



## Taxonomic utility of niche models in validating species concepts: A case study in *Anthophora (Heliophila)* (Hymenoptera: Apidae)

MICHAEL C. ORR<sup>1,4</sup>, JONATHAN B. KOCH<sup>2</sup>, TERRY L. GRISWOLD<sup>3</sup> & JAMES P. PITTS<sup>1</sup>

<sup>1</sup>Biology Department, Utah State University, Logan, Utah, 84321, USA.

E-mail: michael.christopher.orr@gmail.com; james.pitts@usu.edu

<sup>2</sup>Biology Department, Ecology Center, Utah State University, Logan, Utah, 84321, USA. E-mail: jonathan.koch@usu.edu

<sup>3</sup>USDA-ARS Pollinating Insects Research Unit, Logan, Utah, 84321, USA. E-mail: terry.griswold@ars.usda.gov

<sup>4</sup>Corresponding author

### Abstract

Taxonomy has far-reaching effects throughout biology, and incorrect taxonomy can be detrimental in many ways. Polymorphic species complexes, many of which exist in the bee genus *Anthophora* Latreille, lend themselves to such difficulties. This study employs environmental niche mapping (ENM) and traditional morphological analyses to investigate the validity of the subjective synonymy of *Anthophora (Heliophila) curta* Provancher with the senior synonym *A. squammulosa* Dours. Eleven of fifty morphological characters consistently differentiate the two putative species, with an additional five characters sometimes separating them. Additionally, based on over 1000 georeferenced museum specimens, the geographic ranges of the two taxa do not overlap. The two entities also react differently to the bioclimatic variables based on correlation analysis. We further tested the two-species hypothesis by constructing ENMs with informative bioclimatic variables associated with locality records. Their modelled distributions overlapped less than 1%, suggesting discrete environmental boundaries. The variables which contributed most to each species' model also differed. These differences are explored in relation to their habitats. The combined morphological and biogeographic analysis indicates that *A. curta* and *A. squammulosa* are distinct species. Based on the accumulated evidence the synonymy is formally rejected and *A. curta* is recognized as a valid species. Five additional taxa (*A. bispinosa* Cockerell, *A. franciscana* Cockerell, *A. usticauda* Cockerell, *A. u. cinerios* Cockerell, *A. zamoranella* Cockerell) are newly synonymized with *A. squammulosa* and *Anthophora curta* var. *melanops* Cockerell is newly synonymized with *A. curta*. Implications outside of taxonomy are discussed.

**Key words:** Apoidea, Anthophorini, bees, taxonomy, biogeography, Nearctic, MaxEnt, niche modelling

### Introduction

The Anthophorini (Hymenoptera: Apidae) are a tribe of large to small bees (6–30mm) known for their fast flight and generalist floral tendencies (Michener, 2007). A large number of synonymies were made in Brooks' (1988) review of the tribe Anthophorini without any formal argument. One such synonymy was that of *Anthophora (Heliophila) curta* Provancher, 1895 with the senior synonym *Anthophora (Heliophila) squammulosa* Dours, 1870 (Fig. 1). This synonymy came into question during the course of a revision of the New World *Anthophora (Heliophila)* Klug. Upon initial review of determined specimens, there appeared to be two phenotypes of *A. squammulosa*. The distribution of these two entities appeared disjunct, with a northern form in the southwestern United States that encompassed the type locality of *A. curta* and a second form limited to Mexico that included the type locality of *A. squammulosa*. Several morphological characters also seemed to distinguish the two, while others appeared to intergrade between the two entities, suggesting the need to re-examine this synonymy. The situation was further obscured by four additional, currently recognized species from Central America and three historical subspecies in the complex. Caution in analysis of morphological characters is prudent as there are numerous polymorphic species in Anthophorini (Brooks, 1983; Brooks, 1988). As morphology alone has proven inadequate for distinguishing some *Anthophora* Latreille, the incorporation of additional sources of information becomes beneficial. Molecular data is often used under these conditions but recent material for DNA extraction was

study has major implications for the conservation status of these species. With the separation of *A. curta* from *A. squammulosa*, the latter's geographic range and climatic niche are much reduced. The unique distribution of *A. squammulosa*, separate from all other *A. (Heliophila)*, becomes especially apparent. This is of conservation importance because much of Mexico's forests, especially the dry forests, are being logged (Myers *et al.*, 2000; Olson & Dinerstein, 2002). Based on projections by the WWF, virtually all of the ecoregions in which *A. squammulosa* has been detected are soon to be in critical or endangered status (Fig. 5). In contrast, *A. curta* inhabits a number of ecoregions projected to be relatively stable or only vulnerable in the future. The incorrect synonymy of these two species obscured the potential threat to *A. squammulosa* posed by habitat loss. Only through the combination of traditional taxonomy and ENMs did this become apparent. This study demonstrates the value of ENMs in taxonomic studies where molecular data are not available and suggests its usefulness in future studies.

