¿Cretaceous Montiaceae? Reevaluation of the classification of Kuprianovaites deccanensis Nambudiri & Thomas (Caryophyllales)

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ABSTRACT

Kuprianovaites deccanensis Nambudiri & Thomas is a form species referring to fossil ovule/seed-bearing fructifications from the Cretaceous/Paleocene boundary of central India. It has been classified in Montiaceae based on similarities to fruits of *Phemeranthus* Raf. species, in particular a 3-valvate unilocular loculicidal capsule with free-central placentation and seeds with campylotropous ovules. *Kuprianovaites* is likewise similar to fruits of *Talinum* species (Talinaceae), but differs in lacking a conspicuously two-layered pericarp. At the same time, however, available seed images of *Kuprianovaites* show no evidence of an investing aril (pellicle) characteristic of *Phemeranthus* species. Lacking a clear synapomorphy with either Talinaceae or Montiaceae, the morphological and geographical evidence suggest that *Kuprianovaites* is better assigned to the Portulacineae stem group. This classification accords better with current molecular-based divergence estimates. The implications for Portulacineae historical biogeographic interpretation are discussed.

Key words: *Kuprianovaites*, Montiaceae, Talinaceae, Portulacineae, Cretaceous, Gondwana, clade age, vicariance, long-distance dispersal (LDD)

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Introduction

Manchester et al. (2024) published new images of *Kuprianovaites deccanensis* Nambudiri & Thomas, a form species of fossil ovule/seed-bearing fructifications from the Cretaceous/Paleocene boundary (ca. 66 mybp) of central India. The published images show fairly clearly a: (i) \pm globose; (ii); 3-valvate unilocular loculicidal capsule; with (iii) free-central placentation of; (iv) many (ca. 18) seeds; with (v) campylotropous ovules. As the authors partially noted, *each* of the traits i–v is found among several families of the core Caryophyllales clade ("Centrospermae;" Yao et al., 2019). But the *combination* of these traits suggested fruits of certain Portulacineae taxa, in particular *Talinum* Adans. (Talinaceae) and *Phemeranthus* Raf. (Montiaceae). Furthermore, the fruit was born on a naked pedicel that bore a thickening suggestive of perianth scars, which also characterizes *Talinum* and *Phemeranthus* fructifications.

But the pericarp of *Kuprianovaites* lacks the distinctive exocarp-endocarp differentiation of *Talinum* fruits. Thus, Manchester et al. (2024) considered *Kuprianovaites* to be "a good phenetic match with *Phemeranthus*," hence they classified it in Montiaceae. The fossil thus predated by some four million years the Montiaceae crown group oldest age estimate based on fossil-calibrated DNA sequence divergence (Yao et al., 2019; cf. Hershkovitz, 2019; see also below). This, the authors suggested, undermined long-distance dispersal (LDD) explanations for intercontinental Montiaceae disjunctions. Here, I dispute the taxonomic diagnosis of *Kuprianovaites* and discuss the general problem of

paleotaxonomic diagnosis and its consequences for both phylogenetic age estimation and historical biogeographic interpretation.

Reconsideration of the Kuprianovaites taxonomic diagnosis

Although *Kuprianovaites* indeed resembles a *Phemeranthus* fructification and lacks pericarp differentiation, Manchester et al. (2024) seem to have overlooked a critical characteristic of *Phemeranthus* seeds, viz. an enveloping membranous aril or "pellicle" (Carolin, 1987, 1993; Price, 2012). This evidently resistant and usually persistent structure is visible on dehisced seeds to the naked eye. Although I cannot locate an image of a standard anatomical section of a mature but undehisced *Phemeranthus* ovary, I thus suppose that the pellicle should be present and clearly visible. In fact, in a micro-CT (x-ray) scan of a *Phemeranthus* fruit published by Manchester et al. (2024: Fig. 3), it is evident as a thin envelope separated from but enclosing the seeds, and it is clearly absent in the *Talinum* seed scans.

