

1 **Appendix S12**

2 **Critique of Suaza-Gaviria et al. 2017**

3 We perceive many problems in the paper by Suaza-Gaviria, González, and Pabón-
4 Mora (2017) (hereafter SGP), and here express our concerns. We present our critique in
5 two forms. The first is a general critique and the second is a line-by-line critique. There is
6 some unavoidable overlap in information between these two critiques.

7
8 **GENERAL CRITIQUE**

9 **Terminology**

10 The existing literature is already replete with terms used to describe the morphology
11 of flowers and inflorescences in Santalales. Moreover, the unusual inflorescence type
12 seen in *Phoradendreae* has required the use of specialized terms to describe features that
13 are, in some cases, unique among angiosperms. Unfortunately, SGP failed to utilize
14 existing terms and at the same time introduced unorthodox or inappropriate new terms,
15 often inadequately defined, that resulted in frequent confusion in the text.

16
17 **Fig. 7 in SGP and the Concept of Dichasium**

18 In terms of the tree shown in Fig. 7, the authors have generated their own (unique)
19 topology based on several molecular phylogenetic studies from Nickrent et al. (2010) and
20 earlier. Not considered is the more recent analysis (Su et al., 2015) where more genes and
21 more taxa were included. Although the topology at the base of their tree is correct,
22 intergeneric relationships within Viscaceae are depicted as fully resolved, which they are
23 not. Several molecular phylogenies have been published that addressed intergeneric

24 relationships in Viscaceae: Der and Nickrent (2008), Mathiasen et al. (2008), Su et al.
25 (2015), and the present work (Fig. 1). Sister relationships that appear solid are
26 *Korthalsella* with *Ginalloa* and *Phoradendron* with *Dendrophthora*. The relationships
27 among the other three genera (*Arceuthobium*, *Notothixos*, and *Viscum*) have been
28 unresolved.

29 As shown by the diagrams and scoring of the matrix in Fig. 7, SGP have adopted a
30 very liberal concept of what constitutes a dichasium. In fact, they have constrained all
31 members of the order into the cymose (vs. racemose) branching pattern and within that
32 type, only dichasia (and their reductional derivatives) were allowed. The losses of flowers
33 shown as “x” on the Fig. 7 diagrams are in nearly all cases not backed up by any
34 developmental or comparative morphological evidence and stand in contrast to
35 inflorescence descriptions in the literature. The information presented in Fig. 7 is a
36 mixture of factual information and interpretations presented as facts. In addition, the
37 scoring of the matrix is incomplete and in many cases erroneous. Because of these
38 problems, we feel it is best to question every single entry (and blank cell) in the matrix.
39 For the purposes of this review, we have designated the diagrammatic inflorescence
40 figures at the bottom of the matrix A through I (left to right). Not all entries are critiqued
41 but here we discuss the following examples.

42 Schoepfiaceae

43 Schoepfiaceae is scored as having single flowers with abortive second order axes but
44 with bracteoles (type B) or with a single flower on the first order axis with no second
45 order axes and no residual bracteoles (type C). As shown in Appendix S3, the branching
46 pattern for Schoepfiaceae is mainly racemose. This is especially true for two genera now

47 known to be in this family, *Arjona* and *Quinchamalium* that have spikes or racemes. Most
48 authors score *Schoepfia* as having racemes and spikes. Inflorescence type C is
49 represented is scored for 9 of the 16 taxa on the phylogenetic tree, but many of these
50 entries must be questioned.

51 Loranthaceae

52 For Loranthaceae, the full suite of inflorescence types seen in the family is not
53 properly represented in Fig. 7. This scoring gives the impression that only determinate
54 partial inflorescences are found in Loranthaceae, however, both determinate and
55 indeterminate types occur (sometimes in the same inflorescence – i.e. thyrsoid types). For
56 *Psittacanthus*, *Passovia*, and nearly all *Struthanthus*, species have indeterminate
57 inflorescences. In contrast, nearly all *Cladocolea* and *Peristethium* species form
58 inflorescences morphologically terminated by a single flower, and are thus determinate
59 (this includes the *P. archeri* that GSP erroneously call indeterminate). Whether the three-
60 flowered partial inflorescences (or their reductional derivatives) are called a dichasium or
61 not is discussed in text. We, and a number of other authors, have taken a more
62 conservative approach and use the noncommittal term “triad” for the 3-flowered
63 condition. Some of these may be dichasial and some may not, however, the
64 developmental studies to ascertain which is which have generally not been conducted.
65 Moreover, for our Bayesian analyses, we have been extremely liberal and allowed triad to
66 be included with dichasium when producing the matrix for BayesTraits. This does not
67 mean we believe these terms are synonymous (see text).

68

69

70 Thesiaceae

71 Thesiaceae is an example where the Fig. 7 matrix is incompletely scored. This family
72 contains the large genus *Thesium* (ca. 350 species), members of which have at least 11
73 distinct inflorescence types that include both determinate and indeterminate types
74 (Nickrent, unpublished data). The family is represented in Fig. 7 by dichasia (type A) and
75 dichasia reduced to a single terminal flower (type B). Certainly, *Thesium* taxa exist that
76 have monochasia (type F), in contrast to the statement “rarely, the partial inflorescence
77 becomes a monochasium.”

