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Re-evaluating Amarna: A Likelihood-Based Assessment of 18th-Dynasty Genealogies from STR Evidence

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Abstract

The genealogy of Egypt's late 18th Dynasty remains contested, especially the identities and kin ties of Akhenaten, Nefertiti, Tutankhamun, and the mummies KV55, KV35YL, KV21A and KV21B. Using the eight STR loci published by Hawass et al. (2010), we formalize leading scholarly pedigrees (Hawass, Dodson, Phizackerley, Bommas, Tawfik) and closely related variants, then evaluate them with a transparent likelihood framework designed to be readable to non-statisticians. We separate two questions: (Run I) which overall pedigree best fits the STR data when KV21B is left unidentified; and (Run II) conditional on placing KV21B inside the Akhenaten–Nefertiti nuclear family, whether she fits better as Nefertiti or as another daughter of Akhenaten and Nefertiti. Across founder assumptions ranging from maximal endogamy to unrelated founders, Run I yields a stable result: the "sibling-parent" architecture in which both parents of Tutankhamun are children of Amenhotep III and Tiye fits the data best; within that structure, osteological age-at-death evidence for KV55 excludes identification with Akhenaten, pointing instead to Smenkhkare (Bommas model). Run II shows that, within the same best-fitting architecture, KV21B's label (Nefertiti vs. Daughter) depends on founder assumptions and is not decided by STRs alone; only under the most agnostic founder setting do the data clearly prefer "Daughter." Two additional observations emerge: (i) endogamy signals in KV21A and the KV62 fetuses make a fully unrelated-founders scenario unlikely, and (ii) multi-locus sharing between Amenhotep III and Yuya supports a close maternal tie long suspected for Mutemwia. We conclude with a "most likely" working pedigree that integrates these genetic and osteological constraints and outline targeted tests that could confirm or refine it.

1. Introduction

The genealogy of Egypt's 18th Dynasty, and in particular the royal family of the Amarna period, remains one of the most debated topics in Egyptology. The complex relationships between iconic figures such as Akhenaten, Nefertiti, Tutankhamun, and their relatives are central not only to understanding dynastic succession, but also to the interpretation of political, religious, and artistic developments in late New Kingdom Egypt. While numerous genealogical models have been proposed over the past decades, the high degree of endogamy, ambiguous titles, and the scarcity of securely identified mummies have resulted in persistent scholarly disagreement regarding key familial connections.

The advent of ancient DNA analysis has provided new avenues to test long-standing hypotheses. In particular, the landmark study by Hawass and colleagues established short tandem repeat (STR) profiles for several royal mummies, enabling the genetic evaluation of proposed parentage and kinship relations within the Amarna lineage.[1] This dataset has subsequently become the benchmark for genetic reconstructions of 18th Dynasty family trees.

Despite these advances, interpretation of the genetic results remains challenging. The available DNA data is incomplete, and the presence of numerous plausible genealogical arrangements means that genetic compatibility alone is often insufficient to identify the most likely family structure. Furthermore, published family trees by leading scholars—including those by Hawass,[2] Dodson,[3] Phizackerley,[4] Tawfik,[5] and Bommas[6]—differ substantially in their assumptions and conclusions. A systematic, comparative approach is therefore required to evaluate the genetic plausibility of these expert models, as well as potential variants.

The present study seeks to address this gap by testing a set of prominent, published family trees —and relevant variations—against the available STR data. For each genealogical model, we assess its consistency with the established genetic profiles, employing a transparent visual system to track allele inheritance patterns and potential contradictions. In addition, we incorporate a probabilistic framework that integrates historical priors and the likelihood of various

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[1] Zahi Hawass, Yehia Z. Gad, Somaia Ismail, et al., "Ancestry and Pathology in King Tutankhamun's Family," Journal of the American Medical Association 303, no. 7 (2010): 638–647, https://doi.org/10.1001/jama.2010.121.

[2] Ibid.

[3] Aidan Dodson, *Amarna Sunrise: Egypt from Golden Age to Age of Heresy* (Cairo: American University in Cairo Press, 2014), 168–69.

[4] Kate Phizackerley, "DNA Shows that KV55 Mummy Probably Not Akhenaten," *News from the Valley of the Kings* (blog), March 2, 2010, https://kv64.info/2010/03/dna-shows-that-kv55-mummy-probably-not.html.

[5] Tarek Tawfik, Susanna Thomas, and Ina Hegenbarth-Reichardt, "New evidence for Tutankhamun's parents: revelations from the Grand Egyptian Museum," *Mitteilungen des Deutschen Archäologischen Instituts, Abteilung Kairo* 74 (2018): 177–192.

[6] Martin Bommas, *Tutankhamun: A Biography* (London: Routledge, 2025), 304.

inheritance scenarios, aiming to quantify the relative plausibility of each model. Our goal is to clarify which genealogical reconstructions are most strongly supported by the genetic evidence, to identify areas of persistent uncertainty, and to provide a methodological template for future work on ancient dynastic kinship.

2. STRs and Genetic Kinship Analysis in the Amarna Dynasty

2.1. Brief Historical Context

The Amarna period represents one of the most radical and enigmatic episodes in ancient Egyptian history. In Year 5 of his reign, Amenhotep IV abandoned the traditional pantheon in favor of exclusive worship of the Aten, renaming himself Akhenaten and founding a new capital at Akhetaten (modern Amarna).[7] This ideological revolution upended centuries of religious practice and artistic convention, producing a corpus of inscriptions and monuments that depart sharply from earlier New Kingdom styles. Yet within a generation, the Aten cult was largely abandoned, and the old gods—above all Amun—were restored. The rapidity and scope of this reversal continue to provoke debate over the political, theological, and social forces at work.

Figure 1. Busts of Akhenaten and Nefertiti, c. 1340 BC. Pergamon Museum, Berlin; photo by Mary Harrsch, 2016. Image licensed under Creative Commons Attribution-Share Alike 4.0 International (CC BY-SA 4.0).

[7] Cyril Aldred, *Akhenaten: King of Egypt* (London: Thames & Hudson, 1991), 268–69.

At the center of this tumult stands Tutankhamun, the so-called “boy king.” His nearly intact tomb, uncovered by Howard Carter in 1922, captured the world’s imagination and has made him the best-known of all pharaohs. Ironically, despite the abundance of funerary objects bearing his name, the precise identity of his parents—and thus his exact place within the Amarna succession—remains uncertain. Competing hypotheses have variously proposed that he was the son of Akhenaten and Nefertiti[8], of Akhenaten and another consort[9], or even of a short-lived co-regent such as Smenkhkare.[10] [11] [12]

The immediate aftermath of Akhenaten’s death is equally obscure. Names such as Smenkhkare, Neferneferuaten, and Meritaten appear briefly in the archaeological record, but their familial ties and chronological order are hotly contested. The identities of the occupants of Tomb KV55 and the “Younger Lady” in KV35YL likewise defy consensus.[13] Unraveling these relationships is not merely an exercise in pedigree-making: it has direct implications for our understanding of the restoration of the Amun priesthood, the politics of royal marriage, and the very mechanisms by which authority was reclaimed in the years following Amarna.

2.2. Short Tandem Repeats (STRs) and Their Role in Genealogy

Short tandem repeats (STRs), also known as microsatellites, are short sequences of DNA, typically 2–6 base pairs in length, that are repeated in direct succession at specific locations (loci) throughout the genome. These regions are highly polymorphic, meaning the number of repeat units often varies greatly between individuals. This high degree of variability makes STRs powerful tools for distinguishing individuals and establishing biological relationships within and between families.[14]

In human genetics, each individual inherits two alleles at each STR locus—one from the mother and one from the father. Close relatives are therefore more likely to share identical STR alleles. For example, at any given locus, a child must possess one allele present in the mother and one in the father. Siblings often share several alleles due to their common parentage, although the specific

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[8] Aidan Dodson, *Amarna Sunrise*, 167.

[9] See, for example, the general discussion in Dodson, *Amarna Sunrise*, 167, which allows for an unnamed wife; cf. Hawass et al., "Ancestry and Pathology in King Tutankhamun's Family.“

[10] Martin Bommas, *Tutankhamun: A Biography*, 75ff.

[11] Kate Phizackerley, "DNA Shows that KV55 Mummy Probably Not Akhenaten.“

[12] Tarek Tawfik,"New evidence for Tutankhamun’s parents.“

[13] Aidan Dodson, *Amarna Sunrise*, 163–67.

[14] John M. Butler, *Forensic DNA Typing: Biology, Technology, and Genetics of STR Markers*, 2nd ed., Burlington, MA: Elsevier Academic Press, 2005, 1–25.

pattern depends on chance inheritance.[15] This principle underpins the use of STR analysis in forensic science, paternity testing, and, increasingly, in the study of ancient populations where more traditional lines of evidence—such as textual or iconographic sources—are missing or ambiguous.[16]

STR analysis is particularly suited to ancient DNA studies because these loci are short and, thus, more likely to be preserved and successfully amplified even when the genetic material is highly degraded, as is typical in archaeological samples.[17] The technique relies on comparing the repeat-length patterns at specific loci, known as genotyping, which generates an individual genetic "profile." By comparing STR profiles across a set of mummies or skeletal remains, researchers can systematically test proposed parent-child, sibling, or more distant familial relationships, and—critically—exclude those configurations that are genetically impossible.

This approach was famously applied to the royal mummies of the Amarna period by Hawass and colleagues, who analyzed eight STR loci across a sample of individuals believed to belong to the royal family of the late 18th Dynasty.[18] By reconstructing the allelic inheritance patterns, the study could directly support, question, or even exclude certain genealogical relationships proposed on the basis of historical or archaeological evidence.

However, some important caveats remain. While STR analysis is powerful, it cannot always identify relationships with certainty. For example, the probability that two individuals share an allele at a particular locus by chance increases in populations with high levels of endogamy, as was the case in royal lineages of ancient Egypt.[19] Furthermore, STR analysis can only test relationships among individuals for whom ancient DNA can be recovered and securely attributed —a significant limitation in Egyptology, where many key mummies remain unidentified or untested. Nonetheless, when used in conjunction with historical and archaeological data, STR analysis provides a crucial line of evidence for reconstructing the intricate family networks of the Amarna age.

2.3. Application to Ancient DNA: The Hawass et al. (2010) Study

A major breakthrough in the genetic investigation of Egypt's Amarna dynasty was achieved by Hawass et al. (2010), who conducted a systematic analysis of ancient DNA from a set of royal

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[15] Ibid., 14–18.

[16] Hawass et al., "Ancestry and Pathology in King Tutankhamun's Family."

[17] Matthias Meyer et al., "A high-coverage genome sequence from an archaic Denisovan individual," *Science* 338, no. 6104 (2012): 222–226.

[18] Hawass et al., "Ancestry and Pathology in King Tutankhamun's Family."

[19] Ibid.

mummies believed to belong to the late 18th Dynasty.[20] This landmark study combined traditional Egyptological methods with genetic testing to reconstruct parentage, clarify sibling relationships, and test the plausibility of longstanding genealogical hypotheses.

Mummies Analyzed:

The study focused on eleven royal mummies, including some of the most famous individuals of the period. Key figures tested were:

- Yuya (KV46)
- Thuya (KV46)
- Amenhotep III (KV35)
- The “Elder Lady” (KV35EL)
- The “Younger Lady” (KV35YL)
- Unidentified mummy (KV55)
- Tutankhamun (KV62)
- KV21A and KV21B (two female mummies from KV21)
- Two fetal mummies from KV62 (Tutankhamun’s tomb)

Loci Analyzed and Prior Probabilities:

Genetic kinship in the Hawass et al. study was assessed at eight nuclear STR loci. For clarity and visual consistency throughout this paper, we refer to these loci as L1–L8, and map them to their respective marker names in Table 1. Each allele length is represented by a unique color code in our diagrams, as explained in the legend. The allele frequency data (“priors”) used in this analysis are drawn from the comprehensive global STR database compiled by Wolfgang Huckenbeck, which includes population samples from modern Egypt and, where necessary, from the geographically closest available populations.[21] Although modern frequencies cannot fully replicate the allele distribution of the Amarna period, they provide the best available proxy for evaluating the statistical plausibility of observed inheritance patterns in the absence of ancient population-scale data. For locus L3 (D2S1338), Egyptian-specific frequencies were unavailable, so frequencies from the modern Israeli population, as reported in the same database, were used (see Table 1).

This set of markers was selected because of their established use in forensic genetics, their high degree of variability, and their relatively short amplicon size, which increases the likelihood of successful amplification from degraded ancient DNA.[22]

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[20] Ibid.

[21] Wolfgang Huckenbeck, "The distribution of the human DNA-PCR polymorphisms. A worldwide database." University of Düsseldorf (2001), available at: www.uni-duesseldorf.de/WWW/MedFak/Serology/dna.html.

[22] John M. Butler, *Forensic DNA Typing: Biology, Technology, and Genetics of STR Markers.*

Key Achievements:

Hawass et al. were able to:

- Demonstrate with high probability that Tutankhamun was the son of KV55 and KV35YL (the "Younger Lady").
- Show that Amenhotep III and Queen Tiye were likely the parents of both KV55 and KV35YL, thus identifying them as full siblings.
- Exclude certain alternative parentage scenarios based on incompatible allele inheritance.
- Propose new hypotheses for the identification of otherwise anonymous mummies, such as KV35YL and KV21A/B, using both genetic and Egyptological evidence.

Limitations in the Ancient Context:

Ancient DNA studies are inherently challenged by post-mortem DNA degradation, leading to allelic dropout (the failure to detect one or both alleles at a locus), contamination with modern DNA, and chemical modifications that can result in erroneous genotyping.[23]
Despite strict protocols to minimize contamination—such as independent replication in multiple laboratories, the use of negative controls, and authentication criteria—complete genetic profiles could not be obtained for all individuals at all loci. These gaps in the data sometimes allow for multiple plausible genealogical reconstructions.

A further complication arises from the high degree of endogamy and repeated cousin marriage within the royal family, which increases the probability that genetically compatible STR profiles might occur by chance even among individuals who are not in direct parent-child or sibling relationships. Thus, while STR analysis is powerful for excluding impossible genealogies, it is less conclusive for distinguishing between closely related alternatives in such populations.

Nevertheless, the Hawass et al. study established a new benchmark for the genetic analysis of ancient Egyptian royal mummies, providing a dataset that remains the foundation for most subsequent genealogical research on the Amarna period.

2.4. The Null Hypothesis and Visual Representation

In the context of this study, the null hypothesis refers to the genealogical model that aligns with the most direct and widely accepted parent-offspring and sibling relationships as proposed by Hawass et al. (2010), using only those links for which there is both genetic and substantial Egyptological support. This "default" model assumes no unnecessary or speculative connections, treating the simplest explanation that fits all known STR inheritance patterns as the baseline against which all alternative family trees are tested.

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[23] Michael Hofreiter et al., "Ancient DNA," *Nature Reviews Genetics* 2, no. 5 (2001): 353–359.

L1	Length	9	10	11	12	13	16
D13S317	Color						
	Prior	0.0788	0.0631	0.2928	0.2855	0.1056	0.0000
L2	**Length**	**6**	**10**	**13**	**15**		
D7S820	Color						
	Prior	0.0000	0.2985	0.0132	0.0000		
L3	**Length**	**16**	**17**	**19**	**22**	**26**	**27**
D2S1338	Color						
	Prior*	0.0399	0.2822	0.1043	0.0245	0.0153	0.0031
L4	**Length**	**25**	**26**	**29**	**34**	**35**	
D21S11	Color						
	Prior	0.0040	0.0000	0.3250	0.0040	0.0110	
L5	**Length**	**6**	**8**	**10**	**11**	**13**	
D16S539	Color						
	Prior	0.0000	0.0330	0.0670	0.3080	0.1250	
L6	**Length**	**8**	**10**	**12**	**16**	**19**	**22**
D18S51	Color						
	Prior	0.0000	0.0110	0.2360	0.0930	0.0110	0.0000
L7	**Length**	**6**	**7**	**9**	**12**		
CSF1PO	Color						
	Prior	0.0000	0.0071	0.0160	0.2901		
L8	**Length**	**20**	**23**	**24**	**25**	**26**	**31**
FGA	Color						
	Prior	0.1084	0.1628	0.1713	0.0762	0.0396	0.0035

Table 1. Loci Analyzed and Prior Probabilities

The practical value of this null hypothesis lies in its function as a reference framework: all variations—be they minor (such as switching the identity of a single parent) or major (such as postulating otherwise unattested individuals)—are compared to this model. Only when the null hypothesis fails to accommodate the observed genetic data, or when there are compelling archaeological reasons to doubt it, are alternative genealogies considered.

