bullae on the first three tarsomeres. This is a nice example where the bullae formula can be used to support species hypothesis. In the *silvestrii*-group two patterns have been seen in the group as well, the majority of the species do have femoral bullae while *S. perparva* and a sister species (*Strumigenys* ufv-28) don't. The two species in the *hyphata*-group coincide in their absence of tibial glands. The species in the *mandibularis*-group all but *S. borgmeieri* have propleural glands as mentioned above.

In spite of the laborious process of coding specimens for bullae presence or absence, we encourage the cataloging of the bullae formula in *Strumigenys* as a way of supporting the classification at the species level as well as at a species group level.



Fig. 14. Putative propleural and procoxal glands. **A**, *S. planeti* (UFV-LABECOL-000061, *mandibularis*-group) worker in anterolateral ventral view with a black arrow evidencing position of propleural patches on the body; **B**, detail of propleural patches of *S. saliens* (UFV-LABECOL-000057, *mandibularis*-group), white arrow showing the slit and black arrow the spongiform tissue; **C**, excavated propleural patches of *S. perissognatha* (ANTWEB103200, *substricta*-group); **D**, **E** and **F**, *S. goddefroyi* (*goddefroyi*-group), showing propleural patches covered on whitish secretion in **D** (UFV-LABECOL-008281), and a disarticulated and mounted propleuron in **E**, with its porous plate zoomed in **F** (black arrow pointing at a pore); **G**, lateral view of *S. hindenburgi* (ANTWEB1038341, *hindenburgi*-group) with area of procoxal patch evidenced; **H**, disarticulated and mounted procoxa of same species of **G** revealing the procoxal patch as a porous area (UFV-LABECOL-001634), black arrow pointing at one pore.

group	species		c b s p p p m m p m m p p p p p m m m m m m m m m m																									
			a m c r r r s t r s t r r r r r r s s s s s t t t t t	s d p pl c f f f t	t b v x m m m b b b a a a a a a a a a a a a a a a a	e	r r	1 2 3 4 5 1 2 3 4 5 1 2 3 4 5																				
<i>splendens</i>	<i>splendens</i>	w	1	1	0	0	1	1	1	1	1	1	1	1	0	0	0	0	1	1	1	0	0	1	1	1	0	0
<i>splendens</i>	<i>villiersi</i>	w	0	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>splendens</i>	<i>villiersi</i>	q	1	1	0	0	1	1	1	1	1	1	1	1	0	0	0	1	1	1	0	0	1	1	1	1	0	
<i>splendens</i>	<i>inusitata</i>	w	0	0	0	0	1	1	1	1	1	1	1	0	0	0	0	1	1	1	0	0	1	1	1	0	0	
<i>substricta</i>	<i>perissognatha</i>	w	1	1	1	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1	0	1	1	1	1	1	0	
<i>mirabilis</i>	<i>mirabilis</i>	w	1	1	0	0	0	1	1	1	1	1	1	0	0	0	1	1	1	0	0	1	1	1	0	0		
<i>beebei</i>	<i>beebei</i>	q	1	1	0	0	1	1	1	1	1	1	1	1	0	0	1	1	1	0	0	1	1	1	0	0		
<i>beebei</i>	<i>beebei</i>	w	1	1	1	0	1	1	1	1	1	1	1	1	0	0	1	1	1	0	0	1	1	1	0	0		

In the *hindenburgi*-group there is possibly yet another type of unique exocrine gland. Specimens of some species in the group commonly have a plaque of debris at the posterolateral area of the pronotum and, more rarely, posterolaterally on the propodeum as well (Fig. 13, B). If the plaques are removed, a smooth patch is revealed (Fig. 13, C). The patch is much smoother than the surrounding cuticle, both on pronotum and on the propodeum, and there are usually relatively long setae on them. It remains to be investigated if the region is truly glandular, but it seems plausible to imagine the debris plaque being agglutinated by a secretion from the smooth areas.

3.4. *Strumigenys* males

At first look, males of *Strumigenys* are strikingly different from workers and queens, just as is the case in the majority of ants. They do not have any of the peculiar traits of the cephalic capsule, their antennae are 13-segmented, and mandibles are very reduced. Two traits are helpful in revealing them as belonging to the genus: the presence of spongiform tissue (Fig. 15, A) and blister-like bullae. The first is present in many species, varying from dense, to only a few small and inconspicuous outgrowths, or even entirely absent. The second is very hard to observe as the blister-like glands in males appear not to be as sharply defined as in the females. Moreover, it seems that they are absent in some sclerites, even when present on the females for that same sclerite. The transversal carina or spongiform lamella on anterior posttergite IV, the *limbus*, is absent on males (Brendon Boudinot, personal communication). Also absent are the specialized setae on the anterior poststernite IV (sometimes there is a patch of long setae, but they are simple instead of highly modified) make the task of identifying males even harder. We examined 53 specimens of males of Neotropical species, comprising at least 20 morphospecies. We checked tergosternal fusion of

postpetiole in 18 out of those 53 specimens. All males have the ventral margin of the propodeum with a notch similar to that observed in the female castes (Fig. 15, B, white arrow). As in the females, males showed A3 tergosternal fusion in all disarticulated specimens that were tested for that character. Males hardly ever have the metapleural seta and curiously, in some of the specimens that do have it, it was curiously observed on only one side of the body.

Therefore, identification of Myrmicinae males as *Strumigenys* can be confidently made by confirming the presence of the notched ventral margin of the propodeum (Fig. 15 B, white arrow) and the anterior longitudinal carina on petiole poststernite (Fig. 15 B, black arrow).

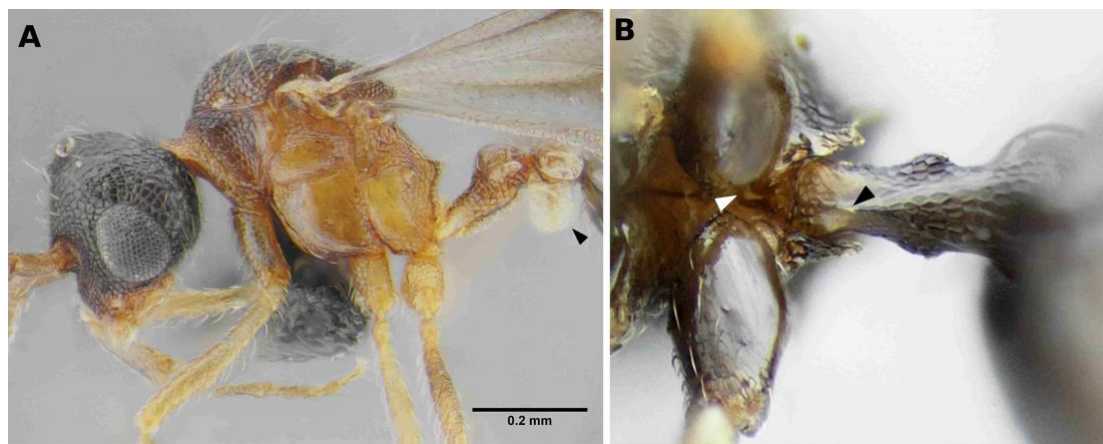


Fig. 15. Important traits for identifying *Strumigenys* males. Spongiform outgrowths on the petiole and postpetiole are not always present as seen in A (black arrow). The notched ventral margin of the propodeum (B, white arrow) and the anterior carina on the poststernite II (B, black arrow), although smaller and harder to see, are "safe characters" for confirming males as *Strumigenys* when spongiform tissue is absent. **A**, *Strumigenys* ufv-62 (UFV-LABECOL-001537); **B**, *S.* aff. *zeteki* (*gundlachi*-group, ANTWEB1041072).

3.5. Defining characters of the SPB-clade

Bolton (1998) provided a set of characters in an attempt to define the "Dacetonini" tribe group ("Dacetonini" + Basicerotini + Phalacromyrmecini tribes). In the following year, Bolton (1999) focused on diagnosing the "Dacetonini" genera, a tribe composed of *Strumigenys*, "*Pyramica*", and the most of the genera treated here as the dacetines. Subsequent papers by Bolton repeated his classification ideas (Bolton 2000; 2003), except for a correction of the tribe name to Dacetini (Bolton, 2000). Despite considering repeated evolution of trap-jaw lineages as a possibility due to the great variability of small details observed among the trap-jaw lineages in the tribe

Dacetini (Bolton, 1999), this author never discussed explicitly the possibility of part of the Dacetini (the dacetines) being only distantly related to the *Strumigenys*, basicerotines and phalacromyrmecines. Such phylogenetic hypothesis came only after Bolton's series of papers when molecular-based phylogenies first showed the pattern with low support and resolution or with a small number of taxa (Brady et al., 2006; Moreau et al., 2006) but then strongly corroborated it when more taxa were included and advanced techniques were used (Ward et al., 2015; Branstetter et al., 2017).

Baroni Urbani and De Andrade (1994) proposed the synonymization of the Basicerotini and the Phalacromyrmecini tribes into the Dacetini, a classification that was readily reversed by Bolton (Bolton, 1994, 1995). After Bolton's papers (1998, 1999, 2003) arguing that the three tribes should be maintained, Baroni Urbani and De Andrade (2007) proposed again a similar classification to their 1994 paper and criticized and/or questioned the validity of several characters used previously by Bolton to support the tribes and genera. Baroni Urbani and De Andrade (2007), although aware of the molecular papers recently published at the time (Brady et al., 2006; Moreau et al., 2006), didn't discuss anything beyond a critique to the finding that *Tatuidris* was found to be a poneroid instead of a Myrmicinae, even though the basicerotines, the dacetines, and *Strumigenys* were not recovered as closely related lineages within the Myrmicinae in one of the papers (Moreau et al., 2006, no phalacromyrmecines included), and in the other paper, *Strumigenys*, the phalacromyrmecine *Pilotrochus*, and the basicerotines were recovered as a clade (the SPB-clade) with the exclusion of the dacetines, which were found to be only distantly related, appearing as a polyphyletic group amidst the fungus-growing ants (Brady et al., 2006).

We reassessed the morphological characters used in series of papers by Bolton and Baroni Urbani and De Andrade trying to understand these characters in light of the topology provided by the most recent molecular results (Ward et al., 2015; Branstetter et al., 2017). We discussed above the most important defining characters of *Strumigenys*. Below, we discuss other characters that we judged important in defining the SPB-clade itself and the smaller clades inside it: the *Strumigenys* (much have already been discussed above), the phalacromyrmecines, the *Strumigenys* + phalacromyrmecines, and the basicerotines (Table 3). Since there has been a lot of disagreement in characters studied by Bolton (1984, 1998, 1999, 2006a and 2006b) and Baroni Urbani and De Andrade (1994, 2006a, 2006b and 2007), we judged

necessary an attempt to understand the reasons of the disagreements, give our opinion, and hopefully, enhance understanding of this outstanding group of ants. We didn't have access to the unpublished thesis of Dietz (2004) and won't comment his findings below.

Table 3. A summary of important characters to define the SPB-clade and lineages within it. Column S represent the genus *Strumigenys*, P the phalacromyrmecines, and B represent the basicerotines. Presence of the character is coded with 1, absence with 0. Exceptions and details are discussed in the text, the table shows only a general pattern.

	S	P	B
Opposing mandibles	1	1	1
Modified labra with specialized setae	1	1	1
Blister-like bullae	1	1	0
Poststernite II carina	1	?	0
Hypertrophied metapleural seta	1	1	0
Ventral propodeal foramen notch	1	?	0
Basal process on mandible	1	0	0
Ventral basigastral hairs	1	0	0
Spongiform outgrowths on postsclerites II and III	1	0	0
Carinated/lamellate edges of posttergites II, III and IV	1	0	1
Node of petiole without a posterior face	0	1	0
Robust downcurved mandibles, teeth alternating in size	0	1	0
Katepisternal groove	0	1	0
Eyes on dorsal margin of scrobe	0	0	1
Two right-angle bents on scape	0	0	1
Antennal fossa offset from scrobe cavity	0	0	1
Broad and sessile presclerites IV	0	0	1
Ventral mesothoracic hair beds	1	1	1
Bizarre pilosity	1	0	1

3.5.1. Opposable mandibles

The SPB-clade is defined by two main characters, the opposable mandibles and the modified labra (Table 3). Opposable mandibles, those in which the inner margins are juxtaposed when mandibles are closed, differ from crossing mandibles, the most common type found in ants in which one mandible partially overlaps the other when closed. Opposable mandibles have been first proposed as a synapomorphy for the Dacetini by Baroni Urbani and De Andrade (1994) and it was confirmed by Bolton as a synapomorphy of his "Dacetonini tribe group" (1998). Outside the SPB-clade it occurs in the dacetines and in the genus *Tatuidris*. The Cretaceous ant genus

Camelomecia (Barden and Grimaldi, 2016) has overall very similar mandibles to those of *Tatuidris* and probably might have had opposable mandibles too. Baroni Urbani and De Andrade (2007) made a correction in their coding of this character for *Pilotrochus* and *Phalacromyrmex*, arguing that the mandibles of the first cross apically and that it could be the case of the latter. In spite of this note, we considered the character still very strong to define the SPB-clade, especially considering that the teeth interlock across most of the length of the mandibles in *Phalacromyrmex* just as it does in the remaining ants in the SPB-clade.

With the finding that the dacetines are not related to the SPB-clade (Brady and al., 2006; Ward et al., 2015), this character is reinterpreted as having arisen at least twice in the Attini, once in the ancestral of SPB-clade and at least once in the dacetines.

We couldn't make the same effort to reassess characters that putatively define the dacetines as we did for the SPB-clade, as the former is not closely related to the *Strumigenys*, the main focus of this paper, but also for not having available specimens of several genera it. However, it is worth mentioning that the opposable mandibles apparently are a synapomorphy of the dacetines as well, even considering the "odd member" *Lenomyrmex* (Fernández and Palacio, 1999), which was surprisingly recovered as a member of the clade in the molecular phylogenies (Ward et al., 2015; Branstetter et al., 2017). We suggest then that this character should be reevaluated for that genus since we weren't able to rule out the possibility of *Lenomyrmex* having crossing mandibles by examining available images. The fact that the opposable mandibles might be a synapomorphy of the two clades in the Myrmicinae in which lineages of trap-jaws evolved brings the following question: are opposable mandibles an exaptation to the evolution of trap-jaw ants? While this idea can be drawn upon the internal SPB-clade phylogeny, where at least three trap-jaw lineages are nested within a big clade of species with gripping mandibles (also opposable), the same is not true for the dacetines. In that clade it is not at all clear whether gripping and opposable mandibles gave rise to trap-jaws, the contrary actually appearing more or as plausible (Branstetter et al., 2017). Moreover, outside the Myrmicinae, the phylogenetic relations of the genera *Myrmoteras* and the *Odontomachus-Anochetus* clade, trap-jaw lineages of the Formicinae and Ponerinae subfamilies, respectively, are also not informative in this respect, since both are not nested within or sisters to groups with opposable mandibles (Larabee et al., 2016; Ward et al., 2016).

3.5.2. Specialized labra

Putting aside the fact that labral morphology is extremely variable within the SPB-clade, we concur with Bolton (1998) that the labral morphology in this group departs radically from the common B-shaped or D-shaped observed in the Myrmicinae and should be interpreted as a defining character of the group, with the difference that we are now excluding the dacetines and considering their modified labra as having originated independently. Our argument might seem contradictory to our opinion about the modified hairs found in the group (see below in the topic "The basicerotine pilosity"), however, there are fundamental differences between the two cases, which makes us consider the modified labra a stronger character than the modified hairs to define the SPB-clade. First, all three main lineages of the SPB-clade have modified labra. Second, it doesn't occur elsewhere in the Myrmicinae, except in the dacetines. Third, the modified labra, together with the mandibles, and approaching mode (behavior), is part of their hunting mechanism, which is very likely a condition present in the ancestor of the SPB-clade.

Baroni Urbani and De Andrade addressed critics to specific labral characters discussed in Bolton 1999 (in their characters 4-8), but not the general pattern proposed by Bolton in the previous paper (1998).

3.5.3. Basal process on mandibles

Baroni Urbani and De Andrade (2006a, 2007) critics of the basal lamella were responded by Bolton (2006a). We agree with Bolton's argument in that reply. Occasional examples of reductions of the basal process in some species of *Strumigenys* don't make the character less valuable, especially considering how widespread it is in the genus and how large the genus is. It is completely absent in phalacromyrmecines and in the basicerotines, provided we don't consider the flattened and lengthened basal tooth of some basicerotines as a homologous structure. Bolton claims that the origins of the basal lamella of *Strumigenys* and the modified teeth seen in some basicerotines are of a different nature, the first being "derived from the mandible itself" and the latter from the basal tooth, but gives no explanation why. We don't see any reasons why the basal lamella of the *Strumigenys* cannot be a modified basal tooth. Interpreting it as so seems strange while examining trap-jaw *Strumigenys*, but in species with more "normal", triangular mandibles, such as *S. agosti* or *S. browni*, it does seem plausible that the basal process is a modified tooth as argued by Baroni Urbani and De Andrade

(2007). Nevertheless, to our diagnosing goals, the dispute over the origin of the structures makes little difference and the important fact is that, in the SPB-clade, the basal process is only widespread in *Strumigenys*. In the basicerotines, if a basal process is present in an initial state of differentiation (as an enlarged basal tooth), it is not helpful to diagnose the entire group as it only rarely occurs.

3.5.4. The phalacromyrmecine mandible

Baroni Urbani and De Andrade (2006b, 2007) argued for the inadequacy of the alternating size of the teeth on the mandibles of the phalacromyrmecines as a character to define the group. Bolton (2006b) responded calling attention to other characteristics of the phalacromyrmecine mandible that must be considered in conjunction with the teeth alternating in size: mandibles robust and downcurved, main teeth increasing in size towards base, and absence of basal lamella. We concur that, taken in conjunction, these traits are not seen in the mandibles of other ants and therefore, the overall morphology of the phalacromyrmecines is a sound trait isolating them in the SPB-clade.

Baroni Urbani and De Andrade (2007, page 28) mentions a denticulate swelling on the basal margin of the mandibles of *Phalacromyrmex fugax*, which according to them could potentially be an atrophied basal lamella. The swelling can be seen in specimens CASENT0217029 and CASENT0179596 of *Ph. fugax* at AntWeb. Considering it is apparently absent in *Pilotrochus* (e. g. specimen CASENT0047617) and *Ishakidris* (e. g. specimen CASENT0235144) and that it little resembles the basal lamella of the *Strumigenys*, we don't consider this hypothesis plausible.

3.5.5. Labio-maxillary complex palpal formula

With the exclusion of the dacetines, it became easier to interpret palpal formula in the SPB-clade. There is a clear tendency to reduction of palpomeres in the group. *Strumigenys* has a fairly constant 1, 1 formula, with occasional species showing 0, 1. The phalacromyrmecines have 3, 2 (*Phalacromyrmex* and *Pilotrochus*) or 2, 2 (*Ishakidris*). The basicerotines have two or one maxillary and two or one labial palps.

3.5.6. Basimandibular seta

Baroni Urbani and De Andrade pointed out that the basimandibular seta, putatively shared between the basicerotines and the phalacromyrmecines, is also present in some species of *Strumigenys*. The seta is absent in all examined species of the genus *Rhopalothrix* (5) and in *Protalaridris armata*. In *Basiceros scambognathus*

and in a sister morphospecies, the seta appears to be present, however, there is a pair of similar, only slightly smaller setae anterior to it. Among the phalacromyrmecines, *Ishakidris* has the seta and its presence must to be confirmed in *Phalacromyrmex* (Bolton, 1998). In *Phalacromyrmex*, it seems to be present at least in one specimen (CASENT0217029, AntWeb). Due to the abundant, fine, and long pilosity of *Pilotrochus*, the basimandibular seta is hard to be confirmed by images, however, one specimen appears to have a longer seta on the spot where it is expected to arise (CASENT0047617).

Although the seta appears to be predominant in the basicerotines, it is not universal, and the character occurs scattered in some unrelated lineages across the SPB-clade.

3.5.7. Blister-like bullae on phalacromyrmecines

Blister-like bullae, a very typical trait of the *Strumigenys*, appears to be present in the phalacromyrmecines as well. It was noted that basimandibular bullae do occur in *Ishakidris* and in *Microdaceton* apart from *Strumigenys* (Bolton, 1998). We now know it has been independently acquired in *Microdaceton*, but it is very likely that it is shared by common ancestry between *Strumigenys* and the phalacromyrmecines. Apart from the ventral basimandibular gland (Bolton, 1998), the phalacromyrmecines might well have femoral and tibial leg blister-like bullae as we argue ahead. By studying images of phalacromyrmecines available on AntWeb, we could detect pale patches on the outer and distal surfaces of the femora and tibiae of some specimens. We made a tentative presence/absence coding for the bullae on these specimens (Table 4).

Table 4. Tentative coding through images for presence of blister-like bullae on the legs of phalacromyrmecines.