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## References

- Bassin, L., Alvarez, N., Pellissier, L. & Triponoz, Y. (2011) Ecological niche overlap in sister species: how do oil-collecting bees *Macropis europaea* and *Macropis fulvipes* (Hymenoptera: Melittidae) avoid hybridization and competition? *Apidologie*, 42, 579–595.  
<http://dx.doi.org/10.1007/s13592-011-0067-z>
- Brooks, R.W. (1983) Systematics and Bionomics of *Anthophora*: The Bomboides Group and Species Groups of the New World (Hymenoptera: Apoidea, Anthophoridae). *University of California Publications in Entomology*, 98, 1–75
- Brooks, R.W. (1988) Systematics and Phylogeny of the Anthophorine Bees (Hymenoptera; Anthophoridae; Anthophorini). *The University of Kansas Science Bulletin*, 53, 436–575.
- Brooks, R.W. (1999) Bees of the genus *Anthophora* Latreille 1803 (Hymenoptera Apidae Anthophorini) of the West Indies. *Tropical Zoology*, 12, 105–124.  
<http://dx.doi.org/10.1080/03946975.1999.10539381>
- Cockerell, T.D.A. (1912) Descriptions and Records of Bees - XLV. *The Annals and Magazine of Natural History*, 10, 21–30.
- Cockerell, T.D.A. (1926) Some bees in the collection of the California Academy of Sciences. *Pac-Pacific Entomologist*, 3, 80–90.
- Cockerell, T.D.A. (1941) Observations on plants and insects in north-western Baja California, Mexico, with descriptions of new bees. *Transactions of the San Diego Society for Natural History*, 9, 337–352.
- Cockerell, T.D.A. (1949) Bees from Central America, Principally Honduras. *Proceedings of the United States National Museum*, 98, 429–490.  
<http://dx.doi.org/10.5479/si.00963801.98-3233.429>
- Danforth, B.N. (1999) Emergence dynamics and bet hedging in a desert bee, *Perdita portalis*. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 266, 1985–1994.  
<http://dx.doi.org/10.1098/rspb.1999.0876>
- Dours, J.M.A. (1870) Monographie iconographique du genre *Anthophora*. *Memoires de la Société linnéenne du Nord de la France*, 2, 5–211.

