Manuscript ID: #14913
Manuscript title: The fossil Osmundales (Royal Ferns) - a phylogenetic network analysis,
revised taxonomy, and evolutionary classification of anatomically preserved trunks and
rnizomes
Editor
Overall. I believe this paper is worthy of publication in PeerJ, but only after what might
amount to a major revision. I stress that the paper should not be rejected. This represents a
great deal of work and is an ambitious and potentially high profile study. Refinement of the
manuscript should greatly increase its reach.
The paper provides valuable information on the stem anatomy of the ferns in question, and
undertakes a phylogenetic analysis that will be of interest to a large number of plant scientists
However, both reviewers provide excellent suggestions for ways in which this paper can be
improved and have significantly higher impact. The comments overlap in a number of areas
but most particularly the need for better organization of the presentation of the data and
results, and clearer presentation of the methods used. It would appear that both reviewers had
some difficulty ferreting out data, and following the results and discussion due to the manner
in which the manuscript is organized. Both also caution about making strong statements that
are potentially not supported (or may appear unsupported, perhaps simply due to the
organization of the paper) by the analyses or that may be unnecessarily inflammatory.
Has been followed; we restructured the original, rather unconventional format of presentation
of Introduction/Material&Methods into a more classic and—hopefully—more readily
comprenensible layout.
Reviewer 1 raises a number of important questions about the analysis, and the presentation of
the data. In addition, the reviewer raises the matter of environmental effects on the anatomica
characters that form the basis of the study. This should be addressed if possible in a revision
The limitation of certain diagnostic value of anatomical features that are potentially
dependent on age, size, and ontogenetic stage of a plant has already been critically discussed
in, e.g., the introduction (e.g., lines 148–165), the annotated character list (e.g., lines 365–
374), and relevant comment sections on particular taxa (e.g., lines 1298–1320). Beyond that,
though, we think that teasing out the potential effects of environmental factors on anatomical
structures and, consequently, on systematic classification would go beyond the scope of this
manuscript (given its already lengthy state). We are developing ideas for a sequel project
about putting the evolutionary history of the group into stratigraphic, geographic, and climatic
contexts, and we look forward to addressing this reviewer's questions concerning
contents, and we rook for which to addressing and reviewer b questions concerning
environmental influences in the manuscript to follow; see below for details].

- 45 and organization of the data, and the way the manuscript is structured. This reviewer also used
- the authors' data matrix to run a parsimony analysis and, from the results of that, suggests that
- 47 the authors do likewise, which would (or would not) support some of their assertions about
- 48 that approach.
- 49 [Has been (mostly) followed; see below for details]
- 50

## 51

## 52 **Reviewer 1**

- 53 Basic reporting
- 54 The authors have conducted a needed analysis for stem anatomy in these ferns and provided
- some standardization of the terms to be applied to allow for improved comparison. This was a
  large task and one that can be valuable for future studies.
- 57 Overall the study seems to have been exhaustive in finding all the species for which stem
- 58 anatomy is known.
- 59 The main weakness I see in this paper is that there are really no methods explained in such a
- 60 way that the work is repeatable.
- 61 [We hope to have clarified this issue by providing much more in-depth explanations in the
- 62 form of restructured and expanded Materials-and-Methods and Results chapters]
- 63
- 64 Experimental design
- 65 Methods: This may be the journal style, but I think that putting the description of all these
- 66 character states into the methods section dilutes the understanding of what methods were used
- 67 for this study. To me, it would be best to describe the methods for obtaining the characters –
- i.e. how did the authors evaluate these characters used in the analysis? Was it just from the
- 69 literature, or reexamination of actual specimens in some cases, how there were examined, etc.
- and then describe the methods of analysis to create the new classification and expose the
- relationships of the taxa. If only literature was used for this study, what was used to determine
- the characters (light microscope photos, SEM photos, drawings, the text descriptions by the
- 73 original authors, etc.)?
- 74 [This has been addressed in a separate Material-and-Methods sub-chapter on Data Acquisition
- 75 (lines 548–563); the general description of Osmundales axis anatomy is now part of the
- 76 introduction chapter.]
- 77

