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Report on the PhD thesis by Jana Čepičková entitled "Cenomanian vegetation of the Bohemian Cretaceous Basin"

The thesis comprises six parts: four published papers, one 'in press' manuscript and a document linking these works.

The linking document summarises the published thesis components that report on Cenomanian vegetation of the Bohemian Cretaceous Basin. This basin accumulated Cretaceous sediments reflecting a variety of sedimentary and ecological environments and the thesis work builds on prior detailed sedimentological analyses conducted by a succession of researchers, but most notably by David David Uličný, upon whose research much of the context for the plant fossils depends.

The linking document is well organised and while the English is easy to follow there are a number of typographical and grammatical mistakes compared to those in the published material. However, since I cannot speak or write in Czech at all I applaud the candidate for her efforts. I do not propose to give a line-by-line list of suggested corrections in this report. If the candidate needs my annotated pdfs I can provided them. Rather, I will focus on a few key topics.

The choice to emphasise the Mesophytic and Cenophytic over the more conventional Mesozoic and Cenozoic is an interesting one and is particularly pertinent to the angiosperm rise to dominance in the middle Cretaceous upon which the thesis focusses. The Bohemian Basin preserves one of the best records of this transition and has been particularly well documented thanks to the multi-decadal perseverance of the team in Prague. This thesis is a product of this team, and is an important contribution. In the 'in press' manuscript entitled "Terrestrial palaeoenvironments from the Cenomanian strata of the Bohemian Cretaceous Basin in Central Europe: evidence of the rise to ecological dominance of angiosperms and the decline of gymnosperms", of which the candidate is the third author of nine, this transition to angiosperm dominance in many communities is extremely well documented. This is one of the most complete and insightful reconstructions of a Cretaceous landscape I have seen and really brings that ancient landscape alive. Looking at the author contributions it is clear that the candidate played on important role in this work. Returning to the linking document, on page 4, first paragraph, there is a remark about papillae trapping dew, but there is no reference. In fact, this phenomenon of extracting water from the atmosphere by *Pseudofrenelopsis* (a close relative of *Frenelopsis alata* and equally water stressed) was commented on in Chapter 4 of "The Cretaceous World" edited by P. Skelton (Cambridge University Press, 2003, ISBN 0 521 83112 1). However, it was not the papillae that did the trapping but fimbrial hairs along the reduced leaf margin. It was surmised that water nucleating there (much as water nucleates overnight on wool, strands on a sweater left on a washing line) formed droplets that ran down between the adpressed leaf and the stem, where the cuticle was thin, and was absorbed by the plant. Thus, these conifers extracted moisture directly from the atmosphere minimising the osmotic roots stress imposed by saline groundwater, which may be why they show unstressed ∂^{13} C signatures documented in one of the thesis papers (Zahajska et al., 2024). A study looking at the distribution of such taxa and coastal fog using numerical climate models might be worth pursuing. Such modelling/fossil biology studies might help explain some of the weak and mixed isotopic signatures reported by Zahajska et al. (2024).

After reviewing the history of research on Cretaceous floras and cuticle studies as well as the geology of the Bohemian Basin, the candidate goes on to discuss the Bohemian Basin records in comparison with those from the USA. The emphasis is on conterminous USA, excluding the abundant Cretaceous floras records in Alaska. In the in press manuscript the authors refer to the "Cretaceous of North America" but again omit the Cretaceous floras of Alaska and Canada. Consequently, the comparisons are only relevant for mid and low latitudes, and this should be recognized.

I really applaud the combination of sedimentary environment analysis, plant mega- and mesofossil studies with palynology to obtain a comprehensive insight into community heterogeneity and plant succession across the topographically subdued but complex landscape. This work sets a new standard for palaeo-environmental reconstruction, even down to distinguishing plant communities on slopes of different aspect. Future studies might look at how communities might have changed under orbitally-driven climate change using new high spatial resolution climate models configured for the Cenomanian. Orbital cycles could be the driver for the oscillatory nature of marine influence in the Bohemian Basin, and a strong impetus for the transition in angiosperm ecological strategies (from ruderal to competitive), since flowering plant biology makes that group particularly successful in fluctuating environments.

