



Studies in Mexican Grasshoppers: *Liladownsia fraile*, a new genus and species of Dactylotini (Acrididae: Melanoplinae) and an updated molecular phylogeny of Melanoplinae

DEREK A. WOLLER^{1,3,4}, PAOLO FONTANA^{2,4}, RICARDO MARIÑO-PÉREZ^{1,4} & HOJUN SONG¹

¹Department of Biology, University of Central Florida, 4000 Central Florida Blvd., Orlando, FL 32816-2368, U.S.A.

²Fondazione Edmund Mach - Centro Trasferimento Tecnologico – Protezione delle piante e biodiversità agroforestale, Via della Val, 2 - Loc. Costa di Casalino, I-38057 Pergine Valsugana, Italy

³Corresponding author. E-mail: asilid@gmail.com

⁴These authors participated equally

Abstract

Liladownsia fraile **gen. nov. sp. nov.** Fontana, Mariño-Pérez, Woller & Song (Lila Downs' friar grasshopper) of the tribe Dactylotini (Orthoptera: Acrididae: Melanoplinae) is described from the pine-oak forest of the Sierra Madre del Sur Mountain Range in Oaxaca, Mexico. Taxonomic placement of this new genus is justified based on morphological characters as well as a molecular phylogeny. Information about the probable host plant, phenology, and known localities is also presented. We also present an updated molecular phylogeny of Melanoplinae, which includes representatives of five of the seven recognized tribes. The monophyly of the subfamily and the included tribes is tested and we find Dactylotini to be paraphyletic because of the placement of *Hesperotettix* Scudder, 1876. We also recover strong close relationships between the new genus and *Perixerus* Gerstaecker, 1873 and *Dactylotum* Charpentier, 1845.

Key words: Melanoplinae, Dactylotini, *Perixerus*, Oaxaca, *Salvia elegans*, aposematic

Introduction

The tribe Dactylotini is one of seven tribes into which the subfamily Melanoplinae is currently divided (Eades *et al.* 2013) and is presently composed of ten genera and 36 species with a distribution across the U.S.A. and Mexico. The first mention of the tribe, as Dactyloti, was by Scudder (1897), but Rehn and Randell (1963) were the first to formally describe Dactylotini. They included 12 genera as typical members of the tribe: *Aztecacris* Roberts, 1947, *Campylacantha* Scudder, 1897, *Chibchacris* Hebard, 1923, *Dactylotum* Charpentier, 1845, *Dasyscirtus* Bruner, 1908, *Dichroplus* Stål, 1873, *Hesperotettix* Scudder, 1876, *Oedomerus* Bruner, 1907, *Paraidemona* Brunner von Wattenwyl, 1893, *Paratyloptropidia* Brunner von Wattenwyl, 1893, *Poecilotettix* Scudder, 1897, and *Perixerus* Gerstaecker, 1873, plus two atypical genera: *Gymnoscirtetes* Scudder, 1897 and *Meridacris* Roberts, 1937.

Of these original 14 genera, *Oedomerus* was transferred to the Conalcaeini tribe by Cohn and Cantrall (1974) and *Chibchacris*, *Dichroplus*, and *Meridacris* were transferred to Dichropli by Amédégnato (1977), leaving Dactyloini with its now-ten members. All the species in the tribe were described between 1843 and 1943 except for four species of the genus *Paraidemona* that were described recently: 1) *P. nuttingi* and 2) *P. olsoni* by Yin and Smith (1989) from Texas, USA and 3) *P. cohni* by Fontana and Buzzetti (2007) and 4) *P. ruvalcaba* by Buzzetti *et al.* (2010), both from Mexico.

Scudder (1897) employed the following characteristics to separate the members of Dactylotini from other tribes: hind tibiae with 6–8 spines only on the exterior margin, but lacking an apical spine on the outer side, face nearly vertical, fastigium of vertex not prolonged, apically obtuse, mesosternal lobes transverse or equally long and broad with the inner margin usually rounded. However, it should be noted, that due to the specific focus of his work, Scudder (1897) was relying chiefly upon his descriptions of only *Dactylotum*, but mentioned that he was also aware that Dactylotini was mainly a Central American group comprised of only two or three genera. Later, Roberts

divided into two major clades, one solely consisting of the South American endemic Dichroplini and the other consisting of the Eurasian Podismini, the North American Dactyloptini, and the North American Melanoplinae. Based on the biogeographic distribution of the tribes, we hypothesize that Melanoplinae originated in South America, progressively diversified northward to Central and North America with one clade eventually colonizing Eurasia. This pattern is consistent with the “out-of-South America” hypothesis, put forth by both Amédégno *et al.* (2003) and Chapco (2006).

