The case for the continued use of the genus name *Mimulus* for all monkeyflowers

Running Title: *Mimulus* for all monkeyflowers

David B. Lowry[1*], James M. Sobel[2], Amy L. Angert[3], Tia-Lynn Ashman[4], Robert L. Baker[5], Benjamin K. Blackman[6], Yaniv Brandvain[7], Kelsey J.R.P. Byers[8], Arielle M. Cooley[9], Jennifer M. Coughlan[10], Michele R. Dudash[11], Charles B. Fenster[12], Kathleen G. Ferris[13], Lila Fishman[14], Jannice Friedman[15], Dena L. Grossenbacher[16], Liza M. Holeski[17], Christopher T. Ivey[18], Kathleen M. Kay[19], Vanessa A. Koelling[20], Nicholas J. Kooyers[21], Courtney J. Murren[22], Christopher D. Muir[23], Thomas C Nelson[14], Megan L. Peterson[24], Joshua R. Puzey[25], Michael C. Rotter[17], Jeffrey R. Seemann[26], Jason P. Sexton[27], Seema N. Sheth[28], Matthew A. Streisfeld[29], Andrea L. Sweigart[30], Alex D. Twyford[31,32], Mario Vallejo-Marín[33], John H. Willis[34], Kevin M. Wright[35], Carrie A. Wu[36], Yao-Wu Yuan[26]

[1]Department of Plant Biology, Michigan State University, East Lansing, MI, 48824, USA
[2]Department of Biological Sciences, Binghamton University (SUNY), Binghamton, NY 13902, USA
[3]Departments of Botany and Zoology, University of British Columbia, Vancouver, BC, V6T 1Z4, Canada
[4]Department of Biological Sciences, University of Pittsburgh, Pittsburgh, PA, 15260, USA
[5]Department of Biology, Miami University, Oxford, OH, 45056, USA
[6]Department of Plant & Microbial Biology, University of California, Berkeley, Berkeley, CA, 94720, USA
[7]Department of Plant & Microbial Biology, University of Minnesota, St. Paul, MN, 55108, USA
[8]Department of Zoology, University of Cambridge, Downing Street, Cambridge, CB2 3EJ, UK
[9]Biology Department, Whitman College, Walla Walla, WA, 99362, USA
[10] Biology Department, University of North Carolina at Chapel Hill, NC, 27599, USA
[11]Department of Natural Resource Management, South Dakota State University, SD 57007, USA
[12]Department of Biology and Microbiology, South Dakota State University, SD, 57007, USA
[13]Department of Ecology and Evolutionary Biology, Tulane University, New Orleans, LA 70118
[14]Division of Biological Sciences, University of Montana, Missoula, MT, 59812
[15]Department of Biology, Queen's University, Kingston, Ontario, Canada K7L3N6
[16]Department of Biology, California Polytechnic State University, San Luis Obispo, CA, 93407, USA
[17]Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ, 86011, USA
[18]Biological Sciences, California State University, Chico, 95929, USA
[19]Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, Santa Cruz, CA, 95060
[20]Department of Biology and Environmental Science, Auburn University at Montgomery, Montgomery, AL, 36124, USA
[21]Department of Biology, University of Louisiana, Lafayette, LA, 70503, USA
[22]Department of Biology, College of Charleston, Charleston, SC, 29424, USA
[23]Department of Botany, University of Hawai'i, Honolulu, HI, 96822, USA
[24]Environmental Studies Program, University of Colorado Boulder, Boulder, CO 80309, USA

[25]Biology Department, William & Mary, Williamsburg, VA 23187, USA
[26]Ecology & Evolutionary Biology, University of Connecticut, Storrs, CT, 06269, USA
[27]Department of Life and Environmental Sciences, University of California, Merced, CA 95343, USA
[28]Department of Plant and Microbial Biology, North Carolina State University, Raleigh, NC, 27695, USA
[29]Institute of Ecology and Evolution, University of Oregon, Eugene, OR 97403, USA
[30]Department of Genetics, University of Georgia, Athens, GA, 30602, USA
[31]Institute of Evolutionary Biology, School of Biological Sciences, Ashworth Laboratories, University of Edinburgh, Edinburgh, UK
[32]Royal Botanic Garden Edinburgh, 20A Inverleith Row, Edinburgh EH3 5LR, UK
[33]Biological and Environmental Sciences, School of Natural Sciences, University of Stirling, Stirling, Scotland, FK9 4LA, UK
[34]Department of Biology, Duke University, Durham, NC, 27708, USA
[35]Calico Life Sciences LLC, South San Francisco, CA, 94080, USA
[36]Department of Biology, University of Richmond, Richmond, VA, 23173, USA