Species	Specimen's code	Femoral	Tibial
<i>Pi. besmerus</i>	CASENT0047618	not seen	possibly on meso and metatibiae
<i>Pi. besmerus</i>	CASENT0005888	elongate, large and diffuse	possibly on mesotibia
<i>Pi. besmerus</i>	CASENT0047617	not seen	possibly on metatibia
<i>Pi. besmerus</i>	CASENT0010642	dubious	possibly on meso and metatibiae
<i>Pi. besmerus</i>	CASENT0003287	elongate	not seen
<i>Ph. fugax</i>	CASENT0103116	dubious	not seen
<i>Ph. fugax</i>	CASENT0179596	possibly on profemora	dubious
<i>Ph. fugax</i>	CASENT0217029	diffuse on all femora	dubious
<i>Ph. fugax</i>	CASENT0235252	possibly on meso and metafemur	not seen
<i>Ishakidris my01</i>	CASENT0235144	dubious	not seen
<i>Ishakidris my01</i>	CASENT0235145	not seen	not seen
<i>Ishakidris my01</i>	CASENT0235131	elongate and diffused	possibly on metatibia
<i>I. ascitaspis</i>	CASENT0249428	possibly on mesofemur	not seen

As discussed in the Material and Methods, bullae might be hard to visualize on the stereomicroscope and to have them revealed on the images can be sometimes just as difficult. The fact that the bullae appear to be present in at least some specimens (even if in one or another leg and not in the others) strongly suggest that phalacromyrmecines do have leg blister-like glands. Even in specimens in which the pale patches are more apparent, they never had sharp bounds and were described as diffused in the table above. Confirmation of this characters on physical specimens is necessary. If confirmed, it will represent an important morphological trait shared between *Strumigenys* and the phalacromyrmecines, since similar leg glands (in terms of morphology and position on the sclerite) on the legs are absent in the Formicidae (Billen et al., 2000).

3.5.8. The antennal fossa, the scrobe, and the curved scape of the basicerotines

Baroni Urbani and De Andrade (2007) claimed that the antennal fossa separated from the scrobe by a cuticular rim was not a basicerotine autapomorphy, as suggested by Bolton (1998). According to them (in their character 22), some species in the basicerotine clade don't have the rim, while some *Strumigenys* do have the antennal fossa separated from the scrobe by a rim. All species of *Strumigenys* they showed as examples, however, have the scrobe surface interrupted (or almost interrupted) by the preocular carina and not by a second carina, which is the condition of the basicerotines (Fig. 16, A-D, white arrows). In those species (*S. smilax*, *S. minkara*, *S. tethepa*, and the species shown in Fig. 60 of Bolton 1999) the preocular carina is either bent dorsally and meeting the dorsal margin of the scrobe (Fig. 16, F) or very well-developed and almost reaching the apex of the scrobe (Fig. 16, J). *S. zapyx* is maybe the sole exception, but it is a very aberrant species in the genus and to us its cephalic morphology matches neither the typical *Strumigenys*, nor the basicerotines. As for the basicerotines that do not possess the rim, they mentioned *E. bruchi* and *E. heliscata*, both not examined by us. We did examine though a sister species to *E. bruchi*, and it does have the rim. We examined at least one species in each basicerotine genera and most of them have a well-defined rim. *E. aff. gravis* has a poorly defined rim (Fig. 16, B, white arrow), which might mirror somehow the condition found in *E. heliscata*. We show below, however, that the rim itself is only part of a structure of main importance to define the basicerotines.

Also, according to Baroni Urbani and De Andrade (2007, their character 18) the character state "scapes bent at base" being a typical basicerotine trait has the same problem of occurring in several *Strumigenys* as well (their examples being *S. decipula*, *S. nannosobek*). They show images of the scapes (in dorsal view) of these *Strumigenys* comparing them to scapes of basicerotines, the pairs supposedly not differing significantly. We think there is a misunderstanding in the inadequacies for this character, as Bolton (1998) described two right-angle bents at the base of the scape of the basicerotines. By comparing disarticulated scapes of basicerotines and *Strumigenys* in dorsal and in posterior view (and not only in dorsal view) the differences arise. The posterior bent is absent or gentle in *Strumigenys* (Fig. 17, A, C and E), while it is commonly very strong and abrupt in the basicerotines (Fig. 17, B, D and F).

The antenna, antennal insertion, and scapes are unique in the basicerotines and taken in conjunction they separate them from the *Strumigenys* and the phalacromyrmecines. Apart from our considerations above regarding the rim enclosing the antennal fossa and the double bent at the scapes, we highlight some additional traits. First, the dorsal margin of the scapes, instead of following anteriorly straight to the antennal insertion area, it is offset dorsally and medially right anterior to the eye (Fig. 16, A and D, black triangles). This forms the "pinched-in dorsolateral margins" of the head posterior to frontal lobes (Bolton, 2003), which is best seen in face view. In some species the dorsal margin of the scrobe fades in this area but the pinched-in margin on top of the frontal lobes remains (Fig. 16, B, C and E). Another important thing is that the antennal fossa, regardless of being separated from the scrobe by a cuticular rim or not, forms another cavity in the basicerotine cranium. It is positioned slightly dorsally, offset from the cavity forming the scrobe (Fig. 16, A-E). On the other hand, in *Strumigenys* and apparently in the phalacromyrmecines, the antennal fossa is barely a shallow cavity within the scrobe area, at its base (Fig. 16, F-J). The antennal fossa being in another level from that of the scrobe, explains the second right-angle bent at the base of the scape in the basicerotines, as the scape shaft can only fit on the scrobe due to it (otherwise it would be directed outwards in rest position). Finally, the scrobe in the basicerotines truly protects the funiculus, and only slightly the scapes. The scrobe ventral margin is very developed, sometimes even into a lamellar projection (Fig. 16, A). As the scapes are not to be protected but in fact part of the "shield" (when antennae are retracted), there is little space in the scrobe for them,

except for a relatively narrow area where the posterior margin of the shaft lies on to some extent.

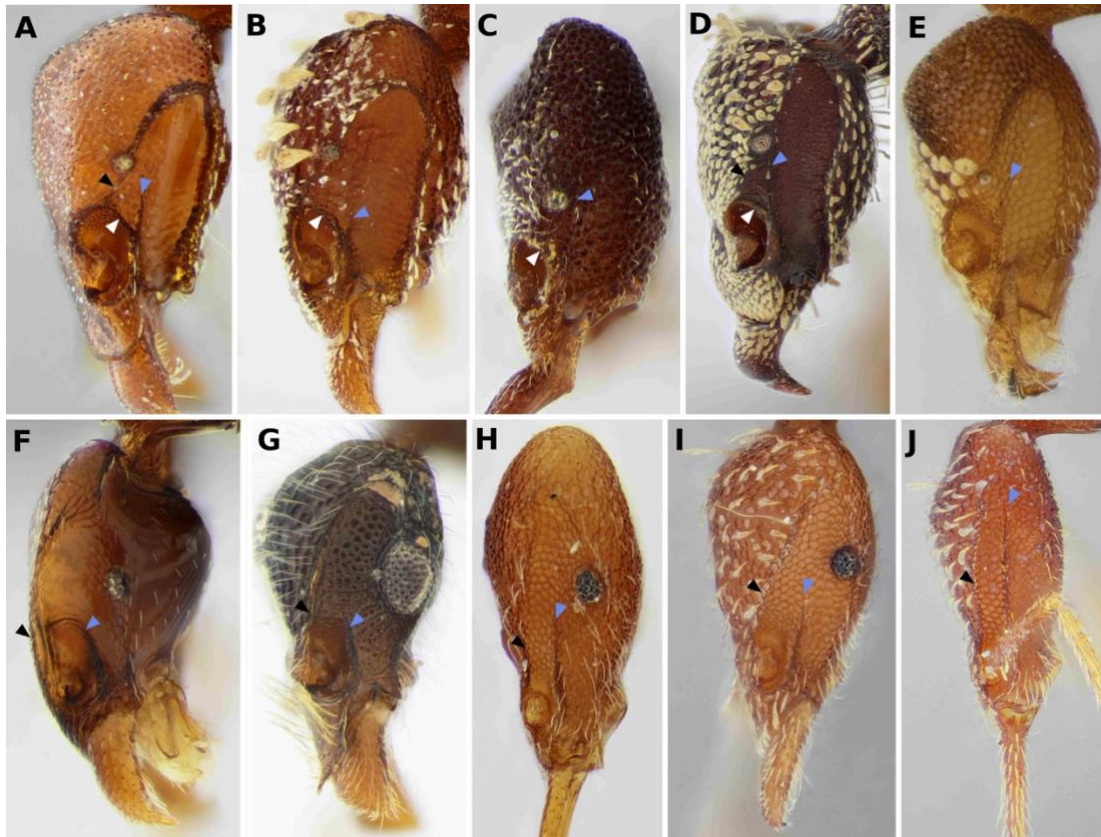


Fig. 16. Comparison of the antennal fossa and scrobe of the basicerotines (A-E) and *Strumigenys* (F-J). **A**, *Eurhopalothrix spectabilis* (UFV-LABECOL-008985); **B**, *Eurhopalothrix* aff. *gravis* (ANTWEB1041007); **C**, *Protalaridris armata* (ANTWEB1041070); **D**, *Basiceros scambognathus* (ANTWEB1032529); **E**, *Rhopalothrix* *ufv_sp1* (UFV-LABECOL-008567); **F**, *S. lilloana* (ANTWEB1041005); **G**, queen of *S. reticeps* (ANTWEB1038995); **H**, *S. chareta* (ANTWEB1032292); **I**, *S. alberti* (UFV-LABECOL-001551); **J**, *S. smilax* (ANTWEB1032491). White arrows pointing to the cuticular rim that closes the antennal fossa in the basicerotines (absent in E and weak in B). Black arrow pointing to the dorsal margin of the scrobe anterior to the eye level (absent or poorly developed in B, C and E). Blue arrow evidencing the preocular carina (poorly developed in B and C).

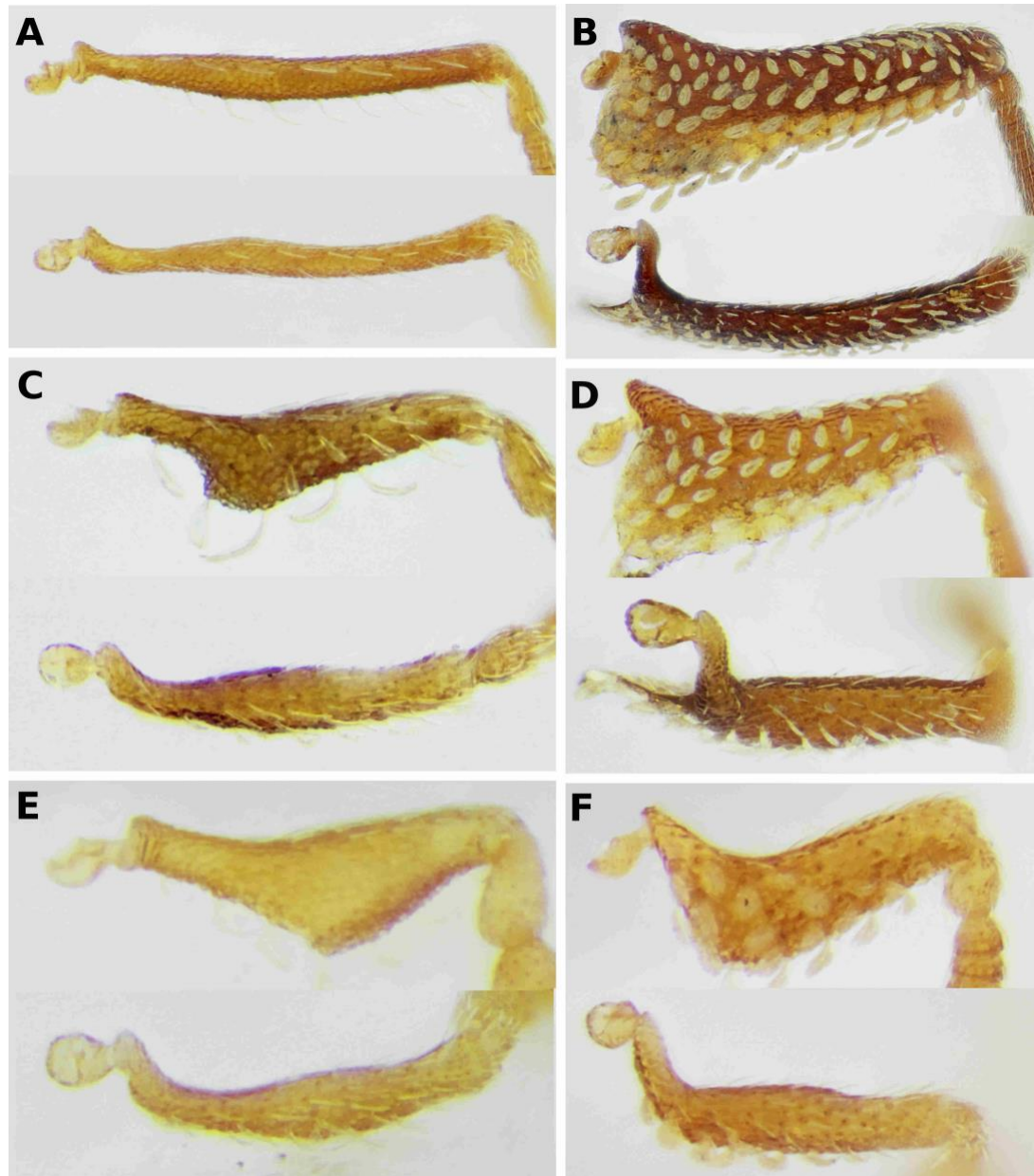


Fig. 17. Scapes of *Strumigenys* (A, C and E) and basicerotines (B, D and F). **A**, *S. chyzeri* (ANTWEB1038333); **C**, *S. crassicornis* (UFV-LABECOL-008999); **E**, *S. emmae* morph 2 (ANTWEB1032299); **B**, *Basiceros scambognathus* (ANTWEB1032529); **D**, *Eurhopalothrix* aff. *gravis* (ANTWEB1041007); **F**, *Eurhopalothrix* aff. *bruchii* (ANTWEB1041020). Top image on each letter box is the dorsal view of scape, except E which is the ventral view. Bottom image in each letter box is the posterior (top) view of scape.

3.5.9. Eyes on dorsal margin of scrobe in the basicerotines

This character has long been noticed (Brown, 1949), but during the time myrmecologists were considering the dacetines as related to the SPB-clade, it was hard to interpret, since many species in that clade have dorsal eyes and the degree of development of the scapes and their shapes varies drastically on them. Assuming the

molecular topology of the Myrmicinae (Ward et al., 2015), the character becomes an excellent one splitting the basicerotines from the *Strumigenys* + phalacromyrmecines. Completely blind species can cause some confusion (e. g. *S. inopinata*), but in such cases other traits must be used for their identification.

3.5.10. Expanded frontal lobes differ between *Strumigenys* and phalacromyrmecines

An important character pointed out in Bolton (1984) has since then been neglected in the following discussion. It is the expanded frontal lobes, which in *Ishakidris* and *Phalacromyrmex* flank the clypeus laterally. In those genera, the frontal lobes set the anterolateral margins of the cephalic capsule. In *Strumigenys* species, when frontal lobes are expanded, they never flank the clypeus laterally and the lateral margins of the clypeus are also the anterolateral margins of the cephalic capsule.

3.5.11. Clavate scapes

Baroni Urbani and De Andrade criticized the use of the clavate scape to define the phalacromyrmecines (in their character 19) as this condition is observed in *S. reticeps* and *S. warditeras*. We were able to find other species with a clavate scape such as *S. perissognatha*, *S. thaxteri*, *S. beebei*, *S. splendens*, *S. inusitata*, and members of the *appretiata*-group (5 species checked). The clavate scapes seem to be a simple feature to evolve and since it is replicated in many *Strumigenys* (probably in many more species outside the Neotropics), we consider it a weak character to define the phalacromyrmecines. Here it is appropriate to justify that cases like those of the mandibles or the katapisternal grooves of the phalacromyrmecines were considered sound characters due to their apparent greater complexity when compared to the clavate scapes and to the fact they are not exactly replicated in any *Strumigenys*, as it is the case here.

3.5.12. Ventral mesothoracic hair beds

The "mesopleural organ" or "mesopleural gland" (Bolton, 2000, 2003) is the lateral patch of fine setae seen anteriorly on the upper katapisternum. Bolton (1999) and Baroni Urbani and De Andrade (2007) called attention to the fact that it is not a paired structure confined to the lateral pleurae, but a continuous ventral line of hairs on mesothorax hidden by the procoxae. According to Bolton (2003) it is restricted to the phalacromyrmecines and many *Strumigenys*, while absent in the basicerotines. Baroni Urbani and De Andrade (2007) argued that there is no indication the structure

is glandular, suggested the term *mesosternal hair beds* to describe the structure, and pointed that the hairs are present in some basicerotines as well. We concur with Baroni Urbani and De Andrade in these respects (Fig. 18) and only suggest a slight modification to the term they proposed. The meso and metasternum are invaginated structure in the Holometabola (Buetel et al., 2013), therefore it is likely that the ventral region of the mesothorax is a folding of the pleurae in ants and not the mesosternum. We suggest a term that doesn't associate the structure directly with a pleural or a sternal area, therefore we will call it the *ventral mesothoracic hair beds* instead. The ventral mesothoracic hair beds, although far from universal in the group, occur scattered among species in the SPB-clade. This peculiar feature is interestingly convergent in some dacetines (*Orectognathus*, *Colobostruma*, *Mesostruma*, and *Orectognathus*), as mentioned by Baroni Urbani and De Andrade (2007).

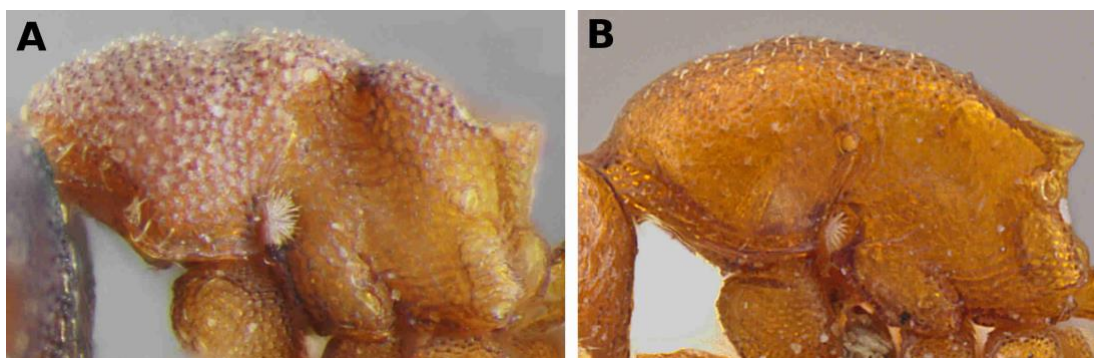


Fig. 18. Ventral mesothoracic hair beds in basicerotines. **A**, *Rhopalothrix* ufv_sp1 (UFV-LABECOL-000718); **B**, *Octostruma convallisur* (MCZ-ENT00511411, photo by John Longino).

3.5.13. The katepisternal grooves of the phalacromyrmecines

Baroni Urbani and De Andrade (2006b, 2007) questioned the presence of the katepisternal groove in *Phalacromyrmex* and *Pilotrochus*. The groove, which presumably channel the substances of a putative glandular region has been pointed out by Bolton as a putative synapomorphy of the Phalacromyrmecini (1998). In their critique, Baroni Urbani and De Andrade (2006b, 2007) show an image of the mesosoma of the holotype of *Ph. fugax* and state that the examination of the specimen showed "no trace of groove". Regarding *Pilotrochus*, Baroni Urbani and De Andrade follow citing Bolton (1984) where he stated the "mesopleural organ" as not subtended by the "open groove seen in *Ishakidris*". While it is true that Bolton has paid little attention to the presence of the groove in *Pilotrochus* and to its value as a diagnosing character for the phalacromyrmecines (Bolton, 1984), it must be noted that later he

stressed its importance (Bolton, 1998). To us, his statement (in 1984) is ambiguous, since it doesn't mean that the groove is absent, but only not present exactly as in *Ishakidris*. Moreover, Bolton (2006b) insisted that, in spite of the variation of the character in the three genera, to say it is absent in *Phalacromyrmex* and in *Pilotrochus* is an exaggeration, and reaffirmed that the groove is *somehow* present in the three genera, either as one main well-defined, deep groove (*Ishakidris*) or as a series of grooves irradiating from the ventral mesothoracic hair bed (*Pilotrochus* and supposedly *Phalacromyrmex*). He follows suggesting that a better term for the structure, which he claims to be absent in *Strumigenys*, would be something as *katapisternal channelling system*.

Our interpretation is that the groove is indeed present and important to define the phalacromyrmecines. Images below confirm the presence of a groove or grooves on the mesopleura of the three phalacromyrmecine genera (Fig. 19). It is undoubtedly present as a deep and wide groove in *Ishakidris* (Fig. 19, E). In *Phalacromyrmex*, it is either present as one main groove with faint striae below (Fig. 19, A and B, the two sides of the same ant) or as two main grooves and additional striae below on the katapisternum (Fig. 19, C and D). It is important to note that the specimen in image D is probably not *Ph. fugax*, but a sister species (see Material and Methods) and the specimen in A and B was sampled in the same locality as the holotype showed in Baroni Urbani and De Andrade (2006b, 2007). Finally, in *Pilotrochus* (3 workers and 2 queens specimens examined: CASENT0003287, CASENT0010642, CASENT0047617, CASENT0005888, and CASENT0047618) there are at least three grooves that irradiates from the mesothoracic hair beds in the workers and two grooves in the queens (worker shown in Fig. 19, F). The term suggested by Bolton (2006b), *katapisternal channelling system*, implies it is part of a glandular structure. Since this hasn't been confirmed, we refrain to use it and suggest the term *katapisternal* (or *mesopleural*) groove/grooves be maintained.