The monophyly of Dichroplini was supported by Chapco (2006), but Chintauan-Marquier *et al.* (2011) found the tribe to be paraphyletic because *Neopedies* did not group with other dichropline species. Our phylogeny is congruent with Chapco (2006) and finds Dichroplini to be monophyletic. According to OSF (Eades *et al.*, 2014), *Apacris*, *Neopedies*, and *Pseudoscopus* are currently unplaced, although the latter two were assigned to Dichroplini by Ronderos (1991). Chapco (2006) found *Apacris* was closely related to other valid dichropline species. Our study finds that all three genera are found near the base of the clade forming Dichroplini, supporting the notion that they probably need to be assigned to Dichroplini. Mayer (2004) erected a new tribe called Prumnini purely based on nomenclatural grounds, but the nominal genus of the tribe, *Prumna*, is placed robustly within Podismini in our phylogeny, which provides no support for the validity of the Prumnini tribe concept.

In terms of classification, *Perixerus* is currently a monotypic genus and *Liladownsia* also appears to be monotypic at this point in time. Although the two genera share much in common, they also, as mentioned earlier, possess some differences, hence why we did not describe the new taxon under *Perixerus*. One of the main reasons is that some of the morphological characters, outlined earlier, that define *Perixerus* as a genus do not adequately describe the new taxon. Furthermore, *P. squamipennis* is known to occur in Puebla, Veracruz (Roberts, 1947), and Oaxaca (Fontana *et al.*, 2008) while *L. fraile* has only yet been found in southern Oaxaca within a habitat in which *P. squamipennis* does not typically live. However, it should be mentioned that during the 2013 expedition both species were collected within the same locality (29 km past San José del Pacífico, Fig. 1C-2), meters from one another, and in grasses, not far from *Salvia elegans* (Fig. 9A&B). Also, it should be noted that the range of *P. squamipennis* appears to be far greater.

We have demonstrated the validity of describing a new genus of Dactyloptini based on several lines of evidence. There is still much to learn about this intriguing insect, especially in terms of aposematism and host-plant association. We think that the people of Oaxaca will be pleased to learn that their beautiful endemic grasshopper, the friar grasshopper, is now named after their beautiful endemic musician, Lila Downs.

Acknowledgments

We thank Dr. Paola Tirello (University of Padova) and Salomón Sanabria-Urbán (UNAM) for helping to collect the material, Dr. Zenón Cano-Santana (Facultad de Ciencias, UNAM) for collecting permits, the World Biodiversity Association (WBA) for supporting the second author, the Entomological Society of America Systematics, Evolution and Biodiversity Section (ESA SysEB) for a Travel Award to the third author. The Orthoptera Species File Grant, “Enhancing digital content for Pyrgomorphidae (Orthoptera: Caelifera) in the Orthoptera Species File” allowed the third author to visit MNHN in Paris, France and Simon Poulain kindly provided the material to review while there. Gabriella M. Alava performed all of the morphological measurements and assisted with the molecular work. Ji Min Noh mounted the most recent material from the 2013 expedition. The first author would also like to thank his wife, Elizabeth C. Kerr-Woller, for her continued support of his myriad scientific endeavors. This study was supported by the U.S. National Science Foundation grants, DEB-1064082 and IOS-1253493 to H.S.

References

- Amédégno C., Chapco, W. & Litzenberger, G. (2003) Out of South America? Additional evidence for a southern origin of melanopline grasshoppers. *Molecular Phylogenetics and Evolution*, 29, 115–119.
[http://dx.doi.org/10.1016/s1055-7903\(03\)00074-5](http://dx.doi.org/10.1016/s1055-7903(03)00074-5)
- Avise, J.C., Arnold, J., Ball, R.M., Bermingham, E., Lamb, T., Neifel, J.E., Reeb, C.A. & Saunders, N.C. (1987) Intraspecific phylogeography: The mitochondrial DNA bridge between population genetics and systematics. *Annual Review of Ecology and Systematics*, 18, 489–522.