Visualizing STR Inheritance: Color Coding, Locus Notation, and Diagram Conventions

Given the complexity of multi-generational STR inheritance and the large number of individuals involved, visual clarity is paramount. To this end, all genealogical diagrams in this paper use a consistent color-coding scheme and a standardized locus notation:

- **Locus Notation (L1–L8):**
  Each of the eight STR loci analyzed is labeled L1 through L8 for simplicity and to avoid confusion with the more technical marker names. The mapping to official STR marker names (e.g., L1 = D13S317) is provided in Table 1, which should be consulted for cross-referencing and allele frequency priors.
- **Color Coding:**
  Each unique allele length at a given locus is assigned a specific color. This color is used consistently across all diagrams for that locus only; the same color does not indicate the same allele at a different locus. This system enables a rapid visual assessment of inheritance: alleles that are shared between parents and offspring at a specific locus will be immediately apparent by matching colors. (See the mapping table for a full listing of allele lengths, corresponding colors, and priors.)

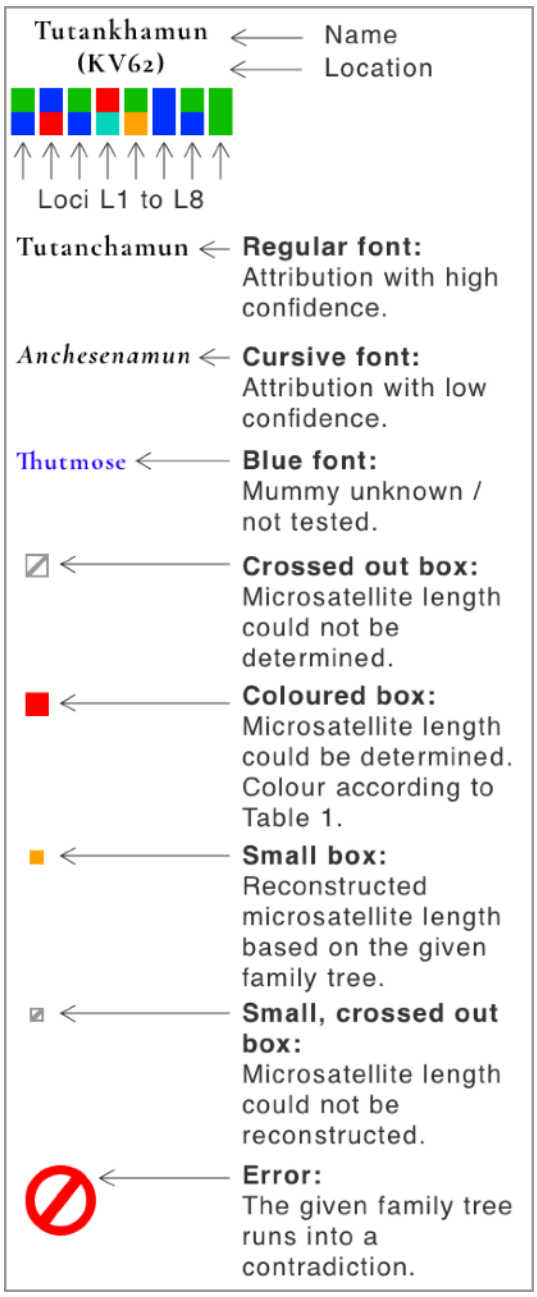

Figure 2. Legend

Interpreting the Diagrams

To interpret these visualizations, the reader should note that for each locus, a child's two alleles must each be present in at least one parent; if this condition fails for any locus, the proposed parentage is genetically impossible under normal Mendelian inheritance. The diagrams are read locus-by-locus (L1–L8), with each individual's allele pair for each locus represented by the corresponding colored boxes in sequence.

Importantly, these diagrams are meant to facilitate comparison between alternative genealogical hypotheses. By standardizing visual elements, even subtle incompatibilities or shared inheritance

patterns are made immediately visible—highlighting where the genetic evidence either supports or contradicts a given family tree.

The Concrete Null Hypothesis in This Study

In constructing the null hypothesis family tree, we have been deliberately conservative in assigning names and relationships. Only those individuals whose mummies are either directly labelled (such as Amenhotep III) or whose identification can be considered highly secure have been given specific names. An exemplary case is Queen Tiye: while her mummy was not labelled, her identity is confirmed by an analysis of a lock of her hair found inside a box inscribed with her name in Tutankhamun's tomb, providing an extraordinary link between the genetic and archaeological records.[24] All other individuals in the trees are referenced by tomb number (e.g., KV55, KV35YL), and speculative or less secure attributions are avoided in the baseline hypothesis.

For the purposes of the null hypothesis, we defaulted to the most straightforward genetic relationships consistent with the data: wherever a putative child shows no allele contradictions with proposed parents across all eight STR loci, the probability that this is indeed a true biological relationship is extraordinarily high. Thus, unless there is a clear conflict or strong Egyptological argument to the contrary, the null hypothesis accepts the simplest relationship suggested by the genetic data.

Kinship Inferences for KV21A and KV21B

This principle allows for additional insight in certain cases. For example, the genetic profile of KV21A indicates not only a close relationship to Amenhotep III, but also—via an independent route—to Thuya, the mother of Tiye. This conclusion is based on the presence of a rare yellow-coded allele at locus L4 (D21S11), with a prior frequency of just 0.0110 in the modern Egyptian population. This allele is shared by Thuya, but not by Tiye, making it highly unlikely to have arisen by chance and strongly suggesting an additional ancestral connection to Thuya in KV21A's lineage.[25] For KV21B, the STR data also points to a close relationship with both Amenhotep III and Thuya; however, in this instance, a secondary connection to Thuya is not necessarily required to explain the observed alleles, and a single descent path may suffice. These inferred, but not fully documented, relationships are represented in our diagrams as dotted lines.

It is important to note, however, that the exceedingly high probabilities for contradiction-free parent-child assignments—such as 99.9997% for eight matching loci—are derived from studies of unrelated individuals in the general population.[26] In the royal house of Egypt's 18th Dynasty,

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[24] Hawass et al., "Ancestry and Pathology in King Tutankhamun's Family."

[25] Wolfgang Huckenbeck, "The distribution of the human DNA-PCR polymorphisms."

[26] John M. Butler, *Forensic DNA Typing: Biology, Technology, and Genetics of STR Markers, 125–28.*

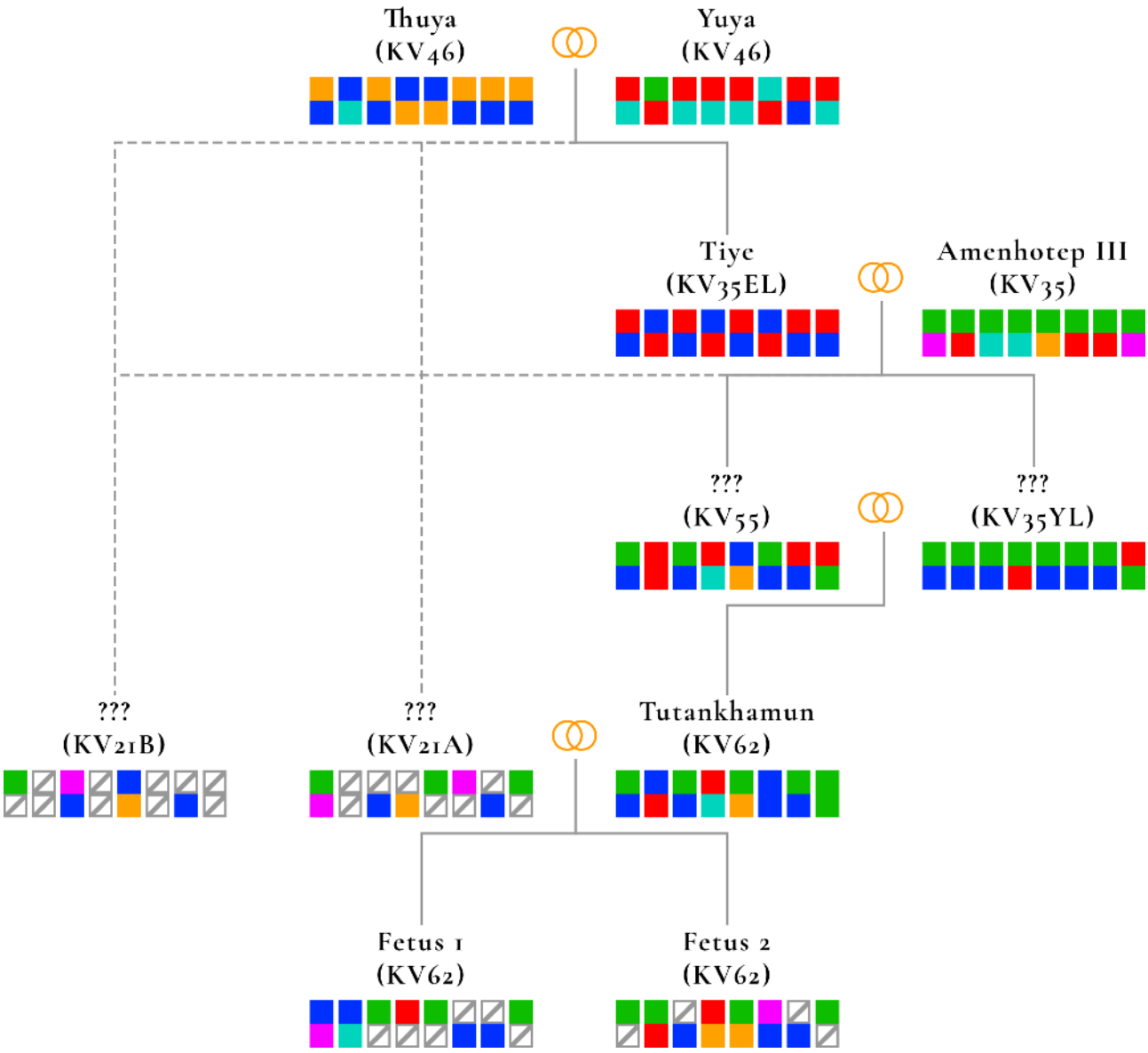

Figure 3. Null Hypothesis

repeated cousin and sibling marriages (endogamy) were the norm, greatly increasing the chance that close relatives share the same alleles simply by descent, rather than direct parentage.

2.5. Practical Limitations and Statistical Considerations

The strength of STR analysis in genealogical studies lies in its ability to exclude impossible relationships. For parent-offspring or sibling ties, even a single locus where the putative child's alleles do not match those of the supposed parents can confidently rule out that relationship, given the rules of Mendelian inheritance.[27]

[27] Ibid, 114–18.

Conversely, the presence of matching alleles at all tested loci does not guarantee a true biological relationship, but it does raise the probability to a high level—especially in the general population. In forensic genetics, the probability that a contradiction-free parent-child pairing across eight independent STR loci is correct exceeds 99.9997%.[28] Even when only three loci are available due to DNA degradation, the probability remains above 99%. These high-confidence figures are the foundation for accepting straightforward, contradiction-free relationships as the null hypothesis in many genealogical reconstructions.

However, these probability thresholds rely on the assumption of a randomly mating (outbred) population. The royal family of Egypt's 18th Dynasty was marked by repeated cousin and sibling marriages—extreme endogamy. This practice greatly increases the chance that even distant relatives may share identical alleles at multiple loci, simply due to the limited pool of ancestral genetic material.

As a result, the chance that two individuals match at all tested loci "by chance" is much higher in the Amarna royal family than in the general population. This undermines the classical confidence levels described above: while exclusions remain robust, confirmations must be interpreted with caution. For Egyptologists, this means that multiple family trees—sometimes surprisingly divergent—can all appear equally plausible genetically, and only a subset can be eliminated on purely genetic grounds.

The potential for ambiguity is further increased by the quality and completeness of the ancient DNA dataset. Many tested mummies yielded partial profiles due to degradation or contamination, resulting in loci with missing data (allelic dropout). In these cases, the absence of a contradiction does not strongly support a relationship; it may simply reflect a lack of information.[29]

Moreover, attributions of certain mummies remain disputed—notably, the identities of the "Younger Lady" (KV35YL), KV55, and the two female mummies from KV21. Assigning a genetic relationship based on a misidentified mummy would lead to a flawed family tree, regardless of genetic compatibility. This uncertainty underlines the necessity of a conservative approach in both naming individuals and interpreting genetic matches.

A further limitation is the presence of untested or unidentified individuals. Some of the most critical figures for resolving Amarna genealogy (such as Nefertiti, Ay, or Kiya) are either missing or cannot be securely identified among the available mummies. Any genealogical model must acknowledge that future discoveries or identifications could substantially revise current conclusions.

Additionally, the lack of population-scale genetic data from ancient Egypt poses an inherent limitation. All allele frequency priors ("probabilities") used in this study are based on modern

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[28] Ibid, 125–28.

[29] Michael Hofreiter et al., "Ancient DNA".

populations, either from Egypt or (where unavailable) from the closest possible neighboring regions. Although this approach is standard and reasonable, population structure and allele frequencies may have shifted significantly over three millennia, adding another layer of uncertainty to any probability calculations.

Lastly, it is important to recognize that alternative genealogical scenarios—even those not presently considered—may become viable with the discovery of new mummies, the application of additional genetic markers, or reinterpretations of the archaeological record. For this reason, the results and likelihoods calculated here should be viewed as provisional and open to revision.

In sum, while STR analysis provides a powerful means of testing and narrowing the field of plausible family trees, the high degree of endogamy, incomplete dataset, uncertainties in mummy identification, and reliance on modern population frequencies all place significant constraints on the degree of certainty attainable. By highlighting these limitations and quantifying probabilities tailored to this specific case, the present study seeks to offer a transparent and realistic assessment—enabling historians and Egyptologists to make better-informed judgments about the kinship networks of the Amarna period.

3. Proposed Family Trees

3.1. Orientation and shared assumptions

In this chapter we review the principal published reconstructions of the Amarna-period genealogy, together with a small number of closely related variants used for sensitivity testing. We begin from a cautious baseline (our "null hypothesis") and then describe what each proposal aims to solve historically and how it fares genetically given the eight STR loci outlined in Chapter 2. Where identities are not secure, we designate individuals by tomb number and mark conjectural relationships with dotted lines; diagram conventions, color coding (within-locus only), and the L1–L8 shorthand follow § 2.3.

Two standing Egyptological ideas shape several variants we display:

- **Ay and Iuy as placeholders.** It has long been proposed that Ay may have been Tiye's brother and Nefertiti's father;[30] his attested wife Tey bears the title "nurse" of Nefertiti,[31] which usually (though not invariably) excludes biological motherhood. We therefore label a plausible earlier consort Iuy[32] (sometimes transcribed Iui/Yui) as a placeholder for Nefertiti's mother. In figures,

[30] Aidan Dodson. *Nefertiti, Queen and Pharaoh of Egypt: Her Life and Afterlife*. American University in Cairo Press, 2020, 21.

[31] Ibid, 17.

[32] Jacobus van Dijk, "Horemheb and the Struggle for the Throne of Tutankhamun," *Bulletin of the Australian Centre for Egyptology* (1996), 29–42.

"Ay" and "Iuy" name a genealogical role, not a proven onomastic identity; dotted lines signal this status.