The apparent absence of a pellicle surrounding the *Kuprianovaites* seeds presents a dilemma. Manchester et al. (2024) noted the similarity of *Kuprianovaites* to both *Talinum* and *Phemeranthus* fructifications, but discarded a relationship with the former because *Kuprianovaites* lacked its derived pericarp trait. But it is clear that *Kuprianovaites* also lacks the derived seed trait of *Phemeranthus*. So we are back to square one.

The solution to this problem is very simple when it is appreciated that *Kuprianovaites* lacks a clear *synapomorphy* with either Talinaceae or Montiaceae. It only bears *similarities*. ¿What are the relations of *Kuprianovaites based on synapomorphy*? Here, it is significant to note that fruits in the Portulacineae sister group, Molluginaceae, also are mostly loculicidal capsules, and this seems to be the ancestral state for the family (Thulin et al., 2016). Molluginaceae and Portulacineae form the "Portullugo" clade (Edwards & Ogburn, 2012, etc.). The difference between Molluginaceae and Portulacineae capsules is that the former are *septate* at maturity, hence the placentation is axile rather than (apparently) free-central (Hofmann, 1994; Thulin et al., 2016). In *Talinum*, the synascidiate portion of the ovary becomes septate during early development, but the septa later disintegrate, yielding free-central placentation (Veselova et al., 2011). Hofmann (1994) reported that septa "obliterate" (beginning in the mesophyll) in all four examined current Montiaceae genera¹ and also in *Talinum, Anacampseros* (Anacampserotaceae), and *Portulaca* (Portulacaceae).² As would be expected given the state of ovary maturation, the *Kuprianovaites*

¹ Hofmann's (1994) tabulation applied the Candollean generic classification of *Calandrinia* Kunth and *Talinum* (see Hershkovitz, 2021a). She did not list the species or number of examined species, hence the correspondence to current classification cannot be ascertained. Nonetheless, one can infer that multiple Montiaceae were examined, and that the septa obliterate in any and all examined species formerly classified in *Calandrinia* and *Talinum*.

² The descriptions of Ronse de Craene (2020 ["2021"]: Table 3) are at odds with earlier reports. He reported that septa "at maturity" are "well-developed and centrally joined" in Montiopsis umbellata (Ruiz & Pav.) D.I.Ford (Montiaceae; reported there as "Calandrinia"), Talinum, and Anacampseros (Anacampserotaceae), as well as in Mollugo and Glinus (Molluginaceae); and "weakly developed" in Claytonia sibirica L. (Montiaceae; reported there as "Montia"). Accordingly, he classified placentation in all these taxa as axile. His Fig. 8 suggests that Lewisia would be classified likewise. Thus, free-central or basal placentation were reported as occurring only in Basella (Basellaceae), Decarya (Didiereaceae), and Portulaca (Portulacaceae). Meanwhile, among many others, Carolin (1993) described placentation in classical Portulacaceae (viz. sensu lato) as "basal or free-central at maturity." The discrepancy may owe to the definition of "at maturity," viz. at anthesis versus at fruit dehiscence. In the latter case, septa (hence axile placentation) persist in Molluginaceae but not among Portulacineae (hence apparently free-central placentation).

images show no evidence of septa. For the sake of argument, it can be *supposed* that they developed but later disintegrated.

If disintegration of capsule septa is considered to be a synapomorphy of Portulacineae, then *Kuprianovaites* can be classified provisionally in this suborder. But that seems to be as far as we can go. Classification in any of the included families requires reference to an additional morphological synapomorphy. On the basis of the absence of synapomorphy, Manchester et al. (2024) excluded *Kuprianovaites* from Talinaceae. It can be provisionally excluded also from Anacampserotaceae, Basellaceae, Cactaceae, Didiereaceae, Halophytaceae, and Portulacaceae. It lacks one or more specialized traits of each of these families.