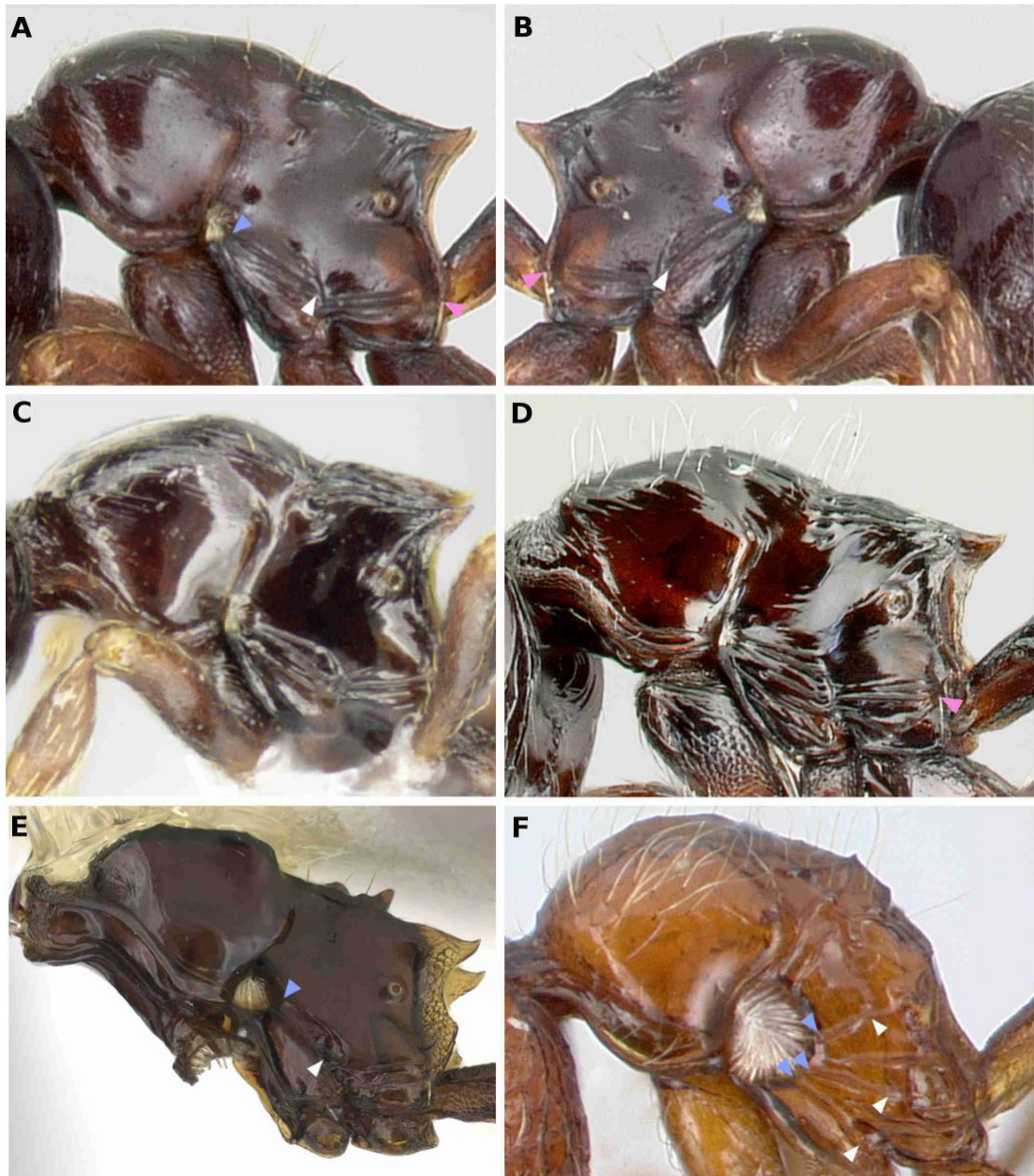


Fig. 19. The katepisternal groove in several phalacromyrmecines. **A to C**, *Ph. fugax*; **D**, determined as *Ph. fugax*, but probably an undescribed, sister species. **E**, *Ishakidris my01* (CASENT0235145, photo by Shannon Hatman); **F**, *Pilotrochus besmerus* (CASENT0010642, photo by April Nobile). **A** and **B** show, left and right sides, respectively, of specimen CASENT0103116 (photo by April Nobile), **C** is specimen CASENT0235252 (photo by Estella Ortega, AntWeb), and **D**, specimen CASENT0179596 (photo by Erin Prado, AntWeb). Blue triangles indicate anterodorsal end of groove, white triangles indicate posteroventral end. Pink triangles show metapleural seta (see discussion in "Ventral mesosoma" section above).

3.5.14. The carina on poststernite II (petiole) in phalacromyrmecines

This character has been discussed above (Fig. 6 and related text) as one of the most important defining characters of the *Strumigenys*, occurring in females and

males. Here we want to stress that it must be checked in the three phalacromyrmecine genera as it can be, just as the blister-like glands, a defining character of the *Strumigenys* + phalacromyrmecines clade, instead of a trait restricted to the *Strumigenys* only. In fact, Bolton mentions in *Ishakidris ascistaps* description a carina ventrally on the petiole (1984). It could well be similar to that found in some *Strumigenys* in which the anterior carina of the poststernite II has extended posteriorly, spanning the entire poststernite. However, only examination of specimens will tell if it is, in detail, similar to the peculiar structure seen in *Strumigenys*, in which a translucent patch and a roughly T-shaped carina is often present in conjunction with the longitudinal carina.

3.5.15. The transversally carinated posttergites II, III and IV of *Strumigenys* and the basicerotines

With the risk of becoming repetitive, as this topic have been briefly discussed in the spongiform tissue section above, here we comparatively discuss the differences of structure of the posterior postsclerites II (petiole), the anterior and posterior portions of postsclerites III (postpetiole), and the anterior postsclerites IV (anterior section of the gaster). The differences are important in setting apart the phalacromyrmecines from *Strumigenys* and the basicerotines.

Posterior margin of the posttergite II (petiole)

In *Strumigenys*, the posterior margin of the node of the petiole bear an arched cuticular outgrowth which can be a simple carina or shelf-like, either lamellate or spongiform (Fig. 20, *b* in A and C). It is only seldom absent in the genus (Fig. 20, B). Posterior to this outgrowth, the sclerite funnels to form a short posterior tube where presclerites III articulate. In other words, in profile the node of *Strumigenys* has a short posterior (descending) margin followed by a short tube-like "posterior peduncle" (Fig. 20, *c* in A-C). In the basicerotine genera, the posterior petiolar conformation is very similar to that of *Strumigenys*, with the difference that the outgrowth on the posterior margin of the node, when present, is only developed into a carina or very short lamella (Fig. 20, *b* in G-I). Despite that, the posterior (descending) margin of the node and the tube-like "posterior peduncle" are present (Fig. 20, *b* and *c* in G-I, note that the node is very low and therefore *b* it is *almost* absent in *Basiceros*). Contrastingly, the phalacromyrmecine genera have a very different, simpler, morphology of the posterior petiole. In profile view, the dorsal margin of the node of their petiole meets the A3

presclerite straight away, not forming a posterior margin (Fig. 20, D-F, the three without *b* and *c*).

Anterior posttergite III (postpetiole)

In *Strumigenys*, presclerites III (helcium) are cup-shaped and arise from a shallowly concave anterior face of the postsclerites III. A transversal carina separates this anterior face from the postpetiole disc dorsally (Fig. 20, *e* in A and C). This carina can be also lamellate, spongiform or rarely very reduced to absent (Fig. 20, B). The concave face is seldom seen *in situ* (Fig. 20, *d* in A is part of presclerites III and the concavity appears between *d* and *e*) and disarticulation of the abdominal segments should be done to reveal them. Among basicerotines, anterior posttergite III conformation is rather similar to *Strumigenys*, except that the transverse carina is never very developed (lamellate or spongiform). In the genus *Rhopalothrix* the carina is reduced to absent. In phalacromyrmecines, on the other hand, the presclerites III are protruded anteriorly and do not originate from a concave anterior surface of the postsclerites. It seems that a dorsal transversal carina setting an anterior from a dorsal surface on posttergite III is completely absent in *Phalacromyrmex* and *Pilotrochus*. In fact, the posttergite III of these two genera appears to be a continuous convexity, with no anterior, dorsal, or posterior well-delimited surfaces. On *Ishakidris*, however, posttergite III is anteriorly carinated and appears to form a minute anterior area between the carina and the base of the presclerites III (Fig. 20, *e* in E).

Posterior posttergite III (postpetiole)

In *Strumigenys* there is a transversal posterodorsal carina on the posttergite III which is often shelf-like, lamellate or spongiform (Fig. 20, *g* in A and C) delimiting the posterior end of postpetiole disc. It is rarely reduced to a simple carina (Fig. 20, *g* in B). In posterior view, postsclerites III funnel slightly (Fig. 8, A) to form a ring-like projection which receives the relatively reduced presclerites IV. *In situ* basicerotine specimens seem to have a similar condition of the posterior postsclerites III, since the posterior posttergite III is almost always carinated (most *Rhopalothrix* species are exceptional in that respect). Disarticulated specimens, however, show they don't have a clearly formed posterior area. Instead, the postpetiole foramen is enlarged to receive the likewise broad presclerites IV (Bolton, 1998, and see "A4 index" above). The phalacromyrmecines don't have a carinated posterior face of the posttergite III, and it

seems that no posterior surface is formed, although they have postsclerites III and presclerites IV narrower than the basicerotines.

Anterior posttergite IV (first gaster segment)

Presclerites IV are narrow in phalacromyrmecines and *Strumigenys* and relatively broad in the basicerotines. In *Strumigenys*, they arise from an anterior truncate anterior area of the postsclerites IV. This area is delimited dorsally by an arched carina (Bolton, 1998, Fig. 20, *h* in A and C), and ventrally by an arched band of specialized hairs (discussed above). The phalacromyrmecines *Phalacromyrmex* and *Pilotrochus* appear to have their presclerites protruded anteriorly and not arising from a flat anterior surface (Fig. 20, D and E). *Ishakidris*, do have a transversal carina anteriorly on posttergite IV and a strongly developed keel-shaped anterior face on the poststernite IV, therefore at least a small anterior face is formed anteriorly on postsclerites IV where presclerites IV arise. Some basicerotines have arched transversal carinae, dorsally and ventrally, delimiting an anterior truncate face of postsclerites IV from the remaining postsclerites (Fig. 21, A). Others have only a posttergite IV anterior carina (Fig. 21, B), although the anterior poststernite IV is still truncate (but not carinated). There is no sign of carinae in some species of *Rhopalothrix*, but those still have a truncate anterior face of the postsclerites IV (Fig. 21, C). Regardless of variation in how the truncate anterior surface formed by the postsclerites IV are in the basicerotines, a common feature is that much of it is occupied by the broadened presclerites IV (Fig 21, compare A-C with D-F).

The only difference between the anterior transversal carina of posttergite IV of the basicerotines and *Strumigenys* is that in the latter it tends to be more developed and is often spongiform or lamellate. Moreover, the only difference of this carina when compared to the ones on posterior posttergite II and on anterior and posterior posttergite III is that it is more developed. For those reason we avoid the term *limbus* here and prefer to treat the structure as a simple carina.

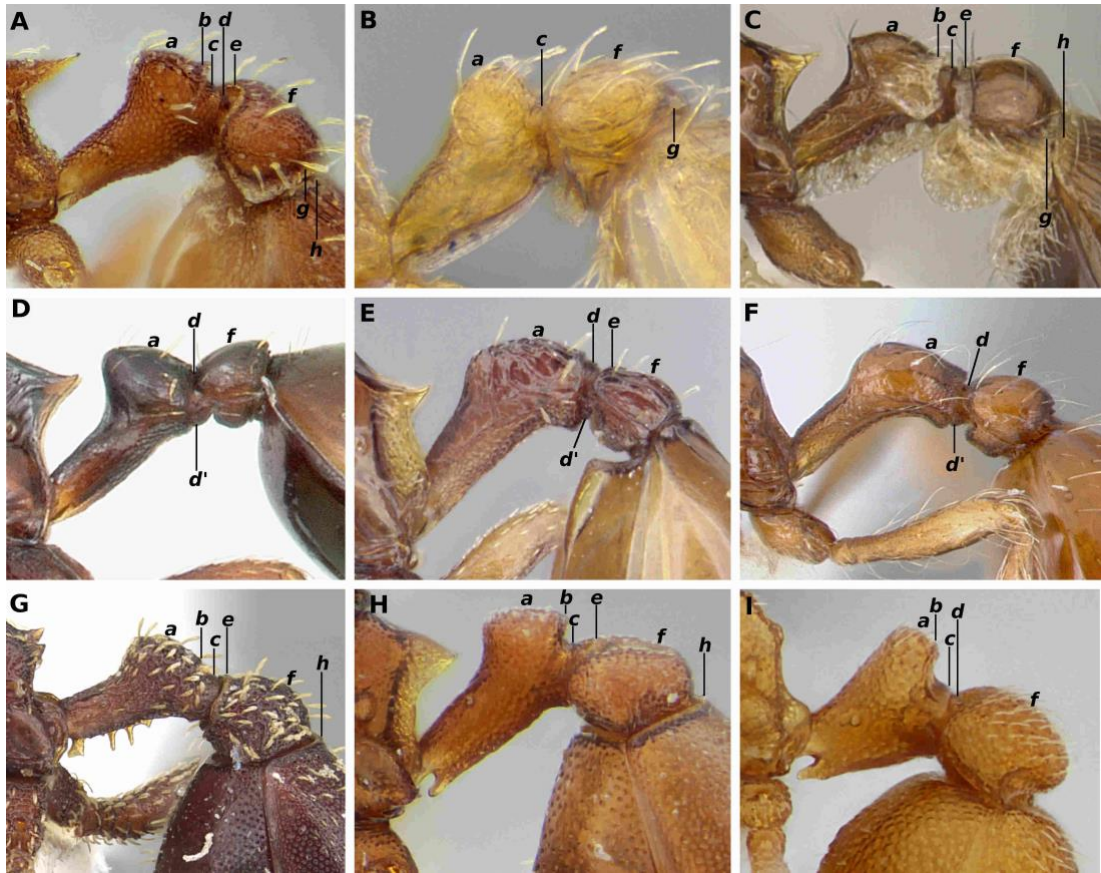


Fig. 20. A comparison between abdominal segments II, III and IV in the SPB-clade. Letters *a - h* infer homologous points among species (see text above for explanation for each letter). **A**, *S. infidelis* (*louisianae*-group, ANTWEB1041097); **B**, *Strumigenys* **sp.n.** H (*emmae*-group, ANTWEB1032333); **C**, *S. dentinasis* (*splendens*-group, CASENT0900191, photo by Will Ericson); **D**, *Phalacromyrmex fugax* (CASENT0103116, photo by April Nobile); **E**, *Ishakidris ascitaspis* (CASENT0249428, photo by Shannon Hartman); **F**, *Pilotrochus besmerus* (CASENT0010642, unknown image author); **G**, *Basiceros disciger* (CASENT0914887, photo by Michele Esposito); **H**, *Eurhopalothrix spectabilis* (UFV-LABECOL-008989); **I**, *Rhopalothrix* ufv-04 (ANTWEB1032474).

3.5.16. Broad presclerites IV of the basicerotines

Bolton (1998) pointed out that the small and constricted presclerites IV were a potential Dacetini + Phalacromyrmecini synapomorphy, contrasting with the broad presclerites IV (and sessile pretergite) of the basicerotines. Baroni Urbani and De Andrade (2007) noted that the small and constricted presclerites were not good to define the Phalacromyrmecini + Dacetini, since that was also the state observed in most Myrmicinae genera. They also criticize, in their character 43, that the narrow versus broad articulation of the postpetiole and gaster wasn't consistent, with many members of one group having the state expected for the other, and vice-versa. To

illustrate that, they show images (their Fig. 24, page 52) of non-disarticulated postpetioles and gasters of two *Strumigenys* and one basicerotine (*Basiceros disciger*), the two *Strumigenys* showing relatively broader postpetioles than *B. disciger*. We think that Baroni Urbani and De Andrade misunderstood that character, since the articulation region can't be seen in non-disarticulated specimens. Confirming the articulation between A3 and A4 as broad or narrow by those images is misleading because the supposedly broad articulation is in fact the posterior posttergite III touching the anterior posttergite IV. However, when a flat posterior A3 face and an anterior A4 face are developed and touching each other, which is the case in the basicerotines and in *Strumigenys*, the real width of the postpetiole foramen and the presclerites IV can't be seen *in situ* (see the discussion of the carinated posttergites II, III and IV in the basicerotines and *Strumigenys* above). The correct way to verify this character in the *Strumigenys* and in the basicerotines is by checking the relative width of the presclerites IV in disarticulated specimens (Fig. 20 below, and Fig. 27 of Baroni Urbani and De Andrade, 2007). We measured the width of pre- and postsclerites of abdominal segment A4 in anterior view and made an "A4 index" to verify if basicerotines consistently have broader presclerites IV in comparison to *Strumigenys*. As the pretergites and posttergites are always broader than the presternites and poststernites, the index is calculated by tergal measurements only, like this: (pretergite width/posttergite width) x 100 (Fig. 20, D). We measured very different *Strumigenys* species and at least one species in each basicerotine genera, including some of the species Baroni Urbani and De Andrade (2007) used to illustrate their argument. Basicerotines have always broader presclerites than the *Strumigenys* (Table 5). Among the *Strumigenys*, the species with broader postpetioles do indeed have broader presclerites IV (Fig. 20, D) than the majority of *Strumigenys* (Fig. 20, E and F). However, there is still a considerable gap between the values of those *Strumigenys* (*S. eggersi*, *S. subdentata*, *S. crassicornis*, *S. aff. zeteki*) and the basicerotines with the smaller values (as the genus *Basiceros* in Table 5). Note that *B. disciger* has a greater value of A4 index than *S. crassicornis*, even though in dorsal view of non-disarticulated specimens it shows a relatively smaller contact zone of the postpetiole and gaster than *S. crassicornis* (Fig. 24 of Baroni Urbani and De Andrade, 2007). The sessile condition of the basicerotines presclerite IV (Bolton, 1998) couldn't be confidently verified, it seems there is still a small constriction at least in some portions between the presclerites and the postsclerites, however no species present an obvious

neck-like constriction as in the majority of *Strumigenys*. As some species of *Strumigenys* appear to have very weak constriction and species without neck-like constrictions can be eventually found (many species haven't been investigated for this trait), we think that to discriminate the presclerites as sessile or not is probably not relevant to diagnose the big groups inside the SPB-clade for the time being.

We conclude that the broad presclerites IV appear to be a typical basicerotine trait which sets them apart from *Strumigenys* and the phalacromyrmecines.

We suspect Fig. 24, A of Baroni Urbani and De Andrade does not depict *S. horvathi* as stated, since the postpetiole in *S. horvathi* seems much narrower and surrounded by spongiform tissue.

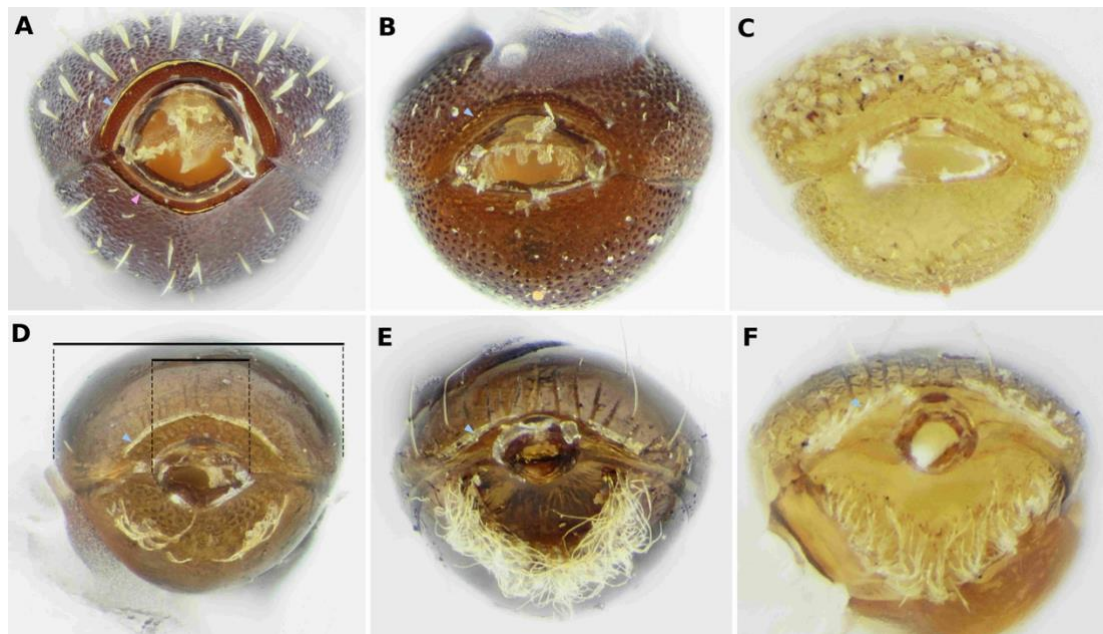


Fig. 21. Comparison between basicerotine and *Strumigenys* presclerites IV. **A**, *Basiceros* aff. *scambognathus* (ANTWEB1041044); **B**, *Octostruma stenognatha* (UFV-LABECOL-008981); **C**, *Eurhopalothrix* aff. *bruchi* (ANTWEB1041020); **D**, *S. crassicornis* (UFV-LABECOL-008999); **E**, *Strumigenys* ufv-10 (UFV-LABECOL-001929); **F**, *S. emmae* morph 2 (ANTWEB1032299). Blue arrows evidencing posttergite IV anterior transversal carina (lamellate or spongiform in *Strumigenys*). Pink arrow in A shows poststernite IV anterior transversal carina. Lines in D represent how A4 index measurements were taken (see text above).

