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

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

2
3 **Running Title: *Mimulus* for all monkeyflowers**

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93 The genus *Mimulus* is a well-studied group of plant species, which has for decades allowed
94 researchers to address a wide array of fundamental questions in biology (Wu & al. 2008;
95 Twyford & al. 2015). Linnaeus named the type species of *Mimulus* (*ringens* L.), while Darwin
96 (1876) used *Mimulus* (*luteus* L.) to answer key research questions. The incredible phenotypic
97 diversity of this group has made it the focus of ecological and evolutionary study since the mid-
98 20th century, initiated by the influential work of Clausen, Keck, and Hiesey as well as their
99 students and collaborators (Clausen & Hiesey 1958; Hiesey & al. 1971, Vickery 1952, 1978).
100 Research has continued on this group of diverse taxa throughout the 20th and into the 21st century
101 (Bradshaw & al. 1995; Schemske & Bradshaw 1999; Wu & al. 2008; Twyford & al. 2015; Yuan
102 2019), and *Mimulus guttatus* was one of the first non-model plants to be selected for full genome
103 sequencing (Hellsten & al. 2013). *Mimulus* has played a key role in advancing our general
104 understanding of the evolution of pollinator shifts (Bradshaw & Schemske 2003; Cooley & al.
105 2011; Byers & al. 2014), adaptation (Lowry & Willis 2010; Kooyers & al. 2015; Peterson & al.
106 2016; Ferris & Willis 2018; Troth & al. 2018), speciation (Ramsey & al. 2003; Wright & al.
107 2013; Sobel & Streisfeld 2015; Zuellig & Sweigart 2018), meiotic drive (Fishman & Saunders
108 2008), polyploidy (Vallejo-Marín 2012; Vallejo-Marín & al. 2015), range limits (Angert 2009;
109 Sexton et al. 2011; Grossenbacher & al. 2014; Sheth & Angert 2014), circadian rhythms
110 (Greenham & al. 2017), genetic recombination (Hellsten & al. 2013), mating systems (Fenster &
111 Ritland 1994; Dudash & Carr 1998; Brandvain & al. 2014) and developmental biology (Moody
112 & al. 1999; Baker & al. 2011, 2012; Yuan 2019). This combination of a rich history of study
113 coupled with sustained modern research activity is unparalleled among angiosperms. Across
114 many interested parties, the name *Mimulus* therefore takes on tremendous biological significance
115 and is recognizable not only by botanists, but also by zoologists, horticulturalists, naturalists, and
116 members of the biomedical community. Names associated with a taxonomic group of this
117 prominence should have substantial inertia, and disruptive name changes should be avoided. As
118 members of the *Mimulus* community, we advocate retaining the genus name *Mimulus* to describe
119 all monkeyflowers. This is despite recent nomenclature changes that have led to a renaming of
120 most monkeyflower species to other genera.

121

122 **How did we get here?**

123

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

135

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

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

149
150 The nomenclatural suggestions made by Barker & al. (2012) have now been adopted by multiple
151 floras, including the Plants of the World Online, the Oregon Flora Project (Oregon State
152 University), and the Jepson eFlora, and are under review at the Flora of North America. In
153 addition, online resources such as the National Center for Biotechnology Information (NCBI),
154 Global Biodiversity Information Facility (GBIF), UniProt, and iNaturalist now use the names
155 from Barker & al. (2012) in lieu of the older classification. Given the widespread and rapid
156 acceptance of the Barker & al. (2012) circumscription, it may be perplexing as to why so many
157 scientists have continued to use the name *Mimulus*. There are three key reasons why the use of
158 *Mimulus* will likely continue by this group of scientists into the future.

159
160 **Reason 1: The botanical community needs a stable circumscription for monkeyflowers**
161

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

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

198
199 It is quite possible that new phylogenetic data will completely upend our current understanding
200 of relationships among species in the Phrymaceae. Thus, our position is that no new
201 nomenclatural changes should be adopted until there is a better understanding of the species tree
202 in this group. It has always been our position that it was premature to rename most of the genus
203 *Mimulus* based on two discordant gene phylogenies, as was done by Barker & al. (2012). Our
204 concern is that prematurely switching to new names may cause additional confusion in the
205 literature, particularly if more robust systematic data are consistent with retaining the original
206 name or indicate yet another name change. Thus, we are reluctant to adopt a new circumscription
207 until we are more assured of its stability. We are not alone in our desire for stability, which has
208 been pointed out by others, including Orchard & Maslin (2005): "Taxonomists must recognize
209 that nomenclature is not a plaything of taxonomy, molecular phylogeny, cladistics or any other
210 special interest group. It is a working tool (a filing system) for all biologists, professional and
211 amateur, and for the wider community, and to be meaningful it needs to be as stable as possible.
212 A naming system that continually changes is not a naming system at all and will be discarded or
213 disregarded."