- Elith, J. & Leathwick, J.R. (2009) Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology and Evolution S*, 40, 677–697.  
<http://dx.doi.org/10.1146/annurev.ecolsys.110308.120159>
- Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E. & Yates, C.J. (2010) A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*, 17, 43–57.  
<http://dx.doi.org/10.1111/j.1472-4642.2010.00725.x>
- Fitzpatrick, M.C., Gotelli, N.J. & Ellison, A.M. (2013) MaxEnt versus MaxLike: empirical comparisons with ant species distributions. *Ecosphere*, 4, 1–15.  
<http://dx.doi.org/10.1890/ES13-00066.1>
- Gonzalez, V.H., Koch, J.B. & Griswold, T.L. (2010) *Anthidium vigintiduopunctatum* Friese (Hymenoptera: Megachilidae): the elusive “dwarf bee” of the Galápagos Archipelago? *Biological Invasions*, 12, 2381–2383.  
<http://dx.doi.org/10.1007/s10530-009-9651-9>
- Griswold, T.L., Parker, F.D. & Hanson, P.E. (1995) The Bees: (Apidae). In: Hanson, P.E. & Gauld, I.D. (Eds.), *The Hymenoptera of Costa Rica*. Oxford University Press, Oxford, pp. 650–691.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25, 1965–1978.  
<http://dx.doi.org/10.1002/joc.1276>
- Hinojosa-Diaz, I.A., Feria-Arroyo, T.P. & Engel, M.S. (2009) Potential distribution of orchid bees outside their native range: the cases of *Eulema polychroma* (Mocsary) and *Euglossa viridissima* Friese in the USA (Hymenoptera: Apidae). *Diversity and Distributions*, 15, 421–428.  
<http://dx.doi.org/10.1111/j.1472-4642.2008.00549.x>
- Hurd, P.D. Jr. (1957) Notes on the Autumnal Emergence of the Vernal Desert Bee, *Hesperapis fulvipes* Crawford (Hymenoptera, Apoidea). *Journal of the Kansas Entomological Society*, 30, 10.
- ITIS (2013) Integrated Taxonomic Information System on-line database. Available from: <http://www.itis.gov/> (accessed 13 June 2013)
- Larkin, L.L., Neff, J.L. & Simpson, B.B. (2008) The evolution of a pollen diet: host choice and diet breadth of *Andrena* bees (Hymenoptera: Andrenidae). *Apidologie*, 39, 133–145.  
<http://dx.doi.org/10.1051/apido:2007064>
- Lozier, J.D., Strange, J.P. & Koch, J.B. (2013) Landscape heterogeneity predicts gene flow in a widespread polymorphic bumble bee, *Bombus bifarius* (Hymenoptera: Apidae). *Conservation Genetics*, 14, 1099–1110.  
<http://dx.doi.org/10.1007/s10592-013-0498-3>
- MacMahon, J.A. & Wagner, F.H. (1985) The Mojave, Sonoran and Chihuahuan deserts of North America. In: Evenari, M., Noy-Meir, I. & Goodall, D.W. (Eds.), *Hot deserts and arid shrublands. Ecosystems of the world 12A*. Elsevier, Amsterdam, pp. 105–201.
- Michener, C.D. (1951) Superfamily Apoidea. In: Muesebeck, C.F.W. & Krombein, K.V. (Eds.), *Hymenoptera of America North of Mexico-Synoptic Catalog*. U.S.D.A. Monograph no. 2, Washington, D.C., pp. 1043–1255.
- Michener, C.D. (1954) Bees of Panamá. *Bulletin of the American Museum of Natural History*, 104, 1–176.
- Michener, C.D. (2007) *The Bees of the World. 2<sup>nd</sup> Edition*. Johns Hopkins University Press, Baltimore, MD, 953 pp. Moldenke, A.R. & Neff, J.L. (1974) *The Bees of California: a catalogue with special relevance to pollination and ecological research. Vol. 1*. Board of Studies in Biology, University of California.
- Müller, A. (1996) Host-plant specialization in western Palearctic Anthidiine bees (Hymenoptera: Apoidea: Megachilidae). *Ecological Monographs*, 66, 235–257.  
<http://dx.doi.org/10.2307/2963476>
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, 403, 853–858.  
<http://dx.doi.org/10.1038/35002501>
- Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'Amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P. & Kassem, K.R. (2001) Terrestrial ecoregions of the world: a new map of life on Earth. *Bioscience*, 51, 933–938.  
[http://dx.doi.org/10.1641/0006-3568\(2001\)051\[0933:TEOTWA\]2.0.CO;2](http://dx.doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2)
- Olson, D.M. & Dinerstein, E. (2002) The Global 200: Priority ecoregions for global conservation. *Annals of the Missouri Botanical Garden*, 89, 199–224.
- Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, 190, 231–259.  
<http://dx.doi.org/10.1016/j.ecolmodel.2005.03.026>
- Provancher, L. (1895) Les dernières descriptions de l'Abbe Provancher. *Naturaliste Canadian*, 22, 79–191.
- R Core Team. (2012) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria, 1731 pp.
- Ricketts, T.H., Dinerstein, E., Olson, D.M., Loucks, C.J., Eichbaum, W., DellaSala, D., Kavanagh, K., Hedao, P., Hurley, P.T., Carney, K.M., Abell, R. & Walters, S. (1999) *Terrestrial Ecoregions of North America A Conservation Assessment*. Island Press, Washington, D.C., 486 pp.