78 Santalaceae

79 Type D (dyads) do not occur in Santalaceae (nor in Misodendraceae, Cervantesiaceae,
80 or Nanodeaceae). The male inflorescence of *Antidaphne viscoidea* is a raceme
81 (indeterminate) with no bracteoles subtending the individual flowers. Fig. 18a from Kuijt
82 (1988) with a cluster of three, sessile female flowers is cited as evidence that the partial
83 inflorescence is a dichasium (this term was not used here by Kuijt). Again, no bracteoles
84 are associated with this cluster. This arrangement could equally arise from metatopic
85 displacement such as concaulescence occurring on a racemose inflorescence. To call the
86 female inflorescence a dichasium is unwarranted and speculative.

87 Viscaceae

88 A “dichasium” that lacks bracteoles (type E) is scored for all Viscaceae genera in Fig.
89 7. This type is rarely seen in *Arceuthobium*, *Korthalsella* or *Ginalloa* and certainly for
90 *Phoradendron* and *Dendrophthora*. Position effects in crowded axillary groups of
91 flowers (*Korthalsella*) do not readily translate into the designation of dichasia. For the
92 eight species of *Notothixos*, most have a fan-like arrangement of flowers referred to in the

93 literature as cymes or cymules. This arrangement is similar to some dichasial *Viscum*
94 where supplementary partial inflorescences develop in the bracteolar nodes, thus
95 appearing superposed. Barlow (1984) describes the cymules as solitary or in determinate
96 or indeterminate conflorescences. An inflorescence of *N. cornifolius* is illustrated in Kuijt
97 (1969 p. 30, Fig. 2-17b). It is apparently this type that is equated with inflorescence type
98 H in Fig. 7, thereby yielding a synapomorphy with *Phoradendreae* (uniseriate, type 2a).
99 This is clearly a case of unwarranted interpretation and speculation as to the homology of
100 these phenotypes. Although a quote from Kuijt (1961) is provided to support this
101 relationship, an earlier quote from the same author (Kuijt, 1959 p. 542) could be
102 proffered: “To conclude on the basis of such a similarity that *Notothixos* is closely related
103 to *Phoradendreae* would indeed be incautious, as evolutionary convergencies (sic)
104 abound in the Viscoideae”. Molecular evidence indicate that *Notothixos* is **not** closely
105 related to *Phoradendreae* (see Fig. 1, this manuscript); thus, the flattened cymule of
106 *Notothixos* must have been derived independently from the 2a inflorescence type of
107 *Phoradendreae*.

108 Indeed, the terms cyme and dichasium have been used to describe inflorescences in
109 *Viscum*. Engler and Krause (1935) indicated *Viscum* inflorescences are composed of
110 simple cymes which are 3-flowered or only 1-flowered as a result of reduction of the
111 lateral flowers. Similarly, Sanjai and Balakrishnan (2006) in their revision of Indian
112 Viscaceae follow Danser (1941) where *Viscum* is said to possess only cymes and, for the
113 3-flowered situation, triads. Similar terminology was used by Barlow (1984); (Barlow,
114 1996). The term dichasium was used by Polhill and Wiens (1998) and Kirkup, Polhill,

115 and Wiens (2000). To our knowledge, there has been no developmental studies conducted
116 on *Viscum* that might provide evidence for the presence of dichasia.

117

118 **Choice of Taxa**

119 Another major concern about the SGP study is their choice of taxa. Only taxa from
120 the Andean area were selected; their coverage included species from *Aetanthus*,
121 *Antidaphne*, *Gaiadendron*, *Oryctanthus*, *Passovia*, *Peristethium*, *Phoradendron*, and
122 *Struthanthus* (The latter is not mentioned, but SGP misidentified “*Passovia* sp.” in Figs.
123 5C-E; it represents a species of *Struthanthus*). Curiously, the largest loranthaceous genus
124 present, *Psittacanthus*, receives no mention in the paper. Other Andean genera not
125 utilized are *Cladocolea*, *Dendrophthora*, *Desmaria*, *Lepidoceras*, *Ligaria*, *Phthirusa*,
126 *Tripodanthus*, and *Tristerix*. This omission of 8 out of 16 genera is serious as some of
127 these genera exhibit unusual inflorescence types or (*Phthirusa*) lack inflorescences
128 entirely and are thus not taken into account by SGP. Within the chosen genera, only in
129 *Phoradendron* is more than one species included. The rationale for the selection of
130 genera and species is not explained. It is significant that neither *Cladocolea* nor *Phthirusa*
131 is mentioned, for they would pose difficult problems for SGP; both genera occur in the
132 Andean area.

133 Our concern with the selection of species is sharpened by the SGP omission of
134 relevant literature or their contents. For example, their repeated reference to
135 *Arceuthobium* inflorescences is done without reference to the detailed exploration of the
136 branching pattern in the genus (Kuijt, 1970). Sexual dimorphism in inflorescences,

137 present in numerous species, has received no mention. No substantial reference is made
138 to the world-wide survey of loranthaceous inflorescences by Kuijt (1981).

139 It may also be questioned whether a few selected mistletoe species, limited to a
140 certain geographical area, can provide an adequate basis for reaching conclusions that
141 extend across a very large order spread around the globe. This reach by SGP is indicated
142 clearly in the Abstract, where it is stated that dichasia are plesiomorphic in the entire
143 order Santalales. Five of the 11 families shown in Fig. 7 contain mistletoes, thus the
144 remaining six are composed of root hemiparasites. Among the mistletoes, those in
145 Amphorogynaceae and Misodendraceae were not included in the morphological and
146 anatomical investigations. And again, to truly address the issue of inflorescence types in
147 the entire order, equal attention should be given to the root hemiparasites as to the
148 mistletoes.