Table 5. A4 index of basicerotines and *Strumigenys* species (see text above for description of the index).

Species	A4 index	Species	A4 index
<i>Basiceros disciger</i>	39.05	<i>Strumigenys alberti</i>	25.84
<i>Basiceros</i> aff. <i>scambognathus</i>	43.00	<i>Strumigenys appretiata</i> -group ufv-10	26.74
<i>Eurhopalothrix</i> aff. <i>gravis</i>	50.79	<i>Strumigenys lilloana</i>	22.00
<i>Eurhopalothrix spectabilis</i>	45.83	<i>Strumigenys crassicornis</i>	33.75
<i>Eurhopalothrix</i> aff. <i>bruchi</i>	48.72	<i>Strumigenys</i> aff. <i>zeteki</i>	30.00
<i>Octostruma rugifera</i>	44.23	<i>Strumigenys eggersi</i>	30.30
<i>Octostruma iheringi</i>	40.00	<i>Strumigenys subdentata</i>	30.00
<i>Octostruma stenognatha</i>	47.27	<i>Strumigenys saliens</i>	23.43
<i>Protalaridris</i> sp.	42.52	<i>Strumigenys louisianae</i> -group ufv-06	25.00
<i>Rhopalothrix</i> ufv_sp1	50.00	<i>Strumigenys rogeri</i>	27.03
<i>Rhopalothrix</i> jtl021	50.00	<i>Strumigenys membranifera</i>	23.68
<i>Talaridris mandibularis</i>	46.94	<i>Strumigenys saliens</i>	23.43
		<i>Strumigenys emmae</i> morph 2	24.24
		<i>Strumigenys godeffroyi</i>	24.32
		<i>Strumigenys chareta</i>	26.19

3.5.17. The basicerotine pilosity

The odd pilosity seen in *Strumigenys* species and pointed out by Bolton (1983, 1999) as characterizing the genus have been criticized by Baroni Urbani and De Andrade (1994) who argue that the specialized pilosity seen in the Basicerotini is, in essence, very similar to *Strumigenys*. These authors show high magnification SEM images as examples of their argument (images 1.B, 2.B and 3B in Baroni Urbani and De Andrade, 1994). We disagree with their conclusion: "it should be evident that no significant differences can be observed among them". In fact, considering only the three images they show (two of basicerotine species and one *Strumigenys*), we conclude the opposite, and describe the differences between the two types as decumbent, leaf-like, and pedunculate in the *Strumigenys* image, and suberect, brush-like, and gradually expanding in the images showing basicerotines. In fact, the latter type is widespread among the basicerotines. The plate below shows different species with these "typical basicerotine" standing setae (Fig. 22 A-D), even though the setae in each species varies a lot in development, in greater detail they look similar (as those of Fig. 22, D). There are scattered exceptions of species where standing pilosity is reduced or absent (e.g. *Rhopalothrix subspatulata*, *Eurhopalothrix spectabilis*) and more rarely species with setae with radically different shape from the brush-like setae. Examples of differentiated setae among the basicerotines is the squamate setae of *Eurhopalothrix bruchi*, the so called "holding hairs" of *Basiceros manni* (Hölldobler

and Wilson, 1986, their Figs. 1.B and 1.C), the short, bristle-like, simple erect pilosity of queens in some species in the genus *Rhopalothrix* (Fig. 22, E), and the exquisite thin, squamate with frayed margins, appressed ground pilosity of *Eurhopalothrix platisquama* and *E. seguensis* (Taylor, 1990, his Figs. 33 and 34). In sum, with the above mentioned exceptions in mind, we agree with Brown and Kempf (1960) in that there is a particular type of setae that helps in diagnosing the basicerotines. The *Strumigenys* have a much larger array of setae types (detailed in Bolton, 1999, 2000), even so, we weren't able to find species in the genus with setae very similar to the common type of the basicerotines. The genus *Caliptomyrmex*, a member of the Crematogastrini tribe, does, in some species, show setae of extreme resemblance to that seen in the basicerotines.

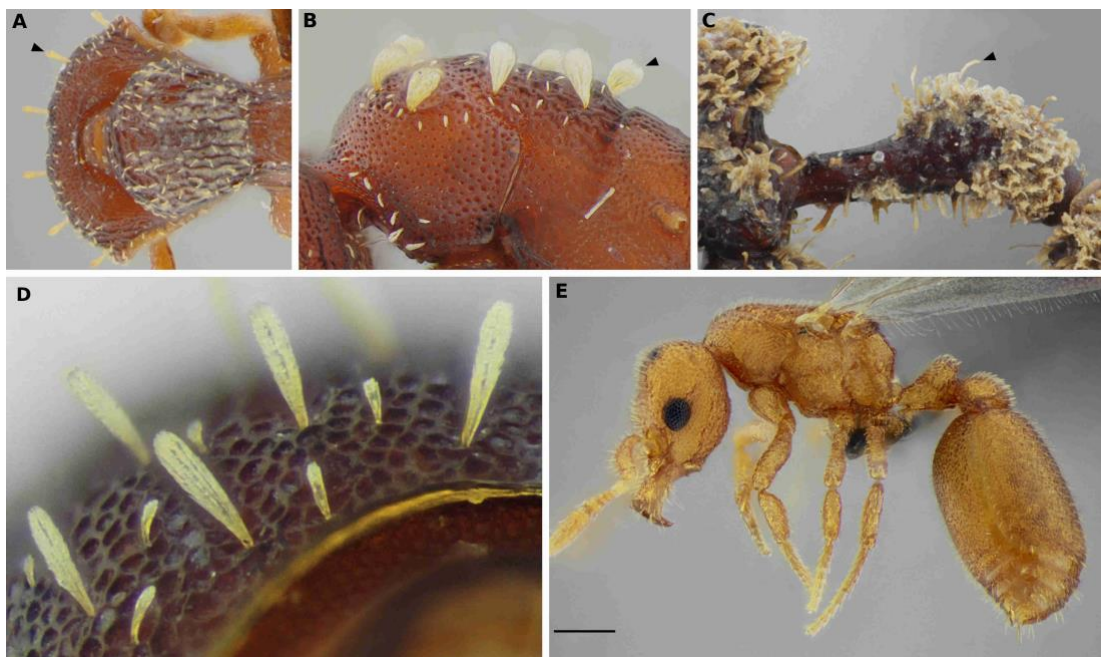


Fig. 22. The common type of suberect, brush-like setae found across the basicerotine (A-C, evidenced by the black arrows and zoomed in D). Although varying from thin (C) to hypertrophied (B), the configuration of the setae is similar (shown in greater detail in Figs. 9.B, 10.C, 11 of Hölldobler and Wilson, 1986). Exceptions to the common type of setae do occur in the clade and can be of lacking of setae (e. g. *Eurhopalothrix spectabilis*), tiny, bristle-like setae (E). **A**, *Octostruma ufv-09* (UFV-LABECOL-000697); **B**, *Eurhopalothrix gravis*; **C**, *Basiceros manni*; **D**, *Basiceros* aff. *scambognathus* (ANTWEB1041044); **E**, *Rhopalothrix ufv-04* (ANTWEB1032824).

On the other hand, we do agree with Baroni Urbani and De Andrade (2007) when they argue (in their character 50) that to call all types of hairs a character, "bizarre pilosity", and use it to classify the entire group is not appropriate. In their publication they were referring to the SPB-clade + the dacetines (the Dacetini *sensu* Baroni Urbani

and De Andrade), while here we are considering the SPB-clade only. Three facts make us think there are reasonable chances that the weird hairs have evolved independently in the SPB-clade. First, the microstructural differences between the basicerotines and the remaining ants in the SPB-clade just discussed. Second, the fact that, although bizarre pilosity is rare in other subfamilies (e.g. *Mystrium*), it is only uncommon in the Myrmicinae (e. g. *Cephalotes*, *Myrmicocrypta*, *Caloptomyrmex*, *Stegomyrmex*, some *Cataulacus*, some *Dacatinops*, some dacetines), so it could have evolved twice or more in a group such as the SPB-clade. And third is the fact that the hairs in the phalacromyrmecine are not clearly bizarre. *Pilotrochus* has abundant, long, and flexuous setae, but all of them are simple setae.

3.5.18. The basicerotine cuticle sculpturing

Baroni Urbani and De Andrade (2007, in their character 49) pointed inconsistencies in the presumably synapomorphic character of the deep punctured sculpture of the first gaster segment (Bolton, 1998). They indicated exceptional species with smooth integument like *Octostruma onorei* and old world *Eurhopalothrix* species (although the first do have punctures at least posteriorly on the poststernite IV, see Fig. 28 of Baroni Urbani and De Andrade, 2007) and mentioned examples where the sculpture of *Strumigenys* matches by much that of a basicerotine, showing the pair *S. margaritae* and *Eurhopalothrix bruchi* as an example (their Fig. 29). Although there are many exceptions of basicerotines with smooth or reticulated gastral sculpturing and therefore varying from the typical deep-punctured sculpturing, the latter type is rare outside the basicerotine clade. Inside it, it occurs frequently in the majority of species of most genera, except in most *Rhopalothrix* species. It also often occurs in other parts of the body (see pronotum in Fig. 22, B). The character is a good indicator of the basicerotines, but might not be considered as a defining character. The majority of species in the genus *Rhopalothrix* have a reticulate gastral sculpture rather than a deep punctate sculpture. Using *E. bruchi* as an example to show that some *Strumigenys* have gastral sculpture similar to the basicerotines (Baroni Urbani and De Andrade, 2007) was a bad choice, because *E. bruchi* itself has exceptional gastral sculpture among basicerotines. *E. bruchi* is in fact a member of the group of species currently in the *Rhopalothrix* just mentioned and should be moved from the *Eurhopalothrix* (Branstetter et al., in prep.). However, indeed, some *Strumigenys* (e.g. *S. superba* and *S. tomodonta*) do have deep-punctured sculpture, resembling that of the basicerotines.

Acknowledgements

We thank Jack Longino, Michael Branstetter, Brendon Boudinot, Livia Pires do Prado, John Lattke and Douglas Booher for informally sharing ideas and personal observations on various topics regarding the taxonomy and phylogeny of the ants treated in this contribution. One of us (JCMC) thanks the Conselho Nacional de Desenvolvimento Científico e Tecnológico CNPq for funding.

References

- Barden, P., and Grimaldi, D. A. Adaptive radiation in socially advanced stem-group ants from the cretaceous. *Current Biology*, 26(4), 515–521, 2016.
- Baroni Urbani, C.; De Andrade, M.L. Correcting our correctors: the “Tribe Phalacromyrmecini.” – notes from the underground website (contact us for the pdf of the letter, the link has apparently expired). 2006.
- Baroni Urbani, C.; De Andrade, M.L. First description of fossil Dacetini ants with a critical analysis of the current classification of the tribe (Amber Collection Stuttgart: Hymenoptera, Formicidae. VI: Dacetini). *Stuttg. Beitr. Naturkd. Ser. B (Geol. Palaontol.)* 198: 1-65, 1994.
- Baroni Urbani, C.; De Andrade, M.L. The ant tribe Dacetini: limits and constituent genera, with descriptions of new species. *Annali del Museo Civico di Storia Naturale Giacomo Doria (Genova)* 99: 1-191, 2007.
- Billen, J. and Espadaler, X. A novel epithelial intramandibular gland in the ant *Pyramica membranifera* (Hymenoptera, Formicidae). *Belgian Journal of Zoology* 132: 175-176, 2002.
- Billen, J., Ito, F. and Bolton, B. Femoral and tibial glands in the ant genus *Strumigenys* (Hymenoptera, Formicidae). *Cell* 130: 111-115, 2000.
- Bolton, B. The Afrotropical dacetine ants (Formicidae). *Bulletin of the British Museum (Natural History). Entomology* 46: 267-416, 1983.
- Bolton, B. A new general catalogue of the ants of the world. Harvard University Press, Cambridge, Mass, 1995, 504 pp.
- Bolton, B. An online catalog of the ants of the world. 2018. Available from <http://antcat.org>. Accessed 25 February 2018.
- Bolton, B. Ant genera of the tribe Dacetonini (Hymenoptera: Formicidae). *Journal of Natural History* 33: 1639-1689, 1999a.
- Bolton, B. Ant genera of the tribe Dacetonini (Hymenoptera: Formicidae). *Journal of Natural History* 33: 1639-1689, 1999b.
- Bolton, B. Diagnosis and relationships of the myrmicine ant genus *Ishakidris* gen.n. (Hymenoptera: Formicidae). *Systematic Entomology* 9: 373-382, 1984.
- Bolton, B. Identification guide to the ant genera of the world. Harvard University Press, Cambridge, Mass. 1994.
- Bolton, B. Maintaining the current Dacetini: any need to correct the correctors? Notes

- from the Underground website (contact us for the pdf of the letter, the link has apparently expired), 2006a.
- Bolton, B. Monophyly of the dacetonine tribe-group and its component tribes (Hymenoptera: Formicidae). *Bulletin of the Natural History Museum* 67: 65-78, 1998.
- Bolton, B. New myrmicine ant genera from the Oriental Region Hymenoptera: Formicidae. *Systematic Entomology* 16: 1-13, 1991.
- Bolton, B. Phalacromyrmecini: defending the defensible. Notes from the Underground website (contact us for the pdf of the letter, the link has apparently expired), 2006b.
- Bolton, B. Synopsis and classification of Formicidae. *Memoirs of the American Entomological Institute* 71: 1-369, 2003.
- Bolton, B. The ant tribe Dacetini. *Memoirs of the American Entomological Institute* 65: 1-1028, 2000.
- Brady, S.G., Schultz, T.R., Fisher, B.L. And Ward, P. S. Evaluating alternative hypotheses for the early evolution and diversification of ants. *Proceedings of the National Academy of Sciences* 103: 18172-18177, 2006.
- Branstetter, M.G., Ješovnik, A., Sosa-Calvo, J., Lloyd, M.W., Faircloth, B.C., Brady, S.G. And Schultz, T.R. Dry habitats were crucibles of domestication in the evolution of agriculture in ants. *Proceedings of the Royal Society B: Biological Sciences* 284: 20170095, 2017.
- Brown Jr., W.L. A Preliminary Generic Revision of the Higher Dacetini (Hymenoptera: Formicidae). *Transactions of the American Entomological Society* 74: 101-129, 1948.
- Brown Jr., W.L. The Neotropical Species of the Ant Genus *Strumigenys* Fr. Smith: Group of *gundlachi* (Roger). *Psyche* (New York) 66: 37-52, 1959.
- Brown Jr., W.L. The neotropical species of the ant genus *Strumigenys* Fr. Smith: group of *smithii* Forel. *Journal of the New York Entomological Society* 61: 101-110, 1953.
- Brown Jr., W.L. Revision of the Ant Tribe Dacetini: IV. Some genera properly excluded from the Dacetini, with the Establishment of the Basicerotini new Tribe. *Transactions of the American Entomological Society*, 1949.
- Brown Jr., W.L. The ant genus *Smithistruma*: a first supplement to the World revision (Hymenoptera: Formicidae). *Trans. Am. Entomol. Soc.* 89(3/4): 183-200, 1964, Plate XVI.
- Currie, C.R., Poulsen, M., Mendenhall, J., Boomsma, J.J. and Billen, J. Coevolved crypts and exocrine glands support mutualistic bacteria in fungus-growing ants. *Science* 311: 81-83, 2006.
- Dejean, A. Étude éco-éthologique de la prédation chez les fourmis du genre *Smithistruma* (Formicidae, Myrmicinae, Dacetini) IV. Le polyéthisme chez *S. truncatidens*. – *Insectes Sociaux* 32: 389-402, 1985.

- Dietz, B.H. Uma revisão de Basicerotini Brown, 1948 (Formicidae: Myrmicinae), suas relações filogenéticas internas e com outras tribos dacetíneas (Dacetini e Phalacromyrmecini). PhD thesis, Universidade de São Paulo, 2004, 245 pp.
- Downs, W.G. Polyvinyl alcohol: a medium for mounting and clearing biological specimens. *Science* 97 (2528): 539-540, 1943.
- Fernández, F., and Palacio, E. *Lenomyrmex*, an enigmatic new ant genus from the Neotropical Region (Hymenoptera: Formicidae: Myrmicinae). *Systematic Entomology* 24: 7-16, 1999.
- Fisher, B.L. The Malagasy fauna of *Strumigenys*. In: Bolton, B., The ant tribe Dacetini. *Memoirs of the American Entomological Institute* 65: 1-1028: pp. 612-710, 2000.
- Hölldobler, B. and Wilson, E.O. Soil-binding pilosity and camouflage in ants of the tribes Basicerotini and Stegomyrmecini (Hymenoptera, Formicidae). *Zoomorphology* 106: 12-20, 1986.
- Keller, R.A. A Phylogenetic Analysis of Ant Morphology (Hymenoptera: Formicidae) with Special Reference to the Poneromorph Subfamilies. *Bulletin of the American Museum of Natural History* 355: 1-90, 2011.
- Kimball, S. and Mattis, P. GIMP. The GNU Image Manipulation Program, 1996.
- Larabee, F.J., Fisher, B.K., Schmidt, C.A., Matos-Maraví, P., Janda, M. and Suarez, A.V. Molecular phylogenetics and diversification of trap-jaw ants in the genera *Anochetus* and *Odontomachus* (Hymenoptera: Formicidae). *Molecular Phylogenetics and Evolution* 103: 143-154, 2016.
- MacGown, J.A., Brown, R.L. Specialized setae and spongiform lobes in *Strumigenys* and *Pyramica* Ants (Hymenoptera: Formicidae). 72-77, 2012.
- Masuko, K. Studies on the predatory biology of oriental dacetine ants (Hymenoptera: Formicidae). I. Some Japanese species of *Strumigenys*, *Pentastruma*, and *Epitritus*, and a Malaysian *Labidogenys*, with special reference to hunting tactics in short-mandibulate forms. *Insectes Sociaux* 31: 429-451, 1985.
- Masuko, K. Studies on the predatory biology of oriental dacetine ants (Hymenoptera: Formicidae). III. Predation on Gamasid Mites by *Pyramica mazu* with a Supplementary Note on *P. hexamerus*. *Journal of the Kansas Entomological Society* 82: 109-113, 2009.
- Moreau, C.S., Bell, C.S., Vila, R., Archibald, S.B., and Pierce, N.E. Phylogeny of the ants: Diversification in the age of angiosperms. *Science* 312: 101-104, 2006.
- Beutel, R.G., Friedrich, F., Ge, S-Q., Yang, X-K. *Insect Morphology and Phylogeny*. 1689-1699, 2013.
- Schneider, C., Rasband, W. and Eliceiri, K. ImageJ. *Nature methods* 9: 671-675, 2012.
- Shattuck, S.O. A revision of the Austral epopostrumiform genera. In: Bolton, B. The ant tribe Dacetini. *Memoirs of the American Entomological Institute* 65: 1-1028. – pp. 30-67, 2000.
- Taylor, R.W. New asian ants of the tribe basicerotini, with an on-line computer

- interactive key to the twenty-six known indo-australian species (Hymenoptera: Formicidae: Myrmicinae). *Invertebrate Systematics* 4: 397-425, 1990.
- Taylor, R.W. The ants of the Papuasian genus *Dacotinops* (Hymenoptera: Formicidae: Myrmicinae). – Taxonomy, phylogeny and zoogeography of beetles and ants: a volume dedicated to the memory of Philip Jackson Darlington, Jr., 1904-1983 33: 41-67, 1985.
- Ward, P. S. *Adetomyrma*, an enigmatic new ant genus from Madagascar (Hymenoptera: Formicidae), and its implications for ant phylogeny. *Systematic Entomology* 19: 159-175, 1994.
- Ward, P. S. Broad-scale patterns of diversity in leaf litter ant communities. In: *Ants: standard methods for measuring and monitoring biodiversity*. pp. 99-121, 2000.
- Ward, P. S., Blaimer, B.B. and Fisher, B.L. A revised phylogenetic classification of the ant subfamily Formicinae (Hymenoptera: Formicidae), with resurrection of the genera *Colobopsis* and *Dinomyrmex*. *Zootaxa* 4072: 343-357, 2016.
- Ward, P.S., Brady, S.G., Fisher, B.L. and Schultz, T.R. The evolution of myrmicine ants: Phylogeny and biogeography of a hyperdiverse ant clade (Hymenoptera: Formicidae). *Systematic Entomology* 40: 61-81, 2015.