Returning to Montiaceae, although unequivocally monophyletic based on genomic evidence, perhaps paradoxically, it cannot be diagnosed currently by any morphological synapomorphy (Hershkovitz, 2021b; cf. Hershkovitz, 1993). Meanwhile, classification of *Kuprianovaites* in *Phemeranthus* is precluded by its lack of the seed trait synapomorphy of the latter.³ *Kuprianovaites* is less similar to other Montiaceae fructifications, which generally have ovate capsules with persistent sepals.⁴

Another *Kuprianovaites* trait of interest is the possible perianth scars on the pedicel. As Manchester et al. (2024) noted, these also are suggestive of both *Talinum* and *Phemeranthus*, in which the perianth generally is caducous, usually abscising at some point in between anthesis and fruit dehiscence (Hershkovitz, 2021a). In the case of *Kuprianovaites*, for the sake of argument, let us assume that indeed perianth scars are present and that indeed the perianth is similarly caducous.

Hershkovitz (2021a) described in detail perianth fate among Portulacineae. Ignoring for the present purposes the peculiar perianths of Cactaceae and Halophytaceae, the perianth in the remaining families comprises an outer whorl of usually two sepal-like organs, believed to be homologous with outgroup bracteoles, and an inner whorl of usually several petaloid organs, believed to be homologous to the monochlamydeous outgroup perianth (Ronse de Craene, 2008, 2013). In Molluginaceae, the variously sepaloid to petaloid perianth organs are persistent in fruit. Among Portulacineae, the supposedly homologous petaloid whorl is persistent only among Basellaceae and Didiereaceae. In the other families, the petaloid whorl is ephemeral.

Meanwhile, besides Talinaceae and *Phemeranthus*, the sepaloid whorl is (sooner or later) caducous in Portulacaceae; caducous or persistent among Anacampserotaceae; persistent among Basellaceae and Didiereaceae (possibly except in the "basal" lineage *Calyptrotheca* Gilg.); and usually and ancestrally persistent among *remaining* Montiaceae. A propos *Kuprianovaites*, once again *Talinum* and *Phemeranthus* share the same state. But this does not matter. Partially because of the homology question⁵

³ Hershkovitz (2019) considered that the monotypic and possibly extinct genus *Schreiteria* Carolin may be sister to *Phemeranthus*. Seeds of this genus lack an investing aril, but its distinctive capsules are slender and greatly elongated. Also, its stomata morphologically/developmentally agree with other Montiaceae and are distinct from those of *Phemeranthus* and all other Portulacineae outgroup families (Hershkovitz, 1993 [Table 3], 2021b; contra Hershkovitz, 2019). Given the consequent uncertainty regarding the relations of *Schreiteria*, its lack of seed investing arils does not seem to rescue the classification of *Kuprianovaites* in Montiaceae.

⁴ There are derived exceptions for each of these traits, but not the combination.

⁵ The typological homology may be a red herring in any case if evolutionary morphological shifts bring one organ into the developmental "field" of another, creating a neontological organ that *behaves* more or less as a prior organ in that same morphological position (Ronse de Craene, 2008). Just as with many "real" angiosperm sepals, Portulacineae sepaloids usually enclose the floral bud, spread open at anthesis, and, if they are persistent, usually close after anthesis and envelop the fruit until dehiscence.

and partially because of variability, the ancestral states of perianth organ persistence among Portulacineae cannot be assessed with certainty at the present time (Hershkovitz, 2021a).

Talinum vs. *Phemeranthus*: a "model conundrum" for paleotaxonomy and phylogenetic age estimation?

Above, I concluded that classification of *Kuprianovaites* in Montiaceae is unjustified, and that it is better classified as Portulacineae incertae sedis. This conclusion has significant implications for the age and geographical metastasis of Portulacineae, which will be discussed further below. But before that, I digress. The *Kuprianovaites* question recalls a more sobering aspect of morphology-based, hence fossil-based classification, hence the consequences for phylogenetic and evolutionary interpretation.