- **Shared STR constraints used below.** From Tutankhamun and the two KV62 fetuses, the mother's genotype at L2 (D7S820) must be {cyan, green}. Independently, KV21A carries L4 (D21S11) yellow and L6 (D18S51) pink that cannot come from the paternal (Amenhotep III/Tiye) side and therefore must be maternal in any model where KV21A is the mother of the fetuses. At L1 (D13S317) KV21A shows green and pink; in our dataset both are traceable to Amenhotep III, making a dual link to him plausible (not proven). These observations motivate, in some variants, a second Thuya-line connection (Thuya → Ay/Iuy → Nefertiti) to explain the L4 and L2 signals independent of Tiye.

To keep the narrative readable, each proposal below is presented in two compact paragraphs: (i) the historical claim/motivation; (ii) the genetic test/outcome. A one-sentence interim assessment closes each subsection.

3.2. Hawass' Proposals

In the 2010 JAMA study, Hawass and colleagues reconstructed the Amarna genealogy from eight STR loci and—taking the burial context of KV55 into account—argued that KV55 is Akhenaten. On the genetic side, they showed that KV55 and the "Younger Lady" (KV35YL) form a parental pair for Tutankhamun; on the archaeological side, they appealed to the Amarna equipment and inscriptions associated with KV55 to support Akhenaten's identification.[33] Hawass later reaffirmed this view in Scanning the Pharaohs (2016)[34] and additionally suggested that KV21A = Ankhesenamun and KV21B is a strong candidate for Nefertiti.[35]

The Egyptological counter-argument focuses on age-at-death. Several osteological assessments —most prominently Eugen Strouhal's response—conclude that the KV55 skeleton is that of a young adult (≈18–26 years)[36], far short of an Akhenaten who ruled ~17 years and is depicted with adult offspring. Hawass allows an age "up to 45," but provides limited justification and does not fully engage the technical points raised by those favoring a younger age.[37] In short: the genetic assignment "KV55 = father of Tutankhamun" is robust, but "KV55 = Akhenaten" remains contested on anatomical grounds.

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[33] Hawass et al., "Ancestry and Pathology in King Tutankhamun's Family."

[34] Zahi Hawass and Sahar Saleem, *Scanning the Pharaohs: CT Imaging of the New Kingdom Royal Mummies*, Oxford University Press, 2016, 123.

[35] Ibid, 142.

[36] Eugen Strouhal. "Biological Age of Skeletonized mummy from tomb KV 55 at Thebes." *Anthropologie (1962-)* 48.2 (2010): 97-112.

[37] Ibid.

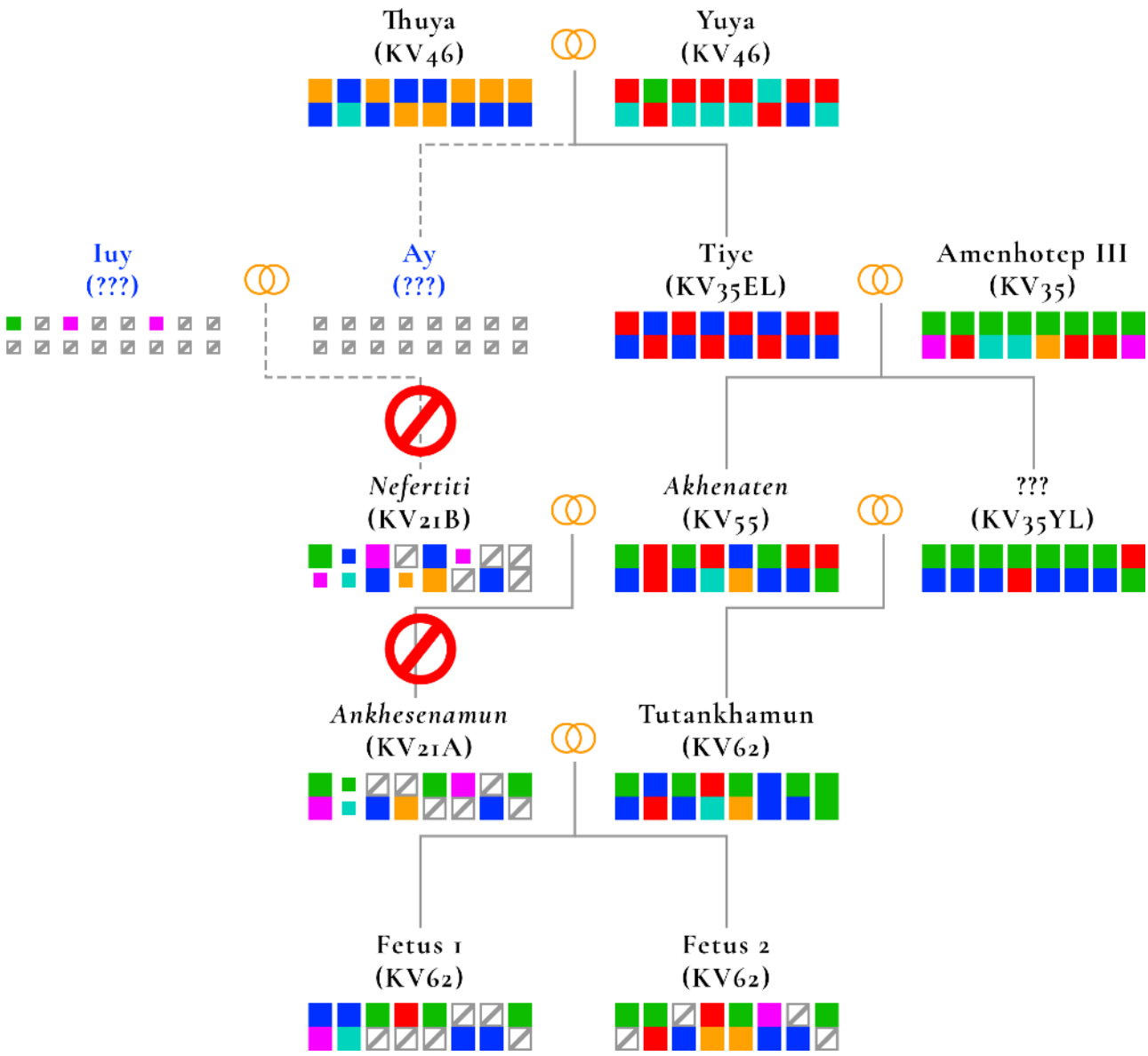

Figure 4. Hawass v1 (KV21B = Nefertiti & KV55 = Akhenaten)

If we combine Hawass' 2010 identification of KV55 as Akhenaten with his 2016 suggestion KV21B = Nefertiti, the tree becomes genetically impossible once we include the fetuses from KV62. At L2 (D7S820) the data are:

Fetus 1: blue / cyan; Fetus 2: green / red; Tutankhamun: blue / red

Therefore the mother of the fetuses must carry green and cyan at L2 (to supply cyan to Fetus 1 and green to Fetus 2). Even though L2 could not be directly read for KV21A, this reconstruction is forced by the offspring. By contrast, KV55 is red/red at L2; any child of KV55 must inherit at least one red allele at L2. A woman with green/cyan at L2 cannot be KV55's daughter, so KV21A cannot be the daughter of KV55 in this configuration. If KV21A = Ankhesenamun (daughter of Akhenaten and Nefertiti) and KV55 = Akhenaten, the L2 requirements contradict Mendelian inheritance. Thus Hawass v1 is excluded.

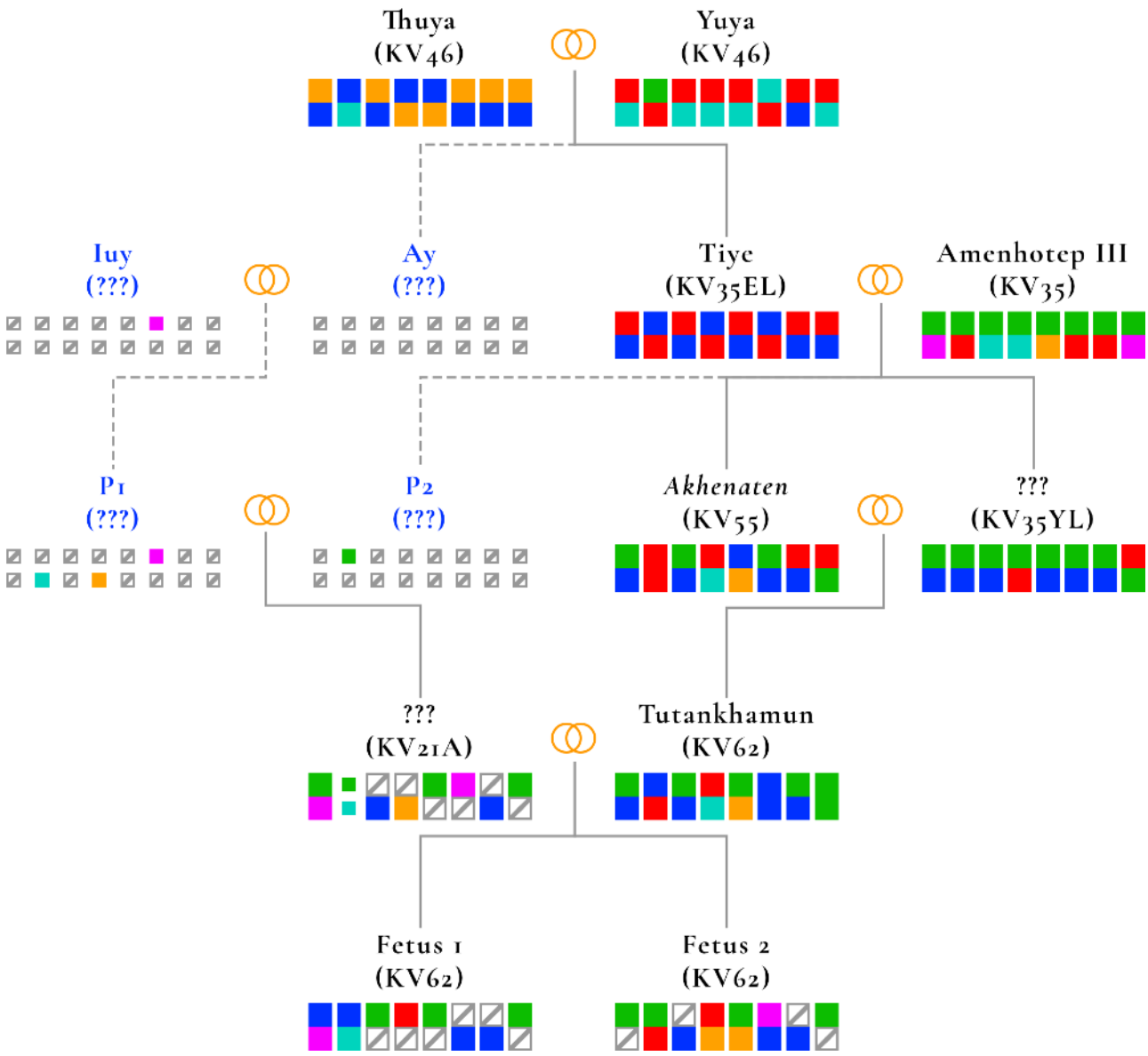

Figure 5. Hawass v2 (KV55 = Akhenaten)

A related knock-on problem appears at L1 (D13S317) if KV21B = Nefertiti and Nefertiti is Ay's daughter: the needed L1 (green/pink) combination for KV21B cannot be sourced from Ay if he descends only from Thuya and Yuya as in many Ay-as-brother-of-Tiye schemes. One could rescue this by positing a cousin-level alternative maternal line also tied to Thuya and Amenhotep III—but given the L2 contradiction above, we do not pursue this already-ruled-out path further.

If we retain "KV55 = Akhenaten" but do not identify KV21B as Nefertiti (and leave KV21A's parents unknown), the contradictions vanish. This variant is consistent with the genetic core of the JAMA results (KV55 + KV35YL → Tutankhamun) and with Hawass' cautious wording in 2010 regarding the KV21 mummies (KV21A very likely the mother of the KV62 fetuses, identity not proven).[38] The dotted lines from Thuya → (Ay as placeholder) → Nefertiti's line capture the additional Thuya-line

[38] Hawass et al., "Ancestry and Pathology in King Tutankhamun's Family."

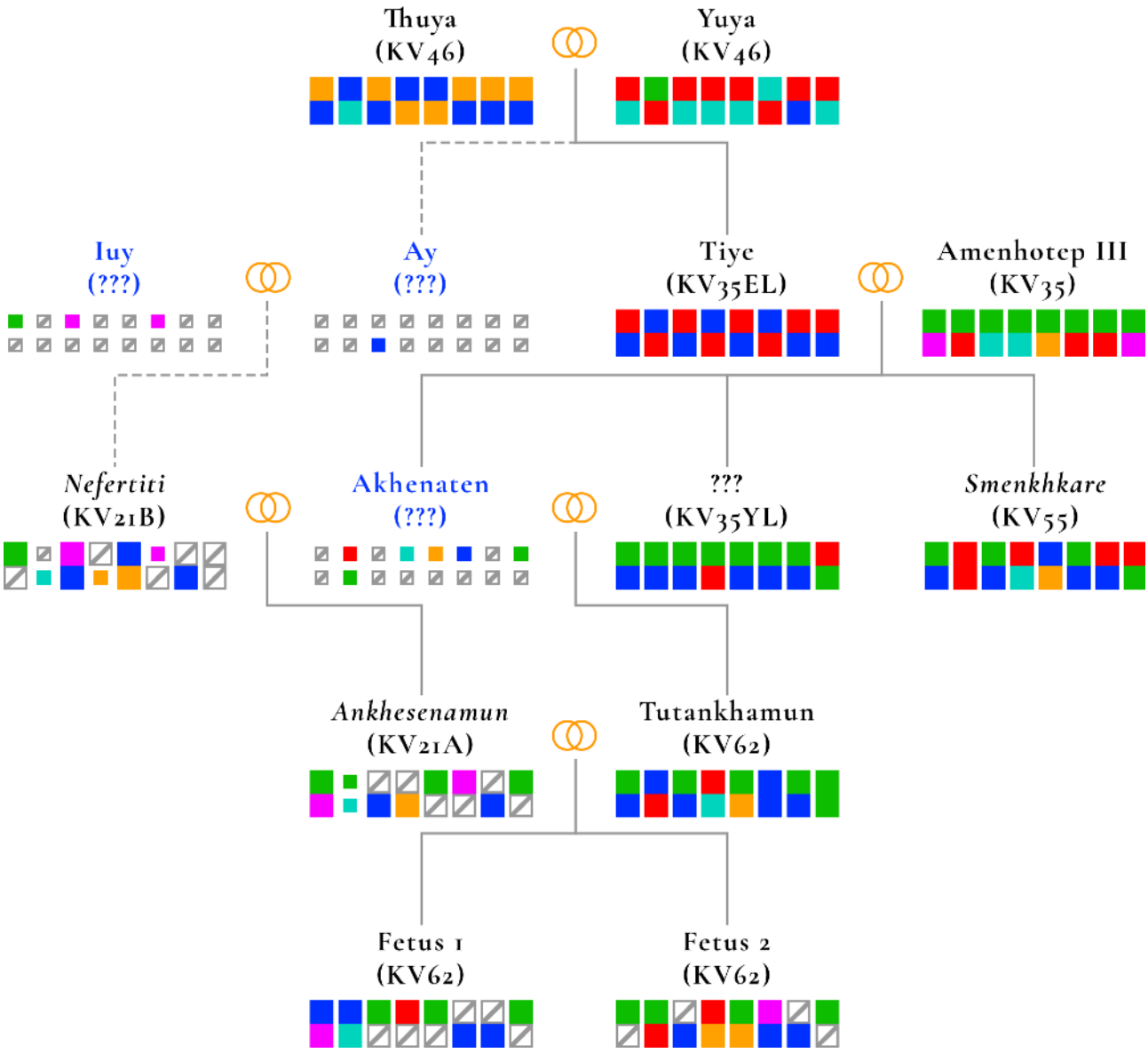

Figure 6. Hawass v3 (KV21B = Nefertiti)

signal seen in KV21A (rare L4 yellow; rare L2 cyan), without forcing Ankhesenamun's parentage to pass through KV55. This is genetically admissible, while acknowledging that the age-at-death objection to "KV55 = Akhenaten" still hangs over the model.[39]

Alternatively, if we accept KV21B = Nefertiti and KV21A = Ankhesenamun, then KV55 cannot be Akhenaten (see above). The most economical assignment is "KV55 = Smenkhkare," still a son of Amenhotep III and Tiye and thus a full sibling of KV35YL. This relocates Akhenaten outside KV55, making him an untested brother in the tree. This configuration satisfies the L2 constraints for the fetuses, dodges the age-at-death argument against KV55=Akhenaten, and remains fully compatible with the strong genetic similarity between KV55 and KV35YL (explained as full sibs).