*Author for correspondence: dlowry@msu.edu

The genus *Mimulus* is a well-studied group of plant species, which has for decades allowed researchers to address a wide array of fundamental questions in biology (Wu & al. 2008; Twyford & al. 2015). Linnaeus named the type species of *Mimulus* (*ringens* L.), while Darwin (1876) used *Mimulus* (*luteus* L.) to answer key research questions. The incredible phenotypic diversity of this group has made it the focus of ecological and evolutionary study since the mid-20th century, initiated by the influential work of Clausen, Keck, and Hiesey as well as their students and collaborators (Clausen & Hiesey 1958; Hiesey & al. 1971, Vickery 1952, 1978). Research has continued on this group of diverse taxa throughout the 20th and into the 21st century (Bradshaw & al. 1995; Schemske & Bradshaw 1999; Wu & al. 2008; Twyford & al. 2015; Yuan 2019), and *Mimulus guttatus* was one of the first non-model plants to be selected for full genome sequencing (Hellsten & al. 2013). *Mimulus* has played a key role in advancing our general understanding of the evolution of pollinator shifts (Bradshaw & Schemske 2003; Cooley & al. 2011; Byers & al. 2014), adaptation (Lowry & Willis 2010; Kooyers & al. 2015; Peterson & al. 2016; Ferris & Willis 2018; Troth & al. 2018), speciation (Ramsey & al. 2003; Wright & al. 2013; Sobel & Streisfeld 2015; Zuellig & Sweigart 2018), meiotic drive (Fishman & Saunders 2008), polyploidy (Vallejo-Marín 2012; Vallejo-Marín & al. 2015), range limits (Angert 2009; Sexton et al. 2011; Grossenbacher & al. 2014; Sheth & Angert 2014), circadian rhythms (Greenham & al. 2017), genetic recombination (Hellsten & al. 2013), mating systems (Fenster & Ritland 1994; Dudash & Carr 1998; Brandvain & al. 2014) and developmental biology (Moody & al. 1999; Baker & al. 2011, 2012; Yuan 2019). This combination of a rich history of study coupled with sustained modern research activity is unparalleled among angiosperms. Across many interested parties, the name *Mimulus* therefore takes on tremendous biological significance and is recognizable not only by botanists, but also by zoologists, horticulturalists, naturalists, and members of the biomedical community. Names associated with a taxonomic group of this prominence should have substantial inertia, and disruptive name changes should be avoided. As members of the *Mimulus* community, we advocate retaining the genus name *Mimulus* to describe all monkeyflowers. This is despite recent nomenclature changes that have led to a renaming of most monkeyflower species to other genera.

How did we get here?

In a recent paper, Barker & al. (2012) proposed splitting the genus *Mimulus* into multiple new genera. This proposed change was based upon a molecular phylogenetic analysis that revealed other small genera, comprising a total of 21 species, were potentially located within the *Mimulus* clade (Figure 1; Beardsley & Olmstead 2002; Beardsley & al. 2004; Beardsley & Barker 2005). The finding that *Mimulus* appears to be a polyphyletic group warranted revision to the genus, as monophyletic groupings are preferred for the designation of genera. Four options were proposed as solutions by Barker & al. (2012): 1) Minimize species name changes by allowing *Mimulus* to remain as a polyphyletic or a biphyletic group; 2) Minimize name changes by grouping all genera into one monophyletic group *Mimulus* L.; 3) Minimize name changes by conserving *Mimulus* L. with a different type species; 4) Divide *Mimulus* into multiple new genera, resulting in many name changes.

Barker & al. (2012) chose to divide *Mimulus* into three major genera (*Mimulus, Erythranthe,* and *Diplacus;* Option 4), the solution which required the most name changes (~136 new combinations). They ruled out Option 1, as monophyletic groupings are preferred. They rejected

Option 3, as it would have resulted in name changes to eight widespread *Mimulus* species and would not recognize some genera that the authors designated as distinct. They also stated that they wanted to move forward without waiting for approval of retypification by the next International Botanical Conference in 2017. The justification given for dismissing Option 2 was made based on a desire to conserve the names of a few small Australian genera: "Maximally enlarging *Mimulus* results in the loss of much useful information in the taxonomic hierarchy that recognizes the Australian-centered genera…each of which has apparent apomorphic features that justify treatment at generic rank." Further, it was argued that the *Erythranthe* and *Diplacus* clades represented distinct radiations in western North America and that each deserved to be recognized by being elevated to the genus level.

The nomenclatural suggestions made by Barker & al. (2012) have now been adopted by multiple floras, including the Plants of the World Online, the Oregon Flora Project (Oregon State University), and the Jepson eFlora, and are under review at the Flora of North America. In addition, online resources such as the National Center for Biotechnology Information (NCBI), Global Biodiversity Information Facility (GBIF), UniProt, and iNaturalist now use the names from Barker & al. (2012) in lieu of the older classification. Given the widespread and rapid acceptance of the Barker & al. (2012) circumscription, it may be perplexing as to why so many scientists have continued to use the name *Mimulus*. There are three key reasons why the use of *Mimulus* will likely continue by this group of scientists into the future.