As detailed in Hershkovitz (2021a), Candolle (1828) classified *Phemeranthus* as a section of *Talinum* s.l. It remained included in *Talinum* s.l. in all subsequent taxonomic treatments up until the end of the 20^{th} Century, and in a few treatments after that. The inclusion in *Talinum* s.l. was based in no small measure on the similarity of the fructification, in particular, the caducous sepals.

Carolin (1987) undertook a morphology-based cladistic analysis of classical Portulacaceae in which he analyzed Candolle's sections of *Talinum* s.l. as separate OTUs. He found *Talinum* s.l. to be polyphyletic. Nonetheless, Carolin (1993) retained *Talinum* s.l. in his generic taxonomy, though he recognized and diagnosed the sections *Talinum* and *Phemeranthus*. He did not comment here on their polyphyly per Carolin (1987).

Hershkovitz (1993) revised and amended Carolin's (1987) analysis, and also found *Talinum* s.l. to be polyphyletic, though not mathematically convincingly so. He nonetheless formally recognized *Phemeranthus* as distinct from *Talinum*. Polyphyly of *Talinum* s.l. was not established convincingly until the molecular phylogenetic analysis of Hershkovitz & Zimmer (1997). It was only *after* this that the separation of these taxa began to materialize in taxonomic literature and databases.

Moving to the present, Manchester et al. (2024) described and amply illustrated a fossil fructification that indeed strongly resembles those of both present day *Talinum* and *Phemeranthus* fruits, even though it cannot be either. But they did not seem to appreciate that these genera historically had been merged, nor the implications. In particular, according to a chronogram accepted by Manchester et al. (2024), these taxa diverged *seventy-five million years ago!* Yet the fructification morphology is so similar as to obfuscate fossil diagnosis across this vast temporal expanse. And Manchester et al. (2024) not only effectively predicated to have *empirically* cross-validated the oldest Montiaceae age estimate, they implied that the *true* divergence must be *older*. No doubt, as I am writing this, a researcher somewhere in this world is in front of a computer, recalibrating the Caryophyllales phylogenetic chronogram, using 66 mybp as the date of Montiaceae crown divergence.

But as I have articulated, classification of *Kuprianovaites* in Montiaceae is not supported by a morphological synapomorphy. Morphology supports classification, at best, in Portulacineae. And according to the same cited chronogram, this crown divergence dates to 75 mybp, which is ca. 10 my older than *Kuprianovaites*. Problem solved...sort of. But it begs the questions of how often this happens in paleotaxonomy, why this happens, and what are the broader consequences. I cannot answer the first question at this time, although elsewhere I pointed out that the diagnosis of a Cenomanian pollen fossil as *Montia* was fanciful (Hershkovitz & Zimmer, 2000). The attribution of *Kuprianovaites* to, specifically, Montiaceae is unjustified, but it is nonetheless insightful and not at all fanciful.

This leads to the second and more important question. Unjustified paleotaxonomic diagnoses happen for several reasons. First, and most obviously, this happens because fossils are usually both fragmentary and axiomatically inadequately preserved.⁶ Second, and more importantly, this happens because of either or both of morphological convergence and symplesiomorphy. This is the case for fruit morphology of *Talinum* and *Phemeranthus* and other examples, certainly throughout angiosperms, but also the entire tree of life.

But from the standpoint of paleotaxonomy, the question of whether morphological similarities among extant taxa represent convergence or symplesiomorphy may be, per se, another red herring. The more important question is what the very existence of these phenomena means for paleotaxonomic diagnosis. For example, it is not clear whether the fruit/seed similarities between *Talinum* and *Phemeranthus* represent convergence or symplesiomorphy.⁷ But that is not so important. What is clear is that the developmental wherewithal for the evolution of a 3-valvate globose capsule with degenerating septa existed not only no later than the date of the Portulacineae crown divergence, but *as early as* the split between Molluginaceae and Portulacineae. Thus, per the Yao et al. (2019) chronogram, fructifications similar to *Kuprianovaites* might be found in deposits at ca. 80 mybp.