149 **Inflorescences in *Phoradendreae***

150 One of the major concepts proposed by SGP, reflected in the matrix scoring in Fig. 7,
151 is that the basic inflorescence type seen in *Phoradendreae* is a dichasium or a derivation
152 of one or more dichasia. This is based upon photographs of living and preserved
153 specimens as well as anatomical sections (light microscopy) and SEM images. SGP
154 introduced a new term and concept called the “floral row” which was used to describe a
155 horizontal grouping of flowers and this was equated with dichasium. The primary
156 evidence that such a morphological grouping of flowers exists (and is dichasial) is the
157 fact that an apical flower occurs above and is slightly older than the two lateral flowers
158 below it (see Fig. 2I). SGP state: “A floral row is a transverse series of flowers in each
159 floral group formed by an odd number of flowers (3, 5, 7, or 9).” This definition is

160 problematic for several reasons. First, a transverse cut through an inflorescence would not
161 pass through all three flowers because the terminal one occurs higher than the laterals.
162 Also, in the 1a (biseriate) type of inflorescence, once the top three flowers are assigned to
163 a “floral row”, only two, not three, flowers remain in each of the lower rows. Here one
164 would have to envision loss of all the terminal flowers for each row, a fact acknowledged
165 by the authors in their Discussion (p. 35); a parallel argument would apply to uniseriate
166 inflorescences. Also, the multiseriate inflorescence type is not accounted for under the
167 dichasium hypothesis. This type occurs in a number of species including *P. falcatum*, *P.*
168 *jalicense*, *P. longifolium*, and *P. leucarpum* but is erroneously denied by SGP.

169 SGP attempted to use vascular trace information to confirm the existence of dichasia
170 in the fertile internodes of *Phoradendreae*. Neither the longitudinal nor transverse
171 sections shown in Fig. 4 (or their Appendix S1) provide convincing evidence that the
172 pattern of strands (traces) forms a system resembling a dichasium. This confirms
173 previous observations such as (Kuijt, 1959 Fig. 10e, 16, 17). Interestingly, in their
174 Discussion SGP state “Although this vascular pattern was previously described by York
175 (1913) and Kuijt (1959), it has not been directly taken as evidence of a condensed system
176 of fused branches” which acknowledges that those authors did not extrapolate beyond
177 available evidence. Thus, there is no evidence from vascular anatomy to support the
178 claim that floral rows are dichasia (or triads), or for that matter, that such rows even are
179 morphological entities. Because the flowers of *Phoradendreae* are sessile and lack
180 bracteoles, the only evidence supporting the concept of a dichasium is the presence in
181 triseriate species of three flowers where the apical is older than the younger laterals.

182 Moreover, there is no anatomical evidence to support the idea that the fertile
183 internodes are coenosomes. Typically cymose partial inflorescences are involved in
184 forming coenosomes (Endress, pers. comm.). Moreover, SGP compare inflorescences of
185 Phoradendreae with those of certain Boraginaceae that possess “syndesmies”, however,
186 these only occur in specialized thyrses with cymes seen in some Boraginaceae that are
187 monochasial. Thus, the inflorescences of Boraginaceae and Santalales are
188 morphologically different.

189 The serial floral arrangement on the fertile internodes of *Phoradendreae* has been
190 much illustrated and discussed in the past (Eichler, 1868, 1878), and as defined above,
191 involves elongating internodes and thus are driven by an intercalary meristem at each
192 base, in such a fashion that the oldest flowers are at the top of the internode and the
193 youngest at the base. SGP do not deny that an intercalary meristem is active at the lowest
194 end of fertile internodes in *Phoradendreae*. However, they deny that individual flowers
195 are generated there; only “floral rows” or “dichasia” are. We would maintain that this
196 distinction is specious; it is difficult if not impossible to visualize how a transverse “floral
197 row” of three flowers can be initiated without the individual flowers being generated. Fig.
198 2G clearly shows the basal origin of an individual flower from the intercalary meristem,
199 with two other, lateral flowers scarcely initiated. It cannot be denied that the upper flower
200 was initiated separately from, and ahead of the other two. The SGP view makes even less
201 sense when considering the numerous *Dendrophthora* species that have uniseriate
202 flowers. We meet with some paradoxical statements seemingly denying the obvious: “No
203 evidence of intercalary meristematic activity connecting the flowers with the
204 inflorescence axis was detected”. Since all flowers of these genera are directly attached to

205 the inflorescence axis, we are puzzled by this statement. The vascular supply of the
206 mature *Phoradendron* flower is attached to that of the inflorescence axis (see Kuijt, 1959
207 Fig. 12c); this is especially evident in *Dendrophthora flagelliformis* (Kuijt, 1969 Fig. 9-
208 11a).

209 Yet “Two opposite floral rows initiate (sic) simultaneously, axillary to their
210 subtending bracts”; and “The subsequent rows initiate (sic) in the axil of a subtending
211 bract ...“ These statements are followed by “Thus we favor considering intercalary
212 growth as the mechanism responsible for the displacement of floral buds to an extra-
213 axillary position, *but not for floral meristem initiation*” (emphasis added). Where do the
214 authors consider that the flowers are initiated? In other words, as mentioned earlier, SGP
215 do agree that there is a meristematic zone at the base of each fertile internode; this zone
216 corresponds to the definition of intercalary meristem (Evert, 2006). Their novel
217 contention is that the “floral row” should be regarded as the remnant of a triad or
218 dichasium, to be followed by further iterations of similar triple units where (commonly)
219 three longitudinal rows are eventually formed. It is exceedingly difficult to understand
220 how they would square this view with a) the obviously continuous production of flowers
221 in each series, b) the existence of multiseriate species of *Phoradendron*, and c) the
222 absence (as they themselves admit) of bracteoles for the flowers generated.