IV. CAPÍTULO II

NEW SPECIES OF NEOTROPICAL *STRUMIGENYS* F. SMITH (HYMENOPTERA: FORMICIDAE: MYRMICINAE)

ABSTRACT

The pantropical hyperdiverse genus *Strumigenys* has around 200 species described for the Neotropics alone. Despite the significant amount of work done in the region, new species keep accumulating in museums. Here six new species of various species groups of the Neotropical *Strumigenys* are described: *S. ufv-20* sp. nov. (*schulzi*-group), *S. ufv-28* sp. nov. (*silvestrii*-group), *S. ufv-27* sp. nov. (*incertae sedis*), *S. ufv-11* sp. nov. (*probatrice*-group), *S. ufv-64* sp. nov. (*mandibularis*-group), and *S. ufv-26* sp. nov. (*silvestrii*-group).

Key-words: *Strumigenys*; Neotropics; Taxonomy.

1. Introduction

The cosmopolitan, hyperdiverse genus *Strumigenys* has 837 described species worldwide (Bolton 2018). In a global review (Bolton, 2000), 75 species were newly described for the Neotropics and the total diversity for this biogeographic region was 183 species in that year. Subsequently, several contributions described another 19 species for the Neotropics (Longino, 2006; Sosa-Calvo et al., 2006; Sosa-Calvo et al., 2010; Rigato and Scupola, 2008; Baroni Urbani and De Andrade, 2007; Lattke and Aguirre, 2015), making a current total count of 202 species. With myrmecology thriving in South and Central America in the last decades, the accumulation of new species of *Strumigenys* in several ant collections has continued and alpha-taxonomical work is in need in order to maintain *Strumigenys* as one of the best known genera among the "big ones".

Considering the current taxonomical state of the genus *Strumigenys*, new species can be roughly divided into two types, the "easily-detectable" and the "hardly-detectable". Idiosyncratic species with one or more conspicuous morphological traits setting it apart from its related species are the easily-detectable type of new species. They tend not to match the diagnosis of any previously described species and during identification they either "stuck" at some point along the identification key or go with difficulty, often failing to agree with the entire set of traits presented in the lugs of the couplet they passed through. Only rarely these type of new species goes smoothly through the key until a species name. Contrastingly, those new species which reveal themselves only after the examination of very large series, sometimes relying on minute morphological traits or measurement differences, are the hardly-detectable type. They tend to match perfectly with the diagnosis of already described species, normally run smoothly in the identification keys until a species, and are sometimes part of previously unidentified species complexes (*sensu* Bickford et al., 2007, not Bolton, 2000).

This contribution describes six new species of Neotropical *Strumigenys*. They are not closely related to each other, are members of various species groups, and could be classified in the "easily-detectable" type of new species. Several other new species of *Strumigenys* have been examined which could be classified as the "hardly-detectable type", part of these are currently being described by the author in revisions of their own groups (they belong to the *louisianae*-group and the *hindenburgi*-group). Another part of these hardly-detectable new species will be uploaded in AntWeb as

morphospecies of *Strumigenys* with the code "ufv" (e.g. *Strumigenys* ufv-09, a member of *appretiata*-group) and this will hopefully stimulate taxonomical work in the near future.

2. Material and Methods

Specimens studied belong to the following institutions:

- Instituto Nacional de Pesquisas da Amazônia (INPA)
- Laboratório de Ecologia de Comunidades (LABECOL) from the Universidade Federal de Viçosa (UFV);

All specimens are currently deposited at LABECOL, at the Universidade Federal de Viçosa. After the publication of this manuscript, part of the specimens will be returned to the insect collection at INPA, part will remain deposited on the LABECOL ant collection, and part will be donated to the Museu de Zoologia da Universidade de São Paulo (MZSP) and to the Departamento de Zoologia da Universidade Federal do Paraná (DZUP) as noted for each specimen under the descriptions below.

Abbreviations for the body measurements taken are: head length (HL); head width (HW); mandible length (ML) or mandible length 2 (ML2); scape length (SL); ommatidia number (OM); Weber's length (WL); petiole length (A2L); posttergite III plus posttergite IV length (A3+A4L); pronotum width (PrnW); petiole node width (A2W); petiole node length (A2 node L), postpetiole disc width (A3W), first gaster tergite width (A4W), metafemur length (mtfmL), metatibia length (mttbL) and metabasitarsus length (mtbtL). Total length (TL) is the sum of ML (or ML2, see below), HL, WL, A2L, A3+A4L and "leg length" (LegL) is the sum of mtfmL, mttbL, and mtbtL. Cephalic index (CI), mandibular index (MI) and scape index (SI) were calculated following Bolton (1983). Detailing of how each measurement was taken is given as follows:

ML: Length of mandibles from anteriormost point of clypeus to apex of mandibles in full-face view. When anterior clypeal margin is concave, then measurement is the size of the vertical line from apex of mandibles to the point where this line meets a transversal line that touches the anteriormost points of anterior clypeal margin (Fig. 1, A, B and G). I recommend this measurement for trap-jaw species, because the insertion of the mandibles coincides to a large extent with the anterior clypeal margin in those (not the case of many other *Strumigenys*, see ML2 below). In trap-jaw species, if the specimen has the mandibles slightly open, then it is still possible to make an ML by

choosing one of the mandibles and measuring it from the apex to the point where the base of the mandible meets the anterior clypeal margin. Such cases do not add much error to the measurement, although specimens with fully closed mandibles should always be preferred and specimens with wide open mandibles should be definitely avoided because in those a significant portion of the base of the mandible is covered by the clypeus.

ML2: The size of the line that goes from apex of mandibles to the point where the outer margin of mandibles meets the clypeus laterally (Fig. 1, B and C). Measuring ML in some non-trap-jaw *Strumigenys* species sub-estimates by much the length of the mandibles, since their insertions can be much posteriorly to the anteriormost point of the clypeus. Moreover, in these cases, if the specimen has the mandibles open, then to make a ML becomes impossible in these non-trap-jaw. I suggest that the ML2 should be an auxiliary measurement, taken in conjunction with ML. It will probably be more suitable in the context of revisions of groups with such mandible and may substitute ML in these situations (e.g. the *probatrix*-group).

HL: Length of head measured from anteriormost point of clypeus to the posteriormost point of vertexal margin in full-face view. When any of these margins are concave medially, then measurement should be taken until the point where the sagittal line meets the imaginary horizontal line touching the pronounced lateral portions of the margin, be it the anterior clypeal or the posterior vertexal margins or both (Fig. 1, G).

HW: Maximum width of the head in full-face view.

SL: Maximum length of scapes excluding bulbus and neck.

WL: Silva and Brandão (2014) measured Weber's length in *Strumigenys* as follows: "diagonal length of mesosoma in profile, from the midpoint of the anterior pronotal declivity to the posterior basal angle of the metapleuron". Here I propose a slightly different way to measure it. Instead of setting the anterior limit of the measurement in the middle of the pronotal declivity, it was set on the top of it, which corresponds to the anteriormost point of pronotum dorsum, normally delimited by a carina (Fig. 1, E). Often in *Strumigenys* the head has well developed vertexal lobes and the pronotal declivity is inserted in between them, so that a great part of the pronotal declivity is hidden in profile. Therefore, determining the midpoint of pronotal declivity in profile can be ambiguous. There is also ambiguity in setting the anterior limit of WL as I did in this work in some cases. It happens in species in which the pronotum declivity

merges gently into the pronotal dorsum and does not form a clear pronotal anterior corner or carina. I am aware that both ways of measuring WL are not free of errors but believe that our adaptation of Silva and Brandão (2014) enhances precision of the measurement. The posterior limit of the measurement at the basal angle of the metapleuron was maintained, the exact spot being marked by the base of the metapleuro-propodeal seta (discussed in Chaul and Silva, *in prep.*) which must not be confused with the often present lower lobe of the propodeal lamella.

A2L: Petiole length in profile view, measured from the basal angle of the metapleuron to the posteriormost point of petiole tergite, at the top edge of the "petiole posterior tube" (Fig. 1, E).

A3+A4L: The length of the line that goes from the edge of the transversal anterior carina of posttergite III (the anterior margin of the postpetiole disc) to the posteriormost point of the posttergite IV (the posterior margin of first gaster tergite). The spongiform tissue, occurring in several species of *Strumigenys*, often makes it difficult to define the limits of the petiole, the postpetiole, and gaster. Additionally, in ants in general the length of the gaster is a measurement that is prone to greater variation due to the conditions of the preservation of the specimen (the presclerites of the gastral segments might be exposed or retracted). Considering these two facts, measuring the gaster length in *Strumigenys* as is normally done in ants, potentially blurs existing size differences or augments insignificant differences between species due to artifacts. The measurement of A3 (postpetiole) plus A4 (first gaster segment) posttergite reduces the error while still covering most of what would be the sum of postpetiole plus gaster lengths, since the abdominal segments V, VI and VII (the last 3 gastral segments) are very small. The measure can be done in profile (Fig. 1, F) or in dorsal view (Fig. 1, D). The measurement was made both in profile and in dorsal view for 45 specimens and the differences are minute. Because the limit between A4 and A5 is often hard to visualize, it is recommendable to take the measurement in dorsal view and with a light source illuminating the ant posteriorly, and thus revealing clearly the posterior margin of A4. The correct position of the specimen to measure A3+A4L in dorsal view is when the anteriormost point of the line measured is in focus together with the posteriormost point in high magnification (40x or more). To extract this measurement from images, a profile image is more suitable (Fig. 1, F).

PrnW: Maximum pronotal width in dorsal view.

A2W: Maximum petiole width in dorsal view excluding lateral spongiform lobes if present (Fig.1, D).

A2nodeL: Maximum length of the petiole node in dorsal view, including the posterior collar if present (Fig.1, D).

A3W: Maximum width of postpetiole disc in dorsal view, excluding lateral spongiform lobes if present (Fig.1, D).

A4W: Maximum width of A4 posttergite (first gaster tergite) in dorsal view (Fig.1, D).

mtfmL: Length of metafemur, including trochanter. Positioning is correct when the base of trochanter and the apex of femur are in focus at the same time in high magnification (40x or more) (Fig.1, I).

mttbl: Length of metatibia, measured when the base and apex are in focus at the same time in high magnification (40x or more) (Fig.1, I).

mtbtL: Length of metabasitarsus, measured when the base and apex are in focus at the same time in high magnification (40x or more) (Fig.1, I).

LegL: a proxy for the length of hind leg given by the sum of mtfmL, mttbl, and mtbtL.

TL: a proxy for the total length of the body given by the sum of ML or ML2, HL, WL, A2L, and A3+A4L.

CI: Cephalic index (HW/HL x 100).

MI: Mandible index (ML/HL x 100).

SI: Scape index (SL/HW x 100).

Terminology used in the descriptions follows Bolton (2000). Names like "gaster", "postpetiole" and "petiole" were used throughout the paper, but whenever a specific structure in one of these parts were described, then the nomenclature of Keller (2011) for the metasoma was applied. Terms like the basiventral gastral pad were abandoned and are explained in Chaul and Silva (*in prep.*).

The images were made by using a Canon 1100D camera attached to a Leica S8APO stereomicroscope coupled with a 2x auxiliary objective. Images were manually taken by focusing the sharpness on different levels of the specimen and were then combined in the software Zerene Stacker to form an image with much greater depth of field than each individual image. The resulting image was treated in the software Gimp (Kimball and Mattis, 1996) for enhancing sharpness, adjust rotation and light intensity. Scales bars were added by using the software ImageJ (Schneider et

al., 2012). One body measurement taken in the in the moment the image was taken (usually head width, Weber's length or pronotal width) was used to calibrate the program and add a scale bar on that image.

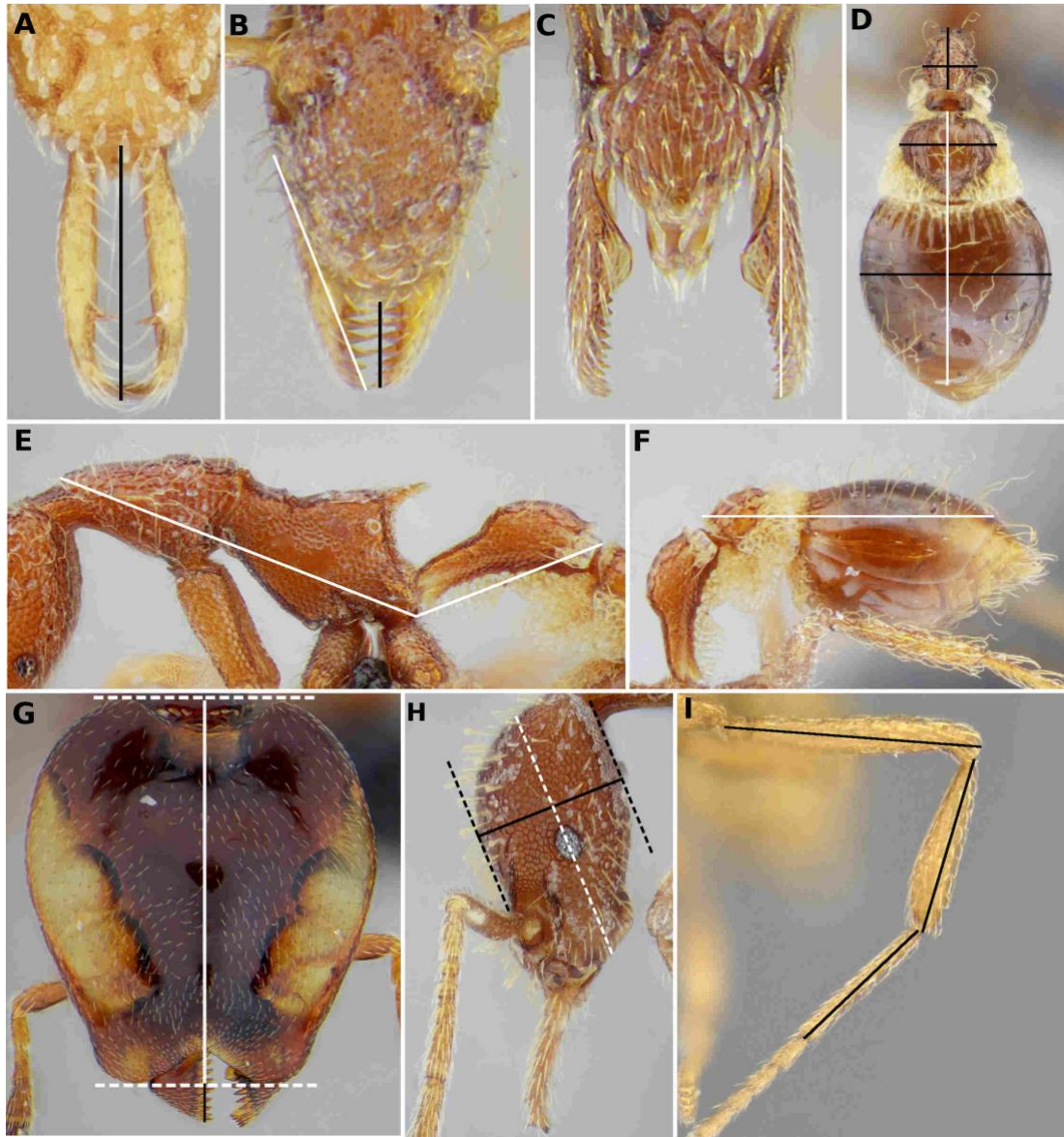


Fig. 1. Examples of how some of the body measurements were taken. A, B, C and G shows how ML (black lines) and ML2 (white lines) were taken. In D, the black lines show, from top to bottom, how A2W, A2nodeL, A3W and A4W were taken. The way A3+A4 was measured dorsally is shown by the white line in D and, in profile, by the white line in F. In E, how WL and A2L were taken. G shows how HL is taken in species with the anterior clypeal margin and the vertexal margin concave (white). ML is also indicated by the black line in G. H shows the way HD is taken. I shows how the three measurements of the hind leg, mtfm, mtb and mtbt are taken.

3. Results

All species described below possess the synapomorphies of *Strumigenys* discussed in Chaul and Silva (*in prep.*), namely the metapleural seta, the notched

ventral margin of the propodeum foramen, the anterior carina on poststernite II (or the translucent patch of the petiole), and the specialized setae anteriorly on poststernite IV. As all species described are based on rare material, therefore no specimens were dissected to confirm tergo-sternal fusion of abdominal segment III (postpetiole).

Currently, there are other taxonomic works under development either by the author or other researchers (Thiago S. R. Silva and Douglas Booher, personal communication) which will describe yet more Neotropical species of *Strumigenys*. The previous papers after the year 2000, this one, and the ones in preparation will render outdated the two identification keys to the Neotropical *Strumigenys* of Bolton (2000). I have included amendments to Bolton's keys in each described species below to ease identification, as did the previous authors, but at this point the many amendments demand that several references are used in conjunction to make a reliable identification and, so, the need for a reformulation of the keys to the Neotropical *Strumigenys* is highly needed.

3.1. Species accounts

3.1.1. *Strumigenys* ufv-20, Chaul sp. nov.

(Fig. 2)

Geographic range. North Brazil and Peru.

Type material. *Holotype worker.* PERU, Madre de Dios, Reserva Nacional Tambopata, Sachavacayoc, -12.855896 -69.361939, 19-31.vii.2012, Winkler (Feitosa, R.; Probst, R.; Camacho, G.; Chaul, J.) [MZUSP, unique specimen identifier ANTWEB1032113]. *Paratype workers.* PERU, Madre de Dios, Reserva Nacional Tambopata, Sachavacayoc, -12.855896 -69.361939, 19-31.vii.2012, Winkler (Feitosa, R.; Probst, R.; Camacho, G.; Chaul, J.) (headless worker) [UFV-LABECOL-001540, unique specimen identifier UFV-LABECOL-001540]; BRAZIL, Rondônia, Jaci-Paraná, -9.451220 -64.376030, 01-27.i.2013, Winkler, (Fernandes, I.) [INPA, ANTWEB1032003].

Diagnosis. Basal lamella triangular. Masticatory margin with 12 teeth, the basal 7 are conspicuous, the apical 5 minute. *Abundant short erect setae dorsally on head without ground pilosity contrasting to them.* Mesosoma, petiole, and postpetiole disc entirely sculptured, without smooth patches. Postpetiole disc more than twice as broad as long.