¿But why not before that? ¿Can we conclude that no currently extinct lineages with free-central placentation evolved along the Portullugo clade stem? This would take us back to ca. 90 mybp. And, for that matter, ¿can we conclude that a lineage with globose 3-valvate capsules with free-central placentation did not exist along any other branch of the centrospermous Caryophyllales phylogeny? This is ad hoc speculation, of course, but not completely. As Manchester et al. (2024) noted, the traits of *Kuprianovaites* exist among other centrospermous Caryophyllales, just not in combination. Application of the same "substitution probability" logic used in the first place to estimate molecular phylogenies, hence age estimates (see also below), would yield some likelihood that the traits existed in combination in a lineage outside of Portulacineae.

As another example, a propos Caryophyllales age, Manchester et al. (2024) cited Samant et al.'s (2020) report of the pantoporate fossil pollen form genus *Periporopollenites* from the same central Indian deposits as *Kuprianovaites*. This presumably centrospermous fossil has been reported worldwide from the latest Cretaceous. But otherwise, it is phylogenetically uninformative, because similar pollen occurs in several centrospermous lineages. Indeed, the basal split of centrospermous Caryophyllales separates the monogeneric Microteaceae from the rest of the order. Microteaceae pollen is pantoporate. Given the lability with which pantoporate pollen evolves in this order (Prieu et al., 2017), *¿is it not unreasonable to suspect that an extinct centrospermous stem group lineage also had pantoporate pollen*? In other words, the oldest such pantoporate grain might be a better marker of the age of the centrospermous stem rather than crown divergence or the divergence of any lineage therein.

The point of the above discussion is to demonstrate how inadequacies of both fossils and fossil diagnoses may result in overconfident association with modern taxa. I suggest that this is the case with classification of *Kuprianovaites* in Montiaceae. Such overconfident associations, in turn, would lead to empirical overestimates of taxon ages that translate into inaccurate calibrations of DNA-based

⁶ Completely adequate preservation would preserve also the genome, which would render trivial fossil diagnosis to at least to the generic, if not species level.

⁷ The fruit morphology of each genus is distinctive within its taxonomic milieu, viz. Montiaceae and the unnamed clade of remaining Portulacaceae. But, as noted first in Hershkovitz (1993; cf. Hershkovitz, 2019, but note correction in Hershkovitz, 2021b: 34), *Phemeranthus* is both morphologically and biogeographically "intermediate" between these groups.

phylogenetic chronograms. This would exacerbate, of course, inadequacies of chronogram estimation itself, which nowadays most commonly applies Bayesian estimation of both ages (ultrametric tree branch lengths) and simplistic DNA base substitution models.⁸ And this is setting aside the large *error bars*, which tend to be ignored in practice. But I cannot evaluate here the actual severity of these problems in current phylogenetic chronography.⁹

Kuprianovaites and Montiaceae historical biogeography

Manchester et al. (2024) concluded that the age of *Kuprianovaites* undermined LDD narratives of Montiaceae historical biogeography. But their brief commentary is both spurious and ill-informed, citing only unsourced information gleaned from a "coffee table" reference, viz. Christenhusz et al. (2017). This encyclopedic tome is intended for scientific educational/informational purposes, not as a data source for scientific *analytical* purposes.

For example, Manchester et al. (2024) parroted almost word-for-word the global Montiaceae distribution detailed by Christenhusz et al. (2017). It is accurate, but "unparsed," and it is ahistorical. In particular, much of this apparently cosmopolitan distribution (viz. Europe, SW Asia, and Africa) owes to that of a *single* and evidently recently evolved cosmopolitan semi-aquatic "weed" (viz. *Montia fontana* L.). This distribution is a red herring for purposes of understanding biogeography of the family as a whole. Eleven of 16 Montiaceae genera are endemic to the Americas, another two are primarily American, one derived lineage is Australian, and the remaining two represent a single derived lineage comprising two monotypic genera, each an insular endemic (cf. Hershkovitz, 2019; see also below).

