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Toward an interdisciplinary 3D animation design process for palaeoart: Visualising Quaternary megafauna from Sri Lanka's Sabaragamuwa Basin

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ABSTRACT

This study examines the use of three dimensional (3D) animation workflows to create scientifically credible palaeoart of extinct Quaternary megafauna from Sri Lanka's Sabaragamuwa Basin. While palaeoart has long played a critical role in visualising prehistoric life, its scientific foundations are often under-reported, and visual reconstructions are rarely subjected to peer review – especially in underrepresented regions like Sri Lanka. There remains a significant gap in both the availability and methodological transparency of palaeoart, despite increasing international calls for standardised and evidence-based practices in the field. This research presents the first photorealistic 3D reconstructions of two extinct Sri Lankan megafauna: *Palaeoloxodon namadicus sinhaleyus* and Quaternary rhinoceros material historically referred to as *Rhinoceros sinhaleyus*. These visualisations were produced through interdisciplinary collaboration between a palaeontologist and digital artist team, merging morphometric data of Ratnapuran fauna with animation and visual effects pipelines. By documenting the full design process and clarifying the scientific and aesthetic decisions involved, this study provides a model for future scientist-palaeoartist collaboration and highlights the communicative power of digital visualisation to enhance public engagement with underexplored palaeontological heritage.

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INTRODUCTION

Scientific visualisation plays a central role in shaping how prehistoric life is understood by both specialists and the public. Palaeoart – the reconstruction of extinct organisms and environments through artistic media – is among its most influential forms, capable of synthesising anatomical, ecological, and behavioural evidence within a single image. However, the scientific reasoning underpinning palaeoart is often under-reported or obscured by artistic convention, limiting its value as a research-informed communicative tool. This issue is particularly evident in underrepresented palaeontological contexts such as Sri Lanka, where visual reconstructions of extinct fauna remain scarce.

To date, only a small number of palaeoartistic representations of extinct Sri Lankan species have been produced, including illustrations by P.E.P. Deraniyagala (1955; 1958), Kelum Manamendra-Arachchi (2005), and Saranath Dhananjaya Senapathi (Jayatunga, 2014). This article presents the first scientifically informed reconstructions of extinct species from Sri Lanka's Sabaragamuwa Basin created using a photorealistic 3D animation workflow. The reconstructions of *Palaeoloxodon namadicus sinhaleyus* and *Rhinoceros sinhaleyus* constitute the first substantial visual updates to these taxa since 1955 (Deraniyagala 1955). Developed through interdisciplinary collaboration between palaeontologists and digital artists, the work is accompanied by a detailed account of the scientific evidence and aesthetic decisions that informed each reconstruction.

This research pursues two objectives: to establish a transparent and methodologically rigorous framework for producing scientifically credible palaeoart using 3D animation pipelines, and to increase visibility of Sri Lanka's palaeontological record within both regional education and international research contexts. By documenting the reasoning behind these reconstructions, this study contributes to ongoing efforts to integrate palaeoart more formally into peer-reviewed scientific discourse.

PALAEOART

Palaeoart is a form of scientific visualisation that depicts prehistoric life through naturalistic representation. Although no single definition is universally accepted, recent scholarship has sought to formalise the term and distinguish it from other forms of palaeontological imagery (Ansón et al., 2015). A recurring feature across these definitions is a commitment to the reconstruction of extinct life grounded in available scientific evidence (Witton et al., 2014).

The concept of palaeoart implies two intersecting evaluative criteria. First, the imagery must demonstrate scientific credibility in its anatomical, ecological, and behavioural depictions. Second, it must possess sufficient aesthetic quality to function as an artistic work, rather than serving a purely illustrative role. This distinction separates palaeoart from technical figures such as skeletal restorations commonly included in palaeontological publications, which are assessed for scientific accuracy but not for artistic merit.

To capture this dual requirement, Ansón et al. (2015) defined palaeoart as: "any original artistic manifestation that attempt[s] to reconstruct o[r] depict prehistoric life according to the current knowledge and scientific evidence at the moment of creating the artwork." (p. 33), emphasising the need for both artistic skill and scientific understanding However, there are many depictions of prehistoric life that fail to meet either scientific or aesthetic standards. Debus and Debus (2002) proposed the term *palaeoimagery* to describe all visual representations of prehistory, regardless of quality or intent. Because the reconstructions presented in this study explicitly aim to meet both scientific and artistic criteria, the term *palaeoart* is used throughout this article.

Origins and Role of Palaeoart

Palaeoart has been closely linked to palaeontology since the early nineteenth century. One of the earliest examples dates to 1800, when Jean Hermann illustrated a speculative restoration of a pterosaur skeleton first described by Cosimo Collini 14 years earlier (Taquet and Padian, 2004). In 1830, Henry Thomas De la Beche published *Duria Antiquior*, a watercolour depicting ichthyosaurs, plesiosaurs, and pterosaurs reconstructed within a shared Jurassic environment based on fossils from Dorset, England. Unlike earlier depictions of extinct organisms as isolated figures, *Duria Antiquior* represented a deliberate attempt to visualise prehistoric life as part of a functioning ecology grounded in contemporary scientific understanding.