223 **Reconstructing Inflorescence Ancestral States**

224 In their Discussion SGP state “The predominant pattern of partial inflorescence
225 architecture that can be traced back to the common ancestor of Loranthaceae, Santalaceae,
226 and Viscaceae and related families consists of dichasia or dichasia-derived cymes (Fig.
227 7).” As outlined above, these authors have “cherry picked” a small number of mistletoes

228 in the order, scored the matrix in Fig. 7 for all examples of what they consider dichasia
229 (and derivations), not scored the matrix for any other inflorescence types, and then
230 conclude that the dichasium is the plesiomorphic state present in the common ancestor to
231 the above families. This methodology is flawed for a number of reasons. To properly
232 address this issue, *all* inflorescence types should have been scored in a matrix that
233 included all extant genera in the order. The phylogenetic tree shown in Fig. 7 does not
234 show or score the inflorescence types in the common ancestor of the above three families,
235 which would be found in Olacaceae s. lat. In the absence of a cladistic tree where
236 inflorescence type is reconstructed, there can be no statements made about the state
237 present in the common ancestor.

238 On p. 34 SGP state "... the most plausible phylogenetic optimization of the dichasium
239 as the plesiomorphic condition in Santalales." These authors have not conducted
240 "phylogenetic optimization" to support statements about the plesiomorphic condition.
241 The current manuscript took a different approach in that we 1) developed a
242 comprehensive morphological character matrix of inflorescence types scored based on all
243 available published literature and our own observations, 2) produced a well-resolved
244 molecular phylogenetic tree for nearly all genera in Santalales, and 3) tested the
245 hypothesis of the dichasium being plesiomorphic in the order using BayesTraits (Meade
246 (Meade and Pagel, 2016).

247

248

250 LINE-BY-LINE CRITIQUE

251 Quotations from SGP are in red font

252 Page 24.

253 1. “Of the 12 families recognized in the order Santalales ... (Nickrent et al., 2010; Kuijt,
254 2015).” Indeed 12 families were recognized by Kuijt (JK), but not by Nickrent (DN),
255 thus, either the first reference should be removed or the contrasting family concepts of
256 both should be discussed and properly referenced. In Nickrent et al. (2010), 18
257 families were recognized. In a latter publication (Su et al., 2015), some holoparasites
258 were included in the order and shown to be composed of two distinct clades that were
259 each recognized as families, Balanophoraceae s. str. and Mystropetalaceae.

260 A general comparison of family concepts for “core” Santalales (not including
261 holoparasites) can be seen in Kuijt (2015) and Nickrent et al. (2010). The updated
262 concept that includes the two holoparasite families was discussed in Su et al. (2015)
263 and is reflected in the classification shown on the Parasitic Plant Connection website
264 (parasiticplants.siu.edu). A general comparison of the treatments by JK and DN shows
265 that that JK recognized some of the segregate families of Olacaceae (e.g. Aptandraceae,
266 Coulaceae, and Schoepfiaceae) but took a more traditional view of Santalaceae and
267 Eremolepidaceae. In contrast, Nickrent et al. (2010) recognized six families that had
268 traditionally been considered Santalaceae. Both JK and DN recognize Viscaceae as a
269 distinct family, which is in contrast to the taxonomy of APG IV where it is lumped
270 into a broadly circumscribed Santalaceae. The new molecular data reported in the
271 current paper provide strong support for the families proposed by Nickrent et al.

272 (2010), thus this classification will be followed here. Different views on family
273 circumscription have little bearing on our criticisms of the SGP paper.

274 2. “Their success and invasiveness rely primarily on ... copious and long lasting flowers.”
275 It is not clear that flower number and longevity in Santalales is greater than in other
276 angiosperm orders, and whether this has anything to do with “success” or invasiveness.

277 3. “Profuse flowering drives the continuous formation of either bisexual or unisexual
278 flowers.” This sentence makes no sense.

279 4. “...Loranthaceae, Santalaceae, and Viscaceae ... encompass most of the variation in
280 terms of inflorescence architecture across Santalales” Although Der and Nickrent
281 (2008) and Nickrent et al. (2010) are cited in this sentence, those works recognized
282 distinct clades (families) in Santalaceae. So one must assume that the taxonomy in
283 those works is being followed. If so, a large amount of variation in inflorescence
284 architecture would be missed, e.g. by excluding Thesiaceae. Within the large genus
285 *Thesium* (ca. 350 species), at least 11 distinct inflorescence types occur (Nickrent
286 unpublished data) that include both determinate and indeterminate types. Moreover, as
287 discussed in our review, this paper looks at only a tiny sampling of species from the
288 sandalwood order.

289 5. “Inflorescences in Loranthaceae and most other members of the order vary from
290 solitary or paired flowers to dichasia.” This is a gross understatement of the diversity
291 of inflorescence types seen in Santalales.

292 6. “Article” is not standard botanical terminology. The term “metamer”, apparently used
293 by SGP as equivalent to a fertile internode, is very rarely used in botany [an exception
294 being found in Bradford (1998)]. Not to be confused with metamere, a zoological term

295 for one unit of a linear series of similar segments or to metamer (metamerism), colors
296 with different spectral properties that are perceived to match.

297 **Page 25**

298 7. “Previous authors have described the inflorescences in the tribe as spikes, ...racemes,
299 ...fascicles.” All of these categories fall into the indeterminate (racemose)

300 inflorescence type of sensu Weberling (1989).” A large number of citations preceded
301 this statement, not all of which are compatible with being interpreted within

302 Weberling’s concepts. For example, Kuijt (1959 p. 541) and Kuijt (2003a p. 14) was

303 fully aware of the unusual nature of the Phoradendreae inflorescence, and admits

304 difficulty with accepting the spike interpretation by Eichler (1868). Nickrent et al.