## 78 Were all the specimens at the same stage of development?

- 79 [This question is impossible to answer and probably marks a never-achievable scale of
- 80 precision. There is general agreement in the scientific community to consider these fossils to
- 81 be at least at a sufficiently similar stage of development to enable comparative systematic
- 82 analysis as we did. Still, we wish to point out that unlike most previous authors we do take
- 83 potential effects of intraspecific variability explicitly into account; please note the critical
- 84 discussion in the relevant introduction, results, and comments chapters on particular taxa, e.g.,
- 85 *Donwelliacaulis versus Itopsidema* (lines 1033–1042) or on *Thamnopteris versus* (formerly)
- 86 *Zalesskya* (lines 1149–1165); the latter genus is here considered synonymous because "[...]
- 87 we see no reason to consider Zalesskya anything but a particularly large and incomplete
- 88 *Thamnopteris trunk.*" Also, please note that our study is the first to move into a direction
- 89 where these effects may be taken into account in the course of analysis in that we attempt to

- 90 provide an as-good-as-it-gets specimen-level coding in order to capture (potentially)
- 91 ontogenetically controlled intraspecific variability. All this has not been done previously.].
- 92
- 93 Were these all from similar environments or were some from wet and others from dry? Would
- 94 this influence the anatomical characters used such as more or less schlerencyma vs
- 95 parenchyma? More could be provided for justification on the analyses done.
- 96 [An interesting idea that is definitely worth pursuing, but we believe that any attempt in this
- 97 direction would go beyond the scope of this manuscript, which we prefer to restrict to mere
- 98 taxonomy and systematics. As mentioned above: We are developing ideas for a sequel project
- about putting the evolutionary history of the group into stratigraphic, geographic, and climatic
- 100 context, and we look forward to addressing this reviewer's questions in the manuscript to
- 101 follow. In general terms, however, since all of the fossils are preserved in fluvial or paludal
- sediments, we infer that all taxa occupied relatively moist settings consistent with the
- **103** preferred habitats of their extant relatives.]
- 104
- 105 What was the rationale for selecting 60% undefined characters to eliminate taxa why not
- 50% or 70%? What is magical about 60%? I did not see an explanation for the choice or areference cited to indicate that this was a standard procedure.
- 108 [This is a subjective choice; an explanation is provided in the methods section (lines 536–547)]
- 110
- 111 Were the characters weighted in any way? Did not say in text or I missed it.
- 112 [No, otherwise we would have mentioned that; we added a remarks to the introduction of the
- 113 methods section to explicitly clarify this (lines 325, 589)]
- 114

115 NeighborNet is a solid analysis as the authors note and generates networks, but it depends on 116 the reliability of the data put into it and it is a planar result. Therefore it would be helpful to

- 117 know how many reticulations were examined, or if any appeared that would warrant 118 additional analyses before accepting them. And so forth – to adequately provide the
- information for someone else to replicate this study. That is what methods should do.
- 120 [We are uncertain what is meant by "alternative reticulations". Any information needed to
- 121 replicate the analysis and to reproduce our results is given in the Material and Methods
- section. All root files, data and all original results are provided in the Supplemental Data
- 123 Archive. Still, since the methodology may be unconventional for some readers, in make our
- rationale perhaps more readily reproducible, we have taken the recent 2016 description of yet
- 125 another species of Osmundaceae rhizome *Millerocaulis zamunerae* as an example to
- demonstrate the inclusion of a new taxon into the matrix in the form of a step-by-step "How-
- 127 To-"tutorial. With this example, we hope to have clarified any remaining uncertainties.]
- 128
- 129 The actual description of the characters for the taxa should be in a description section
- 130 outlining each of the characters and their various states [This has been followed: see lines
- 131 332–480], followed by the analysis of where they appear in the various taxa examined
- 132 [The exact information about which taxon has which character states should be sufficiently
- clear from the matrix file itself and from the annotated spreadsheet in the Supplemental
- 134 Materials. A general overview about which groups are overall characterized by particular