Earlier visualisations of extinct environments were rare and not always intended as serious scientific reconstructions. William Conybeare's 1822 illustration of William Buckland encountering hyenas in Kirkdale Cave, for example, was a satirical image rather than an ecological restoration (Pemberton, 2010). By contrast, De la Beche's work marked a shift toward using palaeoart as a tool for synthesising fossil evidence into coherent environmental narratives. Lithographic reproductions of *Duria Antiquior* were sold to academics for use in lectures (Lescaze, 2017) and, by 1859, model replicas of the Crystal Palace dinosaur sculptures were sold as merchandise, extending the influence of palaeoart across academic, educational, and commercial spheres (Witton et al., 2014).

Today, palaeoart continues to play an important role in communicating palaeontological knowledge to both specialist and non-specialist audiences (Witton et al., 2014). Primary taxonomic publications typically prioritise documentation of anatomical evidence through fossil photography, bone illustrations, skeletal reconstructions, and phylogenetic diagrams. Fully realised palaeoart is less commonly included at this stage, reflecting the focus of initial research outputs on evidentiary description rather than visual synthesis. Reconstructions of complete, fleshed-out organisms therefore more often appear in subsequent publications or as part of public engagement and outreach efforts intended to contextualise scientific finds for wider audiences.

Considerations in Reconstruction

Despite their influence on both scientific and public understanding, the decisions underpinning palaeoartistic reconstructions are rarely subjected to formal peer review, even when works appear in academic contexts (Davis et al., 2022). This is partly due to the infrequent documentation of visual methodologies by palaeoartists themselves (Campbell et al., 2021). As palaeontological knowledge expands – particularly through advances that allow increasingly detailed analysis of fossil material – the scope for artistic licence correspondingly narrows (Witton, 2014; Bertozzo et al., 2020; McDermott, 2020; Campbell et al., 2021). Anatomical reconstructions are therefore constrained by biomechanical plausibility, limiting depictions to poses and behaviours consistent with a species' inferred functional capabilities.

Similar constraints apply to decisions surrounding colouration, body proportions, and soft tissues, including pelage or plumage where relevant. Such features should be defensible in relation to all available evidence at the time of reconstruction, rather than inherited from convention or aesthetic habit (Witton et al., 2014; Davis et al., 2022). Nevertheless, palaeoimagery frequently perpetuates outdated visual tropes – including repeated colour schemes, poses, behaviours, and compositional structures – that owe more to artistic tradition than to contemporary scientific understanding (Naish, 2017).

One of the most egregious of these tropes is the "shrink-wrapping" of prehistoric animals, in which skeletal and muscular forms are depicted as tightly constrained beneath a thin layer of skin. This approach privileges osteology at the expense of soft tissue, resulting in reconstructions that underrepresent the volume, flexibility, and surface complexity seen in extant animals. Comparative anatomy provides clear counterexamples, including the soft-tissue structures of birds and the trunks, ears, and overall mass of elephants, all of which demonstrate how skeletal outlines alone are poor predictors of external form (McDermott, 2020). In response to such limitations, recent palaeoart has increasingly challenged inherited visual conventions. The *All Yesterdays* movement, which emerged in the early 2010s, explicitly sought to disrupt the visual homogeneity of palaeoart by encouraging biologically plausible but unconventional interpretations of extinct animals (Conway et al., 2012; Davis et al., 2022). Rather than abandoning scientific constraint, this approach reframed uncertainty as an opportunity to explore a broader range of defensible anatomical and behavioural possibilities.

Palaeoart and Popular Culture

The relationship formed between a concept and its visual representation during childhood can have long-lasting effects on how that concept is understood into adulthood (Kosslyn et al., 2006). Research suggests that the earliest visual depictions of dinosaurs encountered by children often exert the strongest influence on their lifelong mental models of those animals (Rosset al., 2012). As a result, educational institutions such as museums carry a particular responsibility for the accuracy of their displays, websites, printed materials, and associated merchandise, which exert far greater influence on public understanding – especially among younger audiences – than scientific publications themselves (Campbell et al., 2021).

Museums, however, represent only one avenue through which depictions of prehistoric life are disseminated. Popular culture artefacts – including toys, books, television, film, clothing, and even dino chicken nuggets – arguably play an even greater role in shaping public perceptions of extinct organisms. In such contexts, there is little incentive to reflect contemporary scientific understanding. Instead, popular representations frequently perpetuate outdated reconstructions, favour paedomorphic or exaggerated designs, or modify anatomy and posture to meet commercial or manufacturing constraints, such as ensuring a toy can stand upright (Ross et al., 2012; Witton, 2018).

As a result, palaeoimagery, and palaeoart in particular, "can easily create and perpetuate misconceptions that are carried through generations of iterative popular media" (Davis et al., 2022, p. 1). Mark Witton (2017a) warns that the influence of palaeoart often exceeds those of press coverage or even scientific papers, giving such imagery a disproportionate influence on public perception and, in some cases, on scientific hypotheses themselves. Witton (2017b) further emphasises the importance of actively guiding reconstructions toward greater credibility to shape future representational norms.