[39] Eugen Strouhal. "Biological Age of Skeletonized mummy from tomb KV 55 at Thebes."

Interim assessment

- Hawass v1 (KV55=Akhenaten, KV21A=Ankhesenamun and KV21B=Nefertiti) is genetically excluded by the L2 reconstruction from the fetuses.
- Hawass v2 keeps KV55=Akhenaten but leaves KV21 identities open; genetically viable, osteologically debated.
- Hawass v3 sets KV55=Smenkhkare and allows KV21B=Nefertiti; genetically viable and neutral with respect to age-at-death arguments.

3.3. Dodson's Proposals

Reading the DNA results through an Egyptological lens, Aidan Dodson argues that the mummy in KV55 is Smenkhkare, not Akhenaten. In parallel, he favors a scenario in which Akhenaten and Nefertiti are the parents of both Tutankhamun and Ankhesenamun, who in turn are the parents of the two fetuses from KV62.[40] In later work he further suggests that the "Younger Lady" (KV35YL) is a strong candidate for Nefertiti.[41]

These proposals re-weight the 2010 DNA findings: they keep the historical intuition that Akhenaten and Nefertiti were central to the final Amarna generation, but they reassign KV55 and reinterpret the maternal line.

When we combine KV55 = Smenkhkare with KV35YL = Nefertiti and Ankhesenamun = KV21A, the STR data contradict the tree:

Maternal-only signals in KV21A. KV21A carries a yellow allele at L4 (D21S11) and a pink allele at L6 (D18S51). Both must be supplied by her mother, because neither Amenhotep III nor Tiye (the paternal grandparents in this scenario) carry those alleles in the tested dataset.

Required L2 state for the fetuses. From the fetuses and Tutankhamun we reconstruct the mother's L2 (D7S820) as cyan + green (Fetus 1 has blue/cyan; Fetus 2 has green/red; Tutankhamun has blue/red → the mother must supply cyan and green).

KV35YL lacks all three required maternal alleles. KV35YL has none of {L4-yellow, L6-pink, L2-cyan}. Therefore KV35YL cannot be the mother of KV21A and cannot be the grandmother of the fetuses. Consequently KV35YL ≠ Nefertiti under this configuration.

Thus the "KV35YL = Nefertiti" option is genetically excluded in Dodson's model as framed here (Figure 7. Dodson v1).

If we do not equate KV35YL with Nefertiti—i.e., we treat Nefertiti's mummy as unknown—then the configuration can be made consistent with the STRs: Akhenaten + Nefertiti → (Ankhesenamun, Tutankhamun), with KV55 = Smenkhkare elsewhere in the sibship. KV21A retains the maternal

[40] Aidan Dodson, *Amarna Sunrise*, 168–69.

[41] Aidan Dodson. *Nefertiti, Queen and Pharaoh of Egypt*, 21.

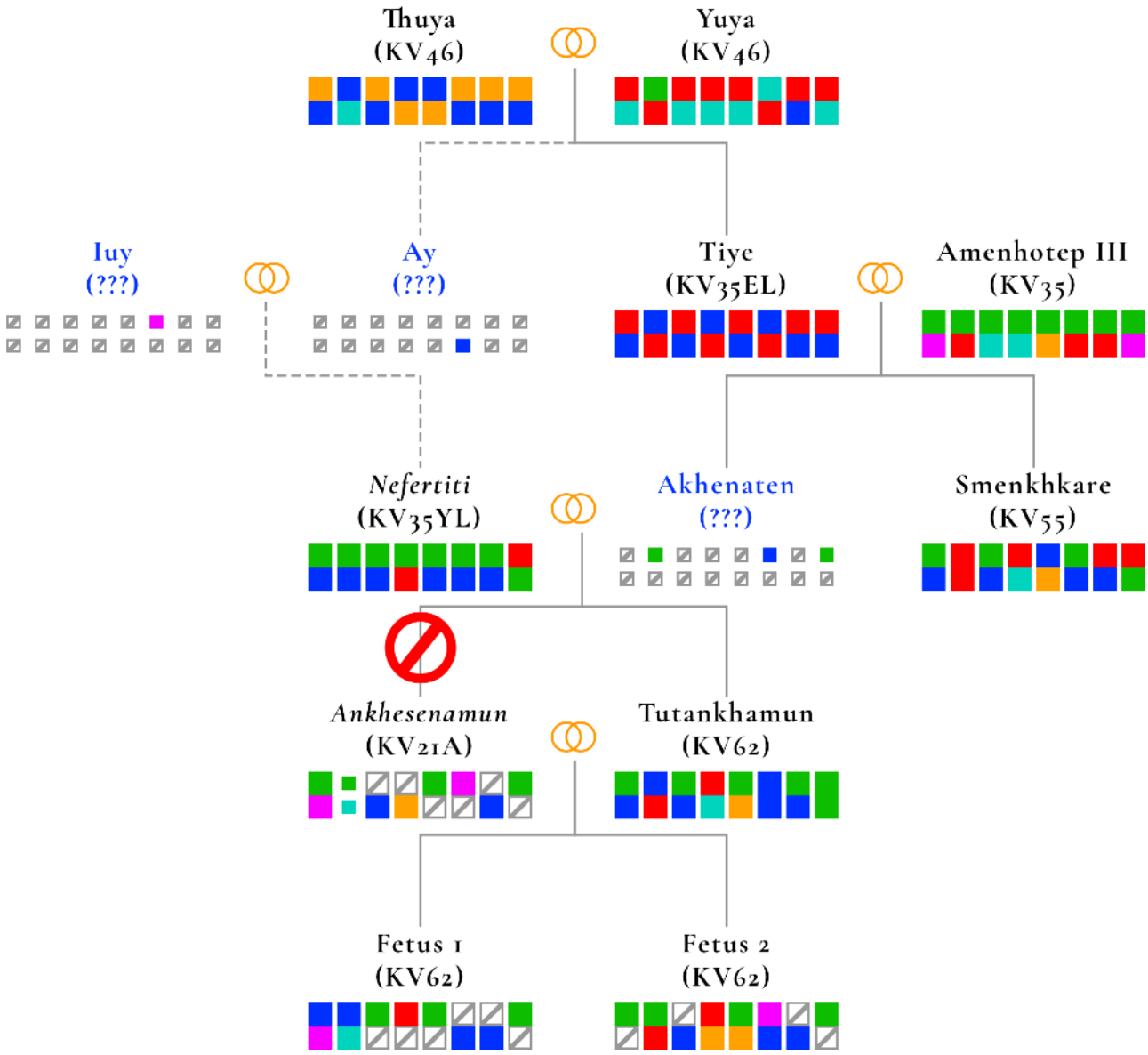

Figure 7. Dodson v1 (KV35YL = Nefertiti)

signals (L4-yellow, L6-pink, L2-cyan) without forcing them onto KV35YL. This preserves Dodson's historical reading while avoiding genetic contradictions.

Interim assessment

- Dodson v1 (KV35YL = Nefertiti) is ruled out by the combined L4, L6, L2 constraints.
- Dodson v2 (Nefertiti unknown) are genetically viable while honoring Dodson's identification KV55 = Smenkhkare.

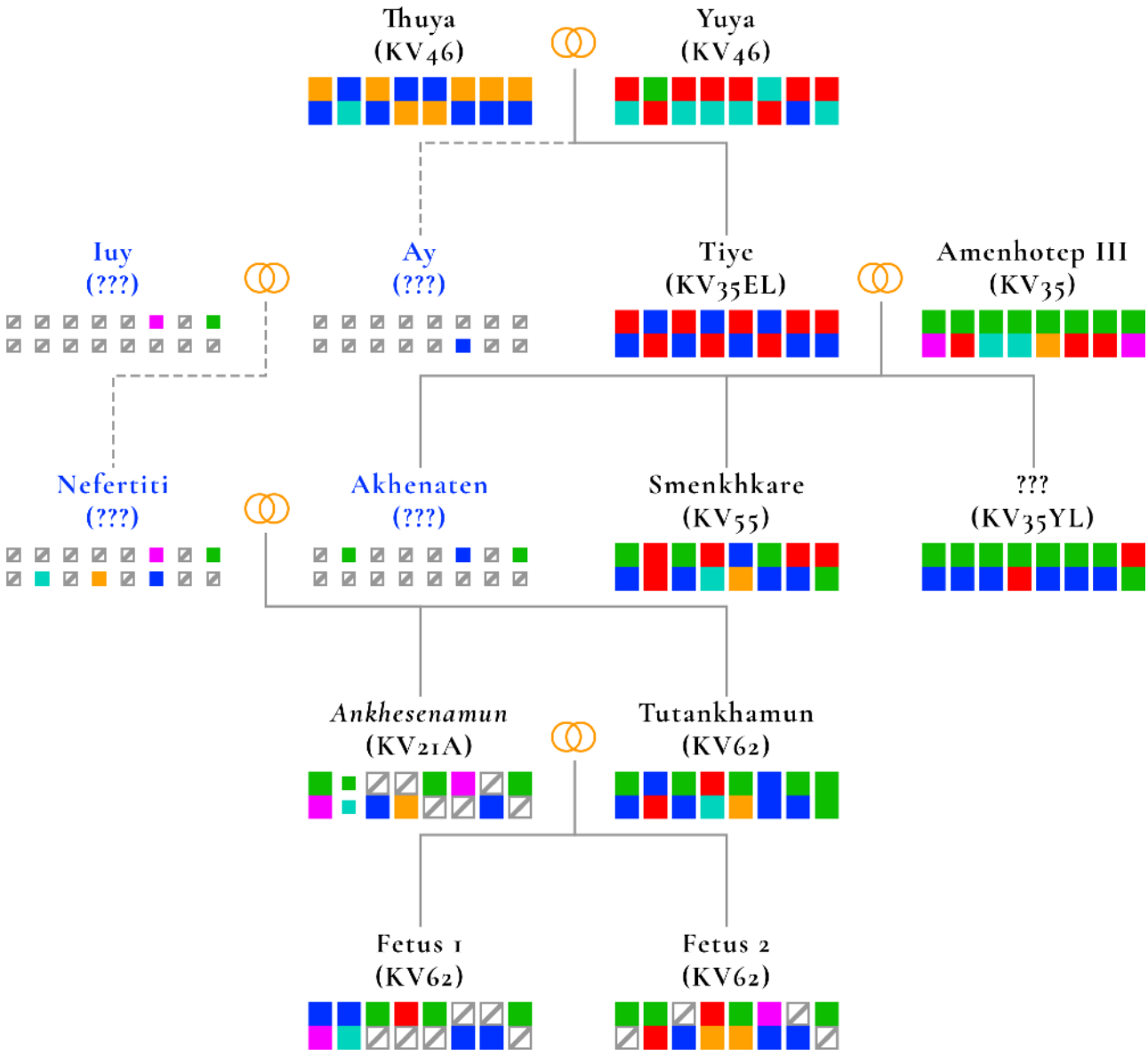

Figure 8. Dodson (Nefertiti unknown)

3.4. Phizackerley's Proposal

Soon after the JAMA study, Kate Phizackerley suggested that the KV55 mummy is Smenkhkare and that the "Younger Lady" KV35YL is Meritaten, eldest daughter of Akhenaten and Nefertiti; in her reading, Tutankhamun is the son of KV55 (Smenkhkare) and KV35YL (Meritaten). She also allowed that KV21B could be another daughter of Akhenaten and Nefertiti.[42] The epigraphic pairing of Smenkhkare–Meritaten is independently supported (e.g., scenes and inscriptions in the tomb of Meryre marking Meritaten as "Great Royal Wife").[43]

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[42] Kate Phizackerley, "DNA Shows that KV55 Mummy Probably Not Akhenaten."

[43] Aidan Dodson, *Amarna Sunset: Nefertiti, Tutankhamun, Ay, Horemheb, and the Egyptian Counter-Reformation*. Oxford University Press, 2009, 29.

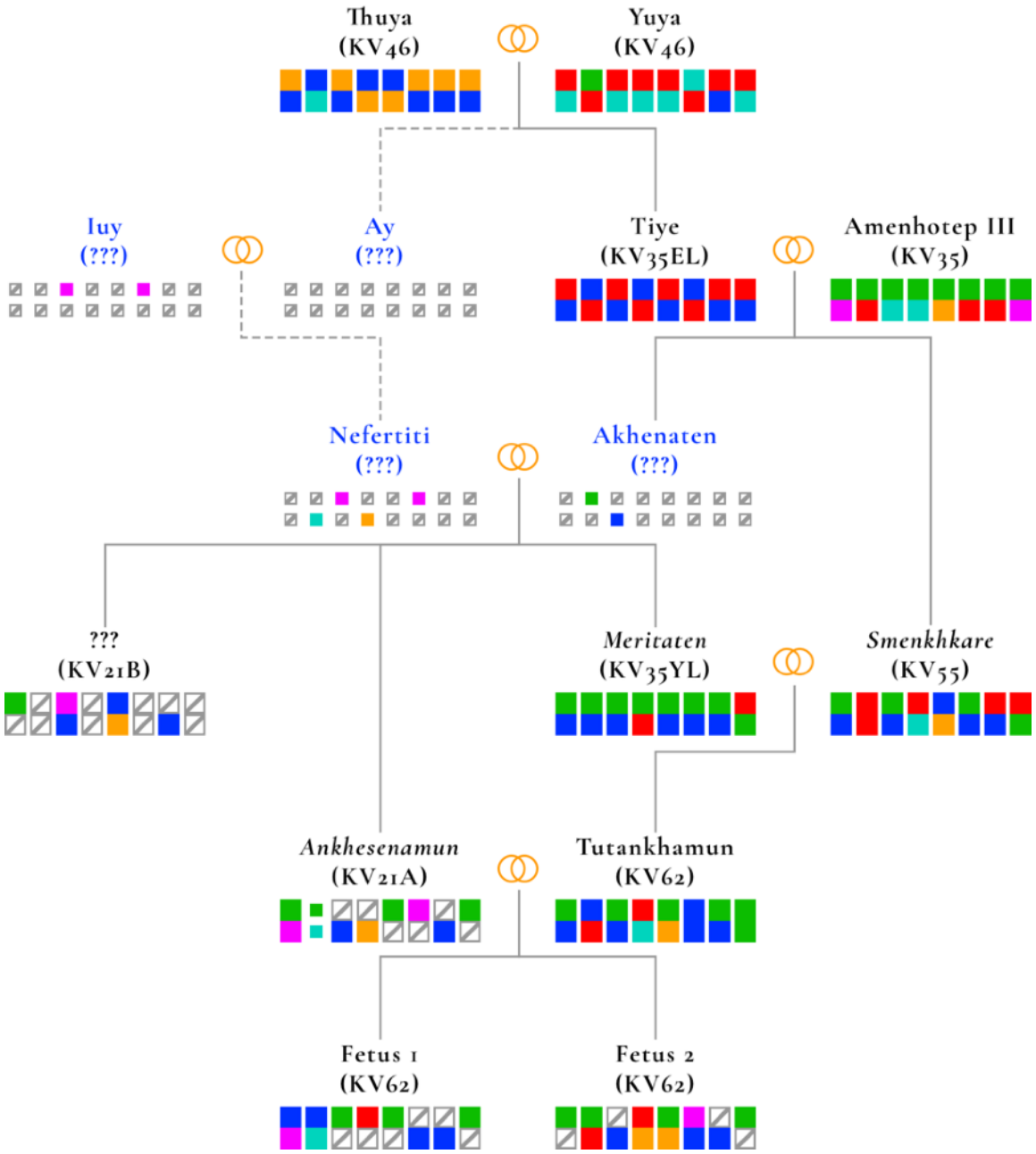

Figure 9. Phizackerley v1 (KV21B = unknown daughter of Akhenaten & Nefertiti)

In the JAMA framework, KV55 and KV35YL were modeled as full siblings—both children of Amenhotep III and Tiye—and, together, as the parental pair of Tutankhamun.[44] One reason this configuration was attractive is that KV55 and KV35YL share a high number of matching STR states across the eight loci—what one typically expects of full siblings (and what, at first glance, can resemble the pattern sometimes seen in parent–child comparisons). However, a true parent–child interpretation is ruled out here, because KV55 and KV35YL do not share an allele at L2 (D7S820)—a requirement for parent–child at every locus.