Reason 1: The botanical community needs a stable circumscription for monkeyflowers

The primary reason for resisting the adoption of the new nomenclature is that we are reluctant to use different names for the organisms we work on until we are convinced that the nomenclature will be stable for the long-term. Unfortunately, given the limited data to support the name changes, we argue that a conservative position is warranted. In particular, the phylogenetic data available are outdated by modern standards (McKain & al. 2018). Prior to the genomic era, it seemed plausible that sequence data from two genes would be sufficient to approximate the species tree. However, given our modern understanding of the prevalence of gene flow and incomplete lineage sorting (Pease & al. 2016; McKain & al. 2018), it is likely that the species tree for the Phrymaceae will change considerably when more data are added. Prior to revision by Barker & al (2012), the Phrymaceae consisted primarily of the genus *Mimulus*, and several small (in some cases monotypic) genera. Grant (1924) originally separated *Mimulus* into two large sub-genera based on morphological placentation traits, *Synplacus* and *Schizoplacus* (Figure 1), and the taxonomic revisions by Barker & al (2012) elevated these groups to genus level, *Erythranthe* and *Diplacus* (Figure 1). Our current state of knowledge of the Phrymaceae is based on chloroplast sequence data (*trnL/F*) and nuclear DNA sequence from the internal and external transcribed spacer nuclear DNA (nrDNA; Beardsley & Olmstead 2002). The chloroplast data suggest that the clade containing *M. ringens* and the Australian *Mimulus* is sister to the clade that includes all other groups, including *Phryma*, *Synplacus*, *Schizoplacus*, and a few other small genera (Figure 1, cpDNA). In contrast, the nrDNA data suggest that *Phryma* is the outgroup to two large clades (Figure 1, nrDNA). One of these clades includes *M. ringens*, the Australian *Mimulus*, and subgenus *Synplacus*. The other clade primarily comprises sub-genus *Schizoplacus*. When data from the chloroplast gene were combined with the nrDNA data, the resulting topology of the species tree resembled the results from the chloroplast data alone (Beardsley &

Olmstead 2002; Beardsley & al. 2004, Beardsley & Barker 2005). This suggests that the chloroplast data were driving the patterns on which Barker's taxonomy was constructed. Unfortunately, trees built from chloroplast data are unreliable because the chloroplast evolves as a single haplotype (McKain & al 2018), frequently spreads to distantly related species by introgression (Rieseberg & Soltis 1991), and often evolves non-neutrally (Wu & Campbell 2007; Bock & al. 2014). Thus, utmost caution is appropriate with regard to the treatment of chloroplast data for phylogenetic questions. We suggest that a modern phylogenetics approach leveraging sequence data from hundreds of nuclear loci and/or an amplicon-based approach incorporating dozens of markers is necessary to gain a better understanding of the species tree topology for the Phrymaceae, as is common in the field (Urive-Convers et al 2016; McKain et al. 2018). The need for more sequence data is illustrated by the comparison of the phylogeny presented in Beardsley & al. (2004) with the modern 41,528-SNP phylogeny from Stankowski & Streisfeld (2015), which shows discordance in the placement of several monkeyflower species.

It is quite possible that new phylogenetic data will completely upend our current understanding of relationships among species in the Phrymaceae. Thus, our position is that no new nomenclatural changes should be adopted until there is a better understanding of the species tree in this group. It has always been our position that it was premature to rename most of the genus *Mimulus* based on two discordant gene phylogenies, as was done by Barker & al. (2012). Our concern is that prematurely switching to new names may cause additional confusion in the literature, particularly if more robust systematic data are consistent with retaining the original name or indicate yet another name change. Thus, we are reluctant to adopt a new circumscription until we are more assured of its stability. We are not alone in our desire for stability, which has been pointed out by others, including Orchard & Maslin (2005): "Taxonomists must recognize that nomenclature is not a plaything of taxonomy, molecular phylogeny, cladistics or any other special interest group. It is a working tool (a filing system) for all biologists, professional and amateur, and for the wider community, and to be meaningful it needs to be as stable as possible. A naming system that continually changes is not a naming system at all and will be discarded or disregarded."