- suites of anatomical features can be found either in the general introduction about axis
- anatomy in Osmundales or in the relevant comments sections dealing with particular taxa in
- the revised taxonomy section. Beyond that, we would prefer to avoid spelling out and
- 138 justifying the coding in text-form because this would probably double the length of the text
- and, in most cases, the raw data for characters possessed by specific taxa has already been
- 140 published in the respective alpha-taxonomic studies cited in our analysis. Nevertheless, please
- 141 note that coding of particular characters in the matrix file and in the spreadsheet file is
- 142 annotated with comments].
- 143
- 144 I found myself jumping around in this paper to follow the reasoning from section to section 145 and then to the figures. So I suggest a separate section for description to provide clarity and 146 logical flow for a reader.
- 147 [We hope to have clarified this issue by restructuring the manuscript. The main text now
- 148 begins first with a comprehensive description of the various anatomical characters of
- 149 osmundalean axes and their respective tissue systems, with brief remarks on what manner this
- 150 structural diversity has been translated into a binary or ternary character list]
- 151
- Discussion this section could have the characters discussed if no separate description section
  is provided. This is probably the place for the rationale for use of NeighborNet as the method.
- 154 [We agree that it is difficult to place the paragraph dealing with the choice of NeighborNet as
- as the preferred analytical tool. We choose to include our justification for this methodology in
- 156 the section "Phylogenetic Analysis" >> "Use of phylogenetic networks". We emphasize that
- 157 Neighbour nets are designed to better handle incompatible signals, and are more sensitive
- 158 with respect to actual ancestor–descendant relationships than are dichotomous trees. The
- 159 distance between two tips in a Neighbour net reflects the actual distance value, which is not
- 160 necessarily the case in dichotomous trees]
- 161

162 The discussion does not really address certain aspects of this artificial classification.

- 163 [Under this assumption, which study would not be artificial? It is more a matter of how164 comprehensively informed the inferences are; see the following comment and reply:]
- 165
- 166 Use of only stem anatomy will bias the study in various ways and should be addressed.
- 167 [This is a good point. We have now highlighted just how reliable stem anatomy is as a source
- 168 of information on the phylogeny of Osmundales: the topology of a network derived from only
- 169 stem-anatomical data of extant taxa is near-perfectly congruent with the topology of a
- 170 network derived from only molecular data of those taxa (see Bomfleur et al. 2015).
- 171 Furthermore, please note that resolution of fossil records of particular lineages based on frond
- 172 fossils perfectly matches the stratigraphic occurrences of the relevant groups as inferred
- independently based on axis anatomy (see Grimm et al. 2015). Finally, it may be important to
- 174 point out that even though our phylogenetic analysis itself is based on only axis anatomy (see
- above), taxonomic decisions are based not only on these anatomical data, but also take into
- account molecular data and frond-morphological data.]
- 177
- 178

- 179 If the developmental stages were not all the same for the specimens examined, how might that 180 influence the characters used?
- [This is partially dealt with in the relevant parts of the introduction (e.g., lines 148–165) and
  comments sections (e.g., lines 1003–1042; lines 1149–1165)]
- 183

184 Is there an environmental effect on stem growth – these stems are pretty much below or close
185 to ground level, so water amount would influence the types of cells produced. Would this