- <http://dx.doi.org/10.1146/annurev.es.18.110187.002421>
- Ball, E.D. (1936) Food plants of some Arizona grasshoppers. *Journal of Economic Entomology*, 29, 679–684.
- Buzzetti, F.M., Barrientos-Lozano, L. & Fontana, P. (2010) New Melanoplineae from Mexico. *Bollettino della Società entomologica italiana*, 142 (3), 99–110.
- Chapco, W. (2006) A note on the phylogenetic position of *Duartettix montanus* within the subfamily Melanoplineae. *Journal of Orthoptera Research*, 15, 59–63.
[http://dx.doi.org/10.1665/1082-6467\(2006\)15\[59:anotpp\]2.0.co;2](http://dx.doi.org/10.1665/1082-6467(2006)15[59:anotpp]2.0.co;2)
- Chapco, W., Kuperus, W.R. & Litzenberger, G.S. (1999) Molecular phylogeny of melanopline grasshoppers (Orthoptera: Acrididae). The genus *Melanoplus*. *Annals of the Entomological Society of America*, 92, 617–623.
- Chapco, W., Litzenberger, G. & Kuperus, W.R. (2001) A molecular biogeographic analysis of the relationship between North American melanoploid grasshoppers and their Eurasian and South American relatives. *Molecular Phylogenetics and Evolution*, 18, 460–466.
- Chapco, W. & Litzenberger, G. (2002) A molecular phylogenetic analysis of the grasshopper genus *Melanoplus* Stål (Orthoptera: Acrididae) - an update. *Journal of Orthoptera Research*, 11, 1–9.
<http://dx.doi.org/10.1006/mpev.2000.0902>
- Chintauan-Marquier, I. C., Jordan, S., Berthier, P., Amédégnato, C. & Pompanon, F. (2011) Evolutionary history and taxonomy of a short-horned grasshopper subfamily: The Melanoplineae (Orthoptera: Acrididae). *Molecular Phylogenetics and Evolution*, 58, 22–32.
[http://dx.doi.org/10.1665/1082-6467\(2002\)011\[0001:ampaot\]2.0.co;2](http://dx.doi.org/10.1665/1082-6467(2002)011[0001:ampaot]2.0.co;2)
- Colombo, P., Cigliano, M.M., Sequeira, A.S., Lange, C.E., Vilardi, J.C. & Confalonieri, V.A. (2005) Phylogenetic relationships in *Dichroplus* Stål (Orthoptera: Acrididae: Melanoplineae) inferred from molecular and morphological data: testing karyotype diversification. *Cladistics*, 21, 375–389.
<http://dx.doi.org/10.1111/j.1096-0031.2005.00068.x>
- Dinghi, P.A., Confalonieri, V. & Cigliano, M.M. (2009) Phylogenetic studies in the South American tribe Dichroplini (Orthoptera: Acrididae: Melanoplineae): is the Paranaense-Pampeano informal genus group a natural clade? *Zootaxa*, 2174, 51–62.
- Eades, D.C., Otte, D., Cigliano, M.M. & Braun, H. (2014) *Orthoptera Species File*. Version 5.0/5.0. Available from: <http://Orthoptera.SpeciesFile.org> (accessed 31 January 2014)
- Edgar, R.C. (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research*, 32, 1792–1797.
<http://dx.doi.org/10.1093/nar/gkh340>
- Flook, P.K., Rowell, C.H.F. & Gellissen, G. (1995) The sequence, organization, and evolution of the *Locusta migratoria* mitochondrial genome. *Journal of Molecular Evolution*, 41, 928–941.
<http://dx.doi.org/10.1007/bf00173173>
- Fontana, P. & Buzzetti, F.M. (2007) New or little known Mexican Melanoplineae (Orthoptera Acridinae). *Atti della Accademia Roveretana degli Agiati*, 8, 7 (B), 73–130.
- Fontana, P., Buzzetti, F.M., & Mariño-Pérez, R. (2008) *Chapulines, langostas, grillos y esperanzas de México: guía fotográfica / Grasshoppers, locusts, crickets and katydids of Mexico: photographic guide*. World Biodiversity Association, Verona Italy, 272 pp.
- García, E. (1973) *Modificaciones al sistema de clasificación climática de Köppen*. Instituto de Geografía, Universidad Nacional Autónoma de México, 2nd Edition, 246 pp.
- Herrera-Ruiz, M., García-Beltrán, Y., Mora, S., Díaz-Véliz, G., Viana, G.S.B., Tortoriello, J. & Ramírez, G. (2006) Antidepressant and anxiolytic effects of hydroalcoholic extract from *Salvia elegans*. *Journal of Ethnopharmacology*, 107, 53–58.
<http://dx.doi.org/10.1016/j.jep.2006.02.003>
- Hubbell, T.H. (1932) A revision of the Puer group of the North American genus *Melanoplus*, with remarks on the taxonomic value of the concealed male genitalia in the Cyrtacanthacridinae (Orthoptera, Acrididae). *Miscellaneous Publications Museum of Zoology, University of Michigan*, 23, 1–64.
- Huelsenbeck, J.P. & Ronquist, F. (2001) MRBAYES: Bayesian inference of phylogeny. *Bioinformatics*, 17, 754–755.
<http://dx.doi.org/10.1093/bioinformatics/17.8.754>
- Isley, F.B. (1938) Survival value of Acridian protective coloration. *Ecology*, 19, 370–389.
<http://dx.doi.org/10.2307/1930592>
- Joern, A. (1979) Feeding patterns in grasshoppers (Orthoptera: Acrididae): Factors influencing diet specialization. *Oecologia*, 38, 325–347.
<http://dx.doi.org/10.1007/bf00345192>
- Kottek, M., Grieser, J., Beck, C., Rudolf, B. & Rubel, F. (2006) World Map of the Köppen–Geiger climate classification updated. *Meteorologische Zeitschrift*, 15 (3), 259–263.
<http://dx.doi.org/10.1127/0941-2948/2006/0130>
- Lanfear, R., Calcott, B., Ho, S.Y.W. & Guindon, S. (2012) PartitionFinder: Combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution*, 29, 1695–1701.
<http://dx.doi.org/10.1093/molbev/mss020>