Identification. Identification of *S. ufv-20* is possible by inserting the following couplet before couplet 37 of the "Key to Neotropical *Pyramica* species" (Bolton, 2000):

A - Vertex with abundant erect setae, without ground pilosity contrasting to the stand pilosity ... **S. ufv-20**

A' - Standing pilosity, when present, tidily arranged in rows of 4 - 6 setae on vertex and contrasting with appressed ground pilosity ... **37**

Description. HW 0.39-0.395, ML 0.08, ML2 0.1, HL 0.48 - 0.515, SL 0.21, OM 18, HD 0.25 - 0.26, WL 0.51 - 0.53, A2L 0.25 - 0.26, A3+A4L 0.465 - 0.485, PrnW 0.28, A2W 0.13, A2nodeL 0.105 - 0.11, A3W 0.22, A4W 0.36, mtfL 0.33 - 0.35, mtbL 0.245 - 0.25, mtbtL 0.175 - 0.18, TL 1.815 - 1.88, LegL 0.75 - 0.78, CI 76.7 - 81.25, SI 53.16 - 53.85, LegI 41.32 - 41.49 (n=2). *Head.* Basal lamella of mandible triangular followed by a total of 12 teeth. The basal seven teeth are more developed than the apical five and can be described as follows: teeth 1 and 2 are more or less blunt, the first being more so than the latter; tooth 3 is acute and the largest on mandible; teeth 4 - 7 are subequal in size and similar to tooth 2. The apical five teeth are divided in four tiny denticles and the apical, which is slightly more developed. Dorsal surface of mandibles covered in tiny, flattened, appressed hairs. Entire cephalic capsule and dorsal surface of scapes reticulate. Clypeus projecting over base of mandibles, with freely projecting hairs on its lateral and anterior margins that vary from flattened laterally to spoon-shaped anteromedially. Other hairs on dorsum of clypeus appressed, spoon-shaped, and smaller than those on the anterior margin, with the exception of an arch of hairs delimiting the clypeus posteriorly that are somewhat more erect. Clypeus surface slightly raised in relation to the portion of the cephalic dorsum just posterior to it. Cephalic dorsum with several erect hairs, which are progressively thinner and longer posteriorly, the ones closer to posterior clypeus margin suberect and spatulate and the ones closer to the vertexal margin, erect and simple. Eyes well developed, with 18 ommatidia. Scrobe well delimited and shallowly concave. Preocular carina well developed, reaching the level of the eye. Antennae 6-segmented. Scapes flattened, with a well developed subbasal bent and with a row of freely projecting setae on its anterior margin, varying from spoon-shaped basally to thinner apically. The setae are as follows: the first one or two (proximal to the subbasal bent) are only slightly curved apically; the following four setae, (distal to the subbasal bent) are curved to the base of scape; the distalmost two or three are curved to the apex of the scape. Dorsal margins of scrobe posterior to the antennal insertions abruptly diverging. The margins having thin translucent shelf-like cuticle which are thicker at their apical third. *Mesosoma.*

Entire mesosoma with a deep reticulate-punctate sculpturing, without signs of smooth patches. Its dorsal outline in profile with two soft convexities, the anterior corresponding to the promesonotum and the posterior, to the propodeum. Several very small, scattered, simple erect hairs confined to promesonotum, which are absent on the propodeal dorsum. A humeral pair and two pairs of lateral mesonotal setae are longer than the remaining hairs in the promesonotum, however they do not stand out as very different from the others around them. Propodeal lamella with an acute spine directed mostly posteriorly and only slightly dorsally on its upper portion. Below this portion, the lamella maintains its width along most of the propodeal posterior face and does not form any clear lobe or indentation on its lower portion. Mesothoracic hairs beds not evident laterally, not forming an evident semicircular area with dense, thin, small setae within. Legs covered with suberect, slightly curved, simple to slightly remiform hairs. Femora, especially mesofemora and metafemora, robust, subcylindrical. Anteroproximal surface of procoxae with somewhat longer setae and shallowly concave. *Metasoma*. Posttergite II (dorsum of petiole) reticulate, posttergite III (dorsum of postpetiole or postpetiole disc) reticulate with sparse, faint superimposed rugulae. Node of petiole in dorsal view slightly broader than long. Postpetiole disc more than twice as broad as long. Spongiform tissue absent on poststernite II (ventral petiole) and present on posttergite II posteriorly (the posterior edge of node of petiole) as a thin, transversal spongiform lamella, thicker laterally than medially. Spongiform tissue on poststernite III (ventral postpetiole) present as two thick ventrolateral triangular outgrowths linked in the middle by a thinner spongiform line, anteriorly on posttergite III (postpetiole disc) as a very thin spongiform lamella, and posteriorly on posttergite III as a transversal lamella that is thinner medially and enlarges posterolaterally. Transversal anterior spongiform lamella on posttergite IV well-developed. Specialized setae anteriorly on poststernite IV (basigastral ventral hairs) arranged as a thin transversal band, hyphae-like. Gaster smooth and costulae anteriorly on posttergite IV (basigastral costulae) well-marked, slightly smaller than postpetiole disc length. Erect, simple hairs scattered on metasomal dorsum. Bullae formula (according to Chaul and Silva, *in prep.*): 11 00 000 100 10000 10000 10000.

Comments. *S. ufv-20* is a member of the *schulzi*-group and resembles slightly *S. cassicuspis*, *S. metrix*, *S. microthrix*, *S. stauroma*, but its pilosity separates it from any of those. The two members of the *schulzi*-group described after Bolton's revision, *S. aequinoctialis* and *S. madrigalae*, differ from *S. ufv-20* by the pilosity as well but also

for having a smooth postpetiole disc. *S. ufv-20* used to have the morphospecies code "*Strumigenys ufv-20*" on AntWeb before this publication. The species has been sampled in winkler extractors twice in localities separated by almost 700 km in the catchment of the Madeira River.

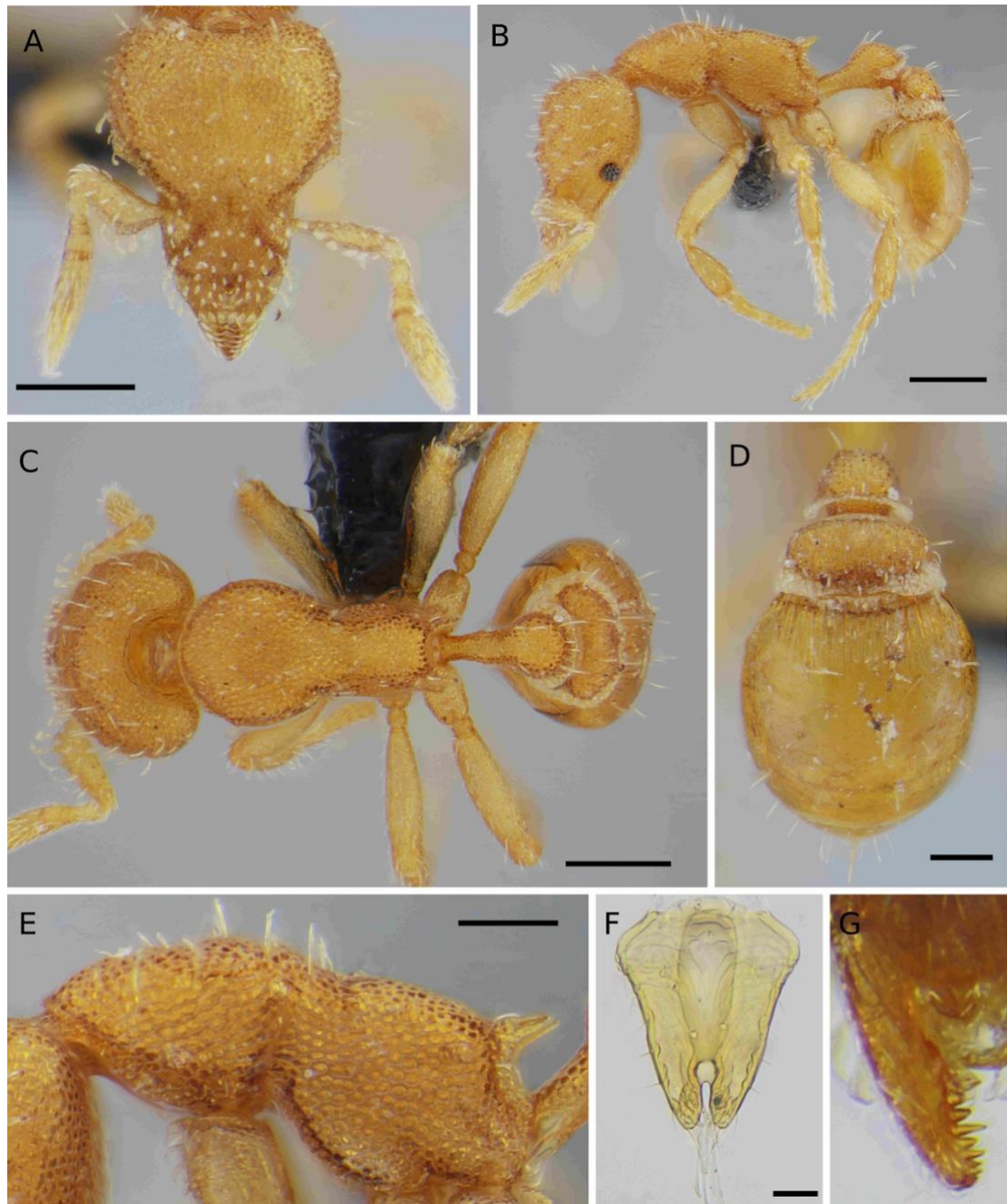


Fig. 2. *Strumigenys ufv-20*, holotype worker (ANTWEB1032697, images A - C) and paratype worker (ANTWEB1032113, images D - G). **A**, face view; **B**, profile; **C**, dorsal view; **D**, dorsum of metasoma; **E**, lateral mesosoma; **F**, labrum; **G**, ventral view of left mandible. Scale bars are 0.2 mm in A, B, C and E; 0.1 mm in D; and 0.02 in F.

3.1.2. *Strumigenys ufv-28*, *Chaul* sp. nov.

(Fig. 3)

Type material. *Holotype worker*: BRAZIL, Amazonas, BR-319, km 300, -4.994 - 61.555, 2009-10-15, winkler 1m² litter, (Baccaro, F. B.) [INPA, unique specimen identifier ANTWEB1032396].

Geographic range. North Brazil.

Diagnosis. Intercalary teeth absent. Four setae on each scrobe dorsal margin curved posteriorly. Head very broad (CI 93.6). Spongiform tissue ventrally on the petiole absent. Standing setae on dorsum of metasoma suberect, gently curved posteriorly, remiform with minute flagellate tips

Identification. *S. ufv-28* will key out as *S. perparva* in the "Key to the Neotropical-Nearctic *Strumigenys* species" (Bolton, 2000). To differentiate them in that key, the first lug of couplet 47, which says "In full-face view upper scrobe margin with a row of 4 - 5 broadly spatulate to spoon-shaped hairs that are curved posteriorly → *perparva*", should be replaced by another couplet as follows:

A - Head clearly longer than wide (CI 80 - 85.7). Humeral, mesonotal and metasoma setae flagellate ... *S. perparva*

A' - Head almost as broad as long (CI 93.6). Mesonotal and metasomal setae remiform with a thin flagellate tips that are very hard to see (often appearing only as remiform setae) ... *S. ufv-28*

Description. HW 0.44, ML 0.26, HL 0.47, SL 0.27, OM 4, HD 0.28, WL 0.48, A2L 0.22, A3+A4L 0.5, PrnW 0.24, A2W 0.105, A2nodeL 0.08, A3W 0.15, A4W 0.34, mtfL 0.365, mttbL 0.27, mtbtL 0.2, TL 1.93, LegL 0.835, CI 93.62, MI 55.32, SI 61.36, LegI 43.26 (n=1). *Head.* Mandibles elongate and linear with an apical fork. Intercalary teeth absent. One preapical pair of teeth situated proximally at the apical third of the mandibles and slightly dorsally oriented rather than completely medially oriented. Cephalic capsule broad (CI 93.6), anterior clypeal margin shallowly concave and vertexal margin deeply concave. Dorsal margin of scrobe abruptly diverging just posterior to the antennal insertion level, the largest spoon-shaped hairs arising from small indentations on the margin and curved posteriorly. Apicoscrobial pair of hairs inconspicuous, curved, only slightly flattened, and subflagellate. Anterior clypeal margin with spoon-shaped setae, except the median pair which is ribbon-like, their

basal halves medially oriented and, after an abrupt curve, their apical halves become anteriorly oriented. The remaining spoon-shaped hairs composing ground pilosity of the cephalic dorsum are reduced in size. Antennae 6-segmented. Scape flattened, subbasal bent well developed, the freely projecting hairs conspicuously long, varying from spoon-shaped to golf-club-shaped or thin, L-shaped (setae on the apical halves of both scapes appear to be abraded in the holotype). Scrobe deep, well-marked across its entire dorsal and ventral margins. Eyes small with 4 ommatidia. Postbuccal groove poorly developed. Dorsum of head shallowly reticulated. *Mesosoma*. A faint medial, longitudinal carina extending across pronotum and mesonotum. Pronotum with a well-developed anterior carina. Humeral pair absent. Mesonotal setae a pair of curved, remiform setae, with a small flagellate tip. Propodeal lamella thinner at midlength but never abruptly tapering, at its upper portion, developed into a posterodorsally oriented pointy tooth, and at its base, with a blunt lobe. Katepisternum, most of metapleuron and the anterior portion of the lateral surface of the propodeum smooth, the remaining mesosomal surface reticulate. Mesothoracic hairs beds not evident laterally, not forming an evident semicircular area with dense, thin, small setae within. In profile and dorsal views, metapleural groove is discernible. Legs covered on elongate subdecumbent flattened setae. *Metasoma*. Poststernite II without spongiform tissue. Posterior posttergite II (posterior edge of node) with a transverse spongiform carina. Spongiform carina present on posttergite III anteriorly (anterior edge of postpetiole disc) as a thin strip, much less developed than posteriorly and posterolaterally on the sclerite, where it is thicker and conspicuous (posterior and lateral edges of postpetiole disc). Poststernite III (ventral postpetiole) with well-developed spongiform lobes. Transverse spongiform carina on posttergite IV present and similar to that posteriorly on posttergite III. Specialized setae anteriorly on poststernite IV (basigastral ventral hairs) present. Costulae anteriorly on posttergite IV (basigastral costulae) slightly longer than postpetiole disc length. Dorsum of node of petiole reticulate. Dorsum of postpetiole disc smooth, at least in its medial portion. Gaster dorsally and ventrally smooth. Metasoma covered with sparse setae similar to the mesonotal pair, however all flagellate tips of the metasomal setae are looped. Bullae formula (according to Chaul and Silva, *in prep.*): 01 00 000 000 10000 10000 10000.

Comments. *S. ufv-28* is a member of the *silvestrii*-group and most similar to *S. perparva*, sharing the peculiar posteriorly curved setae on the dorsal margin of the

scrobe, the relatively long freely projecting setae on ventral margin of the scapes, the shape of the median pair of freely projecting setae on the anterior margin of the clypeus, and the lack of femoral bullae and lack of basimandibular bullae. *S. ufv-28* is, however, larger than *S. perparva*. It is, in fact, one of the larger species in the *silvestrii*-group. Also, it has very small spoon-shaped setae on the middle of the cephalic dorsum area (contrastingly smaller than the adjacent spoon-shaped hairs on scrobe dorsal margin), and has remiform setae with tiny flagellate tips on the mesonotum dorsum and dorsum of metasoma, instead of the typical long, flagellate, standing setae of *S. perparva*.

	CI	MI	SI	TL
<i>S. baccaroi</i>	93.62	55.32	61.36	1.93
<i>S. perparva</i>	80 - 85.71	51.43 - 55.13	69.56 - 81.81	1.41 - 1.71

S. ufv-28 has the broadest head (CI 93) among the *silvestrii*-group species. The CI in this group excluding *S. ufv-28* varies from 75-86 (Bolton, 2000). Additionally, it is the only species which lacks the humeral pair of standing setae, although this must be confirmed when additional specimens are discovered, given that some setae on the gaster and scapes of the unique holotype have clearly been abraded and it is therefore possible that the lack of pronotal humeral setae is an artifact.

S. ufv-28 used to have the morphospecies code "*Strumigenys ufv-28*" on AntWeb before this publication. It is known only by the holotype. There is a chance that boxes with *S. perparva* specimens in ant collections, especially if having specimens from Central Amazon, contain additional specimens of *S. ufv-28* awaiting discovery.

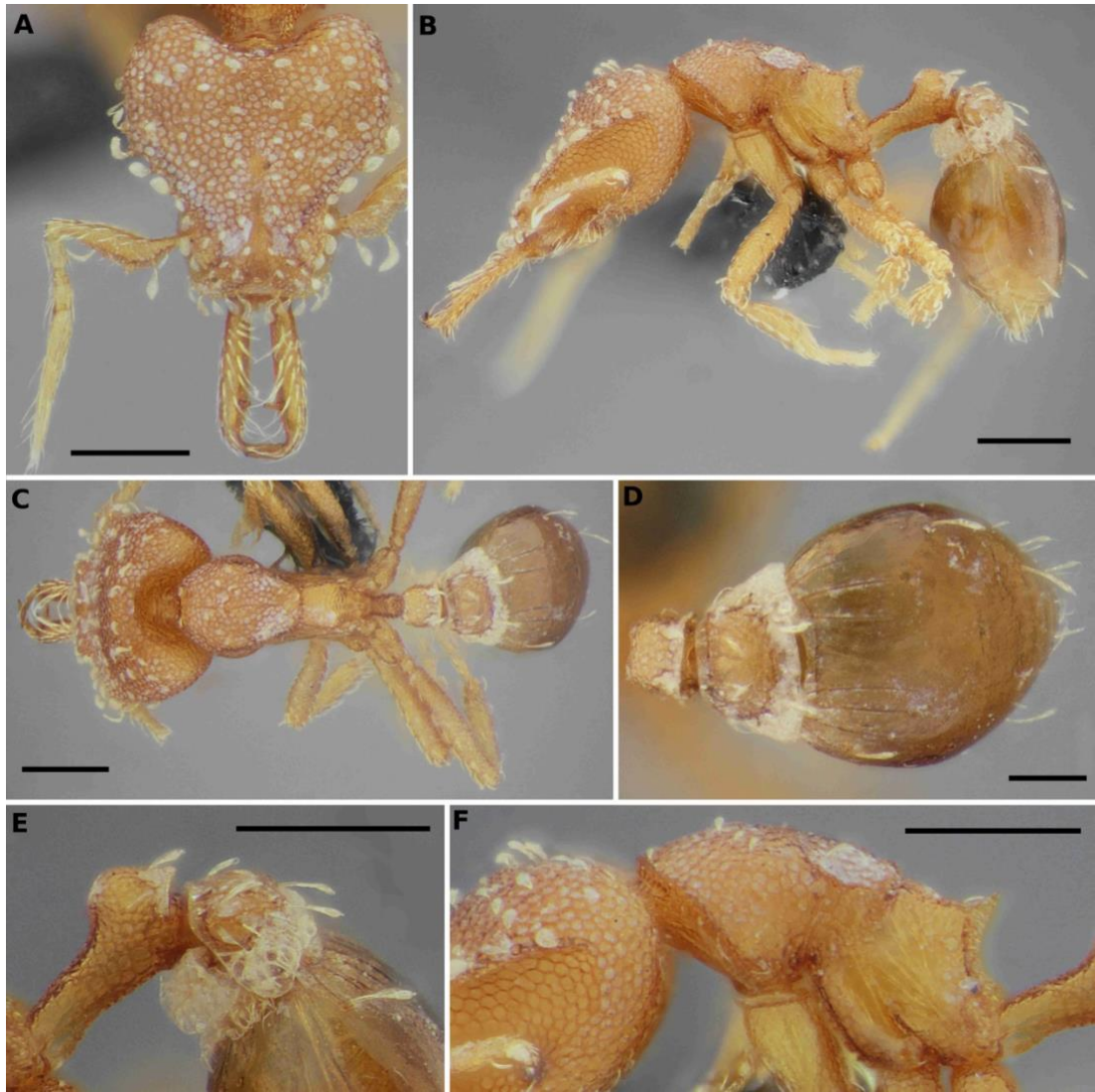


Fig. 3. *Strumigenys ufv-28*, holotype worker (ANTWEB1032396). **A**, face view; **B**, profile; **C**, dorsal; **D**, zooming of dorsum of metasoma; **E**, zooming of A2 and A3 in profile (note the looped, flagellate tips of the remiform setae); **F**, zooming of lateral mesosoma. Scale bars are 0.2 mm, except in D, where it is 0.1 mm.

3.1.3. *Strumigenys ufv-27*, Chaul sp. nov.

(Fig. 4)

Type material. BRAZIL, Amazonas, Manaus, 3 km west of Colosso camp, -2.403701 -59.894830, 2016-08-12-21, Winkler (Boudinot, B.; Fernandes, I.; Chaul, J.) [INPA, unique specimen identifier ANTWEB1032468].

Geographic range. North Brazil.

Diagnosis. Fifth antennomere (preapical) swollen. In face view, the vertexal margins forming well-defined angles (almost right angles) with the scrobes. In profile view, a conspicuous translucent semicircular fenestra on the dorsal outline of the mesosoma, in between mesonotum and dorsal margin of the propodeum.