[44] Hawass et al., "Ancestry and Pathology in King Tutankhamun's Family."

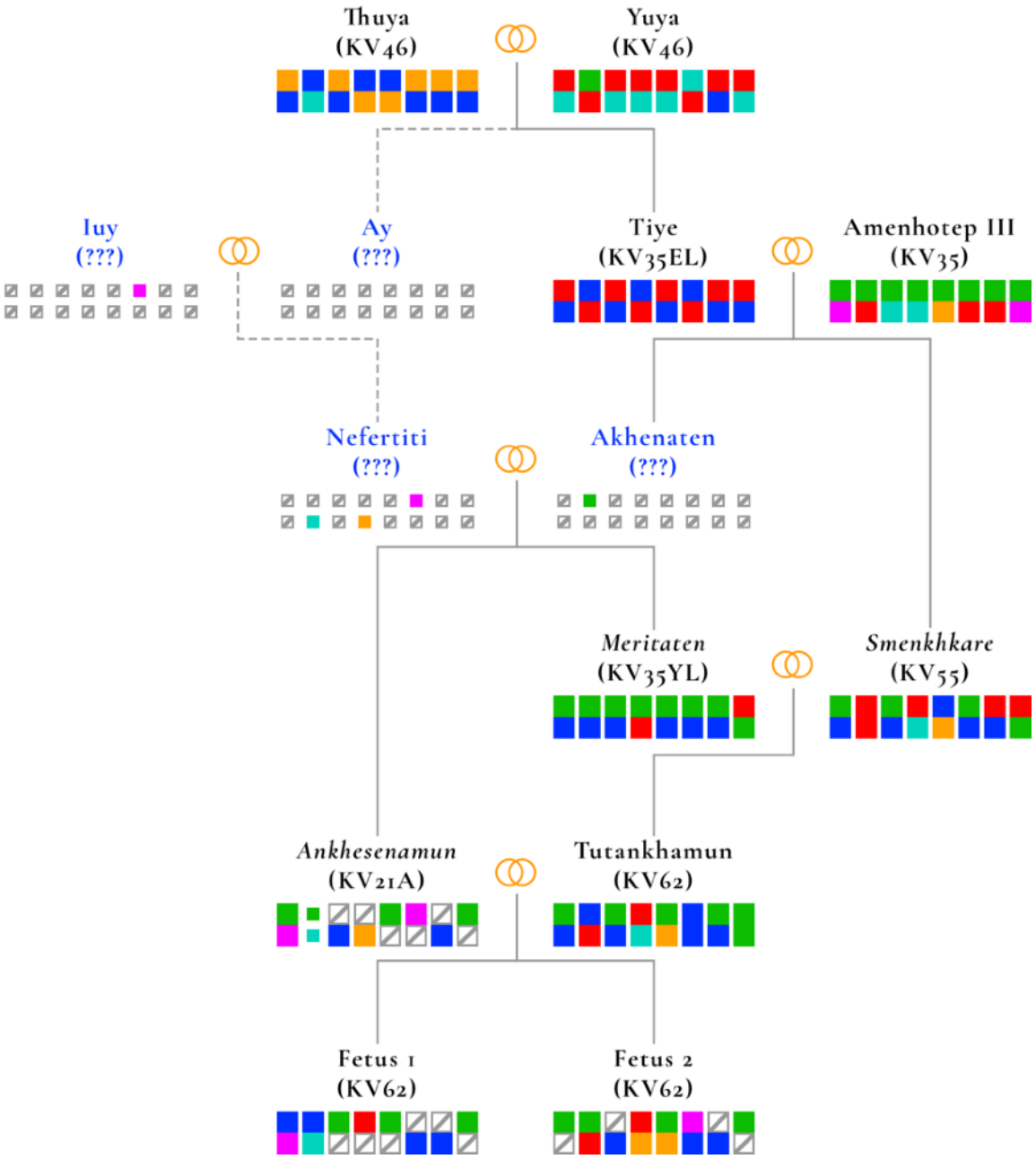

Figure 10. Phizackerley v2 (No assumption regarding KV21B)

Phizackerley reassigns identities while preserving the observed high similarity by proposing KV55 = Smenkhkare and KV35YL = Meritaten. Under standard historical reconstructions, this makes them uncle and niece (Smenkhkare as Akhenaten's brother; Meritaten as Akhenaten's daughter). Especially in an endogamous dynasty, an uncle–niece pair could share many STR alleles. Repeated cousin marriages in the Amarna family compress diversity and raise allele sharing among close relatives; therefore a high match count is not diagnostic of full siblingship in this context. The dataset excludes parent–child for KV55–KV35YL (because of L2), but it remains consistent with full siblings or uncle–niece, to be weighed by historical context and priors.[45]

[45] Ibid.

Crucially, the maternal constraints derived from KV21A and the KV62 fetuses do not defeat Phizackerley's configuration. From the fetuses plus Tutankhamun, the mother must carry cyan and green at L2 (D7S820); KV21A also shows L4 (D21S11) yellow and L6 (D18S51) pink that must be maternal.

The principal challenge is chronological. Meritaten is generally assessed as only ~7–10 years older than Tutankhamun,[46] which makes her motherhood virtually impossible.[47] To maintain this model, the post-Amarna sequence (Smenkhkare/Neferneferuaten interlude) must be lengthened. This move has implications for late-Amarna chronology and remains controversial.

Interim assessment

- Phizackerley v1: KV55 = Smenkhkare; KV35YL = Meritaten; KV21B = daughter of Akhenaten & Nefertiti.
  Genetically viable, but introduces an extra assumption about KV21B's filiation, which will lower its prior weight relative to leaner models.
- Phizackerley v2: Same core model, without assigning KV21B.
  Genetically viable with fewer assumptions; retained as the baseline Phizackerley variant.

3.5. Bommas' Proposal

In his recent synthesis, Martin Bommas identifies the KV55 mummy as Smenkhkare and the "Younger Lady" KV35YL as Baketaten, the youngest attested daughter of Amenhotep III and Tiye. Tutankhamun is then the child of Smenkhkare (KV55) and Baketaten (KV35YL).[48] In this arrangement the genetic structure is identical to the JAMA baseline (both parents of Tutankhamun are full children of Amenhotep III and Tiye), but the names of those parents are reassigned. Akhenaten and Nefertiti remain untested/unknown in the mummy record; they are taken as the parents of Ankhesenamun (KV21A).

This has two immediate attractions: (i) it sidesteps the age-at-death dispute over "KV55 = Akhenaten," and (ii) it requires no additional endogamy beyond the baseline sibling marriage already implied by Tutankhamun's parentage.

On the STR evidence, Bommas's core model is fully compatible. Because Tutankhamun's parents are both children of Amenhotep III and Tiye, the allele-sharing pattern that made the JAMA model work is preserved unchanged; only the historical names of those two individuals differ.

Ankhesenamun (KV21A) is modeled as the daughter of Akhenaten and Nefertiti, which satisfies the maternal-only signals seen in KV21A and inferred from the KV62 fetuses: the mother must

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[46] See for example: Aidan Dodson. *Nefertiti, Queen and Pharaoh of Egypt*, 13; 50.

[47] Aidan Dodson, *Amarna Sunrise*, 156.

[48] Martin Bommas, *Tutankhamun: A Biography*, 304.

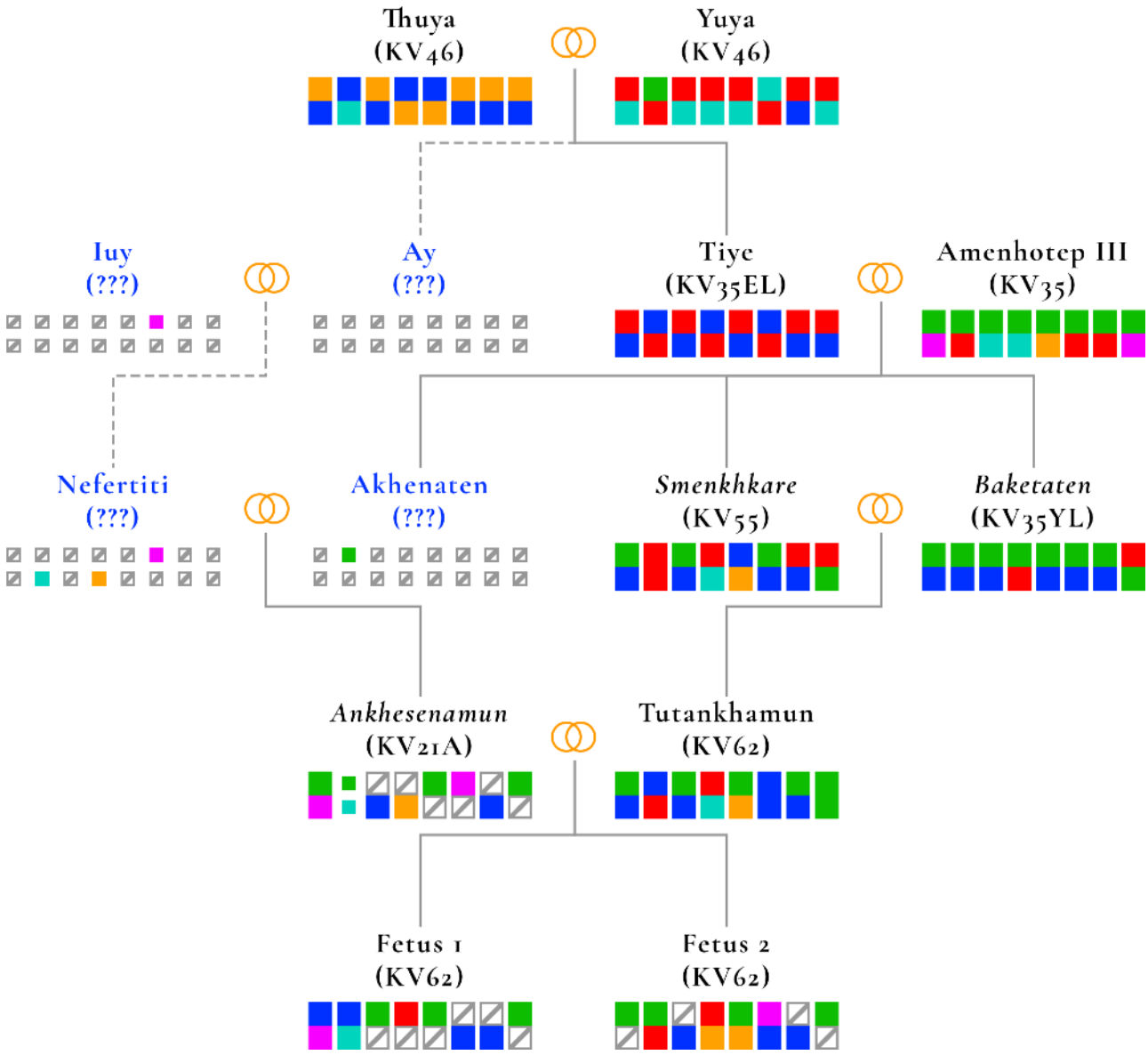

Figure 11. Bommas v1

carry L2 (D7S820) cyan + green, and KV21A carries L4 (D21S11) yellow and L6 (D18S51) pink—states absent in the paternal grandparents Amenhotep III/Tiye, hence necessarily maternal. Assigning these to Nefertiti (rather than to KV35YL) removes the conflicts that defeated other models. (Allele priors: L2–cyan = 0.0132; L4–yellow = 0.0110; see Table 1.)

Nothing in the KV55/KV35YL genotype pairing contradicts Smenkhkare–Baketaten as a full-sibling set; their high match count is expected in that relationship and was the original reason the pair were treated as full children of Amenhotep III and Tiye.

Baketaten is attested with Tiye at Amarna and is generally viewed as a younger daughter of Amenhotep III;[49] her exact birth year is unknown. On many reconstructions she could have

[49] Aidan Dodson, *Amarna Sunrise*, 45.

reached childbearing age by the late Amarna years, making her plausible as Tutankhamun's mother—certainly more so than Meritaten.

Interim assessment

- Bommas v1: Genetically viable, minimal assumptions, neatly resolves the KV55 age debate.

3.6. Tawfik's Proposal

Tarek Tawfik, Susanna Thomas, and Ina Hegenbarth-Reichardt propose that Smenkhkare was not a son of Amenhotep III and Tiye but the son of Thutmose, Akhenaten's elder brother who died before his father. In their reading, Smenkhkare is therefore Akhenaten's nephew and is to be identified with KV55. They further argue that the "Younger Lady" KV35YL is Meritaten, the eldest daughter of Akhenaten and Nefertiti. Tutankhamun is then the child of KV55 (Smenkhkare) and KV35YL (Meritaten).[50] As in other sections of this chapter, Ankhesenamun (KV21A) is modeled as the daughter of Akhenaten + Nefertiti and the likely mother of the two fetuses from KV62.

This configuration departs from the JAMA baseline in two places: (i) KV55 is no longer a son of Amenhotep III/Tiye but their grandson through Thutmose; and (ii) KV35YL is no longer a daughter of Amenhotep III/Tiye but their granddaughter (Meritaten). The historical appeal is that it reconciles Tutankhamun's paternity with a different reading of the late-Amarna succession, while explaining how Smenkhkare could have emerged rapidly as king.

From the STR perspective, the model is admissible, but it carries distinct consequences:

Relationship between KV55 and KV35YL. Under this scheme KV55 (Smenkhkare) and KV35YL (Meritaten) are first cousins (children of two brothers: Thutmose and Akhenaten). In the JAMA dataset KV55 and KV35YL exhibit a very high allele concordance across the eight loci—high enough that Hawass et al. treated them as full siblings. Explaining such high concordance with a first-cousin relationship is not impossible in a dynasty marked by endogamy, but it is less parsimonious than the sibling readings entertained in other models.

As before, the mother of the KV62 fetuses must carry L2 cyan + green, and KV21A carries L4 yellow and L6 pink that must be maternal (since these states are absent in Amenhotep III and Tiye). Assigning Ankhesenamun as the mother (and thus Nefertiti as the maternal source) accommodates those constraints without forcing them onto KV35YL. Hence the core Tawfik configuration is genetically consistent with the observed STRs.

Interim assessment

- Tawfik v1: KV55 = Smenkhkare (son of Thutmose); KV35YL = Meritaten; Nefertiti not identified among known mummies.

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[50] Tarek Tawfik et al., "New evidence for Tutankhamun's parents."