- 186 change the results of the analysis in any way?
- 187 [A detailed analysis of character states and character-state changes in relation to ontogenetic
- 188 development or to stratigraphic age or to environmental factors is beyond the scope of this
- 189 manuscript. As stated in the introduction, the main purpose of this study is to provide a
- 190 uniform framework for the systematic analysis of fossil Osmundales axes under an updated,
- standardized, descriptive terminology. Phylogeny and evolution will be the subject of a
- detailed follow-up project that we look forward to exploring in the future.]
- 193
- 194 Since the authors are using an alternate artificial system of relationships (stem anatomy of
- 195 fossil and modern vs. DNA phylogeny of only modern) their criticisms of some of the
- 196 previous studies are somewhat overstated (e.g. "argument to exclude Osmunda cinnamomea
- 197 from the genus should be obsolete") as some of these classifications might prove to be correct
- 198 if all characters of the plant including frond characters, fertile parts, etc. were to be considered
- in some future analysis and another researcher decided to break up the complex of genera in adifferent analysis.
- 201 [This argument has become obsolete in the course of revision of the manuscript.]202
- Any hypothesis of relationships can vary depending on the taxa used and the characters being
  emphasized, and I'm not convinced that using only the stem anatomy as the determining
  criteria for relationships has the final authority based on their lack of discussion about factors
- that can influence the structure of the stem and its anatomy.
- 207 [We hope to have convincingly demonstrated in a previous publication (Bomfleur et al., 2015:
- 208 p. 15) how well the topology of a classification based solely on axis-anatomical characters
- 209 matches that derived solely from molecular data or from combined molecular and
- 210 morphological data. The congruence is remarkable, which supports our hypothesis that
- analysis of axis anatomy is—in this group—a meaningful approach for resolving systematic
- relationships].
- 213
- 214 Therefore I suggest presenting previous classifications and then presenting the data from their
- analysis which suggests these other classifications should be revised for this particular data in
- this paper. This is particularly important here, because as noted above, the methods are not
- 217 well stated or clear. And their title states that they are only considering the anatomically
- 218 preserved stems and no other information from either modern or fossil material.
- 219 [Has been followed; we have added a short paragraph summarizing the main taxonomic
- 220 changes compared to previous classifications (lines 764–805); in addition, we have compiled
- a large comparative diagram illustrating the nomenclatural and taxonomic history and the
- growing taxic diversity of Osmundales axes in a comparison of selected comprehensive
- taxonomic reviews of the group since the 1970s (see Supplemental Figure S1). In the

- 224 Introduction, we cite these previous major studies dealing with the systematics of fossil and
- extant Osmundales. Part of the objectives of our study is to incorporate into an order-wide
- analysis, the extensive array of data from the large number of fossil taxa erected since the
- 227 previous major systematic review of the order in the 1970s (i.e, following the addition of
- twelve new genera, four new subfamilies, and one new family). Selected major changes are
- discussed in depth in the relevant comments sections.]
- 230
- 231 Validity of the findings
- 232 Mainly noted in the section above the validity cannot be fully judged when the methods are
- not clearly stated, how much material was examined, or whether this paper is completely
- based on a review of previously published material. The parameters for the data analysis need
- to also be presented. Once that is clear, then the validity can be determined The findings are
- certainly a valid opinion for a classification, as all classifications are based on the characters
- used by the authors.
- 238 [These issues have now been addressed in two new materials-and-methods chapters on Data
- Acquisition (lines 548–563) and Analytical Procedures (597–642)]
- 240
- 241 Comments for the author
- Additional line by line comments are below for corrections.
- Line 41 Royal Ferns is the subject of the sentence, should be 'Royal Ferns are' or use the
- ordinal name as the subject for 'Osmundales (Royal Ferns) is' as stated in the abstract.
- 245 [This has been followed.]
- 246
- Line 47 Couper is cited as 1953 here but is 1954 in the Literature Cited. Correct one of the
  references.
- 249 [This has been corrected.]
- 250
- Line 130. Why not use 0 for absent in all cases? This character 1, character 28 and character 29 use 2 for absent, character 33 uses 0 for present and 1 for absent, while most of the other
- characters that have absence as a state use 0. It would be easier for readers to understand the
- analysis and the rest of the statements about characters if there was consistency in the use of
- absence as 0. Or if you prefer keep them all 2, but be consistent for clarity. Does using a
- different number bias the analysis in any way? By selecting a 2 rather than a 0, are you
- 257 implying that you think one is more advanced than another? All that should be clearly stated
- if different numbers are being applied for an absent character depending on the character
- being examined.
- 260 [This has been followed as suggested.]
- 261
- Line 143. Delete 'that'.
- 263 [This item has been left as it was; deleting 'that' renders the phrase potentially ambiguous,
- since it would not be clear whether it is the protoxylem cluster or the parenchyma pocket that
- 265 breaks through towards the pith]
- 266