While these issues have been the subject of sustained discussion within global palaeoart communities, comparable discourse is largely absent in Sri Lanka. Visual representations of the island's prehistoric fauna remain scarce, heightening the importance of examining how such imagery is produced and interpreted within a local context. Given that this study focuses on species recovered from the Sabaragamuwa Basin in southwestern Sri Lanka, it is therefore necessary to situate the role of palaeoart within the country's broader scientific and cultural landscape.

Palaeoart in Sri Lanka

Palaeontological research in Sri Lanka remains comparatively underdeveloped, not due to a lack of fossil material, but as a consequence of structural constraints. These include limited access to research funding, the absence of sustained palaeontology-specific training pathways, and a resulting scarcity of established specialists able to lead long-term research programmes.

Reflecting this broader context, palaeoart production in Sri Lanka has also been limited. The most significant contributions have historically been made by scientists with artistic training, including Paulus Edward Pieris Deraniyagala, Siran Deraniyagala, Saranath Dhananjaya Senapathi, and Kelum Manamendra-Arachchi, (Jayatunga, 2014). Their palaeoartistic output has primarily employed traditional media such as drawing, painting, and sculpture, alongside raster-based digital illustration tools (e.g., Adobe Photoshop). These works typically function as adjuncts to scientific research rather than as independently theorised visual reconstructions.

More recent large-scale palaeoart initiatives include the cement sculptures installed at the Rathnapura National Museum Palaeobiodiversity Museum Park. Created between 2012 and 2014 by Lalith Wijesinghe and D.U. Rajapaksha, these works depict a range of extinct Sri Lankan megafauna and were produced under the supervision of the Department of National Museums to ensure alignment with institutional standards. While significant as public-facing representations, these sculptures were not accompanied by published documentation detailing the scientific assumptions or reconstruction methodologies informing their design.

Among Sri Lankan contributors, P.E.P. Deraniyagala warrants particular attention. In addition to his central role in shaping twentieth-century Sri Lankan palaeontology (Jayatunga, 2014; Atthapattu, 2022), he produced some of the country's earliest palaeoart during the 1930s–1960s as visual interpretations of his fossil discoveries. An accomplished artist as well as a scientist, Deraniyagala integrated zooarchaeological knowledge into drawings, paintings, carvings, and sculptures that functioned simultaneously as research communication and creative practice (Manamendra-Arachchi, 2012).

METHODS

While there is a small, but established, body of palaeoart relating to Sri Lankan fauna, relatively few extinct taxa have been visually reconstructed to date (Sumanarathna et al., 2017; Sumanarathna et al., 2021). Existing representations vary considerably in style and level of anatomical resolution and, although informed by available scientific evidence, tend toward interpretive or stylised depictions rather than photorealistic reconstruction. To date, there are no documented examples of palaeoart depicting extinct Sri Lankan species produced using contemporary digital workflows, including high-fidelity 2D or 3D computer-generated (CG) techniques.

The imagery developed for this research constitutes the first systematic attempt to produce photorealistic CG reconstructions of extinct Sri Lankan megafauna grounded in current palaeontological and comparative anatomical evidence. In addition to the resulting images, this research explicitly documents the scientific assumptions, interpretive uncertainties, and creative decisions underpinning each reconstruction, following best-practice recommendations outlined by Witton (2017a; 2018), Campbell et al. (2021), and Davis et al. (2022). By making these decisions transparent, the palaeoart presented here is positioned as a peer-reviewable research output rather than an illustrative adjunct. In doing so, the study addresses a persistent gap in palaeontology–palaeoart collaboration by formalising an interdisciplinary methodology for producing visually rigorous reconstructions that remain accountable to contemporary scientific knowledge.

Project Origin

Palaeoartists enter collaborative projects from a range of disciplinary backgrounds. Some are trained palaeontologists, while others possess limited formal scientific education and work primarily through consultation with subject-matter experts. In this project, the animation supervisor (J.K.) holds undergraduate training in palaeontology. While this level of training does not support independent scientific interpretation, it proved sufficient to facilitate informed dialogue with the scientific team and to interpret their guidance accurately within the visualisation process.

This intermediary role became particularly important when supervising additional artists involved in the reconstructions, many of whom had no formal background in the natural sciences. The animation supervisor therefore functioned as a liaison between scientific contributors and artistic practitioners, translating scientific constraints into actionable visual decisions while relaying artistic uncertainties back to the research team. Establishing a shared understanding of expectations, limitations, and decision-making authority was essential at the outset of the project. The following sections outline the key points of communication agreed upon prior to commencing the visualisation work.

Scientist considerations. Key communication points from the scientific team centred on public accessibility and regional specificity. These included the need to communicate Sri Lankan palaeontology to non-specialist audiences, to visualise extinct species endemic to the region, and to situate reconstructions within recognisable landscapes such as Sri Pada (Adam's Peak) and Paradise, Kuruwita. The scientists emphasised the importance of conveying species physiology, morphology, and inferred ecological relationships, while explicitly acknowledging the speculative nature of such reconstructions given the fragmentary fossil record. Despite these uncertainties, reconstructions were regarded as valuable tools for efficiently communicating scale, adaptation, and ecological presence. A longer-term objective of the project is the production of a documentary integrating animated reconstructions within live-action footage of ecologically analogous environments.