One of the pervasive features of many of the Bohemian Basin plants is their xeromorphic adaptation reflected in small heavily cutinized leaves with stomata often wreathed by papillae. The studies of cycad (Čepičková and Kvaček, 2020) and angiosperm (Čepičková and Kvaček, 2023, a,b) cuticles underscore the evolutionary convergence in coping with drought stress. These works are well written and illustrated, and document well the critical features of the taxa. This is first class foundational palaeobotanical research, and they put the plants in a detailed depositional context.

A common feature of many of these relatively thick-cuticled plants is the presence not just of papillae but also striations or wrinkles. It is not clear to me if such features afford the cuticle the ability to expand and contract as the leaf takes up or loses water. Did some of these leaves serve as water storage organs? This does not seem to have been considered. Related to this is the suggestion in the 'in press' paper that the *Frenelopsis* leaf mats (also common to *Pseudofrenelopsis*) suggest rare inundations by sea water and wholesale death of the trees. If

this was the explanation then such inundations were exceedingly rare because the trees were able to grow to considerable stature as seen in the large logs exposed on the Isle of Wight, southern England (Alvin, K.L., Fraser, C.J., and Spicer, R.A., 1981, Anatomy and palaeoecology of *Pseudofrenelopsis* and associated conifers in the English Wealden. *Palaeontology* 24:.7). I think it is more likely that this group of conifers was able to supplement their water stress avoidance strategies (sunken stomata with overarching papillae, thick cuticles, reduced leaves, succulent leafy branches and fimbrial hair atmospheric moisture extraction) with mass shedding of leaf load (deciduousness) if conditions became extreme.

Critical to understanding plant biology in the mid Cretaceous Bohemian Basin is the climate. Quantitatively this can be assessed using woody dicot foliar physiognomy. In the 'in press' paper a reference is made to CLAMP (Climate-Leaf Analysis Multivariate Program) on lines 254-256 and line 630 onwards in the 'Palaeoclimate' section. Lines 254-256 say "All the mentioned reference files and datasets are available for download from the CLAMP website: https://www.digitalatlasofancientlife.org/learn/paleoecology/paleoclimate/clamp/ . I have to say this is not the CLAMP website and the information there is misleading and out of date. The correct web address is: <u>http://clamp.ibcas.ac.cn</u> which contains the correct and up-to-date calibration files as well as the ability to do the entire analysis online. If the CLAMP climate variables were obtained using the address in the manuscript they should be checked against the online analysis on the genuine CLAMP website. The CLAMP variables also need to have uncertainties quoted. The statistical uncertainties for any given calibration or given on the CLAMP website (<u>http://clamp.ibcas.ac.cn</u>) but here it seems multiple analyses were performed with different calibrations, in which case the cumulative uncertainties should be given.

That said, the climate is undoubtedly seasonal in terms of precipitation, but better humidity variables can be obtained such as vapour pressure deficit, that is relevant to the water stress arguments. See Spicer, R.A., Yang, J., Spicer, T.E.V., Farnsworth, A., 2020. Woody dicot leaf traits as a palaeoclimate proxy: 100 years of development and application. *Palaeogeography, Palaeoclimatology, Palaeoecology* 562, <u>https://doi.org/10.1016/j.palaeo.2020.110138</u> for a recent overview of CLAMP strengths and weaknesses.

Such issues aside, overall, there is some excellent work in the documents that comprise this thesis. Then taxonomy and palaeobotanical studies are excellent, as is the linking to the palaeoenvironment. The ∂^{13} C on alkanes is innovative, if somewhat needing of more work to understand fully the mixed signals that have emerged. It may be that in a high pCO₂ atmosphere of the mid Cretaceous fractionation responses would be different to those of the present. There is a lot to explore here.

The main criterion for a successful thesis is "is it publishable?". Quite clearly this criterion has been met in the form of four papers and one accepted. What is not entirely clear to me is the candidate's contribution to each paper but work of this kind has to be a team effort and single authorship papers are exceedingly rare in science today. If the supervisors can vouch for the candidate's substantive contribution, then I am happy.

I have enjoyed reviewing this thesis and congratulate the candidate on the breadth and quality of the work.

R. A. Spicer