267 268	Line 210. Delete 'it' – unclear reference to antecedent. Is 'it' the position, the plant, or the stele? Remove 'it' and the sentence seems clearer that position of section is the reference
269	[This has been modified, but we found a hopefully better solution: 'that' has been replaced
270	with 'at which' In this way, it should be clear: effectively it would make no difference
270	whether it is the plant or the stele that is sectioned since in this context the section will
271	always affect both 1
272	
274	Lines 734 and 748 – refers to a 2013 reference with Wang, but only 2014 a and b are listed in
275	Lit cited. Where is this one? Or should it be one of the 2014s?
276	[This has been corrected. I had assumed that nomenclatural novelties were effectively
277	published already at the date of early online publication, but I was unaware that the later date
278	of publication in print will simply replace the earlier online-publication date.]
279	
280	Line 926 Zalessky is this a or b for 1931?
281	[This one was 1935]
282	
283	Line 1153 – ref for Rothwell and Stockey 2008 not in lit cit
284	[Thank you; this has been added]
285	
286	Line 1384 – no date after Chandler for citation
287	[This issue has become obsolete in the course of revision]
289	Line 1821 - Bernhardi needs date of pub 1801?
290	[Well spotted, thank you! However, this issue has become obsolete in the course of revision]
291	
292	Line 1822 – Blume no date for pub 1928?
293	[This issue has become obsolete in the course of revision]
294	
295	Line 1866 – no date for pub. 1907?
296	[This issue has become obsolete in the course of revision]
297	
298	Line 1908 – Gorskii is out of alphabetical order and should precede the Gould reference
299	[This has been corrected]
300	
301	Line 1990 - no Kidston and Gwynne-Vaughn 1914 is cited anywhere in the paper - delete
302	[It is (now): lines 937]
303	
304	Line 2413 – "disparaty" is probably disparity, right?
305	[Yes; thank you. This has been corrected]
306	

## 307 **Reviewer 2** Basic reporting 308 Most of the results are presented in figure captions rather than the body of the text. Please add 309 a section explaining the results of the analyses that stands on its own. Similarly, although 310 there is ample discussion under each taxon in the systematics section, I would like to see a 311 general discussion about how these results challenge or agree with current classifications 312 [This has now been addressed in two sections dealing with "Numerical phylogenetic 313 framework" and the "Revised and annotated classification" (lines 722-805); in addition, we 314 315 have compiled a large comparative diagram illustrating the nomenclatural and taxonomic history and the growing taxic diversity of Osmundales axes in a comparison of selected 316 comprehensive taxonomic reviews of the group since the 1970s (see Supplemental Figure 317 **S**1).] 318 319 320 Experimental design no comment 321 Validity of the findings 322 no comment. 323 324 Comments for the author Recent papers by Bomfleur and associates have produced a series of excellent papers 325 integrating fossil and extant Osmundaceae. The work is of the highest standard and have 326 contributed enormously to our knowledge of these plants. [Thank you!] This paper, however, 327 I think would benefit from some heavy revision and perhaps additional analyses. The authors 328 might feel that my criticisms stem from a philosophical disagreement about the value of 329 neighbour-networks, and that is a fair response. However, I would like to stress here that what 330 I really take issue with is the process of using networks to make decisions, not the networks 331 themselves. I provide more specific comments organized by line number. 332 333 Subgenus Claytosmunda was recently elevated to genus by Metzgar & Rouhan in PPG 1, a 334 new fern classification. Schneider, H., Smith, A.R., Hovenkamp, P., Prado, J., Rouhan, G., 335 336 Salino, A., Sundue, M., Almeida, T.E., Parris, B., Sessa, E.B. and Field, A.R., 2016. A community-derived classification for extant lycophytes and ferns. Journal of Systematics and 337 Evolution. Please revise the text to include this. 338 [This has been followed] 339 340 341 39: Uses of primitive and derived states in the text are fine, but the general application of "primitive" to the clade as a whole in this sentence seems is at risk of conflating the extant 342 plants with their extinct ancestors. I would recommend changing this to something like 343 "contains a high proportion of primitive character states" or something along those lines. 344 345 [This has been followed] 346 568-609: I am not convinced by the author's arguments in favor of an "evolutionary 347 classification". Their reasoning mostly stems from the inconvenience of a cladistics-based 348