Finally, we are concerned about the stability of the current circumscription by Barker & al. (2012) given that it may not have been sufficiently vetted by peer review. The manuscript was published in Phytoneuron, a journal edited by a coauthor on that paper. The editorial policy of Phytoneuron states "Submissions will be reviewed for content and style by the editor, based on his own knowledge and expertise. If deemed appropriate or necessary by the editor, review by other botanical peers will be sought. An indication of the Phytoneuron review process (if beyond the Editor) will appear in the Acknowledgements." The manuscript's acknowledgements in the published paper contain no information about editorial or peer review, other than acknowledging comments "on a late draft" by two colleagues. Subsequent work by Nesom (2014), published in Phytoneuron, is also inconsistent with scientific knowledge of species-level relationships within the section Simiolus of *Mimulus*. For example, Nesom divided annual and perennial populations of *M. guttatus* into two separate species, *Erythranthe guttata* and *E. microphylla*, respectively. Justification for this splitting is directly contradicted by population genetic data, which demonstrate free genetic exchange between annual and perennial populations of *M. guttatus* (Oneal & al. 2014; Twyford & Friedman 2015). Similarly, Tulig & Nesom (2012) recently elevated several taxa within the *M. aurantiacus* complex to species rank based solely on morphological information. Hybrid zones have been well documented for sub-species of *M. aurantiacus* (Thompson 2005), and subsequent work indicates substantial gene flow across these points of contact between incompletely isolated taxa (Sobel & Streisfeld 2015, Stankowski et al 2017). *Mimulus* is arguably one of the most important plant systems in the world for studies of speciation, as we know more about how species form in this group than perhaps any other. Therefore, the lack of alignment between empirical studies of speciation and taxonomic species delimitation seems like an missed opportunity. We thus call for a re-examination and a more rigorous review of this systematic treatment in a traditional peer-reviewed journal.

Reason 2: We do not believe that the name changes were necessary

The splintering of *Mimulus* into multiple genera has primarily been justified based on genera with distinct morphological features being nested within the same clade as traditional *Mimulus* species. Further, the strongest argument for the new nomenclature is that it has utility in placing genus names on groups that have distinct sets of morphological traits. We very much appreciate the contributions made by those who have identified taxonomically useful traits, which will surely be valuable for future research. However, the desired taxonomic hierarchy for the Phrymaceae could be designated with monophyletic sub-genera. The decision to elevate groups to the genus level versus the sub-genus level was a subjective nomenclatural decision. The differences in placentation cited by Barker et al. (2012) to justify elevating *Erythranthe* and *Diplacus* to the genus level have long been recognized (Grant 1924) and thus, do not on their own necessitate breaking up the genus *Mimulus.*

We should also point out that there was uncertainty among the taxonomists who made the suggested name changes on how to proceed with the nomenclature of this group. For example, Nesom (2011) initially renamed the genera *Hemichaena* and *Leucocarpus* to *Mimulus* stating: "*Hemichaena* and *Leucocarpus* are both justifiably accommodated as groups within the bounds of *Mimulus.*" And "In case that it proves desirable to maintain the Australian segregate genera, and to maintain *Phryma* as a distinct genus, the suggestion by Beardsley and Barker (2005) to conserve the name *Mimulus* with a species from within the American lineage is being followed (Nesom and N. Fraga, in prep.)." The following year, a reversal of this course of action was made with the publication of Barker & al. (2012). The contradictions between Nesom (2011) and Barker & al. (2012) clearly illustrate the subjective nature of decisions regarding nomenclature in this group and add to our concerns about the stability of its current circumscription.

Reason 3: *Mimulus* is well recognized in the scientific community

The name changes have already impacted a large number of scientists whose research is focused on *Mimulus*. Barker & al. (2012) dismissed the concerns of these scientists and argued that their research is focused on "relatively few species." The casual dismissal of the interests of the *Mimulus* scientific community by these authors is questionable for four reasons. First, the monkeyflower literature encompasses dozens of different *Mimulus* species across the broader clade (Vickery 1978; Cooley & al. 2011; Grossenbacher & Whittall 2011; Grossenbacher & al. 2014; Sobel 2014; Sheth & al. 2014; Sheth & Angert 2014; Chase & al. 2017; Kooyers & al. 2017; Peng & al. 2017; Li & al. 2018; Medel & al. 2018; Yuan 2019). Second, this argument mischaracterizes the size of the research community that studies *Mimulus*. There are now more than 40 labs worldwide that focus their research effort primarily, if not exclusively, on *Mimulus*. Few non-crop genera, beyond *Arabidopsis*, have this level of research activity. Third, the argument ignores the fact that the instability of nomenclature may cause scientists to lose track or overlook critical datasets, especially in large genomic (e.g. NCBI) and biodiversity (e.g. GBIF) databases. Finally, this research community identifies primarily by the name *Mimulus* and has spent considerable time over the last two decades building that community under the name *Mimulus*. The name *Mimulus* is widely recognized by our colleagues within the evolution community, by non-plant biologists, and by program officers at the National Science Foundation, Department of Energy, and National Institutes of Health. Instability in the names of these species therefore impedes communication of our discoveries to the broader scientific community and to funding agencies. For these reasons we have continued to use the name *Mimulus*.

Where do we go from here?