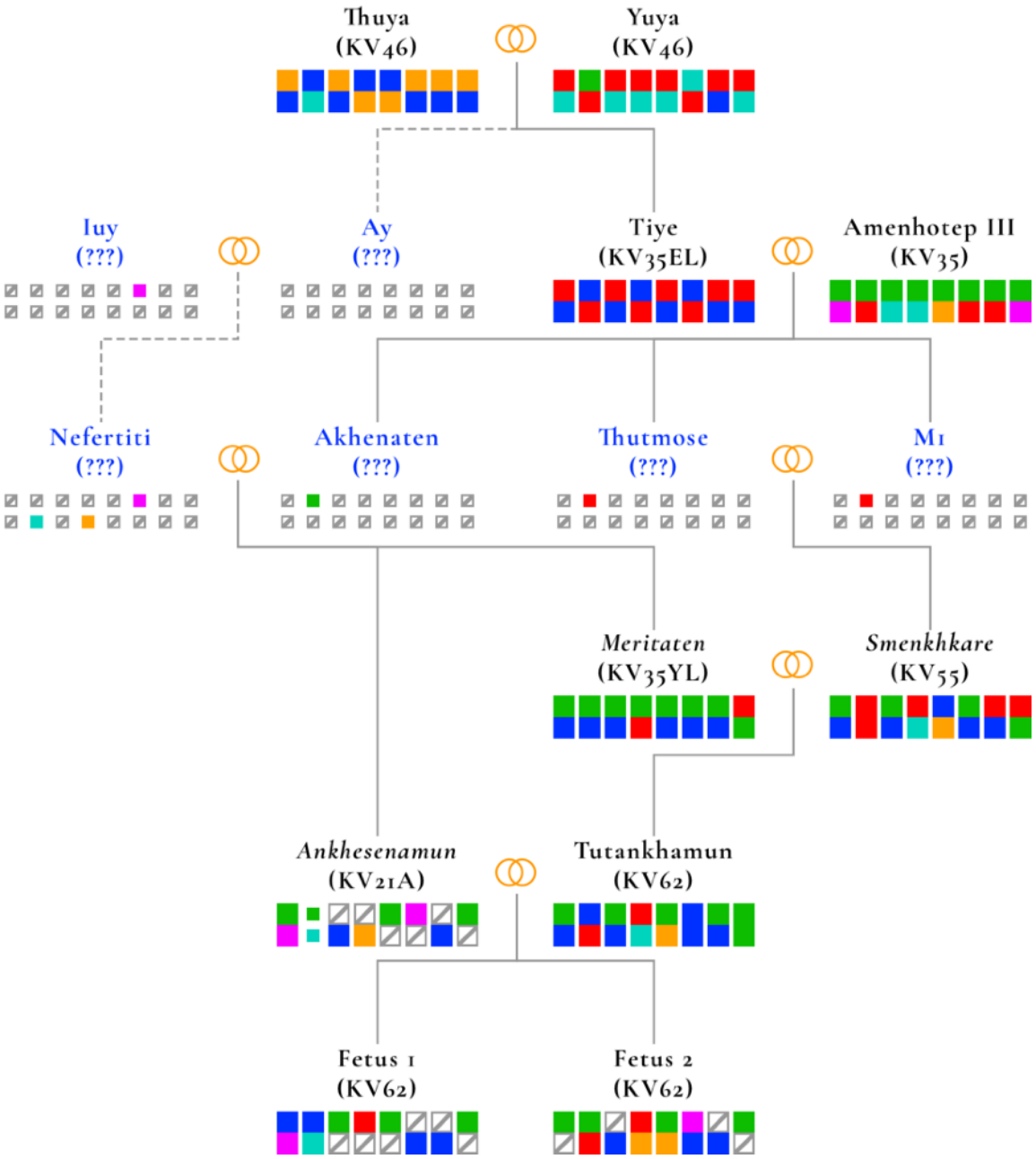

Figure 12. Tawfik v1

Genetically viable; carries a prior penalty for explaining the KV55–KV35YL similarity as first cousins and for two deviations from the null.

3.7. Exploratory Variant

To stress-test our likelihood framework, we include a small set of exploratory trees that—so far as we are aware—have not been advanced in the literature. This variant is not a claim; it is a sensitivity test designed to see how the probabilities move when the same STR evidence is embedded in different but still admissible kinship graphs. We keep the Hawass et al. STR dataset and our locus/color conventions, and we evaluate it with the same priors (see Table 1).

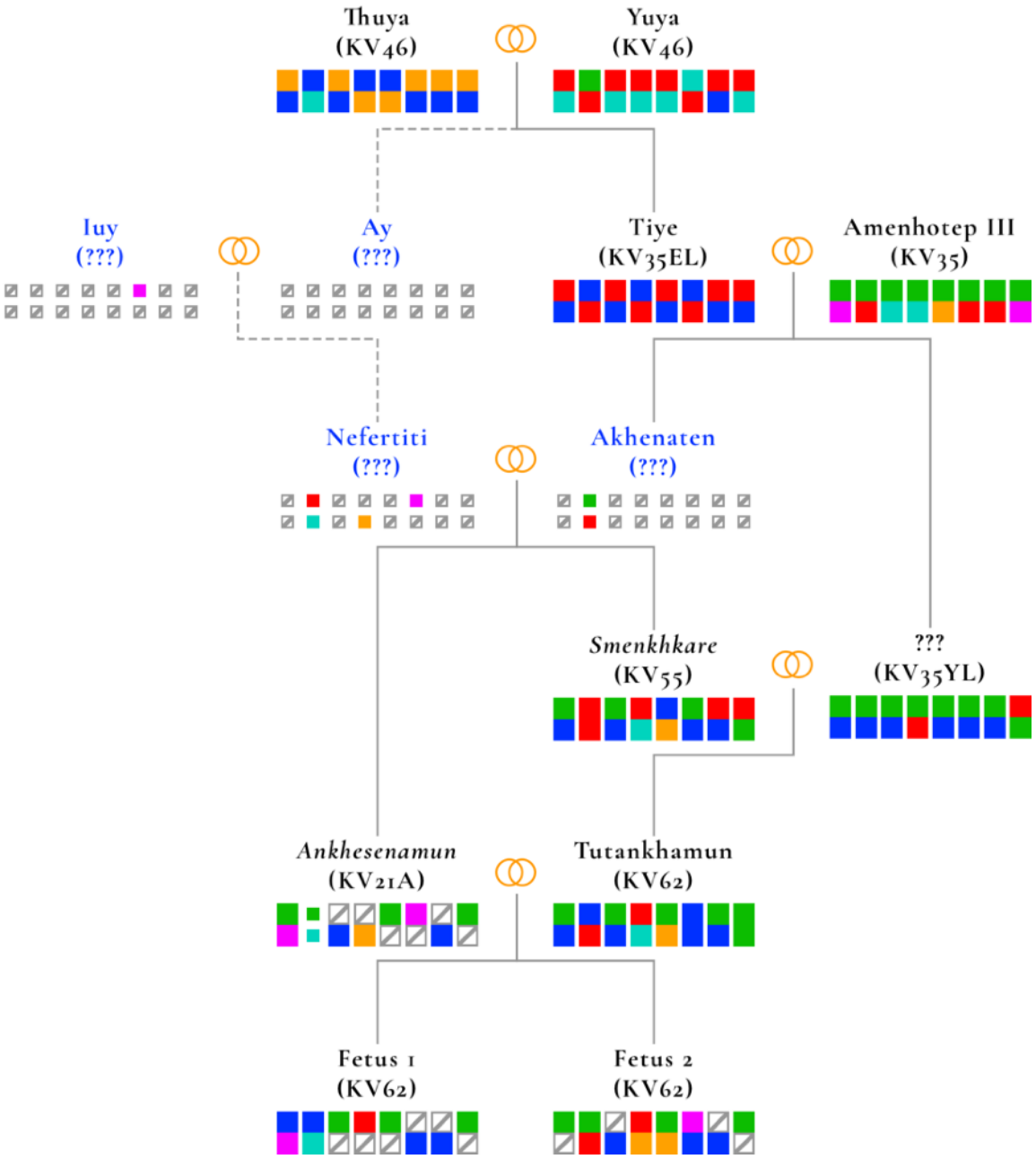

Figure 13. Exploratory Variant E1

In this configuration, KV55 is identified with Smenkhkare, but—unlike the null hypothesis—he is placed one generation lower as the son of Akhenaten and Nefertiti. He marries KV35YL, who remains a daughter of Amenhotep III and Tiye; their child is Tutankhamun. Akhenaten and Nefertiti are also the parents of Ankhesenamun (KV21A), the likely mother of the KV62 fetuses.

The KV55–KV35YL pair shows very high allele concordance across the tested loci in the JAMA data; this pattern originally motivated their treatment as full siblings. Placing KV55 as Akhenaten's son converts the pair into a nephew–aunt marriage (KV35YL being Akhenaten's sister). In an endogamous dynasty, such a close avuncular union can still present many shared alleles without requiring identity at every locus—hence the observed pattern is compatible with this relationship.

The maternal constraints from KV21A and the fetuses remain satisfied: the mother must provide L2 cyan + green; KV21A carries L4 yellow and L6 pink that must be maternal (absent in Amenhotep III/Tiye). Assigning these to Nefertiti keeps the configuration contradiction-free.

Compared with the null, this variant (E1) introduces one structural deviation (moving KV55 down one generation). In our later analysis this adds a parsimony penalty but does not create an allele conflict.

Interim assessment

- The family tree E1 is genetically viable and fit within the known historic facts. However, it introduces an extra assumption regarding KV55 by placing him one generation lower as the son of Akhenaten and Nefertiti.

4. Methodology

Our aim is to compare alternative pedigrees using the STR data by computing, for each tree, a couple-wise likelihood that integrates over parental genotype uncertainty and multiplies Mendelian emission probabilities across all their children and loci. Results are reported as log-likelihoods (logL), differences from the best within a scenario (ΔlogL), and normalized likelihood weights that sum to 100% for the models compared in that scenario.

We treat loci as conditionally independent given the pedigree; all models are evaluated under the same assumption, so comparisons (ΔlogL, weights) are meaningful even if this independence is only approximate.

4.1. STR inputs and prior construction

Loci and states

We analyze a fixed panel of STR loci $\ell \in \mathscr{L}$ (eight in our main analyses). At each locus ℓ, let $\mathscr{A}_\ell$ be the finite set of observed allele labels (the “colors”). Genotypes are unordered pairs:

$$\mathscr{G}_\ell = \big\{\{a,b\} : a,b \in \mathscr{A}_\ell\big\}.$$

Measured vs. unmeasured entries

For any individual i at locus ℓ, if both alleles are measured (a single unordered pair is reported), we treat the prior as a point mass at that pair; if only one allele is measured, we treat that single allele as fixed and the other as unknown; otherwise the locus is unmeasured for i.

Formally, the genotype prior for i at ℓ is a distribution $P_\ell(G_i)$ on $\mathcal{G}_\ell$. For a fully measured genotype $\tilde{g}_{i,\ell} = \{x, y\}$,

$$P_\ell(G_i = \{x, y\}) \;=\; 1, \qquad P_\ell(G_i = g) \;=\; 0 \;\text{ for } g \neq \{x, y\}\,.$$

Parent-independent allele marginals (for unmeasured entries)

For unmeasured allele positions, we use parent-independent allele marginals estimated from the measured alleles available in the dataset at that locus. Denote these empirical marginals by $q_\ell(a)$ for $a \in \mathcal{A}_\ell$, with a small floor to avoid zeros.

$$\text{For all } a \in \mathcal{A}_\ell: \quad q_\ell(a) \;\geq\; \epsilon_0, \quad \sum_{a \in \mathcal{A}_\ell} q_\ell(a) = 1, \quad \text{with } \epsilon_0 \approx 10^{-5}\,.$$

When an individual has one measured allele x and one unknown, we fix that allele and draw the second from q_ℓ. When the individual is completely unmeasured, we draw both alleles independently from q_ℓ and then convert to an unordered genotype (i.e., convolve the two allele marginals and sum symmetric outcomes). Thus, the default parent-independent genotype prior is:

$$P_\ell(\{a, b\}) = \begin{cases} 2\, q_\ell(a)\, q_\ell(b), & a \neq b, \\ q_\ell(a)^2, & a = b\,. \end{cases}$$

Founders and scenario-specific founder priors (a–d)

We treat Amenhotep III, Thuya, Yuya as measured founders. Iuy is unmeasured and receives scenario-specific priors (and in scenario d, Ay as well). These scenarios bracket endogamy assumptions:

- **(a) "maximal endogamy":** at each locus, Iuy's support is restricted to alleles already present in the pedigree (no "new colors" introduced); probabilities are assigned within that restricted support and normalized.
- **(b) "half-related":** at each locus, one Iuy allele is constrained to match the Amenhotep III background (modeled as a spike-and-slab mixture), the other follows q_ℓ.
- **(c) "unrelated Iuy":** both alleles follow q_ℓ (unconstrained support).
- **(d) "unrelated Iuy + unrelated Ay":** as (c) for Iuy and the same construction applied to Ay.

Concretely, these constraints are implemented by zeroing disallowed allele mass and renormalizing. (Zeros are never literal; values $< \epsilon_0$ are replaced by ϵ_0 before renormalization.)

Optional sensitivity: Balding–Nichols correction for founders

As a sensitivity (not in the main tables), an unmeasured founder's genotype prior can be generated from allele frequencies $p_\ell(a)$ via a Balding–Nichols (BN) model with coancestry parameter $\theta \in [0,1)$:

$$P_\ell(\{a,a\}) \;=\; p_\ell(a)\,\big(\theta + (1-\theta)\,p_\ell(a)\big),$$

$$P_\ell(\{a,b\}) \;=\; 2\,(1-\theta)\,p_\ell(a)\,p_\ell(b) \;\; (a<b).$$

In our sensitivity checks, $\theta \in \{0,0.01,0.02,0.03\}$; the main analyses use the scenario-specific priors described above.

4.2. Mendelian transmissions and the observation model

Child prior given parents (Mendelian mixing)

Let the unordered parental genotypes at locus ℓ be $G_f = \{a,b\}$ and $G_m = \{c,d\}$. The child's (latent) unordered genotype G_c has the standard 1/4 mixing over transmissions:

$$P\big(G_c = \{x,y\} \,\big|\, G_f = \{a,b\}, G_m = \{c,d\}\big) = \tfrac{1}{4} \sum_{(u,v)\in\{(a,c),(a,d),(b,c),(b,d)\}} \Big[\mathbf{1}_{\{x,y\}=\{u,v\}}\Big].$$

Observation potential for partial or noisy calls

Let $\tilde{g}_{c,\ell}$, denote the observed child genotype at locus ℓ (it may be fully specified, partially specified—i.e., a single measured allele—or missing). We define an observation potential $O(\tilde{g}_{c,\ell} \mid g)$ for a latent genotype $g \in \mathcal{G}_\ell$ with a small cushion ε (to account for allelic dropout or rare miscalls):

$$O(\tilde{g}_{c,\ell} \mid g) = \begin{cases} 1, & \text{if both alleles measured and } g = \tilde{g}_{c,\ell}, \\ \varepsilon, & \text{if both measured and } g \neq \tilde{g}_{c,\ell}, \\ [3pt]1, & \text{if exactly one allele } x \text{ measured and } x \in g, \\ \varepsilon, & \text{if exactly one measured and } x \notin g, \\ [3pt]1, & \text{if no allele measured at this locus.} \end{cases}$$

We use $\varepsilon = 10^{-3}$. Within any prior distribution (for founders or non-founders), tiny genotype-state masses are floored to min_hap $= 10^{-12}$ and renormalized to prevent numerical zeros.