- Leavitt, J.R., Hiatt, K.D., Whiting, M.F. & Song, H. (2013) Searching for the optimal data partitioning strategy in mitochondrial phylogenomics: A phylogeny of Acridoidea (Insecta: Orthoptera: Caelifera) as a case study. *Molecular Phylogenetics and Evolution*, 67, 494–508.
<http://dx.doi.org/10.1016/j.ympev.2013.02.019>
- Litzenberger, G. & Chapco, W. (2001) Molecular phylogeny of selected Eurasian Podismine Grasshoppers (Orthoptera: Acrididae). *Annals of the Entomological Society of America*, 94, 505–511.
[http://dx.doi.org/10.1603/0013-8746\(2001\)094\[0505:mposep\]2.0.co;2](http://dx.doi.org/10.1603/0013-8746(2001)094[0505:mposep]2.0.co;2)
- Mayer, F.L. (2004) *Primnoa* Fischer-Waldheim 1846, *Sharovia* Otte 1997, *Parahagla* Lin 1982, *Phyllophora erosifolia* Piza 1981 and *Archibrunnea* Otte 1997: naming issues resolved. *Journal of Orthoptera Research*, 13, 161–165.
[http://dx.doi.org/10.1665/1082-6467\(2004\)013\[0161:pfsopl\]2.0.co;2](http://dx.doi.org/10.1665/1082-6467(2004)013[0161:pfsopl]2.0.co;2)
- Miller, M.A., Holder, M.T., Vos, R., Midford, P.R., Liebowitz, T., Chan, L., Hoover, P. & Warnow, T. (2011) The CIPRES Portals. CIPRES. Available from: http://www.phylo.org/sub_sections/portal/ (accessed 24 March 2014)
- Neal, P.R., Stromberg, M.R. & Jepson-Innes, K.A. (1994) Aposematic coloration in *Dactylotum variegatum* (Orthoptera: Acrididae): Support from vertebrate feeding trials. *The Southwestern Naturalist*, 39, 21–25.
<http://dx.doi.org/10.2307/3672187>
- Rambaut, A. & Drummond, A.J. (2003–2009) Tracer v1.5.0: MCMC Trace Analysis Package. Available from: <http://beast.bio.ed.ac.uk/Tracer> (accessed 24 March 2014)
- Rehn, J.A.G. & Randell, R.L. (1963) A preliminary analysis of the lines of the super-tribe Melanoplinae (Orthoptera: Acrididae, Cyrtacanthacridinae). *Proceedings of the Academy of Natural Sciences of Philadelphia*, 115, 1–32.
- Rzedowski, J. (1981) *The vegetation of Mexico*. Editorial Limusa, Mexico, 432 pp.
- Otte, D. (1970) A comparative study of communicative behavior in grasshoppers. Miscellaneous Publications Museum of Zoology, University of Michigan, 141, 1–168.
- Otte, D. & Joern, A. (1977) On feeding patterns in desert grasshoppers and the evolution of specialized diets. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 128, 89–126.
- Otte, D. (2007) *Mexitettix* and *Mexacris*, two new genera of grasshoppers from eastern Mexico (Acrididae: Melanoplinae). *Proceedings of the Academy of Natural Sciences of Philadelphia*, 156, 305–340.