Identification. *S. ufv-27* will key out until couplet 62 of the "Key to Neotropical *Pyramica* species" (Bolton, 2000), where the options in the couplet are *S. doryceps* and *S. browni*. To differentiate between the three species and another new one described below, *S. ufv-11* (which will also stuck in couplet 62), couplet 62 must be substituted by the following amendment:

62 - Basal lamella of mandible short and subtriangular, not visible when mandibles are fully closed ... **A**

62' - Basal lamella of mandible very long and narrow, when mandibles are fully closed, occupying more than half the exposed length of the masticatory margin ... ***S. doryceps***

A - Vertexal corners angled ... ***S. ufv-27***

A' - Vertexal corners round ... **B**

B - Eyes minute, obviously with less than 5 ommatidia. Propodeal spine a small indentation of propodeal lamella. Dorsum of metasoma covered with a combination of long, thin flagellate hairs and curved, flattened pilosity ... ***S. browni***

B' - Eyes conspicuous, obviously with more than 5 ommatidia. Propodeal spine long and sharp, much longer than propodeal lamella subtending it. Metasoma pilosity composed of irregular, subflagellate to wire-like setae ... ***S. ufv-11***

Description. HW 0.375, ML2 0.21, HL 0.55, SL 0.325, OM 3, HD 0.26, WL 0.58, A2L 0.29, A3+A4L 0.52, PrnW 0.22, A2W 0.1, A2nodeL 0.145, A3W 0.15, A4W 0.37, mtfL 0.46, mttbL 0.32, mtbtL 0.31, TL 2.15, LegL 1.09, CI 68.18, SI 86.66, LegI 50.7 (n=1). *Head.* Mandibles triangular elongate, inner margin multidentate and with well

developed basal lamella. Right mandible with 11 small, subequal, triangular teeth, followed by a series of five very small blunt teeth (four plus the apical, which is slightly more developed but still smaller than the basal series of 11). Left mandible as the right one, except for having an additional minute denticle in the basal series, totaling 12 in that series on that mandible. Basal lamellae low, trapezoidal. Mandibles covered on simple to slightly flattened appressed small hairs. Labrum body subrectangular, its body (discounting the lobes) only slight constricted at midheight. In the fully distended position of the labrum, labral lobes are tilted anteroventral. Some small simple setae originating on the labral lobes and a pair of longer sinuous to flagelliform setae with slightly flattened bases. All labral traits have been described *in situ*. Anterior clypeal margin roughly V-shaped. Ground pilosity of appressed, hyaline, spatulate hairs covering the dorsum of cephalic capsule, including dorsum of clypeus. Apicoscrobial and vertexal pair of setae flagellate. Vertexal pair arising from a slightly anterior level on the cephalic capsule than apicoscrobial pair, at about the same level as the eyes. Antennae 6-segmented. Antennomeres covered on simple to slightly flattened ground pilosity, most of them appressed, some scattered ones slightly raised. Row of distinct freely projecting setae on the ventral margin of the scapes absent. Scape subcylindrical and 5th antennomere (preapical) swollen. In face view, dorsal margins of scrobe gradually diverging posteriorly until meeting, in almost right angles, the flat vertexal margins. Vertexal margins are interrupted medially by the well-marked dorsum of the occipital carina. Scrobe has its entire perimeter well-marked, the dorsal margin forming a thin shelf-like projection and the ventral margin being carinated throughout its length, terminating (anteriorly) in a tooth-like projection. Scrobe is long, failing to reach the posterior end of the head in profile by a distance similar to scape's width. Eyes very small, with 3 ommatidia. *Mesosoma*. *Pilosity* on mesosoma composed of small, simple, decumbent ground pilosity and very long flagellate pairs of humeral and mesonotal setae. Mesosoma with a large pleural smooth patch, spanning most of mesopleura, metapleura and an anterior portion of lateral propodeum, remaining areas of mesosoma reticulate. Anterior margin of mesopleura shallowly excavated, allowing visualization in profile of the mesothoracic hairs beds. Irregular lamellate projections on midheight of anterior katepisternal margin. Anterior pronotal carina poorly marked medially, so that division between pronotal neck and pronotum dorsum is not conspicuous. Faint median longitudinal line starting at midlength of pronotal neck and spanning the entire promesonotum. Mesonotum dorsum with a pair of lateral translucent

small cuticular projections right on top of mesonotal spiracles, the "epimeral lobes". In dorsal view, mesonotum strongly tapering posteriorly and propodeum dorsum strongly tapering anteriorly, so that in dorsal view there is a thin cuticular bridge linking mesonotum to the propodeal dorsum at the metanotal groove level. In profile, the region has a translucent fenestra, appearing as a "pinched" area of the cuticle. Propodeal lamella well-developed, forming small, thin and acute, posteriorly directed teeth in its upper portion and a round lobe on its lower portion. Legs covered on decumbent spatulate setae. *Metasoma*. Petiole node elongate in dorsal view. Spongiform tissue extremely developed on poststernite II (ventral petiole) and on lateral posttergite II (sides of petiole node), the lateral outgrowths linked by a thin spongiform collar on the posterior edge of the node. Posttergite III (postpetiole disc) surrounded by spongiform tissue which is denser laterally and posterolaterally. Poststernite III (ventral postpetiole) with two dense lateral lobes. Transversal spongiform carina on anterior posttergite IV well-developed. Specialized setae anteriorly on poststernite IV (ventral basigastral hairs) well-developed, appearing in smaller magnification as a loose spongiform tissue. Basigastral costulae longer medially than laterally, medially about as long as postpetiole disc length. Dorsum of petiole node shallowly reticulate, postpetiole disc, dorsal and ventral gaster smooth. *Metasoma* covered dorsally on flagellate setae. Bullae formula (according to Chaul and Silva, *in prep.*): 10 00 111 000 00000 00000 00000.

Comments. This species is unlike any other *Strumigenys* and forcing it into any given group of species would not be more than a mere guess. *S. ufv-27* is known by the holotype alone. It used to have the morphospecies code "*Strumigenys ufv-27*" on AntWeb before this publication.

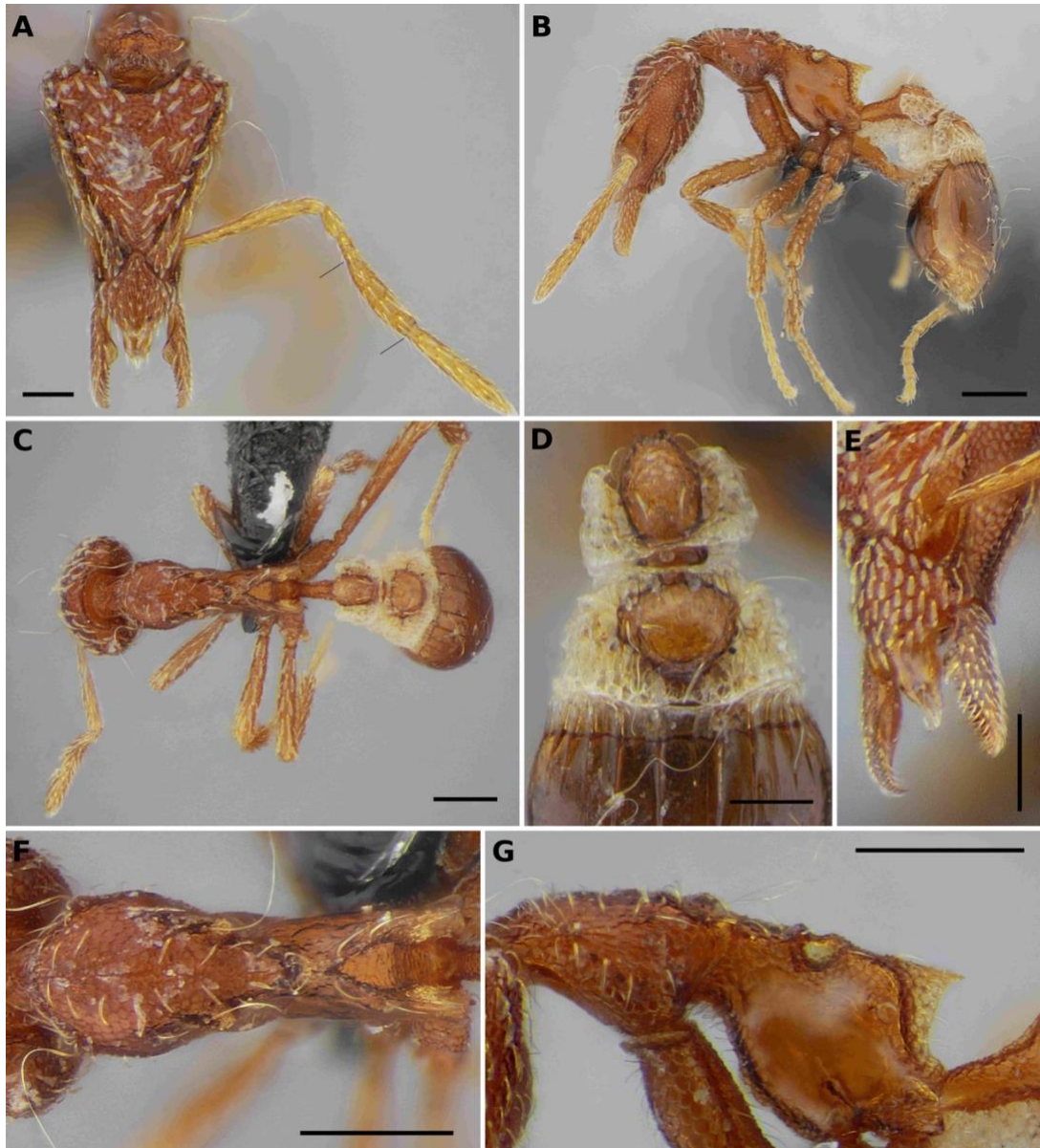


Fig. 4. *Strumigenys* ufv-27, holotype worker (ANTWEB1032697). **A**, face view, swollen 5th antennomere evidenced by the thin black oblique lines.; **B**, profile; **C**, dorsal view; **D**, dorsum of AII, AIII and anterior AIV; **E**, anteroventrolateral detail of the mandibles and labrum; **F**, dorsum of mesosoma; **G**, lateral mesosoma. Scale bars are 0.1 mm in A, D, and E and 0.2 mm in B, C, F, and G.

3.1.4. *Strumigenys ufv-11* Chaul sp. nov.

(Fig.s 5)

Type material. *Holotype worker.* BRAZIL, Minas Gerais, Viçosa, Fragmento Florestal, 1994 (Sperber, Lopes and Louzada) [MZUSP, unique specimen identifier ANTWEB1032112]. Paratype workers: BRAZIL, Minas Gerais, Viçosa, Mata do Paraíso, -20.803959 -42.855107, 2017-02-13, Berlesate (Borlini, P.) [DZUP, unique specimen identifier ANTWEB1032460]; BRAZIL, Minas Gerais, Viçosa, Mata do Paraíso, -20.803146 -42.856782, 2017-08-21-22, winkler sample (Moura, M. N.; Micolino, R.) [UFV-LABECOL, unique specimen identifier ANTWEB1032422].

Diagnosis. Very elongate body and legs. Ground pilosity composed of thin, subflagellate to flagellate hairs, standing pilosity of long, flagellate to wire-like setae. Basal lamellae of mandibles entirely covered by anterior clypeal margin in full face view when mandibles are closed. Spongiform "curtain" on poststernite II notched at about its midlength. Small smooth patch in between anepisternum and metapleuron.

Identification. The coiled hairs on the anterior margin of scapes makes ambiguous the decision if there are hairs curved to the base of the scapes in *S. ufv-11*. For that reason, the first difficulty in keying *S. ufv-11* will be deciding between the lugs in couplet 31 of "Key to Neotropical *Pyramica* species" (Bolton, 2000). Specimens that go through the the first lug of couplet 31 will then stuck at couplet 42. Those that go in in the second lug of couplet 31 will stuck at couplet 62, the couplet in which *S. browni* is contrasted to *S. doryceps* (*S. ufv-11*'s sister, see below). For the moment, a provisional suggestion would be to modify couplet 62 and add another couplet to insert *S. ufv-11* in the key. However, it seems clear that only a more radical change in the structure if the key will make smoother the keying of all specimens of *S. ufv-11* as well as many other species of *Strumigenys* described after 2000. The changes in couplet 62 for keying *S. ufv-11* have been added in the amendment presented above (see under *S. ufv-27*).

Description. HW 0.42 - 0.43, ML 0.08, ML2 0.18 - 0.21, HL 0.81 - 0.84, SL 0.39 - 0.4, OM 12, HD 0.28 - 0.31, WL 0.83 - 0.85, A2L 0.45 - 0.46, A3+A4L 0.72 - 0.8, PrnW 0.29 - 0.305, A2W 0.14 - 0.155, A2nodeL 0.2 - 0.23, A3W 0.25 - 0.27, A4W 0.5 - 0.53, mtfL 0.635 - 0.68, mttbL 0.44 - 0.47, mtbtL 0.48 - 0.52, TL 3.02 - 3.16, LegL 1.55 - 1.67, CI 51.19 - 51.85, SI 92.86 - 93.02, LegI 51.15 - 52.85 (n = 3). *Head.* Head including mandibles very elongate. In face view, mandibles very small (MI 9.7),

elongate triangular, its dorsal surfaces smooth, covered with very small, simple, appressed hairs. Outer margins of mandibles confluent with lateral clypeal margins. Basal lamellae of mandibles triangular, its basal margin slightly tilted dorsally. Masticatory margin with 12 teeth, the first one originating very close to the lower portion of basal lamella. The basal six teeth are large and acute, growing in size until tooth 3 (the largest on the mandible) and then becoming gradually smaller until tooth 6. Seventh is even smaller than 6 and can be triangular or truncated. Teeth 8 to 11 are very small and truncated and tooth 12, the apical, is slightly larger than the previous and triangular (but still smaller and less acute than the basal 7). Tips of mandibles downcurved, so that the row of small truncated teeth are best seen with the head tilted. Basal half of labrum body (excluding the apical lobes) with margins diverging and converging back and then following subparallel along the second half of the body. Lobes about a quarter the length of labrum body, converging slightly towards each other and separated by a wide notch. Each lobe with three simple setae and a longer, flattened and sinuous seta arising from their apices. Clypeus longer than wide, reticulate-punctate, its anterior margin strongly convex projecting over mandibles and covering basal lamellae of mandibles. Antennae 6-segmented. Scapes covered with appressed fine hairs and a row of freely projecting long, curved to coiled, wire-like setae on its anterior margin, most of them not obviously curved basally or apically. Apical and preapical antennomeres taken together slightly longer than scape, preapical antennomere as thick as apical. Fifth antennomere not swollen. Dorsal head reticulate-punctate with superimposed fainting rugulae, and ground pilosity composed of simple, irregularly coiled to subflagellate hairs. A pair of long, wire-like to flagellate apicoscrobial hairs. Vertexal standing setae are absent, although ground pilosity are overall longer posteriorly on the head. Dorsal margin of scrobe forming a thin translucent projection. Scrobe not conspicuously deep, its dorsal margin well-marked, apical margin (the curve where dorsal margin meets the ventral margin) and ventral margins poorly marked, the latter fading anteriorly to the eyes. Compound eyes with about 12 ommatidia, not seen in full face view. Preocular carina terminates much anterior the level of the eyes in profile view. *Mesosoma*. Mesosoma elongate. Dorsally, promesonotal suture manifested as a feeble ridge. Pronotum reticulate with superimposed fainting rugulae, mesonotum reticulate only. Metanotal impression a shallow groove, anteriorly marked by thin feeble transversal carina and with a short median longitudinal carina across it. Dorsum of propodeum, mesopleura, metapleura

and lateral propodeum reticulate, with only a small smooth patch in between mesopleuron (a small upper anepisternal portion) and metapleuron. A pair of thin triangular lamellate projections laterally on mesonotum, on top of mesothoracic spiracle, directed laterad and upwards. Humeral pair of setae long, flagellate, arising from a pair of small protrusions. Similar but slightly smaller and thinner pairs of flagellate setae are also present anterolaterally on the pronotum posterior to the humeral pair, anterolaterally on the mesonotum, and mediolaterally on the mesonotum (arising from the tip of the mesonotal lamellate projections). Ground pilosity on dorsum of mesosoma as on the head. Mesothoracic hair beds poorly developed. Ground pilosity dorsally on mesosoma composed of thin, long subflagellate hairs. Propodeal teeth sharp and long, in profile directed posteriorly and slightly dorsally, subtended by a thin propodeal lamella which descends with regular width until the level of the bulla, where it forms a very small round lobe. Very long legs, reticulate, covered on hairs similar to mesosomal ground pilosity. All pairs of legs with tiny rounded to oval, distally placed bullae on the femora, hind femora having the largest and middle femora, the smallest. Slit-shaped well developed distally placed bullae on hind and middle tibia, and tiny and oval bullae distally on protibiae. *Metasoma*. Petiole elongate, evenly and gently curved in profile view. The anterior face of node gradually ascending from peduncle and merging into dorsal face, making anterior and dorsal faces of node not obviously distinguishable. Node longer than high. Postpetiole disc with longitudinal rugae which are well-marked laterally and shallow to fainting medially. Spongiform tissue on poststernite II strongly developed as a thin and tall curtain, notched at about its midlength. Posttergite II posteriorly (posterior edge of node of petiole) with a thin strip of spongiform tissue connecting two pyramidal spongiform posterolateral lobes. Spongiform tissue well developed on poststernite III (ventral postpetiole), with two large and dense lateral outgrowths linked in the middle by a thinner strip. On posttergite III (postpetiole disc), a thin, transversal, spongiform anterior lamella and well-developed spongiform lobes posterolaterally which gradually becomes thinner where they are linked posteriorly. Spongiform transverse lamella anteriorly on posttergite IV well-developed. Specialized setae anteriorly on poststernite IV (basigastral ventral hairs) reduced. Dorsum of metasoma covered on long, irregular, flagellate hairs. Gaster smooth and shiny. Thin, curved, and simple pilosity on gastral sternites as well as dorsally around the sting. Basigastral costulae

well-marked but small, about half the length of postpetiole disc. Bullae formula (according to Chaul and Silva, *in prep.*): 01 00 111 111 10000 11000 11100.

Comments. *S. ufv-11* is most similar to the Ecuadorian *S. doryceps* and the Central and North American *S. probatrix*, both constituting the *probatrix*-group. However, *S. ufv-11* differs from both by having a short, triangular rather than a long, subrectangular basal lamellae, which is an important trait defining the *probatrix*-group. The shape of the basal lamellae of the *hyphata*-group, as well as overall habitus, match that of *S. ufv-11* to a degree that a relation with this group can't be discarded. Still, the labrum in the *hyphata*-group is very typical (the main body having a constriction at midlength) and does not resemble that of *S. ufv-11*. For the moment, *S. ufv-11*, especially due to its great resemblance to *S. doryceps*, is considered a member of the *probatrix*-group. Two interesting similarities between *S. ufv-11* and *S. doryceps* are the well-developed and medially notched spongiform curtain on poststernite II and the short but well-marked basigastral costulae.

S. ufv-11 can be easily separated from *S. doryceps* by having the outer margins of the mandibles confluent with clypeus instead of bulging basally before meeting the clypeal lateral margin; by the small smooth patch on sides of mesosoma as opposed to a large smooth patch; and by the basal lamellae of mandibles not visible in full face view. *S. ufv-11* can be easily separated from *S. probatrix*, the other member of the group, by the freely projecting setae on anterior clypeal margin which are not tidily arranged and spatulated as in the latter, by the shape of the basal lamella, by the dense and abundant spongiform tissue on ventral petiole, and by its ferruginous brown color instead of dark brown. Regarding the members of the *hyphata*-group, *S. ufv-11* can be easily differentiated from *S. cincinnata* by its much larger size and from *S. hyphata* by the clypeal pilosity, among other traits.

Despite intense sampling effort in the type locality, the species has been sampled only once in a pitfall trap and twice in winkler extractors, each of these sampling events yielding a single worker. Although nothing is known about its biology, its long body and legs suggest it forages on the upper stratum of the litter or maybe on rotten logs or cavities inside them, but not amidst the deeper and denser litter or in the soil.

S. ufv-11 used to have the morphospecies code "*Strumigenys ufv-11*" on AntWeb before this publication.

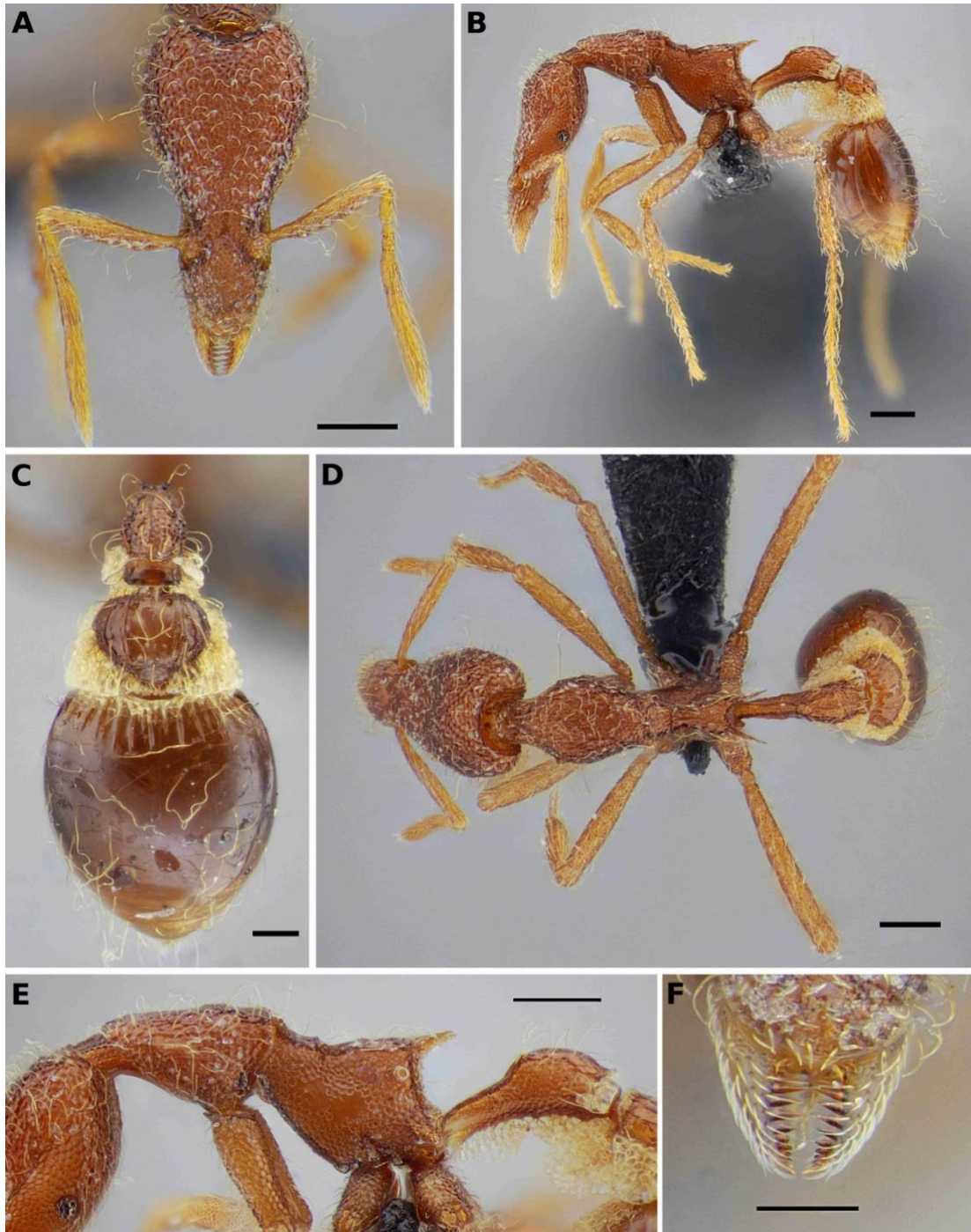


Fig. 5. *Strumigenys ufv-11*, paratype worker (ANTWEB1032460). **A**, face view; **B**, profile; **C**, dorsum of metasoma; **D**, dorsal view; **E**, lateral mesosoma; **F**, anteroventral detail of the mandibles. Scale bars are 0.2 mm in A, B, D and E and 0.1 mm in C and F.