- classification. I consider it a great strength that a newly scored trait can change a topology and
- transform synapomorphies in plesiomorphies. Many of the "weaknesses" presented can also
- be viewed as strengths. I suggest dialing back this critique and focusing on justification of the

352 353 354 355 356 357 358 359 360 361	evolutionary classification. I don't agree that its better, but I do feel that classifications involve many subjective decisions and the authors are free to make theirs. [Thank you; we emended our critique and we delivered a detailed explanation for our approach and preference for the use of Neighbor-nets. We contend that our approach provides a robust methodology for our objectives based on the dataset of available anatomical characters. We point out that unlike many previous studies, our work provides full documentation of root and raw files and supporting material free to download, use and modify so that anyone interested can simply make use of the full data set we gathered to undertake any alternative analytical approaches that they may choose.]
362	611: Nomenclatural remarks. It seems pretty evident to me that these names will be
363	effectively published. Is this statement necessary?
264	[Ves: we have been informed this paragraph is necessary per journal guidelines]
265	[10s, we have been informed this paragraph is necessary per journal guidennes]
266	Pasults and Discussion. Is the aditorial standard of PearI to include all of your results and
267	discussion in the figure captions? It would be nice to have a paragraph explaining your major
260	findings that stands on its own and not have to read about the major results in the figure
360	caption
370	Touche This has been addressed in the form of additional results chapters ]
370	[Touche. This has been addressed in the form of additional results enapters.]
372	The authors make a compelling argument as to why a bifurcating phylogenetic tree might not
373	be the best way to analyze their data: it would suffer badly from conflicting topologies and the
374	strict consensus would include large polytomies. However, I disagree that this is reason not to
375	perform the analysis. I analyzed the included dataset under parsimony using TNT and.
376	although the strict consensus includes large polytomies, it also includes some nicely resolved
377	clades. I find these results useful because they provide a way to distill the dataset down to the
378	most robust relationships. Single most parsimonious trees and Measures of clade support can
379	also be evaluated to get more out of the data. These analyses also have the benefit of directly
380	using the character data that was generated, and not relying in a distance matrix. I would
381	suggest that the authors conduct some type of bifurcating tree analyses [they probably already
382	have] to be included as a supplementary file. I understand that the authors might disagree
383	here, the title of the paper mentions "network analysis" after all. This brings me to the larger
384	question. Are neighbor-net analyses alone appropriate for drawing the conclusions that are
385	made here? Frankly, I don't think they are. I don't have any problem with the analyses
386	themselves, I find them to be a useful way of examining the dataset. However, I am concerned
387	with the interpretation of the results and how they were used to make taxonomic decisions.
388	Most of the statement to this effect are in the figure captions where the authors make
389	statements emphasizing the shape of their networks, such as "note the clear divergence".
390	But many of these "clear divergences" could be interpreted differently. The "clarity" of
391	divergence also differs based on the taxa included. In figure 10, Itopsidemoideae is "clearly"
392	distinguished from Guaireoideae, but in Fig. 9 that is not the case; they both belong to the
393	same undifferentiated arm of the network. This example makes me wonder if any analysis
394	including as few taxa as Fig. 10 would give us some sort of "differentiated" pattern. Unless
395	some other criteria by which taxonomic decisions are based can be introduced, these choices
396	seem particularly subjective to me. I don't doubt that the authors are defining "good" taxa, but