Artist considerations. The artistic team required clear expectations regarding timelines, production scope, and deliverables to manage scientific expectations realistically. This was particularly important given constraints on equipment availability and the reliance on student collaborators rather than full-time industry professionals. The team outlined the cumulative demands of 3D production, including modelling, rigging, animation, simulation, and rendering, alongside downstream processes such as lighting, environment interaction, compositing. The time-intensive nature of each stage was emphasised, as were the benefits of designing assets for reuse across multiple outputs and media formats. Considerations of visual storytelling and adaptability were therefore treated as production requirements rather than aesthetic preferences.

Production considerations. During initial discussions, the palaeontologist (A.R.S.) proposed visualising ten extinct megafaunal species from the Sabaragamuwa Basin within a 12-month period. These included three species of family Elephantidae, two from Rhinocerotidae, two from Felidae, and one species each from Hippopotamidae, Bovidae, and Crocodilia: *Palaeoloxodon namadicus sinhaleyus, Hypselephas hysudricus sinhaleyus, Elephas maximus sinhaleyus, Rhinoceros sinhaleyus, Rhinoceros kagavena, Hexaprotodon sinhaleyus, Bibos sinhaleyus, Panthera leo sinhaleyus, Panthera tigris,* and *Crocodylus sinhalyeus.*

Given the substantial anatomical divergence across these families, the animation supervisor advised that the proposed scope exceeded the available time and resources. It was therefore recommended that the project focus on a smaller number of taxa within a reduced six-month timeframe, allowing the development of proof-of-concept reconstructions and the establishment of a reliable production workflow. Both parties agreed to this revised strategy, with the aim of completing fully composited visualisations of *Palaeoloxodon namadicus sinhaleyus* and *Rhinoceros sinhaleyus.* In this context, compositing refers to the integration of rendered digital elements with live-action imagery to achieve visually coherent and spatially credible results.

Technical Considerations

A range of approaches exist for visualising extinct species. Historically, palaeoart has been produced using traditional media such as drawing and painting. Over the past 25 years, increased access to capable graphics software and consumer-grade computing hardware has led many artists to adopt digital workflows. These can be broadly categorised as either two-dimensional (2D) or three-dimensional (3D) in approach.

Two-dimensional workflows typically rely on raster-based image editing software that provides digital analogues of traditional artmaking practices, such as drawing and painting with simulated media. In addition to digital painting, such software enables techniques including photo-manipulation and photocollage. Photo-manipulation may involve altering photographs of extant animals to approximate the size or proportions of extinct taxa, while photocollage – often referred to as “photobashing” – combines visual elements from multiple extant species into a composite reconstruction. In practice, these techniques are frequently used in combination, as seen in the work of palaeoartists Mauricio Antón and Julius T. Csotonyi (Ansón, 2015).

However, reliance on photo-manipulation and collage techniques carries well-documented risks. As Ansón et al. caution, “[w]hen we transplant directly the many subtle and distinctive aspects in the life appearance of an animal, what we are creating is the very same animal, recognizable although deformed” (2015, p. 33). Such approaches can inadvertently preserve species-specific anatomical signatures that are inappropriate for the extinct taxon being reconstructed. These limitations have prompted some practitioners to adopt 3D workflows, which afford greater control over morphology, proportion, and presentation, as well as the use of virtual cameras that allow a subject to be examined and depicted from any viewpoint.

Within a 3D workflow, extinct species are constructed as digital models that can be sculpted, textured (i.e., assigned surface colour and material properties), posed, lit, and rendered within fully virtual environments. Conceptually, this process is closer to sculpture than illustration, though in practice it is highly technical and shaped by software-specific constraints and conventions. Commonly used applications for 3D palaeoart include generalist modelling and animation software, alongside specialist digital sculpting tools. A detailed comparison of such software ecosystems is beyond the scope of this article, except where directly relevant to the methods adopted here.

A central technical consideration for this research was the requirement that reconstructed species be capable of believable integration within real-world environments. A longer-term objective of the project is to animate these reconstructions within present-day landscapes that serve as ecological analogues for Quaternary habitats. Consequently, the imagery needed to support photorealistic rendering from multiple viewpoints, under varied lighting and environmental conditions, and to remain suitable for posing or animation. These requirements are best met by a 3D pipeline and align with the existing professional expertise of the animation supervisor.

The selection of software was guided by several pragmatic factors. These included access to software licences, which range from open-source solutions to commercial packages requiring substantial per-seat costs; the availability of computing hardware with sufficient graphics-processing capability; and the technical proficiency of the production team. High-performance hardware and advanced software offer limited benefit without the skills required to deploy them effectively. Accordingly, software and hardware choices were matched to the existing competencies and institutional resources available to the project.

Through the facilities at Auckland University of Technology (Auckland, New Zealand) and the technical training embedded within AUT’s Animation, Visual Effects and Game Design major, the project was able to utilise industry-standard software across all stages of production, supported by high-performance computing infrastructure. The primary tools employed included Autodesk Maya 2023 (Autodesk, 2023a), Maxon ZBrush 2023 (Maxon, 2023), Adobe Substance Painter 9.0 (Adobe, 2023a), Adobe Photoshop 2023 (Adobe, 2023b), and Adobe After Effects 2023 (Adobe, 2023c). Within this pipeline, Maya functioned as the central production environment, integrating modelling, animation, fur simulation, lighting, and rendering using Arnold Renderer for Maya 7.1.3.2 (Autodesk, 2023b).