Since we still do not have a good sense of the historical relationships of the taxa in this group of plants, we suggest retaining the name *Mimulus* for all monkeyflowers until more phylogenetic data are available. Ideally, a more robust phylogeny will be developed soon, allowing for a new circumscription to be proposed prior to the International Botanical Congress in 2023. Once that phylogeny has been published, we suggest two routes for retaining the name *Mimulus* across as broad a swath of monkeyflowers as possible based on alternative phylogenetic topologies:

Suggestion 1.

If *Phryma* is found to be sister to all monkeyflowers, as in the nrDNA tree (Figure 1), we propose that all species within the monophyletic clade containing monkeyflowers be renamed as *Mimulus* (Option 2 of Barker & al. 2012). Grouping all of the species into one genus, *Mimulus*, would maximize name stability, which would be especially useful if new data suggest different phylogenetic relationships within the larger clade. While Option 4 of Barker & al. (2012) resulted in the renaming of at least 136 species, Option 2 results in the introduction of only 13 new name combinations. Further, as noted by Nesom (2011) and Barker & al. (2012), most of these species from *Uvedalia*, *Thyridia*, *Elacholoma*, *Hemichaena*, and *Leucocarpus* already have names in *Mimulus*.

Suggestion 2.

If *Phryma* is found to be nested within the clade containing monkeyflowers, as in the *trnL/F* (Figure 1), we also propose that the entire clade be renamed to *Mimulus*. However, if it is determined that renaming *Phryma* to *Mimulus* is untenable, we suggest that the name *Mimulus* be conserved across a much larger swath of the clade by changing the type species to a species within sub-genus *Synplacus* (Option 3 of Barker & al. 2012). We propose that *Mimulus guttatus* be designated as the new type species for *Mimulus*, as it is widely studied by scientists and geographically widespread across western North America. *Mimulus guttatus* occurs within the center of diversity of monkeyflowers, in contrast to *Mimulus ringens,* whose type species status is largely a historical artifact due to the east-to-west direction of exploration of North America by Europeans. The conservation of the name *Mimulus* by changing the type species would likely bring *Leucocarpus* and *Hemichaena* into *Mimulus*. However, *M. ringens* and the Australian monkeyflowers would likely need to be given a different genus name. Further, a new phylogeny may confirm the results of the nrDNA data and show that *M. guttatus* and *M. ringens* are actually more closely related to each other than they are to sub-genus *Schizoplacus*. This would potentially entail elevating *Schizoplacus* to the genus level. However, if *Schizoplacus* is found to be sister to *Synplacus*, we suggest that both sub-genera be named *Mimulus* following retypification. There is precedent for conservative name changes accomplished via designation of a new type specimen to maintain a genus name for a larger clade of species, as has been done with the genus *Acacia* (Orchard & Maslin 2005; McNeill & Turland 2011). The justifications for conserving *Acacia* with a new type are very similar to the justifications for conserving *Mimulus.*

We have provided several reasons above for why we have continued to use *Mimulus* to describe all monkeyflowers. Until modern genomic data can help resolve the considerable uncertainties described above, we will continue to use the name *Mimulus* in publications, presentations, and communication with the general public. In addition, we strongly advocate that *Mimulus* be used in databases and floras until the circumscription of this group is more stable.

AUTHOR CONTRIBUTIONS

All authors contributed to the writing of the manuscript.

LITERATURE CITED

Angert, A.L. 2009. The niche, limits to species' distributions, and spatiotemporal variation in demography across the elevation ranges of two monkeyflowers. *P. Natl. Acad. Sci. USA* 106: 19693–19698.

Baker, R.L. & Diggle, P.K. 2011. Node-specific branching and heterochronic changes underlie population-level differences in *Mimulus guttatus* (phrymaceae) shoot architecture. *Am. J. Bot.* 98: 1924–1934.

Baker, R.L., Hileman, L.C. & Diggle, P.K. 2012. Patterns of shoot architecture in locally adapted populations are linked to intraspecific differences in gene regulation. *New Phytol.* 196: 271–281.

Barker, W.R., Nesom, G.L., Beardsley, P.M. & Fraga, N.S. 2012. A taxonomic conspectus of Phrymaceae: a narrowed circumscription for Mimulus, new and resurrected genera, and new names and combinations. *Phytoneuron* 39: 1-60.

Beardsley, P.M. & Olmstead, R.G. 2002. Redefining Phrymaceae: the placement of *Mimulus*, tribe *Mimuleae*, and *Phryma*. *Am. J. of Bot.* 89: 1093-1102.

Beardsley, P.M., Schoenig, S.E., Whittall JB & Olmstead RG. 2004. Patterns of evolution in western North American *Mimulus* (Phrymaceae). *Am. J. Bot.* 91: 474-489.