[http://dx.doi.org/10.1635/0097-3157\(2007\)156\[305:mamtng\]2.0.co;2](http://dx.doi.org/10.1635/0097-3157(2007)156[305:mamtng]2.0.co;2)
- Roberts, H.R. (1947) Revision of the Mexican Melanoplinae (Orthoptera: Acrididae: Cyrtacanthacridinae) Part I. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 99, 201–230.
- Ronderos, R.A. (1991) El género *Neopedies* Hebard, 1931 (Orthoptera, Acrididae, Melanoplinae). *Revista de la Sociedad Entomológica Argentina*, 49 (1–4), 27–47.
- Scudder, S.H. (1897) *Guide to the genera and classification of North American Orthoptera found north of Mexico*. Cambridge, USA, 87 pp.
- Stamatakis, A., Hoover, P. & Rougemont, J. (2008) A rapid bootstrap algorithm for the RAxML Web-Servers. *Systematic Biology*, 57, 758–771.
- Smith, T.R. & Capinera, J.L. (2005) Host preferences and habitat associations of some Florida grasshoppers (Orthoptera: Acrididae). *Environmental Entomology*, 34, 210–224.
<http://dx.doi.org/10.1603/0046-225x-34.1.210>
- Sun, H., Zheng, Z. & Huang, Y. (2010) Sequence and phylogenetic analysis of complete mitochondrial DNA genomes of two grasshopper species *Gomphocerus rufus* (Linnaeus, 1758) and *Primnoa arctica* (Zhang and Jin, 1985) (Orthoptera: Acridoidea). *Mitochondrial DNA*, 21, 115–131.
<http://dx.doi.org/10.3109/19401736.2010.482585>
- Sword, G.A. & Chapman, R.F. (1994) Monophagy in a polyphagous grasshopper, *Schistocerca shoshone*. *Entomologia Experimentalis et Applicata*, 73, 255–264.
<http://dx.doi.org/10.1111/j.1570-7458.1994.tb01863.x>
- Sword, G.A. & Dopman, E.B. (1999) Developmental specialization and geographic structure of host plant use in a polyphagous grasshopper, *Schistocerca emarginata* (= *lineata*) (Orthoptera: Acrididae). *Oecologia*, 120, 437–445.
<http://dx.doi.org/10.1007/s004420050876>
- Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M. & Kumar, S. (2011) MEGA5: Molecular Evolutionary Genetics Analysis using Maximum Likelihood, Evolutionary Distance, and Maximum Parsimony Methods. *Molecular Biology and Evolution*, 28, 2731–2739.
<http://dx.doi.org/10.1093/molbev/msr121>
- Yin, X.C. & Smith, R.L. (1989) Three new grasshoppers from the Western United States (Orthoptera: Acrididae). *Pan-Pacific Entomologist*, 65 (2), 166–171.
- Zhang, D.C., Han, H.Y., Yin, H., Li, X.J., Yin, Z. & Yin, X.C. (2011) Molecular phylogeny of Pamphagidae (Acridoidea, Orthoptera) from China based on mitochondrial cytochrome oxidase II sequences. *Insect Sciences*, 18, 234–244.
<http://dx.doi.org/10.1111/j.1744-7917.2010.01359.x>