Although alternative software packages could have been used at each stage of production – such as modelling in Blender (Blender Foundation, 2025), texturing in Mari (Foundry, 2025a), or compositing in Nuke (Foundry, 2025b) – the tools selected were chosen for their compatibility with the project's longer-term goals of animation, environmental integration, and methodological reproducibility. At the level of producing individual still illustrations, there is relatively little difference in the visual outcomes achievable using these platforms; in such cases, software choice is primarily a matter of familiarity, efficiency, and pipeline fluency rather than intrinsic capability.

These distinctions become more consequential when moving beyond isolated images into temporally extended or large-scale production contexts. For example, node-based compositing systems such as Nuke offer clear advantages over layer-based tools like After Effects when managing complex, multi-pass visual effects sequences typical of documentary or cinematic production. Similarly, high-end texture painting applications such as Mari may offer advantages for managing extremely high-resolution or multi-UDIM assets in animation pipelines, though such capabilities exceed the requirements of the present study.

Production Considerations

The central production task was the creation of anatomically credible and visually convincing 3D models for each extinct species. The quality of the base model has a decisive influence on every subsequent stage of the pipeline, including posing, texturing, simulation, lighting, and compositing. High-quality creature modelling is both technically demanding and time-intensive, particularly when models are built entirely from first principles within a 3D environment. Given the project's scope and resource constraints, a hybrid strategy was adopted in which existing models of extant species were used as morphological starting points.

To support this approach, the animation supervisor acquired high-quality digital models of extant taxa that share morphological similarities with the extinct species under study. These assets provided a reliable baseline for both macro-scale anatomy and fine surface detail, allowing artists to concentrate on modifying key morphological features rather than constructing entire bodies from scratch. This approach also enabled rapid iteration in response to scientific feedback from A.R.S. and M. Aouititen (personal communication), as targeted anatomical revisions could be implemented without necessitating wholesale reconstruction. Under conditions of limited time and personnel, this strategy represented a more efficient and scientifically responsive use of artistic labour.

Stock models of extant species were purchased from TurboSquid (www.turbosquid.com), an online marketplace for professional-grade digital assets, with the specific assets used in this study listed in Table 1. To ensure suitability for palaeoart reconstruction, candidate models were required to meet the following core criteria:

- The model exhibits sufficient anatomical fidelity for the extant species, including accurate overall proportions, soft tissue definition, and high-resolution surface detail (e.g., wrinkles, pores, scales).
- The extant species demonstrates a close morphological relationship to the extinct taxon to be reconstructed, minimising the extent of structural modification required.
- The model possesses clean, production-ready topology, characterised predominantly by quadrilateral faces. This supports smooth deformation during posing, preserves continuous anatomical curvature, and reduces the likelihood that technical artefacts (e.g., pinching or creasing) are misinterpreted as biological features.
- The native file format is compatible with the software pipeline employed in this research.

Together, these criteria ensured that each extant model could function as a robust technical and anatomical substrate for modification into its extinct counterpart. Additional features were considered advantageous, though not essential to the baseline sculptural task, and were therefore treated as optional:

TABLE 1. Extant 3D models purchased as the anatomical basis for reconstruction of the extinct taxa studied.

Extinct taxon	Extant base model	Year	URL
Palaeoloxodon namadicus sinhaleyus	*Elephas maximus*	2019	https://www.turbosquid.com/3d-models/asian-elephant-anatomy-3d-model-1387620
Rhinoceros sinhaleyus	*Ceratotherium simum*	2018	https://www.turbosquid.com/3d-models/rhinoceros-rigged-3d-model-1327559

- Inclusion of downstream production elements such as UV layouts, texture maps, animation rigs, test animations, fur systems, or render setups.
- Stylistic and topological consistency across selected models to support asset reuse and pipeline coherence.

Based on these criteria, models of *Elephas maximus* and *Ceratotherium simum* were selected as the primary morphological bases for adapting *Palaeoloxodon namadicus sinhaleyus* and *Rhinoceros sinhaleyus*, respectively.

Given the requirement to develop multiple megafaunal assets within a fixed timeframe, additional personnel were necessary to meet production deadlines. As the project budget did not permit the engagement of industry professionals, senior undergraduate students from the Animation, Visual Effects and Game Design major at Auckland University of Technology were recruited as interns. Students were selected based on demonstrated technical competence and participated as part of their formal internship requirements. During 2022, nine student interns contributed to the project; a further six interns participated during 2023. Their contributions spanned multiple stages of the pipeline, including 3D modelling, UV layout, texturing, rigging, animation, simulation, lighting, rendering, and compositing.