- this will be lost on any reader who is not an expert in the group. I suspect that since the
- 398 authors have a strong grasp of the distribution of character states, they are seeing patterns in
- the results are not apparent to the rest of us. This relates to another problem, networks don't
- tell us anything about the distribution of character states, homoplasy, or synapomorphies. Can
- 401 you state whether your ingroup is monophyletic based on these results? It appears that any
- 402 knowledge of character data is drawn from the descriptions of taxa. Would it be more
- 403 straightforward to simply circumscribe taxa using a traditional morphological taxonomic
- 404 approach?
- 405 [Our assessments are based on the available information on the anatomy of the group, the
- 406 modern-day molecular-phylogenetic framework, and reconstructions which are most
- 407 appropriate for handling the complex (non-treelike) signal. In order to make this approach
- 408 (and our reasoning for using 2-dimensional networks rather than a 1-dimensional tree)
- 409 perhaps more readily convincing, we performed a full bootstrap support analysis under all410 three currently used optimality criteria and added more details about the general signal
- 411 structure in our matrix, which is non-tree-like for the most part. Trees will inevitable be
- 412 misled by such signals, and can only incomprehensively reflect the signals provided by
- patterns of morphological differentiation. We, therefore, still refrain from generating one or
- 414 more dichotomous trees from our matrix, but we wish to stress again that underlying raw data,
- 415 including root, batch, and results files, are provided as Supplemental Materials so other
- 416 workers can employ any alternative analytical approaches that they may choose (as apparently
- 417 did the  $2^{nd}$  reviewer in this case)].
- 418

I appreciate that you have italicized diagnostic characters in the descriptions. It's not clear to
me however at what level they are diagnostic. Does that mean that they have no homoplasy?
Or no homoplasy within their clade? Can you provide a bit more explanation?

- 422 [These italicized features are the ones diagnostic at the level of the relevant taxon diagnosis,
- 423 e.g., the combination of italicized features in a genus diagnosis is what differentiates this
- 424 particular genus from others in the same group. One could argue that other features would
- then not be necessary, but that might turn problematic if more distantly related genera show
- the similar features by pure convergence. Consider, e.g., the multiple occurrence of highly
- 427 perforated steles in different groups of Osmundales. The principle is similar to that of Miller,
- 428 1971; we modified the original, perhaps somewhat-too-brief explanatory note and hope to429 have clarified this issue (lines 849–862).]
- 430
- Although there is ample discussion under each taxon in the systematics section, I would liketo see a general discussion about how these results challenge or agree with current

433 classifications.

- 434 [This has been addressed in a new, short summary paragraph and in the accompanying435 Supplemental Figure S1.]
- 436

4371301: You state "As long as the inclusion of the Plenasium species group in Osmunda

remains universally accepted, then any argument to exclude Osmunda cinnamomea from the

- 439 genus should be obsolete". I disagree because your logic is essentially phenetic and ignores
- the fact that Osmunda and Osmundastrum can exhibit plesiomorphic traits, and Plenasium
- 441 (which is nested in them) has derived traits.

442 [Point taken; with our adoption of the latest taxonomic revision, however, this has been