305 (2010) when describing inflorescences across all Viscaceae used the term fascicle to

306 refer to the dense clusters of flowers seen in *Viscum*, not individual inflorescences in

307 *Phoradendreae*. This term was used in Polhill and Wiens (1998): “dichasia sessile or

308 peduncled, solitary or fascicled, axillary, or axillary and terminal.”

309 8. “... axillary dichasial (i.e. cymose) inflorescences in Lorantheae and other

310 Santalales.” This discounts the fact that other types (e.g. indeterminate inflorescences)

311 occur in Santalales. It also presumes the dichasium is plesiomorphic in the order,

312 something that should be tested, not assumed *a priori*.

313 9. “an article is ... formed by two subtending bracts, followed by an internode and two

314 axillary floral groups”. This definition is arbitrary and confusing because the bracts are

315 formed at the apex of the earlier (lower) internode and are morphologically contiguous

316 with that internode. Note that the term “internode” is used here, which is equated

317 elsewhere with “article” and “metamer”. In any case, an “article” is not formed by
318 bracts.

319 10. “A floral group is the aggregation of one or more floral rows axillary to the
320 subtending bract, which corresponds to a partial inflorescence.” This definition is
321 confusing for several reasons. Earlier in the paper, the term “floral row” was used to
322 describe the horizontal grouping of flowers (equated with dichasium). It can be
323 imagined that one row is equivalent to a partial inflorescence (this needs to be
324 demonstrated), but two or more rows presents difficulties, especially if these are
325 subsets of the “floral group”. The term “floral group”, as defined here, conflicts with
326 (duplicates?) the term “floral area” (Kuijt, 1959 p. 527) that constitutes the entire
327 flower bearing area on one side of the fertile internode. Finally, Weberling (1989)
328 defines a partial inflorescence as “any more or less separated lateral part of an
329 inflorescence.” Even with a floral row corresponding to a (reduced) dichasium, can
330 these units be considered separated?

331 11. “A floral row is a transverse series of flowers in each floral group formed by an odd
332 number of flowers (3, 5, 7, or 9).” This definition is based upon an interpretation. First,
333 a transverse cut through a Phoradendreae inflorescence would not pass through all
334 three flowers because the terminal one occurs higher than the laterals. Also, in the 1a
335 (biseriate) type of inflorescence, once the top three flowers are assigned to a “floral
336 row”, only two, not three, flowers remain in the lower rows. Here one would have to
337 envision loss of all the terminal flowers for each row. Other than the order in which
338 the terminal vs. the lateral flowers are initiated, there is no evidence (e.g. from
339 vascular stands) that the flowers in a “floral row” are arranged in a dichasium.

- 340 12. “a floral column is the longitudinal series that results when two or more floral rows
341 are formed and aligned to each other.” A term was already in existence for decades for
342 these columns: flower series. The inflorescences in *Phoradendreae* have been
343 described as flower seriation types (e.g. 1a, 1b, 2a, etc.) where a terminal flower,
344 directly above the bract, is median and other flowers that form along the flanks are
345 lateral. Moreover, this definition excludes uniseriate species from having “floral
346 columns”.
- 347 13. “For Loranthaceae, we consider that each axillary dichasium (cyme) corresponds to a
348 partial inflorescence.” Not all Loranthaceae are cymose, or are mixtures of different
349 determinate and indeterminate components (i.e. a thyse).
- 350 14. The three species of *Phoradendreae* were chosen based on the number of flowers per
351 “article” (fertile internode). The first two species can be either biseriate or triseriate
352 depending upon the sex of the plant and geographic location, and the third is triseriate.
353 All of the photos, however, show triseriate examples. These species were “cherry
354 picked” among the hundreds of other species, some of which do not easily conform to
355 the reconceived interpretation that floral rows equal dichasia.
- 356 15. The six Loranthaceae chosen to represent “different inflorescence construction” are,
357 as above, not representative of the diversity seen in the family (see Kuijt, 1981).
358 Indeed, 5 of the 6 are in subtribe Psittacanthinae, all closely related with X=8 base
359 chromosome numbers.
- 360 16. The mistletoe *Antidaphne viscoidea* was chosen to represent seven diverse clades
361 ranging from Opiliaceae to Amphorogynaceae (see Fig. 7). This species is not even
362 representative of the genus for other species have very different inflorescences. Taxon

363 choice for this study was apparently driven by availability and presence in the Andes,
364 two factors that have little or no bearing on the evolutionary issues the authors are
365 trying to address.

366 **Page 26.** Figure 1. A-C are misidentified, and do not represent *Dendrophthora avenia*;
367 they are probably a *Phoradendron*, instead.

368 **Page 27.** Figure 2. A-L are misidentified, and do not represent *Dendrophthora avenia*;
369 they are probably a *Phoradendron*.

370 **Page 29.** Figure 4. The section shown in G provides no evidence that the vascular traces
371 leading to the three flowers represent branching consistent with a dichasium.

372 **Page 30.** Figure 5. C, D, AND E are misidentified, and are *Struthanthus* sp., female, not
373 *Passovia* sp.

374 **Page 31**

375 17. “*Dendrophthora avenia* - Individuals of this species are uniformly ochre-reddish in
376 color”. The description of this species in Kuijt (2000) gives yellow to orange-green for
377 the color. The specimen for this mistletoe was collected in 2013. Given this date and
378 the color of the shoots in Fig. 1A-C, it is likely that this photo was taken from an
379 alcohol preserved specimen.