Reconstruction Challenges

The most immediate constraint on reconstruction reliability is the quantity and quality of fossil material available for a given taxon. The species visualised in this article are represented by extremely limited fossil remains, in some case by isolated dental elements alone (e.g., *Palaeoloxodon namadicus sinhaleyus*). Although a small number of palaeoart representations exist for these taxa, all known examples were consulted during the development of the revised reconstructions presented here. In particular, the palaeoart sketches produced by P.E.P. Deraniyagala produced as part of his research publications – most notably *The Pleistocene of Ceylon* (1958) – served as important historical reference points.

In cases where fossil evidence is sparse, reconstruction necessarily involves retrodiction – a form of constrained inference that extrapolates plausible morphology from extant or better-documented phylogenetic relatives. This process blends scientific reasoning with informed artistic judgement, guided by comparative anatomy, functional morphology, and ecological context. Campbell et al. (2021) have questioned the reliability of retrodiction in relation to hominin reconstructions, and their critique is relevant to prehistoric reconstruction more broadly. Nevertheless, when direct empirical evidence is minimal, palaeoartists must draw on comparative analogues and ethological inference to bound the range of plausible forms. The key methodological challenge is therefore not the avoidance of retrodiction, but its careful constraint.

Despite the limited fossil record for the two taxa reconstructed in this study, it is essential to identify explicitly the empirical material that informed the reconstructions. Photographs and osteological descriptions of all known fossils attributed to *Palaeoloxodon namadicus sinhaleyus* and *Rhinoceros sinhaleyus* were compiled from the available scientific literature. Several fossils described by Deraniyagala in the mid-twentieth century are now missing; moreover, no specimen or catalogue numbers were reported for this material in the original published sources. As such, the sources cited below represent the most complete photographic documentation available as of 2026. For *P. namadicus sinhaleyus*, the consulted material includes the holotype upper first molar (Deraniyagala, 1955, Plate 13), lower molars (Deraniyagala, 1958, Plates XLI, XLVI), and two fragmentary molar teeth (Sumanarathna et al., 2021, pp. 219–220). For *R. sinhaleyus*, consulted material includes a lower molar (Deraniyagala, 1955, Plate 13), the holotype second molar (Deraniyagala, 1958, Plate XLVII), a right mandibular body (Deraniyagala, 1958, Plate XLIX), first and second upper molars (Jayatunga, 2014, p. 14; Sumanarathna et al., 2021, pp. 231–235), and a proximal portion of a scapula (Sumanarathna et al., 2017, p. 22).

For both taxa, the available fossil material consists primarily of dentition, with the addition of a mandibular fragment and a proximal scapula portion in the case of *Rhinoceros sinhaleyus*. Dental morphology is critical for taxonomic identification and can offer indirect insights into diet and feeding strategy, but it provides limited information about postcranial anatomy, body proportions, or soft-tissue morphology. As a result, reconstruction beyond the cranial region necessarily depends on comparative reference to closely related taxa.

The three-dimensional reconstructions presented here for *Palaeoloxodon namadicus sinhaleyus* were produced by modifying an existing digital model of an adult *Elephas maximus*. This decision was guided by the need for a complete, articulable proboscidean body whose anatomy could be independently evaluated against living reference material. Because *E. maximus* is extant, its skeletal structure, soft-tissue relationships, and range of anatomical variation can be directly verified using photographic, osteological, and observational data, allowing errors introduced during digital modification to be identified and corrected.

By contrast, although *Palaeoloxodon antiquus* represents a close Eurasian sister taxon with unusually complete fossil material, any existing digital reconstructions of this species necessarily embed prior interpretive assumptions that cannot be readily audited or disentangled. For this reason, a pre-existing *P. antiquus* model was not adopted as a starting point. Instead, the *Elephas maximus* model functioned as a technically robust base mesh, providing a fully articulated proboscidean body suitable for large-scale proportional adjustment without inheriting unexamined speculative decisions.

Comparative anatomical guidance for post-cranial morphology was drawn primarily from published osteological reconstructions and functional analyses of *Palaeoloxodon antiquus*, for which substantially more complete skeletal data are available than for *Palaeoloxodon namadicus*, and no post-cranial material is currently known for *P. namadicus sinhaleyus.* This included a study based on the well-documented Neumark-Nord 1 material from Germany, including a schematic reconstruction of an adult male *P. antiquus* assembled from the best-preserved bones of individuals 152-E9 and 175-E23A (Larramendi et al., 2017). These studies informed conservative adjustments to body mass distribution, limb proportions, and cervical musculature in the *Elephas maximus* base model. Cranial morphology was guided principally by published comparative analysis of *P. namadicus*, which constrain skull proportions, tusk orientation, and craniofacial structure across the genus (Larramendi, 2020). Estimates of overall body size were further informed by published measurements of *P. namadicus* material from the Narmada Valley and other Indian localities, including femoral remains used to infer shoulder height and body mass (Larramendi, 2016). The Sri Lankan material attributable to *P. namadicus sinhaleyus* is extremely limited, consisting only of isolated molars described by Deraniyagala (1955; 1958) as smaller than those of the *forma typica*. Accordingly, this local material was used primarily to support taxonomic attribution and the plausibility of a modest reduction in overall body size, rather than to infer detailed cranial or post-cranial anatomy. For the purposes of this reconstruction, *P. namadicus sinhaleyus* was modelled at 80% of the estimated maximum shoulder height of the largest mainland *P. namadicus*. This proportion was not reported by Deraniyagala and should not be understood as a direct osteometric estimate derived from Sri Lankan material. Rather, it represents a conservative interpretive scaling decision made in this study, informed by Deraniyagala's qualitative description of reduced stature and by comparative evidence from insular dwarfing in other palaeoloxodont taxa (Baleka et al., 2021). Because the visualisations in this study were generated by modifying complete digital models of extant animals selected as close phylogenetic analogues, it is necessary to revisit the caution raised by Ansón et al. (2015) regarding photo-manipulation and collage in palaeoart reconstruction. While their critique was directed primarily at 2D practices, the underlying concern – the inadvertent retention of species-specific anatomical signatures – applies equally to 3D workflows. However, digital sculpting affords a higher degree of control over anatomical continuity, allowing artists to adjust proportions, surface topology, integumentary details, and musculature in a spatially coherent manner rather than through planar distortion. This is not meant to imply that 3D reconstructions are immune to error. However, when applied rigorously, digital sculpting techniques enable anatomical transformation without reducing the result to a merely deformed version of the extant analogue.