Beardsley, P.M. & Barker, W.R. 2005. Patterns of evolution in Australian *Mimulus* and related genera (Phrymaceae~ Scrophulariaceae): a molecular phylogeny using chloroplast and nuclear sequence data. *Aust. Syst. Bot.* 18: 61-73.

Bock, D.G., Andrew, R.L. & Rieseberg L.H. 2014. On the adaptive value of cytoplasmic genomes in plants. *Mol. Ecol.* 23: 4899-4911.

Bradshaw, H.D., Wilbert, S.M., Otto, K.G. & Schemske, D.W. 1995. Genetic mapping of floral traits associated with reproductive isolation in monkeyflowers (*Mimulus*). *Nature* 376:762-765.

Bradshaw, H.D. & Schemske D.W. 2003. Allele substitution at a flower colour locus produces a pollinator shift in monkeyflowers. *Nature* 426: 176-178.

Brandvain, Y., Kenney, A.M., Flagel, L., Coop, G. & Sweigart, A.L. 2014. Speciation and introgression between *Mimulus nasutus* and *Mimulus guttatus*. PLoS Genetics 10: e1004410.

Byers, K.J.R.P., Vela, J.P., Peng F., Riffell, J.A. & Bradshaw H.D. 2014. Floral volatile alleles can contribute to pollinator-mediated reproductive isolation in monkeyflowers (*Mimulus*). *Plant J.* 80: 1031-1042.

Chase, M.A., Stankowski, S. & Streisfeld MA. 2017. Genomewide variation provides insight into evolutionary relationships in a monkeyflower species complex (*Mimulus* sect. Diplacus). *Am. J. Bot.* 104: 1510-1521.

Clausen J. & Hiesey W.M. 1958. Experimental studies on the nature of species. IV. Genetic structure of ecological races. Carnegie Institution of Washington Publication 615. Washington, DC.

Cooley A.M., Modliszewski, J.L. Rommel, M. & Willis J.H. 2011. Gene duplication in *Mimulus* underlies parallel floral evolution via independent trans-regulatory changes. *Curr. Biol.* 21: 700-704.

Darwin, C. 1876. The effects of cross and self fertilisation in the vegetable kingdom. D. Appleton and Company, New York, NY, USA.

Dudash M.R. & Carr D.E. 1998. Genetics underlying inbreeding depression in Mimulus with contrasting mating systems. *Nature* 393: 682.

Fenster, CB & Ritland, K. 1994. Quantitative genetics of mating system divergence in the yellow monkeyflower species complex. *Heredity* 73: 422-435.

Fenster, C.B., Diggle, P.K., Barrett, S.C. & Ritland, K. 1995. The genetics of floral development differentiating two species of *Mimulus* (Scrophulariaceae). Heredity 74: 258-266.

Ferris, K.G. & Willis, J.H. 2018. Differential adaptation to a harsh granite outcrop habitat between sympatric *Mimulus* species. *Evolution* 72: 1225-1241.

Fishman, L. & Saunders A. 2008. Centromere-associated female meiotic drive entails male fitness costs in monkeyflowers. *Science* 322: 1559-1562.

Grant, A.L. 1924. A monograph of the genus *Mimulus. Annals of the Missouri Botanical Garden* 11: 99-388.

Greenham, K., Lou, P., Puzey, J.R., Kumar, G., Arnevik, C., Farid, H., Willis, J.H. & McClung, C.R. 2017. Geographic variation of plant circadian clock function in natural and agricultural settings. *J. Biol. Rhythm.* 32: 26-34.

Grossenbacher, D.L. & Whittall, J.B. 2011. Increased floral divergence in sympatric monkeyflowers. *Evolution* 65: 2712-2718.

Grossenbacher, D.L., Veloz, S.D. & Sexton, J.P. 2014. Niche and range size patterns suggest that speciation begins in small, ecologically diverged populations in North American monkeyflowers (*Mimulus* spp.). *Evolution* 68: 1270-1280.

Hellsten, U., Wright, K.M., Jenkins, J., Shu, S., Yuan, Y., Wessler, S.R., Schmutz, J., Willis, J.H. & Rokhsar, D.S. 2013. Fine-scale variation in meiotic recombination in Mimulus inferred from population shotgun sequencing. *P. Natl. Acad. Sci. USA* 110: 19478-19482.

Hiesey, W.M., Nobs, M.A. & Björkman, O. 1971. Experimental studies on the nature of species. V. Biosystematics, genetics, and physiological ecology of the *Erythranthe* section of *Mimulus*. Carnegie Institute of Washington Publication, 628, 1-213.

Kooyers N.J., Greenlee A.B., Colicchio J.M., Oh M., & Blackman B.K. 2015. Replicate altitudinal clines reveal that evolutionary flexibility underlies adaptation to drought stress in annual *Mimulus guttatus*. *New Phyt.* 206: 152-165.