380 18. “... the accessory buds develop simultaneously forming pseudowhorls.” The term
381 “whorl” cannot be used for accessory buds as the accessory flowers are not formed
382 from a joint inflorescence apex, but from an “unorganized meristematic field” as far as
383 is known to date.

- 384 19. The terms “pit” and “fovea” are used for the cup-like depressions in which the
385 flowers sit. Kuijt (2003b) uses “cup” or “alveolus”. No need to introduce new
386 terminology.
- 387 20. The sections in Appendix S1 do not convincingly show that the strands (traces) end
388 up in each floral row. This confirms what Kuijt (1959) reported. It shows there is no
389 evidence from vascular anatomy to support the claim that floral rows are dichasia.
- 390 21. “The presence of both peripheral traces and a central vascular cylinder is apparent at
391 the base of each article.” These are not clearly shown in S1.
- 392 22. “bracteal tubular sheath”. These are labeled “b” in only some of the figures cited.
- 393 23. “Two opposite floral rows”. As mentioned above, these flowers are not in a
394 horizontal row - the top flower is above the other two, as shown in Fig. 3F.
- 395 24. The text about the length of “articles” (fertile internodes) being correlated with the
396 number of flowers is apparently speculation, for no data are presented to support this
397 hypothesis. Really, this type of information should be in the Discussion, if included at
398 all.
- 399 **Page 32**
- 400 25. “Floral rows always have odd numbers of flowers ...” As per the comment for p. 25,
401 this is not true in biseriate inflorescence types.
- 402 26. “... longer peripheral vascular traces that serve the floral groups ...” This is not
403 evident on Fig. 4C.
- 404 27. “... white, funnel-shaped flowers ...” The flowers of *Gaiadendron* are mostly yellow
405 (sometimes slightly orange). White flowered plants are seen in Central Colombia in
406 the mountains around Bogotá. The flowers in *Gaiadendron* are never funnel-shaped.

407 This term (funnel form) is usually applied to sympetalous flowers (*Gaiadendron* is
408 apopetalous).

409 28. “Inflorescences have indeterminate growth.” Kuijt (1981) indicates that *Gaiadendron*
410 in Costa Rica has determinate or indeterminate racemes whereas in South America it is
411 indeterminate. Whether there is a real geographic difference here requires further work.

412 29. “... dichasia axillary to opposite, decussate bracts.” This is not a good description of
413 the inflorescence (see Kuijt, 1981; Kuijt, 2015). It is a compound system, probably a
414 thyse (raceme of triads). Calling the flowers “sessile” is not accurate as some are
415 sessile whereas others are not. There is no mention of recaulescence of the bracts to
416 the lateral peduncles in dichasia.

417 30. “Partial inflorescences consist of two flowers, which retain their respective bracteoles
418 and a vestigial terminal flower.” (Kuijt, 1981, 2009) describes a number of
419 *Psittacanthus* and all *Aetanthus* as having dyads as a result of losing the median flower.
420 Whether the lumps of tissue labeled in Fig. 6J and S2E are vestigial flowers is
421 speculation without a proper developmental study.

422 31. For *Orycanthus* “... inflorescences are reduced to the terminal flower of the
423 dichasium, flanked by the bracteoles ...” The description of the inflorescence / flower
424 morphology is Results. That these represent reduced dichasia is interpretation and
425 therefore belongs in the Discussion.

426 32. For *Peristethium archeri* “No terminal flower is formed in the inflorescence, which
427 indicates indeterminate growth.” The inflorescence in this species is normally
428 terminated by a flower, hence growth is determinate (Kuijt, 2015). The angle of the
429 photo in Fig. 5I does not provide sufficient information to judge whether a terminal

430 flower exists or not. The photo in Fig. 5H is very young and again does not provide
431 sufficient information. See Kuijt (2011 Fig. 4).

432 33. Discussion “The predominant pattern of partial inflorescence architecture that can be
433 traced back to the common ancestor of Loranthaceae, Santalaceae, and Viscaceae and
434 related families consists of dichasia or dichasia-derived cymes (Fig. 7).” These authors
435 have “cherry picked” a small number of taxa in the order, scored the matrix in Fig. 7
436 for all examples of what they consider dichasia (and derivations), and then concluded
437 that the dichasium is the plesiomorphic state present in the common ancestor to the
438 above families. To properly address this issue, *all* inflorescence types should have
439 been scored in a matrix that included a broad sample of all or most genera in the order.
440 The phylogenetic tree shown in Fig. 7 does not show or score the inflorescence types
441 in the common ancestor of the above three families, which would be found in
442 Olacaceae s. lat. In the absence of a cladistic tree where inflorescence type is
443 reconstructed, no meaningful statements can be made about the state present in the
444 common ancestor.

445 **Page 33.**

446 34. Figure 6. The arrowhead in B shows an apical meristem. Indeterminate growth is a
447 process, not a structure. In J, what evidence is there that the tissue labeled with a black
448 X is actually a vestigial flower? In K, the white asterisk is supposed to represent lateral
449 flowers, but their positioning on the figure confuses this concept.

450 **Page 34**

451 35. Figure 7 has so many problems it is probably best to question every single entry in the
452 matrix. The reason for this is that the scoring for the diagrammatic inflorescence

453 figures at the bottom of the matrix (here designated A through I, left to right) is a
454 mixture of observation (fact) as well as interpretation represented as fact. For example,
455 starting at the bottom of the tree, Schoepfiaceae is scored as having single flowers,
456 with (type B) or without (type C) bracteoles. Two genera in this family, *Arjona* and
457 *Quinchamalium*, have indeterminate spikes or racemes. Under this interpretation, the
458 partial inflorescences would have to lose the basic components that define the
459 dichasium: lateral flowers and their pedicels as well as the bracteoles.