- Sheffield, C.S. & Perron, J. (2013) Annotated catalogue of the bees described by Léon Provancher (Hymenoptera: Apoidea). *The Canadian Entomologist*, 146, 1–53.  
<http://dx.doi.org/10.4039/tce.2013.64>
- Sipes, S.D. & Wolf, P.G. (2001) Phylogenetic relationships within *Diadasia*, a group of specialist bees. *Molecular Phylogenetics and Evolution*, 19, 144–156.  
<http://dx.doi.org/10.1006/mpev.2001.0914>
- U. S. National Pollinating Insects Database (2011) United States Department of Agriculture, Agriculture Research Service, Bee Biology and Systematics Laboratory, Logan, Utah (accessed 12 October 2013)
- Wilson, J.S., Clark, S.L., Williams, K.A. & Pitts, J.P. (2012) Historical biogeography of the arid-adapted velvet ant *Sphaerophthalma arota* (Hymenoptera: Mutillidae) reveals cryptic species. *Journal of Biogeography*, 39, 226–352.  
<http://dx.doi.org/10.1111/j.1365-2699.2011.02580.x>
- World Wildlife Fund (2002) WWF Biomes. Available from: <http://worldwildlife.org/biomes/> (accessed 2 July 2013)

**APPENDIX 1.** Detailed descriptions of the useful characters from the morphological analysis. Numbers here correspond to those of the in-line Table 1.

1. Scutum surface sculpting—Differentiates both sexes

The scutum in *Anthophora curta* is pitted throughout as in *Anthophora squammulosa*. Despite this, clear reflections are visible throughout the scutum due to its smooth surface. In contrast, *A. squammulosa* has a more tessellate scutum and very few, if any, reflections as a result. It should be noted that the anterior limit of the scutum is smooth and shiny in both species.

2. Wing 1<sup>st</sup> submarginal cell setae—Differentiates both sexes

There are at most setae along the veins of the first submarginal cell in *A. curta*, as is typical for the New World *A. (Heliophila)*. *Anthophora squammulosa* is the only species of New World *A. (Heliophila)* with setae reaching into the first submarginal cell. There are normally at least five such setae in the cell, although rarely they may be worn off and only the point of attachment is visible. In such a case, this point of attachment will often appear similar to, although less well-defined than, the papillae seen at the edge of the wing in *Anthophora*.

3. Propodeal enclosure surface—Differentiates both sexes

The propodeal enclosures are quite similar in extent in these two species, but within them the level of tessellation is distinctly different. The propodeal enclosure of *A. curta* is only weakly tessellate, allowing for an appreciable degree of reflection. The propodeal enclosure of *A. squammulosa* is comparatively more coarsely tessellate, giving it a duller appearance overall.

4. Mandible form—Differentiates females

The female mandible of *A. curta* is a short, linear blade as is typical of the New World *A. (Heliophila)*. The tip of the mandible in *A. squammulosa* is comparatively much closer to that of *A. peritomae*, which has an elongate, scoop-like mandible tip. Although not as greatly enlarged as that of *A. peritomae*, the scoop of *A. squammulosa* is still distinctly elongate and the subapical tooth appears slightly reduced in comparison as a result.

5. Legs overall setae color—Differentiates females

The legs of *A. squammulosa* are clothed in noticeably darker setae than those of *A. curta*. This is most obvious when looking at the long fringe of setae on the posterior of the fore leg's tibia and basitarsus, which are a smoky gray to black in *A. squammulosa* and a white to light brown color in *A. curta*. This is also seen on the inner edge of the mid and hind femur, where the white setae of *A. curta* are again opposed by the smoky black setae of *A. squammulosa*.

6. T1 erect setae color—Differentiates females

There are very long, erect setae present on T1 in addition to the appressed setae. These setae are all white in *A. curta*. In *A. squammulosa*, an appreciable number of these erect setae are instead black, intermixed with the dominant white setae. This may not be the case in specimens whose setae have been worn off.

7. Female S5 setae color—Differentiates females

In the apical half of S5, there are relatively longer setae in both species. These setae are typically a mix of white to light brown in *A. curta*, while in *A. squammulosa* they are largely dark brown to black, with few if any light setae.

8. Scape integument color—Differentiates males

The integument of the scape is quite commonly maculated in the New World *A. (Heliophila)*, this maculation found on the underside such that it is visible when the antennae are raised. The species *A. squammulosa* follows this trend, with strong maculations typically present from the base to tip of the scape, although in some specimens it is somewhat reduced. There is no such maculation present in any observed specimens of *A. curta*.