Kooyers N.J., James B., & Blackman B.K. 2017. Competition drives trait evolution and character displacement between *Mimulus* species along an environmental gradient. *Evolution* 71: 1205–1221.

Li, Q., Grossenbacher, D.L. & Angert AL. 2018. The effect of range overlap on ecological niche divergence depends on spatial scale in monkeyflowers. *Evolution* 72: 2100-2113.

Lowry, D.B & Willis, J.H. 2010 A widespread chromosomal inversion polymorphism contributes to a major life-history transition, local adaptation, and reproductive isolation. *PLoS Biol.* 8: e1000500.

McKain, M.R., Johnson, M.G., Uribe-Convers, S., Eaton, D. & Yang, Y. 2018. Practical considerations for plant phylogenomics. *Appl. Plant Sci.* 6: e10.

McNeill, J. & Turland, N.J. 2011. Major changes to the code of nomenclature—Melbourne, July 2011. *Taxon* 60: 1495-1497.

Medel, R., Gonzalez-Browne, C., Salazar, D., Ferrer, P. & Ehrenfeld, M. 2018. The most effective pollinator principle applies to new invasive pollinators. *Biol. Lett.* 14: 5.

Moody, A., Diggle, P.K. & Steingraeber, D.A. 1999. Developmental Analysis of the Evolutionary Origin of Vegetative Propagules in *Mimulus gemmiparus* (Scrophulariaceae). *Am. J. Bot.* 86: 1512–1522.

Nesom, G.L. 2011. Recognition and synopsis of *Mimulus* sect. *Tropanthus* and sect. *Leucocarpus* (Phrymaceae). *Phytoneuron* 28: 1–8.

Nesom, G.L. 2014. Updated classification and hypothetical phylogeny of *Erythranthe* sect. Simiola (Phrymaceae). *Phytoneuron* 81: 1–6.

Oneal, E., Lowry, D.B., Wright, K.M., Zhu, Z. & Willis, J.H. 2014. Divergent population structure and climate associations of a chromosomal inversion polymorphism across the M imulus guttatus species complex. *Mol. Ecol.* 23: 2844-2860.

Orchard, A.E., Maslin, B.R. 2005. The case for conserving *Acacia* with a new type. *Taxon*. 54: 509-512.

Pease, J.B., Haak, D.C., Hahn, M.W., Moyle, L.C. 2016. Phylogenomics reveals three sources of adaptive variation during a rapid radiation. *PLoS Biol.* 14: e1002379.

Peng F., Byers K.J., & Bradshaw H.D. 2017. Less is more: Independent loss-of-function OCIMENE SYNTHASE alleles parallel pollination syndrome diversification in monkeyflowers (*Mimulus*). *Am. J. Bot.* 104: 1055-1059.

Peterson, M.L., Kay, K.M. & Angert, A.L. 2016. The scale of local adaptation in Mimulus guttatus: comparing life history races, ecotypes, and populations. *New Phytol.* 211: 345-356.

Ramsey, J., Bradshaw, H.D., Schemske, D.W. 2003. Components of reproductive isolation between the monkeyflowers *Mimulus lewisii* and *M. cardinalis* (Phrymaceae). *Evolution* 57: 1520-1534.

Rieseberg, L.H. & Soltis, D.E. 1991. Phylogenetic consequences of cytoplasmic gene flow in plants. *Evol. Trend. Plant.* 5: 65-84.

Schemske, D.W. & Bradshaw, H.D. 1999. Pollinator preference and the evolution of floral traits in monkeyflowers (*Mimulus*). *P. Natl. Acad. Sci. USA* 96: 11910-11915.

Sexton, J.P., Strauss, S.Y., & Rice, K.J. 2011. Gene flow increases fitness at the warm edge of a species' range. *P. Natl. Acad. Sci. USA* 108:11704-11709.

Sheth, S.N. & Angert, A.L. 2014. The evolution of environmental tolerance and range size: a comparison of geographically restricted and widespread *Mimulus*. *Evolution*. 68: 2917-2931.

Sheth, S.N, Jiménez, I., &Angert, A.L. 2014. Identifying the paths leading to variation in geographical range size in western North American monkeyflowers. *J. Biogeogr.* 41: 2344-2356.

Sobel, J.M. 2014 Ecogeographic isolation and speciation in the genus *Mimulus*. *Am. Nat.* 184: 565-579.

Sobel, J.M. & Streisfeld, M.A. 2015. Strong premating reproductive isolation drives incipient speciation in *Mimulus aurantiacus*. *Evolution* 69: 447-461.

Stankowski, S., & Streisfeld, M.A. 2015. Introgressive hybridization facilitates adaptive divergence in a recent radiation of monkeyflowers. *Proceedings of the Royal Society B: Biological Sciences* 282: 20151666.