460 Figure 7 also shows many examples where the scoring of the matrix is incomplete.
461 Thesiaceae is represented by dichasia (type A) and dichasia reduced to a single
462 terminal flower (type B). As mentioned above, the genus *Thesium* alone has at least
463 11 different inflorescence types, including indeterminate ones. And certainly taxa exist
464 that have monochasia (type F), in contrast to the statement “rarely, the partial
465 inflorescence becomes a monochasium.”

466 In terms of the tree shown in Fig. 7, the authors have generated their own (unique)
467 topology based on several molecular phylogenetic studies from Nickrent et al. (2010)
468 and earlier. Not considered is the more recent analysis (Su et al., 2015) where more
469 genes and more taxa were included. Although the topology at the base of their tree is
470 correct, intergeneric relationships within Viscaceae are depicted as fully resolved,
471 which they are not. Several molecular phylogenies have been published that addressed
472 intergeneric relationships in Viscaceae: Der and Nickrent (2008), Mathiasen et al.
473 (2008), Su et al. (2015), and the present work (Fig. 1). Sister relationships that appear
474 solid are *Korthalsella* with *Ginallia* and *Phoradendron* with *Dendrophthora*. The

475 relationships among the other three genera (*Arceuthobium*, *Notothixos*, and *Viscum*)
476 have been unresolved.

477 Additional errors in scoring are as follows:

- 478 • *Arceuthobium* is listed as having dichasia, but Kuijt (1970) is not mentioned
- 479 • Phoradendreae, *Ginalloa*, *Notothixos*, *Viscum*, *Arceuthobium*, Cervantesiaceae and
480 Opiliaceae are listed as having dichasia; in only male *Viscum* is it partly true.
- 481 • *Misodendrum* is erroneously listed with dyads, as are Santalaceae AND Nanodeaceae.
- 482 • Dichasia with lateral flowers deleted: Schoepfiaceae, Loranthaceae, Thesiaceae,
483 Nanodeaceae, Santalaceae, Amphorogynaceae.
- 484 • *Korthalsella* is listed as having a series of dichasia above its single bracts. Nothing of
485 the sort is true.

486 36. "... the most plausible phylogenetic optimization of the dichasium as the
487 plesiomorphic condition in Santalales." SGP have not conducted "phylogenetic
488 optimization" to support statements about the plesiomorphic condition. This was done
489 with BayesTraits (Meade and Pagel, 2016) in the present paper using a well-resolved
490 molecular phylogenetic tree and a comprehensive examination of inflorescence types
491 in all genera of the order.

492 37. SGP present five ways in which a dichasium can be reduced. They indicate these are
493 independent events but no data supporting this claim are presented. From this
494 discussion, it seems that any part of the dichasium can be lost and the resulting partial
495 inflorescence will still be interpreted as a (derived, modified) dichasium. Following
496 these rules, nearly any type of inflorescence can be related back to dichasial origins,
497 including spikes and racemes. For example, the male inflorescence of *Antidaphne*

498 *viscoidea* is a raceme (indeterminate) with no bracteoles subtending the individual
499 flowers. Figure 18a from Kuijt (1988) with a cluster of three, sessile female flowers is
500 cited as evidence that the partial inflorescence is a dichasium (this term was not
501 applied there by Kuijt). Again, no bracteoles are associated with this cluster. This
502 arrangement could equally arise from metatopic displacement such as concaulescence.
503 To call the female inflorescence a dichasium is extrapolation and speculation.

504 38. “Molvray, Kores, and Chase (1999) and Kirkup, Polhill, and Wiens (2000) proposed
505 sessile dichasia as the plesiomorphic condition for the family.” Neither of these
506 workers examined all the genera in the family, with outgroups, or conducted a robust
507 analysis of inflorescence type. Thus the interpretation is speculation.

508 39. “... the loss of bracteoles does not compromise the dichasial organization of the
509 flowers in Viscaceae.” As stated above, it appears that any and all floral parts that
510 define a dichasium can be lost (e.g. peduncle, lateral flower pedicels, lateral flowers,
511 and bracteoles) and the resulting inflorescence would still be considered a dichasium
512 by the authors. Thus, the data presented in Fig. 7 appear to support a foregone
513 conclusion.

514 40. “... typical dichasia present in *Arceuthobium* and *Viscum* ...” A true dichasium (as
515 we define it here) is not seen in Viscaceae. A “dichasium” that lacks bracteoles (type
516 E) is scored for all genera in Fig. 7. Even this type is rarely seen in *Arceuthobium*,
517 except for male plants of *A. americanum*. The same is true for *Korthalsella* and
518 *Ginalloa* and certainly for *Phoradendron* and *Dendrophthora*. For the 8 species of
519 *Notothixos*, most have a fan-like arrangement of flowers referred to in the literature as
520 cymes or cymules. In some dichasial *Viscum*, supplementary partial inflorescences

521 develop at the nodes, thus appearing superposed. Barlow (1984) in Flora of Australia
522 describes the cymules as solitary or in determinate or indeterminate conflorescences.