214
215 Finally, we are concerned about the stability of the current circumscription by Barker & al.
216 (2012) given that it may not have been sufficiently vetted by peer review. The manuscript was
217 published in *Phytoneuron*, a journal edited by a coauthor on that paper. The editorial policy of
218 *Phytoneuron* states "Submissions will be reviewed for content and style by the editor, based on
219 his own knowledge and expertise. If deemed appropriate or necessary by the editor, review by
220 other botanical peers will be sought. An indication of the *Phytoneuron* review process (if beyond
221 the Editor) will appear in the Acknowledgements." The manuscript's acknowledgements in the
222 published paper contain no information about editorial or peer review, other than acknowledging
223 comments "on a late draft" by two colleagues. Subsequent work by Nesom (2014), published in
224 *Phytoneuron*, is also inconsistent with scientific knowledge of species-level relationships within
225 the section *Simiolus* of *Mimulus*. For example, Nesom divided annual and perennial populations
226 of *M. guttatus* into two separate species, *Erythranthe guttata* and *E. microphylla*, respectively.
227 Justification for this splitting is directly contradicted by population genetic data, which
228 demonstrate free genetic exchange between annual and perennial populations of *M. guttatus*
229 (Oneal & al. 2014; Twyford & Friedman 2015). Similarly, Tulig & Nesom (2012) recently
230 elevated several taxa within the *M. aurantiacus* complex to species rank based solely on

231 morphological information. Hybrid zones have been well documented for sub-species of *M.*
232 *aurantiacus* (Thompson 2005), and subsequent work indicates substantial gene flow across these
233 points of contact between incompletely isolated taxa (Sobel & Streisfeld 2015, Stankowski et al
234 2017). *Mimulus* is arguably one of the most important plant systems in the world for studies of
235 speciation, as we know more about how species form in this group than perhaps any other.
236 Therefore, the lack of alignment between empirical studies of speciation and taxonomic species
237 delimitation seems like a missed opportunity. We thus call for a re-examination and a more
238 rigorous review of this systematic treatment in a traditional peer-reviewed journal.

239

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

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

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

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

264

265 The name changes have already impacted a large number of scientists whose research is focused
266 on *Mimulus*. Barker & al. (2012) dismissed the concerns of these scientists and argued that their
267 research is focused on “relatively few species.” The casual dismissal of the interests of the
268 *Mimulus* scientific community by these authors is questionable for four reasons. First, the
269 monkeyflower literature encompasses dozens of different *Mimulus* species across the broader
270 clade (Vickery 1978; Cooley & al. 2011; Grossenbacher & Whittall 2011; Grossenbacher & al.
271 2014; Sobel 2014; Sheth & al. 2014; Sheth & Angert 2014; Chase & al. 2017; Kooyers & al.
272 2017; Peng & al. 2017; Li & al. 2018; Medel & al. 2018; Yuan 2019). Second, this argument
273 mischaracterizes the size of the research community that studies *Mimulus*. There are now more

274 than 40 labs worldwide that focus their research effort primarily, if not exclusively, on *Mimulus*.
275 Few non-crop genera, beyond *Arabidopsis*, have this level of research activity. Third, the
276 argument ignores the fact that the instability of nomenclature may cause scientists to lose track
277 or overlook critical datasets, especially in large genomic (e.g. NCBI) and biodiversity (e.g.
278 GBIF) databases. Finally, this research community identifies primarily by the name *Mimulus* and
279 has spent considerable time over the last two decades building that community under the name
280 *Mimulus*. The name *Mimulus* is widely recognized by our colleagues within the evolution
281 community, by non-plant biologists, and by program officers at the National Science Foundation,
282 Department of Energy, and National Institutes of Health. Instability in the names of these species
283 therefore impedes communication of our discoveries to the broader scientific community and to
284 funding agencies. For these reasons we have continued to use the name *Mimulus*.

285

286 **Where do we go from here?**

287

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

294

295 Suggestion 1.

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

305

306 Suggestion 2.

307 If *Phryma* is found to be nested within the clade containing monkeyflowers, as in the *trnL/F*
308 (Figure 1), we also propose that the entire clade be renamed to *Mimulus*. However, if it is
309 determined that renaming *Phryma* to *Mimulus* is untenable, we suggest that the name *Mimulus*
310 be conserved across a much larger swath of the clade by changing the type species to a species
311 within sub-genus *Synplacus* (Option 3 of Barker & al. 2012). We propose that *Mimulus guttatus*
312 be designated as the new type species for *Mimulus*, as it is widely studied by scientists and
313 geographically widespread across western North America. *Mimulus guttatus* occurs within the
314 center of diversity of monkeyflowers, in contrast to *Mimulus ringens*, whose type species status
315 is largely a historical artifact due to the east-to-west direction of exploration of North America
316 by Europeans. The conservation of the name *Mimulus* by changing the type species would likely
317 bring *Leucocarpus* and *Hemichaena* into *Mimulus*. However, *M. ringens* and the Australian
318 monkeyflowers would likely need to be given a different genus name. Further, a new phylogeny
319 may confirm the results of the nrDNA data and show that *M. guttatus* and *M. ringens* are actually

320 more closely related to each other than they are to sub-genus *Schizoplacus*. This would
321 potentially entail elevating *Schizoplacus* to the genus level. However, if *Schizoplacus* is found to
322 be sister to *Synplacus*, we suggest that both sub-genera be named *Mimulus* following
323 retypification. There is precedent for conservative name changes accomplished via designation
324 of a new type specimen to maintain a genus name for a larger clade of species, as has been done
325 with the genus *Acacia* (Orchard & Maslin 2005; McNeill & Turland 2011). The justifications for
326 conserving *Acacia* with a new type are very similar to the justifications for conserving *Mimulus*.

327
328 We have provided several reasons above for why we have continued to use *Mimulus* to describe
329 all monkeyflowers. Until modern genomic data can help resolve the considerable uncertainties
330 described above, we will continue to use the name *Mimulus* in publications, presentations, and
331 communication with the general public. In addition, we strongly advocate that *Mimulus* be used
332 in databases and floras until the circumscription of this group is more stable.

333

334 AUTHOR CONTRIBUTIONS

335

336 All authors contributed to the writing of the manuscript.

337

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596 **FIGURE LEGENDS**

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

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