- 443 rendered obsolete in the course of revision.]
- 444

Here, you also mention the "potentially misinformative molecular data" the results in the 445 paraphyly of Osmunda s.s. and cite Bomfleur, 2015. This is an important topic and I am glad 446 you raised the issue here. In Bomfleur 2015 you cite conflicting signal from markers and 447 448 insufficient outgroup selection as reasons why the molecular data might be giving an inaccurate result. The outgroup problem has been addressed in the recent phylogeny of Testo 449 & Sundue 2016 [Testo, W. and Sundue, M., 2016. A 4000-species dataset provides new 450 insight into the evolution of ferns. Molecular Phylogenetics and Evolution, 105, pp.200-211], 451 but those authors find the same result as Metzgar. The marker selection is different from 452 Metzgar, but overlapping for a couple of markers. Thus it seems to weigh in on the issue. 453 [We corresponded with Dr Testo regarding this issue. He provided us with his primary data 454 and the full tree and agreed with our opinion that the analysis in Testo & Sundue does not 455 456 address the issue of (inevitable) ingroup-outgroup long-branch attraction. In fact, their gene 457 sample will likely aggravate the branching artefact. Dr Testo informed us that the tree only served as a vehicle to study the disparate molecular-evolutionary rates within the different 458 lineages of pteridophytes and does not see any reason why it should reject our conclusions as 459 outlined in the 2015 paper. Note further that Testo & Sundue's tree also flips the fastest 460 evolving crowngroup of pteridophytes. Dr Testo informed us that this striking conflict to the 461 PPG I tree could not be resolved. This demonstrates that outgroup-inferred roots, even using a 462 comprehensive as possible, outgroup sample may simply be wrong (all splits in the subtree 463 are identical, only the root is completely placed opposite than in the PPG I tree). The 464 465 phylogenetic (via-the-tree) distance between the Osmundaceae root node (MRCA of Osmundaceae and most other ferns) and the MRCA of all Osmundaceae in Testo & Sundue's 466 inference is 3(!)-times higher than the largest root-tip distance within the Osmundaceae. This 467 would explain the much-too-young Osmundaceae ingroup divergences. The closest relatives 468 of Osmundaceae (Marattiales) are 6-times-or-more distant from the MRCA of the 469 Osmundaceae than the largest root-tip distance within Osmundaceae. Hence, we are confident 470 that our initial conclusions are still valid.] 471

472

1145: You state that this is "a plain example of the failure of strict-cladistic systematics". This

is a gratuitous comment that doesn't need to be here since you don't actually perform these

analyses or use a strict cladistic classification. [Point taken; statement has been deleted.] Also,

isn't another solution simply to re-circumscribe Todea? Furthermore, you're admission that its

status is "ambiguous" seems to deflate it as a good example of a "failure".

478 Supplement: I am confused by the inclusion of molecular sequence data and tree in the data479 file since these are not discussed in the text at all.

480 [The molecular data in the matrix file are a remnant of our previous analysis (Bomfleur et al.

481 2015) upon which the new matrix was built. The molecular data were simply left in there for

the sake of completeness. We added a brief explanation in the matrix description addressing

483 this issue.]

484

485	2077: probably is misspelled
486	[Could not find a misspelled "probably" anywhere near line 2077; we hope to have caught the
487	typo anyway in the course of revision.]
488	
489	
490	ADDITIONAL CHANGES TO THE MANUSCRIPT:
491	We have modified the original files and matrix root files to incorrect the sharpes requested
492 493	As a consequence, all analyses have been re-run and all relevant results (text and illustrations)
494	have been modified accordingly.
495	
496	In addition, we have performed comprehensive analysis of support values, and incorporated
497 498	chapters.
499	
500 501	We have carefully re-evaluated the text and have made minor grammatical improvements throughout.
502	
503	We have re-organized the sections of the text to provide a more logical flow of background
504 505	information, results and discussion.
506 507	We have improved the resolution of the geochronological ages of clades down to epoch level.
508 509	We have made minor amendments to the references.
510	We have made minor amendments to the figures to accommodate the changes to the text and
511 512	the new systematic treatment of extant Osmundaceae genera published recently by PPG I. (2016).
513	
514	
515	We wish to thank the editor and both reviewers for the fair, constructive, and helpful
516	comments. We trust that these changes meet with your approval and we look forward to
517	your decision on our revised manuscript.
518	
519	Yours sincerely,
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521	
522	
523	Benjamin Bomfleur
524	on behalf of all authors