523 An inflorescence of *N. cornifolius* is illustrated in Kuijt (1969 p. 30, Fig. 2-17b). It
524 is apparently this type that is equated with inflorescence type H in Fig. 7, thereby
525 yielding a synapomorphy with *Phoradendreae* (uniseriate, type 2a). This is clearly a
526 case of broad interpretation and speculation as to the homology of these phenotypes.
527 Although a quote from Kuijt (1961) is provided to support this relationship, an earlier
528 quote from the same author could be proffered: “To conclude on the basis of such a
529 similarity that *Notothixos* is closely related to *Phoradendreae* would indeed be
530 incautious, as evolutionary convergencies abound in the Viscoideae” (Kuijt, 1959 p.
531 542). Molecular evidence presented herein indicate that *Notothixos* is *not* closely
532 related to *Phoradendreae*; thus, the flattened cymule of *Notothixos* must have been
533 derived independently from the 2a inflorescence of *Phoradendreae*.

534 41. “Molvray et al. (1999) postulated the “floral triads” (= dichasia) as symplesiomorphic
535 at least in *Ginalloa* and *Korthalsella* ...” We do not consider all cases of floral triads
536 to be dichasia. Plus, postulation about a character being plesiomorphic, without
537 empirical evidence, is simply speculation.

538 **Page 35**

539 42. “This developmental pattern suggests that these three flowers conform [to] an
540 ontogenetic unit in terms of time and space, comparable to a dichasium.” Are the
541 partial inflorescences dichasia or simply “comparable to a dichasium”? Based on
542 ontogeny, one can speculate on the origin of the inflorescence units, but because of
543 reductions and other changes over a long phylogenetic history, one cannot be certain

544 that these are derived from dichasia. Because of the way the matrix in Fig. 7 is
545 constructed, one is given the impression that these character states are absolute and
546 unambiguous, not that the scoring is based upon uncertain hypotheses with associated
547 assumptions.

548 43. "...such ontogenetic unit[s] repeats itself [themselves] basipetally as serial accessory
549 dichasia." As shown above, *Phoradendreae* inflorescences other than the triseriate
550 type require additional assumptions to conform to the idea that subsequent floral rows
551 represent dichasia. For the biseriate condition, the median flower must be lost in all
552 rows below the first. For uniseriate inflorescences, all lateral flowers of the dichasium
553 must be lost. Further interpretational latitude is required to account for multiseriate
554 inflorescences. SGP acknowledge this at the end of the first column and beginning of
555 the second on page 35.

556 44. "The main difficulty with interpreting the floral rows as dichasia lies in the lack of
557 bracteoles in the sessile flowers of *Phoradendreae*." The lack of bracteoles is precisely
558 our point. We fully agree and would have erred on the side of caution instead of
559 presenting hypotheses as facts.

560 45. "... the term intercalary has been used ambiguously (e.g. Kuijt 1986a)" No
561 ambiguity occurs in Kuijt's usage of "intercalary" when it is accompanied by
562 qualifying terms. So, in Kuijt (1986 p. 14) we see: "flowers produced basipetally by
563 intercalary action" and on p. 67 for *Dendrophthora* "flowers produced as in
564 *Phoradendron*, in intercalary fashion." Intercalary can be used in several ways in
565 *Phoradendreae* such as intercalary meristem (with reference to the production of

566 flowers) or intercalary cataphylls (scale-like appendages that occur in three possible
567 positions - see Kuijt 1959, p. 508).

568 46. “However, none of these studies [referring to York and Kuijt] have documented the
569 development of flowers directly from intercalary meristems.” SGP do not deny that
570 an intercalary meristem is active at the lowest end of fertile internodes in
571 Phoradendreae. However, they deny that individual flowers are generated there; only
572 triads (“floral rows” or “dichasia”) are. We would maintain that this distinction is
573 specious; it is difficult if not impossible to visualize how a transverse “floral row” of
574 three flowers can be initiated without the individual flowers being generated. Fig. 2G
575 clearly shows the basal origin of an individual flower from – what else? – the
576 intercalary meristem, with two other, lateral flowers scarcely initiated; it cannot be
577 denied that the upper flower was initiated separately from, and ahead of the other two.

578 47. “Thus we favor considering intercalary growth as the mechanism responsible for the
579 displacement of floral buds to an extra-axillary position, but not for floral meristem
580 initiation.” Where do the authors consider that the flowers are initiated? See comments
581 in text of rebuttal paper.

582 **Page 36**

583 48. “Although this vascular pattern was previously described by York (1913) and Kuijt
584 (1959; fig. 10e), it has not been directly taken as evidence of a condensed system of
585 fused branches.” This is exactly correct. These authors did not extrapolate beyond the
586 available evidence (as SGP have done).

587 49. “However, these two types of racemose inflorescences fail to explain the dichasial
588 arrangement observed during ontogeny (Figs. 2, 3) and fixed during phylogeny (Fig.

589 7) as well as the basipetal development observed in each article.” As shown in
590 comments 11 and 42, dichasia are never observed during floral ontogeny in
591 *Phoradendreae* and evidence from vascular anatomy is lacking. Aside from the fact
592 that the scoring of the matrix for Fig. 7 is flawed, there is nothing in that figure that
593 indicates the dichasium is fixed (whatever this means) during phylogeny.

594 50. “Furthermore, the terms spike or raceme have only limited value to describe an
595 inflorescence...” We acknowledge this terminology shortcoming, as has been done
596 since Kuijt (1959, p. 541).

597 51. “Thus, the number of articles per inflorescence and the number of dichasia per article
598 appear to have limited use in taxonomy, because the same numbers can be found in
599 species of *Dendrophthora* and *Phoradendron* ...” This statement is providing little new
600 information. Kuijt (1959) on page 529 said: “I wish to point out first a few features
601 which are not taken into account in the classification below. The first of these are the
602 number of fertile internodes per spike, and the number of flowers per series. These two
603 features I know to vary greatly within some species, or differ between some closely
604 related species and should, on the whole, perhaps not be taken too seriously.”

605

606

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