Stankowski, S., Sobel, J.M., Streisfeld, M.A. 2017. Geographic cline analysis as a tool for studying genome-wide variation: a case study of pollinator-mediated divergence in a monkeyflower. *Mol. Ecol.* 26: 107-122.

Thompson, D.M. 2005. Systematics of *Mimulus* subgenus *Schizoplacus* (Scrophulariaceae). *Syst. Bot.* 75: 1-213.

Tulig, M.C., & Nesom, G.L. 2012. Taxonomic overview of *Diplacus* sect. *Diplacus* (Phrymaceae). Phytoneuron 45: 1-20.

Troth, A., Puzey, J.R., im, R.S., Willis, J.H. & Kelly, J.K. 2018. Selective trade-offs maintain alleles underpinning complex trait variation in plants. *Science* 361: 475-478.

Twyford, A.D. & Friedman J. 2015 Adaptive divergence in the monkeyflower *Mimulus guttatus* is maintained by a chromosomal inversion. *Evolution* 69: 1476-1486.

Twyford, A.D., Streisfeld, M.A., Lowry, D.B. & Friedman, J. 2015 Genomic studies on the nature of species: adaptation and speciation in *Mimulus*. *Mol. Ecol.* 24: 2601-2609.

Uribe-Convers, S., Settles, M.L., & Tank, D.C. 2016. A phylogenomic approach based on PCR target enrichment and high throughput sequencing: Resolving the diversity within the South American species of *Bartsia* L. (Orobanchaceae). *PLoS One* 11: e0148203.

Vallejo-Marín, M. 2012. *Mimulus peregrinus* (Phrymaceae): A new British allopolyploid species. *Phytokeys* 14: 1-14.

Vallejo-Marín, M., Buggs, R. J., Cooley, A. M., & Puzey, J. R. 2015. Speciation by genome duplication: Repeated origins and genomic composition of the recently formed allopolyploid species *Mimulus peregrinus*. *Evolution* 69: 1487-1500.

Vickery, R.K. 1952. A study of the genetic relationships in a sample of the *Mimulus guttatus* complex. PhD Dissertation Dept. of Biological Sciences, Stanford University.

Vickery, R.K. 1978. Case studies in the evolution of species complexes in *Mimulus*. *Evol. Biol.* 11: 405-507.

Wright, K.M., Lloyd, D., Lowry, D.B., Macnair, M.R. & Willis JH. 2013. Indirect evolution of hybrid lethality due to linkage with selected locus in *Mimulus guttatus*. *PLoS Biol.* 11, e1001497.

Wu, C.A. & Campbell, D.R. 2007. Leaf physiology reflects environmental differences and cytoplasmic background in *Ipomopsis* (Polemoniaceae) hybrids. *Am. J. Bot.* 94: 1804-1812.

Wu, C.A., Lowry, D.B., Cooley, A.M., Wright, K.M., Lee, Y.W. & Willis, J.H. 2008. Mimulus is an emerging model system for the integration of ecological and genomic studies. *Heredity* 100: 220-230.

Yuan, Y.W. 2019. Monkeyflowers (*Mimulus*): new model for plant developmental genetics and evo-devo. *New Phytol.* 222: 694-700.

Zuellig M.P. & Sweigart A.L. 2018. A two-locus hybrid incompatibility is widespread, polymorphic, and active in natural populations of *Mimulus*. Evolution 72: 2394-2405.

FIGURE LEGENDS

Figure 1. Phylogenetic hypotheses in the monkeyflowers (redrawn from data presented in Beardsley and Olmstead 2002 and Beardsley & al 2004). The type specimen for the genus *Mimulus* is the eastern North American species *M. ringens*, which appears to be sister to a radiation of Australian taxa. Grant (1924) separated *Mimulus* into two sub-genera based on morphological traits, *Synplacus* and *Schizoplacus*. These highly diverse groups are further divided into cohesive morphological sections that contain several well-studied ecological model systems, such as *M. guttatus, M. lewisii*, and *M. aurantiacus*. Phylogenies based on DNA sequences indicate that several very small genera are nested within the diversity present in *Mimulus:* e.g. *Leucocarpus, Berendtiella, Hemichaena,* and *Phryma.* However, phylogenetic hypotheses are based on only a small number of chloroplast (*trnL/F*) and nuclear loci (*ITS/ETS*), and substantial uncertainty exists at levels relevant to recent taxonomic revisions. For example, *Phryma* (dashed) is placed sister to the entire group according to the nuclear loci (nrDNA), and nested within *Mimulus* for the chloroplast locus (cpDNA). Further, the placement of *M. ringens* and related Australian species is uncertain (bold), with nrDNA indicating them to be sister to subgenus *Synplacus*, and cpDNA placing them sister to the entire group. Bold and dashed branches are used to highlight discordances between the nrDNA and cpDNA phylogenies.