The three-dimensional reconstruction presented here for *Rhinoceros sinhaleyus* was produced by modifying an existing digital model of an adult *Ceratotherium simum*. This decision was made for technical rather than phylogenetic reasons: the model provided a complete, articulable rhinocerotid body with stable topology, musculature, and limb structure suitable for large-scale proportional adjustment during digital sculpting. Because *C. simum* is extant, its anatomy can also be checked directly against photographic, zoological, and osteological reference material, allowing modifications to be evaluated against an independently verifiable living animal.

However, *Ceratotherium simum* did not function as the primary anatomical analogue for the final reconstruction. As a highly derived grazing rhinoceros with cranial, dental, and postcranial specialisations distinct from Asian browsing and mixed-feeding taxa, it served only as a base mesh. Anatomical inference for *Rhinoceros sinhaleyus* was instead guided by the available Sri Lankan fossil material and by comparative reference to extant and fossil Asian rhinoceroses considered more closely related to the species.

As stated above, the consulted fossil material for *Rhinoceros sinhaleyus* consists primarily of dentition, together with a right mandibular body and a proximal scapula fragment. These remains are sufficient to support taxonomic identification and provide limited insight into feeding ecology, relative size, and aspects of mandibular structure, but they do not permit direct reconstruction of full cranial form, postcranial proportions, musculature, or integument. Accordingly, reconstruction beyond the preserved elements necessarily depended on comparative reference to closely related taxa.

Comparative anatomical guidance was drawn primarily from *Rhinoceros unicornis* and *Rhinoceros sondaicus*, together with published discussion of fossil rhinoceroses from the Shivalik Hills that have been considered relevant to the placement of *Rhinoceros sinhaleyus* (Deraniyagala, 1958; Groves and Leslie, 2011; Sumanarathna et al., 2021). These sources informed conservative modifications to the *Ceratotherium simum* base model, including adjustment of head shape, lip form, horn proportions, skin fold development, body build, and overall scale. In particular, the reconstruction avoids reproducing the broad-muzzled, strongly grazing-adapted cranial profile characteristic of *Ceratotherium simum*. Instead, the preserved dentition and mandibular material of *Rhinoceros sinhaleyus* are more consistent with feeding on softer vegetation and were therefore taken to support a less robust cranial construction.

Because no complete limb bones or diagnostic cranial remains are presently known for *Rhinoceros sinhaleyus*, body size and body proportions could not be reconstructed directly from Sri Lankan postcranial measurements. Deraniyagala's description of the species as "somewhat smaller than the living *R. unicornis*" (1958, p. 116), together with its brachyodont, relatively square molars and inferred affinities with smaller or less heavily built Asian Rhinoceros taxa, was therefore used to support a conservative reduction in overall scale relative to *Rhinoceros unicornis* rather than a precise osteometric estimate. The resulting model should accordingly be understood as an evidence-constrained comparative reconstruction: grounded in the known Sri Lankan fossil material but necessarily extended through reference to extant and closely related fossil rhinoceroses where direct evidence is absent.

Production Pipeline

The reconstruction workflow followed a conventional visual effects (VFX) production pipeline comprising reference development, three-dimensional modelling, surface and material definition, deformation through rigging, and final lighting, rendering, and compositing. In this context, these terms refer to the following:

- Modelling: the construction of a digital geometric representation of form.
- Surface and material definition: the specification of properties such as colour, reflectance, and roughness.
- Rigging: the creation of an internal control structure that allows posing while preserving underlying morphology.
- Rendering and compositing: the generation and assembly of images under controlled illumination.

This pipeline aligns with established VFX and digital creature-development practice (Okun and Zwerman, 2020), with minor modifications to accommodate iterative scientific consultation and the production of high-resolution static imagery rather than animated sequences (Figure 1). Because the workflow relied primarily on commercial production tools developed for professional use rather than academic publication, support for some technical procedures is drawn from industry-standard references and software documentation in addition to scholarly sources. For each species visualised in this research, one or more structured discussions were conducted via videoconferencing to ensure shared understanding between scientific and artistic contributors regarding anatomical constraints, evidentiary limits, and visual priorities. These consultations were integrated at key points within the pipeline to allow scientific feedback to inform modelling and surface development before downstream stages introduced additional technical or aesthetic inertia.