Manchester et al. (2024) went on to cite the unsourced 13 mybp Montiaceae age estimate reported in Christenhusz et al. (2017). This is another red herring, first because it is an "outlier" among calibrated tree estimates,¹⁰ and second, because it was "erroneous." The source of this estimate, not cited by Christenhusz et al. (2017), most likely was Ocampo & Columbus (2010). Christenhusz et al. (2017), hence Manchester et al. (2024), seemed to have overlooked Ocampo et al. (2013; cf. Ocampo & Columbus, 2012), where the *same* authors *corrected* their estimate to *30 mybp*. Meanwhile, Arakaki et al. (2011) and Ogburn & Edwards (2015) graphically indicated Montiaceae divergence in the mid-30 mybp range. Unfortunately, neither work explicitly stated the Montiaceae age. Thulin et al.'s (2018) and Hancock et al.'s (2018) estimates broke the 40 mybp barrier, before Yao et al. (2019) increased it to 62 mybp.

But the point that Manchester et al. (2024) were making was that the *Kuprianovaites* undermined the "argument" of Christenhusz et al. (2017) for LDD-mediated Montiaceae global metastasis. But no "argument" was made. It was simply a declarative statement logically deduced from the age they reported. Still, it is another red herring. Hershkovitz (2019) pointed out that not even the Yao et al. (2019) 62 mybp estimate undermined the evidence for primarily LDD-mediated Montiaceae metastasis, because the multiple intercontinental disjunction ages remained too young to be explained by plate tectonics (see also below).

⁸ Elsewhere, I have referred to such models as "fake models," and to Bayesian estimation as "induction on steroids" (Hershkovitz, 2018, 2021c).

⁹ I am unable to evaluate here the fossil evidence used by Yao et al. (2019). The information, published as supplementary data, evidently is proprietary and not "open access."

¹⁰ Before tree calibration methods were developed and adequate data available to apply them, Hershkovitz & Zimmer (2000) estimated Montiaceae age at 8–16 mybp. This was based on average substitution rates then estimated for herbaceous plants. They reported that the woody plant rate yielded a Montiaceae age of 80 mybp.

Hershkovitz (2019) also pointed out that the mere *existence* of a terrestrial route contemporary with the presumed ancestor of modern disjunct taxa is necessary, but not sufficient evidence for vicariance. LDD, except in the case of water dispersal, is not substrate-specific. It occurs over land as well as water. Vicariance requires minimally that the disjunct taxa are descendents of an ancestral species whose range, at one time or another, actually traversed the eventual rift zone. The zone must have been ecologically *hospitable* to the ancestral taxa. Since rifting itself induces ecological modification/instability, that hospitability might have preceded the age of rifting. Thus, in the absence of actual rift zone fossils, the age of the vicariance event is unknown empirically, rendering *both* vicariance and LDD as credible but still speculative hypotheses.

Meanwhile, Hershkovitz (2019) articulated a phylogeny-based narrative in which Montiaceae originated in far-western South America, whether before or after the Gondwana split. The Andean orogeny then separated *Phemeranthus* and *Schreiteria* from the ancestor of the remainder of the family on the western slope. This ancestor disproportionately diversified. All lineages native to other land masses are phylogenetically more derived, thereby younger and implicating LDD (but see Hancock et al., 2018).

In fact, however tantalizing are the increasingly older age estimates, even the phylogenetic evidence for vicariance-mediated *Portulacineae* metastasis is limited. The basal lineages are either entirely American (Halophytaceae) or primarily American, with non-American taxa being derived (Basellaceae, Cactaceae, Montiaceae, and *each* of the four "ACPT" clade lineages¹¹). Only one deep lineage, the Didiereaceae crown, diversified only in Africa. But the age of the Portulacineae crown is either Gondwanan or it is not. A scenario consistent with the Yao et al. (2019) age is that Portulacineae diversified in Gondwana, Montiaceae and most of the remainder establishing in the west and the Didiereaceae ancestor establishing in the east. After the split, some of the consequently South American lineages dispersed to Africa. Alternatively, ignoring possibly inaccurate molecular-based age estimates, Portulacineae may have diversified after the split. In this case, only a single "ad hoc" but hardly implausible LDD hypothesis would be required to explain Didiereaceae.