4.3. Couple-wise likelihood (parents integrated once)

For a given tree, let $C_{f,m}$ be the set of children of father f and mother m. At each locus ℓ , the couple term integrates once over the parents' genotype priors and multiplies the Mendelian emission across all their children:

$$\mathscr{L}_\ell(f,m) \;=\; \sum_{G_f \in \mathscr{G}_\ell} \; \sum_{G_m \in \mathscr{G}_\ell} P_\ell(G_f)\, P_\ell(G_m) \; \prod_{c \in C_{f,m}} \left[\; \sum_{G_c \in \mathscr{G}_\ell} P\big(G_c \,\big|\, G_f, G_m\big)\, O\big(\tilde{g}_{c,\ell} \mid G_c\big) \right].$$

The whole-tree (log-)likelihood sums over loci and couples:

$$\log \mathscr{L}(\text{tree}) \;=\; \sum_{\ell \in \mathscr{L}} \; \sum_{(f,m)} \log \mathscr{L}_\ell(f,m)\,.$$

Important: This formulation prevents "shape-shifting" parents across siblings; a single pair (G_f, G_m) must explain all children of the couple at that locus.

4.4. Model comparison within a scenario

Within any fixed comparison set (e.g., a–d for Run I or the two KV21B identities for Run II), we report:

Differences from the best:

$$\Delta \log L_i \;=\; \log L_i \;-\; \max_j \log L_j\,.$$

Normalized likelihood weights (sum to 100% within the set):

$$w_i \;=\; \frac{\exp(\Delta \log L_i)}{\sum_k \exp(\Delta \log L_k)} \;\times\; 100\,\%\,.$$

These are invariant to additive constants (e.g., adding or removing loci shifts all logL by the same constant but leaves $\Delta \log L$ and w_i unchanged).

Optional Bayes factor for a two-model comparison (e.g., "KV21B = Nefertiti" vs "KV21B = Daughter" within the same structure):

$$\mathrm{BF}_{A:B} \;=\; \exp\big(\log L_A - \log L_B\big)\,.$$

4.5. Two-stage evaluation design

We evaluate the pedigrees in two complementary runs, each answering a different question and using a different comparison set. Within each run, likelihoods are made comparable by using the same loci, observation model, and prior construction rules; weights always sum to 100% within a run and must not be compared across runs.

Run I — Structural comparison

Goal: compare alternative pedigree structures without forcing a particular identification for KV21B. KV21B is treated as an unspecified female node (with the same prior construction as other unmeasured individuals). Any name claims (e.g., "KV21B = Nefertiti") are not enforced in this run; we ask which structure best explains the STR data.

Run II — Identification within structure

Goal: within a fixed structure, compare identity hypotheses about KV21B—typically "KV21B = Nefertiti" vs "KV21B = daughter of Akhenaten and Nefertiti". The only difference between the two models in a given structure is the set of pedigree constraints implied by that identification (which parents/children that node connects to and, hence, which couple-wise emissions it contributes to). This isolates the evidential contribution of the identity claim itself.

Formalization

Let $\mathscr{M}^{(I)} = \{M_1^{(I)}, \ldots, M_{K_I}^{(I)}\}$ be the set of structural models for Run I, and for Run II let $\mathcal{S}$ index the chosen structures, each with two identity hypotheses H_{Nef} and H_{Dau}. For each model M (in either run) we compute the couple-wise, multi-locus log-likelihood $\log \mathscr{L}(M)$ exactly as in Sections 4.1–4.4.

Within a run, we summarize with differences from the best and normalized likelihood weights:

$$\Delta \log L_i^{(I)} \;=\; \log \mathscr{L}\Big(M_i^{(I)}\Big) \;-\; \max_j \log \mathscr{L}\Big(M_j^{(I)}\Big),$$

$$w_i^{(I)} \;=\; \frac{\exp\big(\Delta \log L_i^{(I)}\big)}{\sum_{k=1}^{K_I} \exp\big(\Delta \log L_k^{(I)}\big)} \times 100\,\%\,.$$

$$\Delta \log L_{s,h}^{(II)} \;=\; \log \mathscr{L}\Big(M_{s,h}^{(II)}\Big) \;-\; \max_{h' \in \{\text{Nef,Dau}\}} \log \mathscr{L}\Big(M_{s,h'}^{(II)}\Big),$$

$$w_{s,h}^{(II)} \;=\; \frac{\exp\big(\Delta \log L_{s,h}^{(II)}\big)}{\sum_{h' \in \{\text{Nef,Dau}\}} \exp\big(\Delta \log L_{s,h'}^{(II)}\big)} \times 100\,\%\,.$$

For a two-hypothesis comparison inside a fixed structure s, we may also report the Bayes factor (with equal model priors inside the pair):

$$\mathrm{BF}_{\mathrm{Nef:Dau}}(s) \;=\; \exp\Big(\;\log \mathscr{L}\Big(M^{(II)}_{s,\mathrm{Nef}}\Big) \;-\; \log \mathscr{L}\Big(M^{(II)}_{s,\mathrm{Dau}}\Big)\Big)\,.$$

4.6. Practical settings and robustness

- **Error cushion and floors.** We use $\varepsilon = 10^{-3}$ in the observation potential andmin_hap $= 10^{-12}$ for genotype-state floors. Rankings are robust to moderate changes (e.g., $\varepsilon \in [10^{-4}, 10^{-2}]$.
- **Sensitivity to founder assumptions.** Scenario-specific founder priors (a–d) are our primary analyses. BN founders with θ are a sensitivity only; they do not change the qualitative ordering in our datasets.
- **Bootstrap over loci (optional).** To gauge stability, resample loci with replacement and recompute$\Delta \log L$; percentile bands (2.5/50/97.5) summarize variability attributable to locus selection.

4.7. Scope and limitations

- The approach is couple-wise: it uses per-individual genotype priors that are parent-independent for non-founders (inherited from the prior construction step) and integrates parents once per couple per locus. We do not perform full pedigree peeling; i.e., we do not update parent priors upward using child observations. This is intentional for comparability across published structures; it also keeps the results driven by transparent prior choices.
- Because we compare models within the same scenario and locus panel, the decisive quantities are $\Delta \log L$ and the normalized weights w_i.

5. Results

We report results in two stages, as defined in §4.5. Run I ranks the overall genealogical structures without fixing an identity for KV21B; this avoids penalizing models for optional name-assignments. Run II then asks a narrower, conditional question: if KV21B must be placed inside the Akhenaten–Nefertiti nuclear family, does she fit better as Nefertiti or as another daughter of Akhenaten and Nefertiti?

How to read the tables and figures

- **Founder scenarios (a–d).** Each scenario encodes a different assumption about the founders (Amenhotep III, Thuya, Yuya, Iuy/Ay; see §4.2–§4.3). We report results within each scenario; stability across scenarios is a key robustness check.
- **ΔlogL (log-likelihood).** Values nearer to 0 are better. Differences of ~2–3 log units indicate about a ten-fold disadvantage; ~6–7 log units indicate a hundreds- to thousands-fold disadvantage.
- **Weight % (relative weight).** Within each set and scenario, model weights are normalized to sum to 100%. Do not compare Weight % across Run I and Run II—they are separately normalized.[51]

5.1. Run I — Models without identifying KV21B

Question: *Given the same STR evidence, which overall genealogy fits best when we do not force a specific identity for KV21B?*

Models evaluated: We include all contradiction-free trees that make no additional claim about KV21B: Hawass v2, Bommas v1, Dodson v2, Phizackerley v2, Tawfik v1, and Variant E1. Each is scored across founder scenarios a–d using the common priors, locus mapping, and handling of missing data described in Chapter 4.

What to expect: Because Run I compares structures only, it tells us which pedigrees the STR data favor before we add the extra constraints that come with identifying KV21B. In §5.2 (Run II) we will hold structure constant within each framework and test, head-to-head, whether KV21B fits better as Nefertiti or as another daughter.

Headline result

Two trees tie for first in every scenario and together account for essentially all the weight (see Table 2):

- Hawass v2 — KV55 = Akhenaten; KV35YL remains the other parent of Tutankhamun; KV21 identities left open.
- Bommas v1 — KV55 = Smenkhkare; KV35YL = Baketaten; KV21 identities left open.

Interpretation

On the STR data alone, the DNA cannot choose between “KV55 = Akhenaten” and “KV55 = Smenkhkare” when the rest of the structure is kept minimal. In both trees, Tutankhamun’s parents are modeled as two children of Amenhotep III and Tiye, and it is precisely that structural feature—supported by the allele flows—that the STRs reward. Which name sits in KV55’s box must

[51] ΔlogL values are in natural logs; Weight % is the softmax of ΔlogL within each set.

Scenario a)	ΔlogL	Weight %
Bommas v1	+0.000000	49.41 %
Hawass v2	+0.000000	49.41 %
Phizackerley v2	-4.708225	0.45 %
Variant_E1	-4.761561	0.42 %
Dodson v2	-5.140399	0.29 %
Tawfik v1	-7.557721	0.03 %

Scenario b)	ΔlogL	Weight %
Bommas v1	+0.000000	49.50 %
Hawass v2	+0.000000	49.50 %
Phizackerley v2	-4.893016	0.37 %
Variant_E1	-4.917931	0.36 %
Dodson v2	-5.304051	0.25 %
Tawfik v1	-7.910825	0.02 %

Scenario c)	ΔlogL	Weight %
Bommas v1	+0.000000	49.69 %
Hawass v2	+0.000000	49.69 %
Variant_E1	-5.395808	0.23 %
Phizackerley v2	-5.404183	0.22 %
Dodson v2	-5.735910	0.16 %
Tawfik v1	-8.937620	0.01 %

Scenario d)	ΔlogL	Weight %
Bommas v1	+0.000000	49.86 %
Hawass v2	+0.000000	49.86 %
Phizackerley v2	-6.108482	0.11 %
Variant_E1	-6.216474	0.10 %
Dodson v2	-6.577771	0.07 %
Tawfik v1	-10.586797	0.00 %

Table 2. In all four founder scenarios, Hawass v2 and Bommas v1 tie for first and together account for ~100% of the evidence; other models trail by hundreds-fold to thousands-fold.

therefore be decided by non-genetic considerations (age-at-death assessments, burial context, historical sequence).

Across all four founder scenarios, the remaining four models receive only residual support:

- **Dodson v2** (ΔlogL −5.140399 to −6.577771; Weight % ~0.29–0.07%):
  Here Akhenaten + Nefertiti are cast as the parents of Tutankhamun (and of Ankhesenamun), with KV55 = Smenkhkare elsewhere in the sibship. This pulls one of Tutankhamun's parents away from the measured pair (Amenhotep III/Tiye) and forces rare-allele introductions and less "natural" transmissions at key loci. The model remains feasible but is outscored by the two minimal winners by many orders of magnitude.
- **Variant E1** (ΔlogL −4.761561 to −6.216474; Weight % ~0.42–0.10%):
  KV55 = Smenkhkare is moved one generation down (as son of Akhenaten & Nefertiti) and marries KV35YL (a child of Amenhotep III & Tiye). This "nephew–aunt" structure is still Mendelian, but it demands extra founder states and breaks the simple, high-efficiency route that the winners exploit, so the score drops.
- **Phizackerley v2** (ΔlogL −4.708225 to −6.108482; Weight % ~0.45–0.11%):
  KV35YL = Meritaten, with Tutankhamun as the child of Smenkhkare (KV55) and Meritaten (KV35YL). Genetically admissible, but again it replaces one of the Amenhotep III/Tiye links in Tutankhamun's parentage and pays for that in the likelihood.
- **Tawfik v1** (ΔlogL −7.557721 to −10.586797; Weight % ~0.03–0.00%):
  Both KV55 and KV35YL are moved down one generation (Smenkhkare as son of Thutmose; KV35YL = Meritaten). This has to recreate the very high observed KV55–KV35YL concordance without using Amenhotep III/Tiye as their parents. It is possible under endogamy, but statistically very expensive; the STRs almost never choose that route.

Any design that keeps both parents of Tutankhamun as children of Amenhotep III & Tiye is strongly preferred. Each step that moves a parent away from that measured pair imposes a multiplicative penalty, because the tree must now summon rarer founder alleles and more constrained transmissions to explain the same observations.

Crucially, the ranking does not change as we sweep the founder assumptions from maximal endogamy (a) to fully unrelated Iuy and Ay (d). The absolute log-likelihoods shift slightly (as expected when we allow or restrict founder colors), but:

- The same two trees tie for first every time.
- Their combined weight hovers around ~100% in every scenario.
- Mid-tier models (Dodson v2; Variant E1; Phizackerley v2) stay far behind, and Tawfik v1 remains negligible.

This stability is exactly what we want to see: the principal conclusion does not depend on how aggressively we assume endogamy at the unknown founder nodes.

What this means for the historical debate

1. KV55's identity is not decided by the DNA. The STRs are happy with either "KV55 = Akhenaten" or "KV55 = Smenkhkare," provided Tutankhamun's parents remain the two children of Amenhotep III & Tiye. Any preference between those two therefore belongs to osteology, context, and chronology, not to the eight STR loci.
2. Minimal commitments win. Avoiding extra name-assignments allows the data to flow through the measured grandparents with the fewest rare assumptions. Models that push parentage away from Amenhotep III/Tiye pay a price and drop in the ranking.
3. Endogamy does not rescue alternative parentages. Even under the most endogamous assumptions, models that move Tutankhamun's parent(s) off the Amenhotep III/Tiye line remain strongly disfavored.

5.2. Run II — Conditional placement of KV21B (Nefertiti vs. Daughter)

What this run asks: Here we hold each published framework fixed and ask a narrower, conditional question: if KV21B must be tied into the Akhenaten–Nefertiti nuclear family, does she fit better as Nefertiti or as another daughter of Akhenaten and Nefertiti? Each base tree from Run I was duplicated into two variants that differ only in that single identification; all other assumptions (priors, locus mapping, founder scenarios a–d) are identical (§4.4).

Headline result

Across all four founder scenarios, the Bommas framework again yields the best KV21B-identified models. Within each framework, the data favor "KV21B = another daughter" over "KV21B = Nefertiti" in scenarios a–c by a small margin and in scenario d by a decisive margin. The precise gap varies with the founder assumptions but the direction is stable under the corrected couple-wise likelihood (see Table 3).

What the numbers say (read across scenarios)

- **Scenario a (maximal endogamy at Iuy):** Best pair within Bommas shows ΔlogL = 0.569 in favor of Daughter (Weight 59.71% vs 33.81%); $BF_{\text{Nef:Dau}}$ ≈ 0.57:1. Small but consistent tilt to Daughter; Hawass shows the same direction (smaller weights).
- **Scenario b (Iuy related to Amenhotep III):** ΔlogL = 0.399 favoring Daughter (56.41% vs 37.86% in Bommas); $BF_{\text{Nef:Dau}}$ ≈ 0.67:1. Again a mild Daughter edge; Hawass mirrors this.
- **Scenario c (Iuy unrelated):** ΔlogL = 0.127 favoring Daughter (51.06% vs 44.97% in Bommas); $BF_{\text{Nef:Dau}}$ ≈ 0.88:1. Essentially a near-tie with a slight Daughter lead; Hawass matches the direction.