3.1.5. *Strumigenys* ufv-64, Chaul sp. nov.

(Fig.s 6)

Type material. *Holotype worker.* BRAZIL, Amazonas, Manaus, 3 km W of Colosso Camp, -2.404892 -59.893775, 12-21.viii.2016, Winkler (Boudinot, B.; Fernandes, I.; Chaul, J.) [INPA, unique specimen identifier ANTWEB1032465].

Geographic range. North Brazil.

Diagnosis. Well-developed propleural glands. Bullae on femora very large and located close to midlength on each leg. Mandibles short and with outer margins converging from base to apex. Abundant erect to suberect remiform setae on dorsum of head, mesosoma and metasoma.

Identification. *S. ufv-64* keys out until couplet 22 of the "Key to the Neotropical-Nearctic *Strumigenys* species" (Bolton, 2000). In the couplet, it does not match well neither lugs, in spite of agreeing more with the lug ending in *S. borgmeieri*. The couplet 22 should be modified and an additional couplet must be added to include *S. ufv-64* as follows:

22 - Mandibles relatively short, $MI < 75$. In full-face view outer margins of mandibles approximately parallel or slightly converging at full closure ... **A**

- Mandibles relatively long, $MI > 85$. In full-face view outer margins of mandibles diverge anteriorly at full closure ... **24**

A - Propleural glands absent. With the exception of specialized standing setae (vertexal, humeral), the remaining pilosity on dorsum of head, mesosoma, and metasoma appressed and spatulate. First gaster tergite might have a combination of appressed small spatulate hairs and larger suberect short stout clavate hairs. Proximal and distal preapical teeth subequal in length. Postpetiole disc in profile dome-shaped ...

S. borgmeieri

A' - Propleural pair of glands well-developed. Abundant erect to suberect remiform setae on dorsum of head, mesosoma, and metasoma. Proximal and distal preapical teeth with clearly different lengths, the former having about half the length of the latter. Postpetiole disc posteriorly inclined, its anterior face much longer than posterior face ... ***S. ufv-64***

Description. HW 0.48, ML 0.33, HL 0.7, SL 0.48, OM 20, HD 0.44, WL 0.73, A2L 0.37, A3+A4L 0.75, PrnW 0.34, A2W 0.16, A2nodeL 0.14, A3W 0.2, A4W 0.55, mtrL 0.68, mttbL 0.47, mtbtL 0.44, TL 2.88, LegL 1.59, CI 68.57, MI 47.14, SI 1, LegI 55.21. Mandibles elongate, relatively small (MI 47.14), with two pairs of preapical teeth and an apical fork. Their outer margins slightly converging from base to apex. Apical fork with one intercalary tooth and apicoventral tooth longer than apicodorsal. In profile view, mandibles are not coplanar with head coronal plane, instead, they are inclined anterodorsally. Mandibles covered with conspicuous slightly flattened, thin, subdecumbent hairs. A concavity present basally on the lateral (outer) surface of the mandible. Anterior clypeal margin shallowly convex. Head gradually broadening posteriorly. Vertexal lobes well-developed. Dorsum of scapes and cephalic capsule reticulate, dorsum of head with superimposed rugae. Scrobes virtually absent, the lateral surfaces of the head not concave neither delimited by carina, except for a small extension of the frontal lobes that fades at the level of the eye, representing a remnant of the dorsal margin of the scrobe. Preocular carina tall and sharp, but small. Eyes large, with 20 ommatidia. Postbuccal groove shallow. Simple, small, anteromedially directed, decumbent hairs on ventral head surface. Dorsum of head and clypeus covered on abundant, suberect, remiform setae which gradually increases in size from clypeus to vertex. The individual seta is composed of a basal stalk and an expanded apex with frayed tips. Antennae 6-segmented. Antennae covered on setae similar to that of the mandibles, except the anterior scape margins which have a distinct row of freely projecting, apically curved setae slightly thicker than the surrounding hairs.

Mesosoma. Outline of the dorsum of mesosoma with two convexities, the promesonotum and the propodeum, well divided by a shallow but distinct metanotal groove. Propodeum dorsal margin in profile sloping down until meeting the propodeal lamella. Propodeal lamella with an upper and a lower indentation, both somewhat fusing to each other medially in the lamella, making the entire propodeal lamella M-shaped in profile. The lamella terminates at midlength of the metapleural gland bulla. Mesosoma reticulate, except for smooth patches covering most of katepisternum. Dorsum of pronotum with superimposed irregular striae. Propleural glands present as a pair of large spongiform, semi-elliptical patches, each with a wide, smooth groove originating on their anterior margins (on "top" of them) and anteriorly directed. Pilosity on dorsum of mesosoma (promesonotum and posterolaterally on propodeum as well) as on dorsum of head, but slightly longer on promesonotum. Pronotal and mesonotal

pairs of standing setae, although present, remain inconspicuous among the abundant standing pilosity which has the same shape as them. Legs covered on abundant hairs similar but slightly longer than those of the mandibles. Bullae on femora extremely developed, the profemoral the longer pair. They are elliptical, situated at about midlength of dorsum of each femora. *Metasoma*. Pilosity on metasoma as on dorsum of head and mesosoma, but slightly longer. Petiole and postpetiole mostly reticulate, gaster smooth. Postpetiole disc in profile view posteriorly inclined, forming an anterior face which is longer than the posterior face. Dorsum of petiole node reticulate but with a posterior portion just anterior to transversal collar of spongiform tissue where reticulation fades. Postpetiole disc with weak reticulation on the anterior face and reduced sculpturing on the posterior face. Basigastral costulae about as long as postpetiole length. Spongiform tissue relatively small on sclerites and "foliaceous". On poststernite II (ventral petiole) present as a very thin strip. On posttergite II (petiole node) more developed posteriorly and posterolaterally and inclined dorsally. Present around posttergite III (postpetiole disc), the anterior transversal outgrowth connected to the posterolateral outgrowth. Present on poststernite III as well-developed lateral lobes connected by the middle. On posttergite IV (first gaster tergite) as a transversal outgrowth as thin as that of anterior postpetiole. Specialized setae anteriorly on poststernite IV (basigastral ventral hairs) inconspicuous, poorly developed. Bullae formula (according to Chaul and Silva, *in prep.*): 11 10 111 111 11000 11110 11110.

Comments. The propleural glands (Fig 6, G), which are described in detail in Chaul and Silva (*in prep.*), are present in the majority of species of the *mandibularis*-group (15 out of the 19 described species of the group). *S. borgmeieri* is an odd species in the *mandibularis*-group due to its pilosity and mandibles and is also the only one without propleural glands among the ones examined by us. The absence of that structure in *S. borgmeieri* was initially thought to be another trait pushing it away from the *mandibularis*-group. The discovery of *S. ufv-64*, clearly a sister of *S. borgmeieri*, with well-developed propleural glands present (even though quite different in detail from the more typical propleural glands seen in the group), implies that *S. borgmeieri* is indeed within the *mandibularis*-group and have secondarily lost the glands. The grooves anterior to the glands in *S. souzai* suggest a channeling system of secretions produced within the propleural spongiform patches.

With the exception of *S. ufv-64*, the propleural glands of each species in the *mandibularis*-group have similar structure, composed of conspicuous cavities covered on spongiform tissue with a slit-shaped longitudinal opening close to the inner edge of the spongiform tissue. The differences in morphology between the propleural glands of *S. ufv-64* (see description above) and the remaining species in the *mandibularis*-group are significant, but still smaller than that seen between the *mandibularis*-group members and other species of *Strumigenys* outside it which possess the structure (e. g. *S. perissognatha*, *S. goddefroyi*, *S. precava*).

S. ufv-64 and *S. borgmeiri* share the following traits:

Subparallel (*S. borgmeieri*) or slightly converging (*S. ufv-64*) mandibles when fully closed instead of diverging apically as is the case in the other species in the *mandibularis*-group;

Preapical teeth very close to each other and much less developed than in the remaining of the species in the *mandibularis*-group.

Pilosity strikingly distinct from the remaining species in the *mandibularis*-group, even though also differing to a lesser degree between both species (see Identification above and comments about variation of pilosity in *S. borgmeieri* below).

Although the mandibles of *S. ufv-64* are atypical for a trap-jaw species (converging from base to apex instead of being subparallel or divergent from base to apex), the basilateral concavities support the hypothesis that *S. ufv-64* is a trap-jaw just as the other members of its group.

S. ufv-64 used to have the morphospecies code "*Strumigenys ufv-64*" on AntWeb before this publication.

Variation in pilosity in *S. borgmeiri* must be considered in further studies of the *mandibularis*-group. Specimens of *S. borgmeiri* from Pará State of Brazil (ANTWEB1032494) as well as from Sergipe State of Brazil have the first gaster tergite covered only on decumbent small spatulate setae, while the specimen from Costa Rica (INBIOCRI001283734) has suberect clavate hairs on it.



Fig. 6. *Strumigenys* ufv-64, holotype worker (ANTWEB1032465). **A**, face view; **B**, profile; **C**, dorsal; **D**, dorsum of anterior metasoma; **E**, lateral head; **F**, lateral mesosoma; **G**, Propleural glands. Scale bars are 0.2 mm in A, B, C, E and F and 0.1 mm in D and G.

3.1.6. *Strumigenys ufv-26*, Chaul sp. nov.

(Fig.s 7)

Type material. BRAZIL, Minas Gerais, Serra do Cipó, Próx. Cachoeira da Capivara, entrada p/ estátua “Juquinha”, -19.252962 -43.551720, 13.v.2016, Epigaeic + hypogaeic winkler, (Chaul, J; Epifânio, S.) [MZUSP, unique specimen identifier ANTWEB1032697].

Geographic range. Southeast Brazil

Diagnosis. Intercalary teeth absent. One preapical tooth only, without a sign of additional teeth or denticles on the inner margin of mandibles. Eyes very reduced. Metasoma with various thin, flagellate setae originating amid the recurved, flattened ground pilosity.

Identification. *S. ufv-26* keys out smoothly until couplet 9 in the "Key to the Neotropical-Nearctic *Strumigenys* species" (Bolton, 2000). In the couplet, it does not match well the lugs, in spite of fitting better the lug which terminates in *S. longispinosa*, a radically different species. *S. ufv-26* can be inserted in the key by adding the following couplet in between couplet 7 and 9 in the key:

A - Eyes conspicuous, more than 10 ommatidia ... **go to couplet 9**

A' - Eyes minute, much less than 10 ommatidia ... ***S. ufv-26***

Description. HW 0.38, ML 0.24, HL 0.46, SL 0.31, OM 4, HD 0.27, WL 0.485, A2L 0.25, A3+A4L 0.52, PrnW 0.25, A2W 0.13, A2nodeL 0.07, A3W 0.185, A4W 0.385, mtfL 0.35, mttbL 0.23, mtbtL 0.195, TL 1.955, LegL 0.775, CI 82.61, MI 52.17, SI 81.58, LegI 39.64 (n=1). *Head.* Mandibles linear with one pair of preapical teeth and with an apical fork without intercalary teeth. Anterior margin of clypeus shallowly convex with freely projecting hairs that are medially curved, spoon-shaped, except for the median pair which is sinuous ribbon-like or spatulate. Cephalic capsule entirely reticulate, its dorsum covered on spoon shaped setae. A pair of thin, subflagellate vertexal setae positioned very posteriorly on vertex (right seta has been abraded). Apicoscrobial pair similar to vertexal, it too oddly posteriorly positioned, slightly past the posterior end of the scrobe, the scrobe's curve. Scrobe poorly marked and shallow. Eyes minute, with 4 ommatidia. Preocular carina almost reaching the level of the eye. Postbuccal groove very shallow. Scapes subcylindrical, with all freely projecting setae on its anterior margin curved apically and not much distinct from other setae on

dorsum of scapes; funiculus with minute appressed pubescence. *Mesosoma*. Reticulate, except for a smooth patch spanning katepisternum, metapleura and a small portion of the lateral surfaces of the propodeum. Ground pilosity on promesonotum dorsum composed of slightly raised spoon-shaped hairs. Very thin flagellate humeral and mesonotal pair of standing setae, the humeral pair longer than the mesonotal. Propodeal lamella thin, with a small spine on its upper portion and a larger, truncated lobe below its midlength, the tip of this lobe is at about the level of the uppermost point of the bullae; propodeal lamella abruptly ending below the lower lobe. Legs reticulate punctate, covered on thin, spatulate, subdecumbent, small hairs. *Metasoma*. Petiole entirely reticulate, postpetiole disc smooth, and gaster smooth, except for basigastral costulae which is thin and, at least medially, longer than postpetiole disc. Dorsum of petiole and postpetiole covered with elongate spoon-shaped hairs as on mesosoma; on dorsum of gaster these hairs are more elongate, curved, and grass-like. Among them several thin flagellate setae originate. Similar scattered flagellate setae also present ventrally on gaster. Spongiform tissue on poststernite II absent. Collar of lamellate spongiform tissue posteriorly and posterolaterally on posttergite II (posterior edge of node of petiole) slightly dorsally raised. Thin lamellate spongiform tissue anteriorly on posttergite III (the anterior edge of postpetiole disc). A pair of very well-developed posterolateral spongiform lobes on posttergite III (the posterior edge of postpetiole disc), both linked posteriorly by a thin collar of spongiform tissue. Poststernite III (ventral postpetiole) with a dense spongiform transversal curtain. Anterior edge of posttergite IV (the first gaster tergite) with a transversal, shelf-like, spongiform lamella. Specialized setae anteriorly on poststernite IV (basigastral ventral hairs) dense and conspicuous. Bullae formula (according to Chaul and Silva, *in prep.*): 11 00 111 000 10000 00000 00000.

Comments. During the examination of the unique holotype the specimen was damaged and has lost one hind leg and had its gaster separated from the body. The gaster is mounted beneath the remaining of the body and has had some of its pilosity abraded. All images were taken before the incident.

S. ufv-26 is a member of the *silvestrii*-group. Among the species in that group, it is most similar to *S. epelys* for having a very similar ground pilosity, specially on the gaster, which is not found in another species in the group. *S. ufv-26* can be differentiated from *S. epelys* by the presence of flagellate setae on the head, mesosoma

and metasoma (entirely absent in *S. epelys*), by the freely projecting setae on the anterior margin of the scapes which are all curved apically (some curved basally in *S. epelys*), and by the absence of minute denticles in addition to the preapical teeth on the inner margin of mandibles (present proximal to midlength in *S. epelys*). Furthermore, *S. ufv-26* is slightly larger than *S. epelys* and they possibly have small differences of body proportions, however more specimens of both species must be measured to ascertain that.

	CI	MI	SI	TL	Leg L
<i>S. thiagoi</i>	82.61	52.17	81.58	1.96	0.78
<i>S. epelys</i>	76.2 - 80.1	47.1 - 50	93.75	1.67 - 1.72	0.69

S. ufv-26 used to have the morphospecies code "*Strumigenys ufv-26*" on AntWeb before this publication. The species was sampled within a vegetation type called Capões de Mata, which are a series of small, offset, Atlantic Forest fragments immersed within grasslands matrices in high altitudes of the Cerrado, the Brazilian savanna (Coelho et al., 2018). In a single sampling event in one those fragments, two new species of *Strumigenys* have been sampled, *S. ufv-26* and one to be described in the revision of the *louisianae*-group (Chaul, *in prep.*). Those fragments, which might harbor yet more new species with close relatives living elsewhere, as is the case of the pair *S. ufv-26* and *S. epelys*, might represents an interesting opportunity to understand speciation.



Fig. 7. *Strumigenys ufv-26*, holotype worker (ANTWEB1032697). **A**, face view; **B**, profile; **C**, dorsal view; **D**, dorsum of AII, AIII and anterior AIV; **E**, lateral mesosoma; **F**, lateral metasoma. Scale bars are 0.2 mm in all images, except in D where it is 0.1 mm.

References

- Baroni Urbani, C.; De Andrade, M. L. The ant tribe Dacetini: limits and constituent genera, with descriptions of new species. *Annali del Museo Civico di Storia Naturale Giacomo Doria (Genova)*, 99: 1–191, 2007.
- Bickford, D. et al., Cryptic species as a window on diversity and conservation. *Trends in Ecology and Evolution*, 22(3): 148–155, 2007.
- Bolton, B. The Afrotropical dacetine ants (Formicidae). *Bulletin of the British Museum (Natural History). Entomology*, 46: 267–416, 1983.
- Bolton, B. The ant tribe Dacetini. *Memoirs of the American Entomological Institute*, 65: 1–1028, 2000.

- Bolton, B. An online catalog of the ants of the world. Available from <http://antcat.org>. Accessed -- February 20-- 2018.
- Coelho, M. S. et al., Forest archipelagos: A natural model of metacommunity under the threat of fire. *Flora: Morphology, Distribution, Functional Ecology of Plants*, 238: 244–249, 2018.
- Kimball, S.; Mattis, P. GIMP. The GNU Image Manipulation Program, 1996.
- Lattke, J. E.; Aguirre, N. Two new *Strumigenys* F. Smith (Hymenoptera: Formicidae: Myrmicinae) from montane forests of Ecuador. *Sociobiology*, 62(2): 175–180, 2015.
- Longino, J. New species and nomenclatural changes for the Costa Rican ant fauna (Hymenoptera: Formicidae). *Myrmecologische Nachrichten*, 8: 131–143, 2006.
- Rigato, F.; Scupola, A. Two new species of the *Pyramica gundlachi*-group from Ecuador (Hymenoptera Formicidae). *Biodivers. South America*, I. Mem. Biodiver., 1: 477–481, 2008.
- Schneider, C.; Rasband, W.; Eliceiri, K. ImageJ. *Nature methods*, 9(7): 671–675, 2012.
- Silva, T. S. R.; Brandão, C. R. F. Further Ergatoid Gyne Records in the Ant Tribe Dacetini (Formicidae: Myrmicinae). *Neotropical Entomology*, 43(2): 161–171, 2014.
- Sosa-Calvo, J.; Schultz, T. R.; Lapolla, J. S. A Review of the Dacetine Ants of Guyana (Formicidae: Myrmicinae). *Journal of Hymenoptera Research*, 19(1): 12–43, 2010.
- Sosa-Calvo, J.; Shattuck, S. O.; Schultz, T. R. Dacetine ants of Panama: new records and description of a new species (Hymenoptera: Formicidae: Myrmicinae: Dacetini). *Proc. Entomol. Soc. Washington*, 108(4): 814–821, 2006.

V. CONCLUSÕES GERAIS

Os resultados dos capítulos desta dissertação trataram da Taxonomia Alfa de parte do gênero *Strumigenys* (Myrmicinae: Attini) e da reinterpretação morfológica do clado-SPB (*Strumigenys* + phalacromyrmecíneas + basicerotíneas) de formigas Attini (Formicidae: Myrmicinae) à luz de recentes resultados moleculares. A diversidade do gênero *Strumigenys* foi incrementada na região Neotropical pela descrição de seis novas espécies raras. Já a reinterpretação morfológica do clado-SPB, tentou determinar sinapomorfias para os nós do clado-SPB. Uma série de possíveis sinapomorfias são listadas para o clado-SPB como um todo, bem como para suas subdivisões internas que são: as basicerotíneas isoladamente, para o clado *Strumigenys*-phalacromyrmecíneas, as phalacromyrmecíneas isoladamente, ou *Strumigenys* isoladamente. Os caracteres morfológicos estudados foram extraídos da literatura, principalmente das várias contribuições de Baroni Urbani & De Andrade e de Bolton. Para *Strumigenys*, além da reinterpretação de caracteres da literatura, cinco novas sinapomorfias do gênero são pela primeira vez descritas. A reinterpretação morfológica dos clados recuperados pelas recentes técnicas moleculares é apenas ocasionalmente realizada, sendo que no presente momento a acumulação de informação filogenética ocorre sem uma caracterização morfológica adequada das novas linhagens propostas, mesmo em casos onde existem abundantes dados morfológicos disponíveis na literatura. O presente trabalho é uma contribuição no sentido de diminuir este descompasso entre produção de dados moleculares e reinterpretação morfológica das linhagens, com enfoque no clado-SPB. Futuros trabalhos no clado-SPB necessitam, principalmente, diagnosticar clados menores dos que foram aqui tratados, especialmente aqueles em que há evolução independente de formas similares (e. g. mandíbulas alongadas em sub-divisões do gênero *Strumigenys* e em linhagens de *Octostruma* e *Rhopalothrix*).