¿Where does Kuprianovaites *fit into this scenario?* If it represents an extinct early Portulacineae lineage, then it would support the vicariance scenario, since it establishes the presence of Portulacineae in eastern Gondwana. But Manchester et al. (2024) seem to have overlooked "the elephant in the room." In particular, they argued that *Kuprianovaites* from the latest Cretaceous of central India is Montiaceae. At *that* time, the Indian subcontinent was *insular* and at \pm its maximum distance from both Africa and Asia (see, e.g., Samant et al., 2020). So...*¿how did* Kuprianovaites *GET there?* Even if *Kuprianovaites* is a Portulacineae stem lineage, vicariance would require an otherwise unsupported Portulacineae stem divergence at 100+ mybp. Thus, ironically, Manchester et al. (2024) seem to be disputing arguments for LDD with evidence for...*LDD*!

Manchester et al. (2024) concluded their work by remarking that, "this example demonstrates that, despite having a crown group that includes many weedy species, an extant angiosperm family may still have its origin in deep time, even predating the Cenozoic." This conclusion seems to be a non sequitur and, besides, nonsensical. Their work did not otherwise refer to "weediness" of Montiaceae or a plausible relation between "weediness" and clade age. For example, Papaveraceae is a weedy lineage, and its crown group age has been estimated at ca. 120 mybp...much older than Portulacineae (Peng et al., 2023). And besides this, Caryophyllales s.l. is a weedy order. In fact, angiosperms as a whole can be considered as a "weedy" crown group (cf. Peng et al. 2023). If anything, what Manchester et al. (2024) demonstrated

¹¹ A clade comprising Talinaceae and its sister, a clade comprising Anacampserotaceae, Cactaceae, and Portulacaceae (Hershkovitz, 2021a).

is that lineages that supposedly diverged in "deep time" (e.g., 75 mybp) can have remarkably similar fructification morphology.

Concluding remarks

Because of its morphology, age, and geography, *Kuprianovaites* is a significant and intriguing discovery, especially given its excellent preservation, structural detail, and the paucity of putative Caryophyllales macrofossils. But it is practically axiomatic that paleotaxonomic sampling can only *increase* the estimated age of a lineage, because older fossils increase the estimate, while younger fossils do not decrease it. Meanwhile, if neotaxonomic sampling has taught us anything, it is that increased sampling axiomatically increases the degree of estimated homoplasy. This lesson must not be lost upon paleotaxonomy, especially given the aforementioned inherent shortcomings of fragmentary fossils in taxonomic diagnosis. And it is important to appreciate that the practical consequence of misdiagnosis is miscalibration of DNA-based phylogenetic chronograms, which leads to downstream errors in evolutionary analysis. Maybe current tree-derived clade ages *already* are overestimated.

Alternatively, while I reject the classification of *Kuprianovaites* as Montiaceae, I cannot prove that it is incorrect, nor that Montiaceae did not arrive to India vicariously from Africa. If this proves to be the case, then indeed modern angiosperm lineages are much older than current chronograms would suggest. This perhaps validates the more panbiogeographic notions of Wang (2018), who intimated that Portulacineae date back to the Carboniferous. Taken to its logical extreme, we might believe that all modern lineages *already* were differentiated when the earth's crust first formed. And if I recall correctly from my stoner years on the Quad at the University of Illinois in the mid-1970s, that is pretty much what the evangelical Brother Max and Brother Jed¹² preached every day. Maybe Manchester et al. (2024) have unwittingly provided evidence that the evangelicals were right all along.

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