Scenario a)	ΔlogL	Weight %
Bommas v1 (daughter)	+0.000000	59.71 %
Bommas v1 (Nefertiti)	-0.568716	33.81 %
Hawass v3 (daughter)	-3.071894	2.77 %
Hawass v3 (Nefertiti)	-3.640610	1.57 %
Variant E1 (daughter)	-3.951762	1.15 %
Phizackerley v1 (daughter)	-5.291508	0.30 %
Variant E1 (Nefertiti)	-5.633712	0.21 %
Phizackerley v1 (Nefertiti)	-5.726077	0.19 %
Dodson v2 (daughter)	-5.927043	0.16 %
Dodson v2 (Nefertiti)	-6.437226	0.10 %
Tawfik v1 (daughter)	-7.980888	0.02 %
Tawfik v1 (Nefertiti)	-8.415457	0.01 %

Scenario b)	ΔlogL	Weight %
Bommas v1 (daughter)	+0.000000	56.41 %
Bommas v1 (Nefertiti)	-0.398812	37.86 %
Hawass v3 (daughter)	-3.175092	2.36 %
Hawass v3 (Nefertiti)	-3.573904	1.58 %
Variant E1 (daughter)	-4.110985	0.92 %
Phizackerley v1 (daughter)	-5.480409	0.24 %
Variant E1 (Nefertiti)	-5.607837	0.21 %
Phizackerley v1 (Nefertiti)	-5.737620	0.18 %
Dodson v2 (daughter)	-6.076593	0.13 %
Dodson v2 (Nefertiti)	-6.403018	0.09 %
Tawfik v1 (daughter)	-8.335041	0.01 %
Tawfik v1 (Nefertiti)	-8.592252	0.01 %

Scenario c)	ΔlogL	Weight %
Bommas v1 (daughter)	+0.000000	51.06 %
Bommas v1 (Nefertiti)	-0.127045	44.97 %
Hawass v3 (daughter)	-3.505138	1.53 %
Hawass v3 (Nefertiti)	-3.632184	1.35 %
Variant E1 (daughter)	-4.586503	0.52 %
Variant E1 (Nefertiti)	-5.808015	0.15 %
Phizackerley v1 (daughter)	-6.018496	0.12 %
Phizackerley v1 (Nefertiti)	-6.019327	0.12 %
Dodson v2 (daughter)	-6.443203	0.08 %
Dodson v2 (Nefertiti)	-6.479125	0.08 %
Tawfik v1 (daughter)	-9.385718	0.00 %
Tawfik v1 (Nefertiti)	-9.386550	0.00 %

Scenario d)	ΔlogL	Weight %
Bommas v1 (daughter)	+0.000000	96.48 %
Hawass v3 (daughter)	-4.066059	1.65 %
Bommas v1 (Nefertiti)	-4.395825	1.19 %
Variant E1 (daughter)	-5.347810	0.46 %
Phizackerley v1 (daughter)	-6.684984	0.12 %
Dodson v2 (daughter)	-7.190217	0.07 %
Hawass v3 (Nefertiti)	-8.461884	0.02 %
Variant E1 (Nefertiti)	-10.794458	0.00 %
Phizackerley v1 (Nefertiti)	-10.909653	0.00 %
Tawfik v1 (daughter)	-10.982130	0.00 %
Dodson v2 (Nefertiti)	-11.428642	0.00 %
Tawfik v1 (Nefertiti)	-15.206799	0.00 %

Table 3. Only in scenario d do we have a clear preference for the identification of KV21B as a daughter of Nefertiti and Akhenaten. In scenarios a-c, the interpretation of KV21B as daughter is preferred, but the likelihood weight for Nefertiti is still reasonably high.

- Scenario d (Iuy and Ay unrelated): ΔlogL = 4.396 favoring Daughter (96.48% vs 1.19% in Bommas); $BF_{\text{Nef:Dau}} \approx 0.012{:}1$ (~81:1 for Daughter). Decisive support for Daughter; the Hawass pair shows the same pattern.

Formally, the Bayes factor we quote is:

$$\text{BF}_{\text{Nefertiti:Daughter}} = \exp\Big(\log L_{\text{best (KV21B = Nefertiti)}} - \log L_{\text{best (KV21B = Daughter)}}\Big).$$

Plugging in the best-in-class pairs yields ~0.57:1 (scenario a), ~0.67:1 (b), ~0.88:1 (c), and ~0.012:1 (d) — i.e., mixed across plausible founder assumptions, with one case (d) showing decisive preference for "Daughter."

Model-by-model reading

- **Bommas framework (KV55 = Smenkhkare; KV35YL = Baketaten).**
  Still the strongest overall once KV21B is anchored inside the nuclear family. Within this framework the identity signal is consistently toward "Daughter" across a–c (small gaps) and decisive in d.
- **Hawass framework (KV55 = Smenkhkare in this set).**
  Always below Bommas in absolute fit, but the same direction holds: Daughter > Nefertiti in a–c by modest margins, and strongly in d.
- **Phizackerley frameworks.**
  Daughter is favored in a–b, essentially a tie in c, and decisively favored in d.
- **Dodson frameworks.**
  Daughter > Nefertiti in a–d, with tiny gaps in a–c and a clearer lead in d.
- **Exploratory Variant (E1).**
  Middle of the pack and far from the leaders, but Daughter is preferred in all four scenarios. The advantage is small-to-moderate in a–c and large in d.
- **Tawfik framework.**
  Daughter > Nefertiti in a–d, but the weights are near zero regardless, and the identification does not alter the overall verdict.

What it means for KV21B—and for the bigger picture

1. **KV21B's placement is not decided by STRs alone.**
   Across realistic founder assumptions, the STR data are compatible with both "KV21B = Nefertiti" and "KV21B = Daughter" — except under the most agnostic founder setting (both Ay and Iuy unrelated), where the evidence shifts strongly toward "Daughter." Absent new genetic

information (additional loci, mtDNA, etc.) or decisive archaeological/epigraphic evidence, we refrain from a single global identification.

2. **Forcing KV21B inside the family does not overturn Run I.**
   The structural message from Run I holds: the overall pedigree that best fits the STRs keeps both parents of Tutankhamun as children of Amenhotep III and Tiye—i.e., the Bommas architecture. Once KV21B is forced inside, that architecture still dominates; what changes is only which label for KV21B the data prefer under different founder assumptions.

3. **Why scenario d pushes toward "Daughter."**
   When Ay and Iuy are modeled as unrelated founders, identifying KV21B as Nefertiti tends to require explaining more of KV21A's maternal signals and the fetuses' L2 {cyan, green} through specific, low-frequency founder alleles on a line that is otherwise unmeasured; this "imports" probability costs. Labeling KV21B as another daughter of Akhenaten and Nefertiti relaxes those founder-specific demands and lets the required alleles travel along paths already present in the nuclear family, which the data reward.

Bottom line for Run II

- **KV21B identity (conditional on being inside the nuclear family):**
  - **Scenarios a–c:** differences are small; a mild preference for "Daughter" over "Nefertiti".
  - **Scenario d (Ay and Iuy unrelated):** clear preference for KV21B = Daughter.
- **Historical reading:** The DNA alone does not settle whether KV21B is Nefertiti. Under minimal assumptions about founders, the signal leans to "another daughter," but a conclusive identification will require additional evidence.

6. Conclusion

This study reframes the Amarna genealogy as a problem of relative likelihood: given eight STR loci and explicit founder assumptions, which pedigrees most efficiently explain the observed transmissions? Two design choices proved decisive. First, we separated structure from identification (Run I vs. Run II), so optional name labels do not depress a model's score. Second, we replaced heuristic compatibility counts with a couple-wise likelihood that integrates parents once per locus and multiplies Mendelian emissions across all their children, with a small observation cushion for partial calls. This corrects the main weaknesses we identified initially and makes the rankings interpretable as likelihood weights within each comparison set.

Run I (structures): Across founder scenarios from maximal endogamy to fully unrelated Iuy/Ay, two closely related architectures—both making Tutankhamun the child of two children of Amenhotep III and Tiye—exhaust essentially 100% of the weight. In one the KV55 box is labeled

Akhenaten (Hawass-type), in the other it is Smenkhkare with KV35YL as Baketaten (Bommas-type). On the STRs alone, the DNA does not choose between these labels; it chooses the structure they share. Given the osteological age-at-death assessments that place KV55 as a young adult, the anatomical evidence then tips the identification away from Akhenaten and toward Smenkhkare—without altering the genetic structure the likelihood favors.

Run II (KV21B identity within structure): When KV21B is forced into the Akhenaten–Nefertiti nuclear family, the same best-fitting structure continues to dominate. Within each framework, the STRs show a consistent, small preference for "KV21B = another daughter" over "KV21B = Nefertiti" in scenarios a–c, and a decisive preference for Daughter in scenario d (both Iuy and Ay unrelated). Using the convention $\mathrm{BF}_{\mathrm{Nef:Dau}}$, we obtain ≈ 0.57:1, 0.67:1, 0.88:1, and 0.012:1 across a–d respectively. These are modest signals in a–c—consistent in direction but not conclusive—and overwhelming only under the fully unrelated-founders stress test. We therefore refrain from a global identification of KV21B on STRs alone.

Substantive implications

Three patterns deserve emphasis:

1. **Sibling-parent solution for Tutankhamun.** The data strongly prefer pedigrees in which both of Tutankhamun's parents are children of Amenhotep III and Tiye. This retains the allele "flow" that the eight-locus panel rewards and explains why alternatives that move one parent off that line incur steep multiplicative penalties. Combined with osteology, this favors Smenkhkare (KV55) as father and Baketaten (KV35YL) as mother.
2. **Maternal signals and endogamy.** KV21A's L4-yellow and L6-pink (absent on the Amenhotep III/Tiye side) and the fetuses' L2 requirement {cyan, green} indicate additional maternal-line endogamy best modeled by a second connection to Thuya (via Ay/Iuy as placeholders). This makes a "fully unrelated founders" world (scenario d) historically unlikely, even though we keep it as a useful boundary check.
3. **Amenhotep III / Yuya affinity.** Broad, multi-locus sharing between Amenhotep III and Yuya is more parsimoniously explained by a close maternal tie (often hypothesized for Mutemwia)[52] than by chance in an outbred population. With only eight loci and endogamy, this is suggestive rather than probative, but the signal justifies targeted testing in future work.

Proposed synthesis pedigree (most likely arrangement)

As a practical synthesis of Runs I–II and the osteological context, we propose the pedigree below as the most likely arrangement given the present STR evidence. It is structurally closest to

[52] Cyril Aldred, *Akhenaten: King of Egypt*, 220.

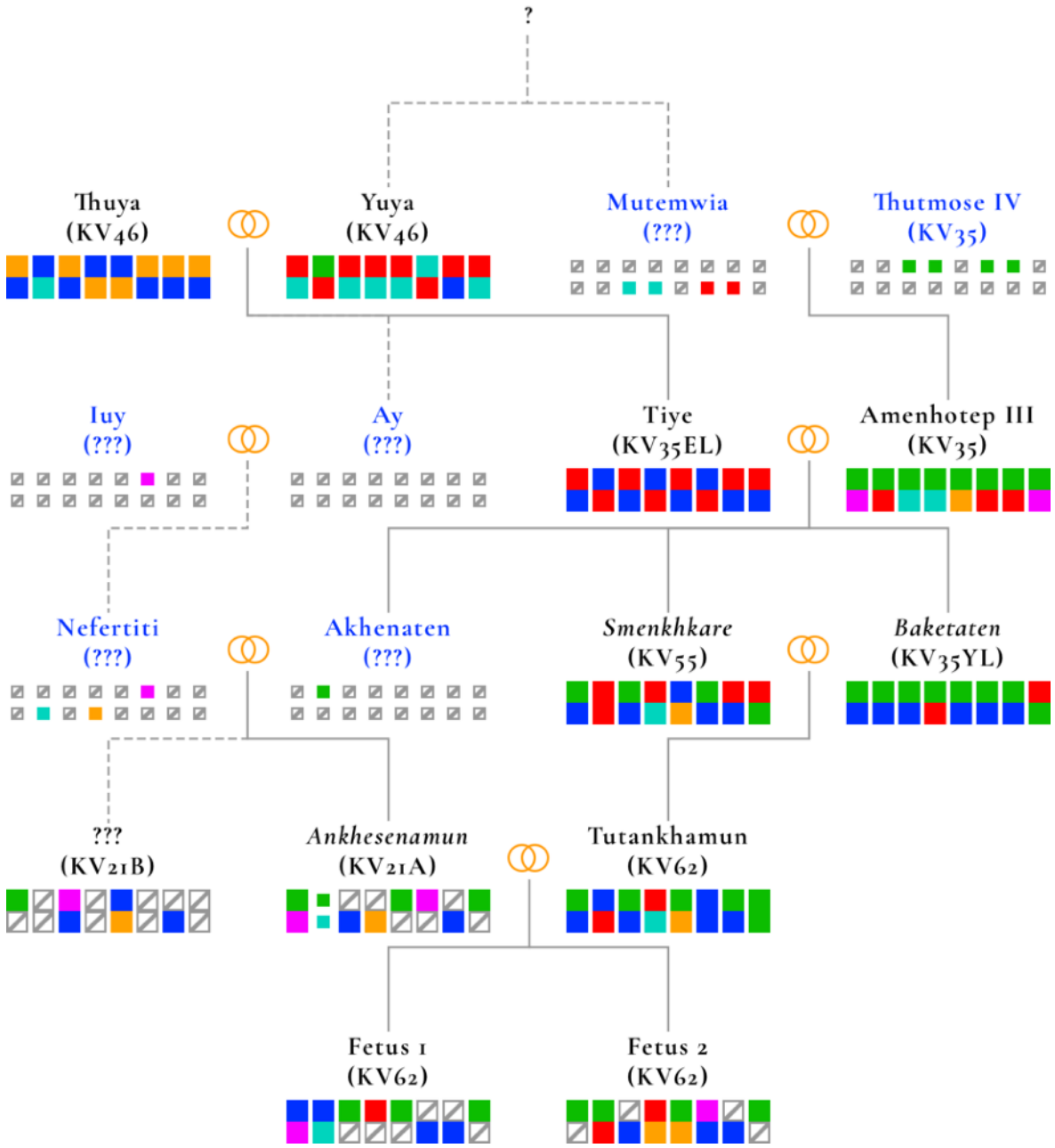

Figure 14. Proposed synthesis pedigree (most likely arrangement). Solid lines are relationships directly supported by the STR panel (and standard historiography). Dotted lines mark hypotheses suggested by STR patterns but not established on STRs alone: (i) KV21B as a daughter of Akhenaten × Nefertiti; (ii) a close maternal link between Mutemwia and Yuya. See text for justification and Run I/II weights.

Bommas (best-fitting framework in both runs), with two cautious additions that the STRs suggest but do not by themselves prove.

- Tutankhamun's parents: Smenkhkare (KV55) × Baketaten (KV35YL).
  This is the sibling-parent solution preferred by the STRs in Run I; the identification of KV55 as Smenkhkare is then carried by osteology (young adult at death), not by the DNA alone.

- Amenhotep III's parents: Thutmose IV × Mutemwia.
  This anchors the maternal line explicitly and sets up the allele-sharing pattern the STRs reward.
- KV21B as daughter: Akhenaten × Nefertiti → KV21B.
  This implements the "Daughter" hypothesis tested in Run II. The STRs favor Daughter over Nefertiti in scenarios a–c by small margins and decisively in d; hence we include KV21B as their daughter but mark the connection as dotted to reflect that the strength is modest in a–c (strong in d).
- Mutemwia–Yuya affinity: a putative close maternal tie between Mutemwia and Yuya.
  Multi-locus sharing is more parsimoniously explained by a close kinship than by chance in an outbred population; we depict this as a dotted kin line (e.g., avuncular/cousin-grade), signaling a hypothesized link pending direct testing.

Conventions for the figure: Solid lines = relationships directly supported by the STRs and/or standard historiography; dotted lines = hypothesized/indirect connections (supported by STR trends but not conclusive on their own). Use node labels with both the common name and the archaeological tag (e.g., "KV55 (Smenkhkare)", "KV35YL (Baketaten)"). If useful, use a light tint on nodes with measured genotypes and a white fill for inferred nodes.

Limitations and next steps

Our conclusions rest on eight STRs, partial profiles, and modern frequency proxies; they are resilient across founder scenarios but necessarily provisional. Three concrete advances would sharpen the picture: (i) targeted capture for genome-wide aDNA (autosomal SNPs, mtDNA, Y) on the key mummies to separate endogamy-driven coincidences from identity-by-descent and to model population structure explicitly; (ii) osteological re-evaluation of KV55 (and KV35YL) under current standards; (iii) if accessible, genetic testing of Mutemwia and Thutmose IV to test the Mutemwia–Yuya link directly.

Bottom line: The structure favored by the STRs is stable, the name on KV55 is decided by osteology rather than DNA, and—conditional on placing KV21B inside the family—the evidence leans Daughter in most founder settings and is decisive only under the most agnostic one. These are not monuments; they are the best-fitting explanations given the present data, and they provide a transparent scaffold for testing with the next increment of evidence.

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