These ideas were formalised through the creation of orthographic drawings (Figure 2) depicting each species from multiple viewpoints conducive to 3D modelling (i.e., anterior, posterior, lateral, and dorsal). These drawings functioned as image planes within the modelling environment, providing a consistent spatial framework against which major morphological features could be aligned and evaluated across views.

3D modelling. The model of *Rhinoceros sinhaleyus* was developed by modifying a 3D model of *Ceratotherium simum*, while *Palaeoloxodon nama-*

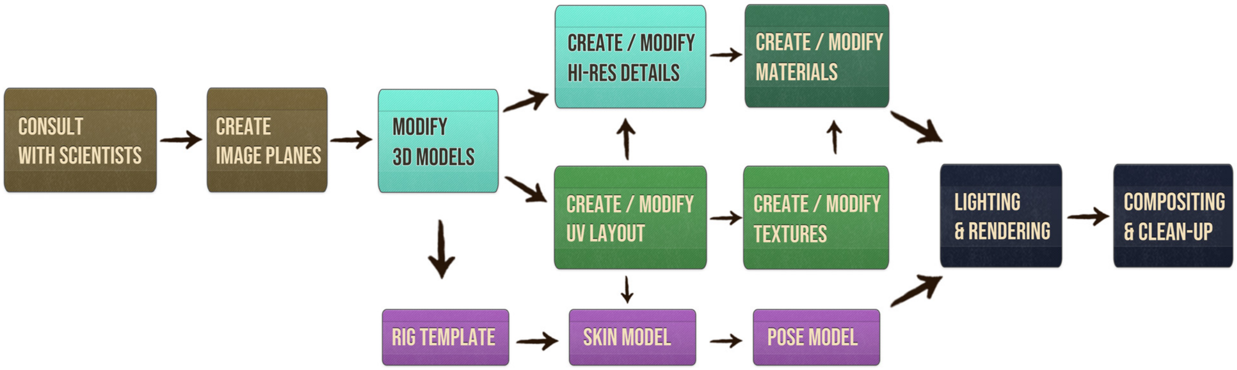

FIGURE 1. Production pipeline used throughout this project.

dicus sinhaleyus was constructed from a model of *Elephas maximus* (Figure 3). In both cases, the modelling process involved systematic adjustment of proportions, volumetric relationships, and anatomical features to align the base meshes of each extant species with the known or inferred morphology of the corresponding extinct taxon. These modifications were informed by comparative anatomical reference and iterative scientific feedback.

Most modelling was undertaken in Maxon ZBrush for high-resolution digital sculpting, with Autodesk Maya used for structural refinement and integration into the broader production pipeline. This combination supported detailed anatomical modification while preserving compatibility with downstream processes, including rigging, lighting, and rendering. The use of digital sculpting in this context was not merely technical, but methodological: it enabled iterative modification of form in response to anatomical evidence and specialist review while maintaining continuity across the same underlying asset.

Materials and texturing. Establishing visual realism in a 3D reconstruction extends beyond accurate form, proportion, and surface detail to include the definition of materials assigned to different anatomical regions, such as skin, eyes, oral tissues, and hooves or toenails. Each material incorporates a shader that governs how light interacts with the surface, controlling properties such as colour, reflectance, roughness, and subsurface response. These properties are typically modulated using texture maps, which provide spatially variable control across the model's surface (Okun and Zwerman, 2020).

To enable texture mapping, the three-dimensional (X-Y-Z) surface of each model is projected into two-dimensional (U-V) space. For complex organic forms, this process commonly involves dividing the model into multiple sections that can be flattened with minimal distortion. These sections may be distributed across multiple UV tiles to increase effective texture resolution and preserve fine-scale surface detail in the rendered result (Okun and Zwerman, 2020). Figure 4 depicts the UV layout for *Palaeoloxodon namadicus sinhaleyus*, and Figure 5 depicts the UV layout for *Rhinoceros sinhaleyus*. Although the stock models used in this project included pre-existing UV layouts, subsequent morphological modification necessitated UV adjustment to ensure that image-based textures remained aligned with their intended anatomical locations on the revised geometry.

All stock models included a set of texture files describing the surface appearance of the animal's integument. These encoded multiple visual attributes, including base colour ("albedo" and "diffuse" maps), surface micro-variations affecting light reflection ("roughness" maps), and fine-scale surface relief visible at render time ("normal" and "displacement" maps), among others (Figure 6). Most stock textures were retained with minor modification to accommodate changes in underlying geometry. Where existing textures were insufficient, new textures were generated using Adobe Substance Painter and Maxon ZBrush through the projection of high-resolution photographic reference of the corresponding extant species' skin onto the modified 3D models (Figure 7). This step was important not only for visual finish, but for preserving biologically plausible variation across the skin surface rather than relying on uniform or procedurally generic texture treatment, consistent with comparable palaeontological visualisation workflows (Gu et al., 2025).

Rigging. A further critical stage in the pipeline involved enabling the models to be posed through

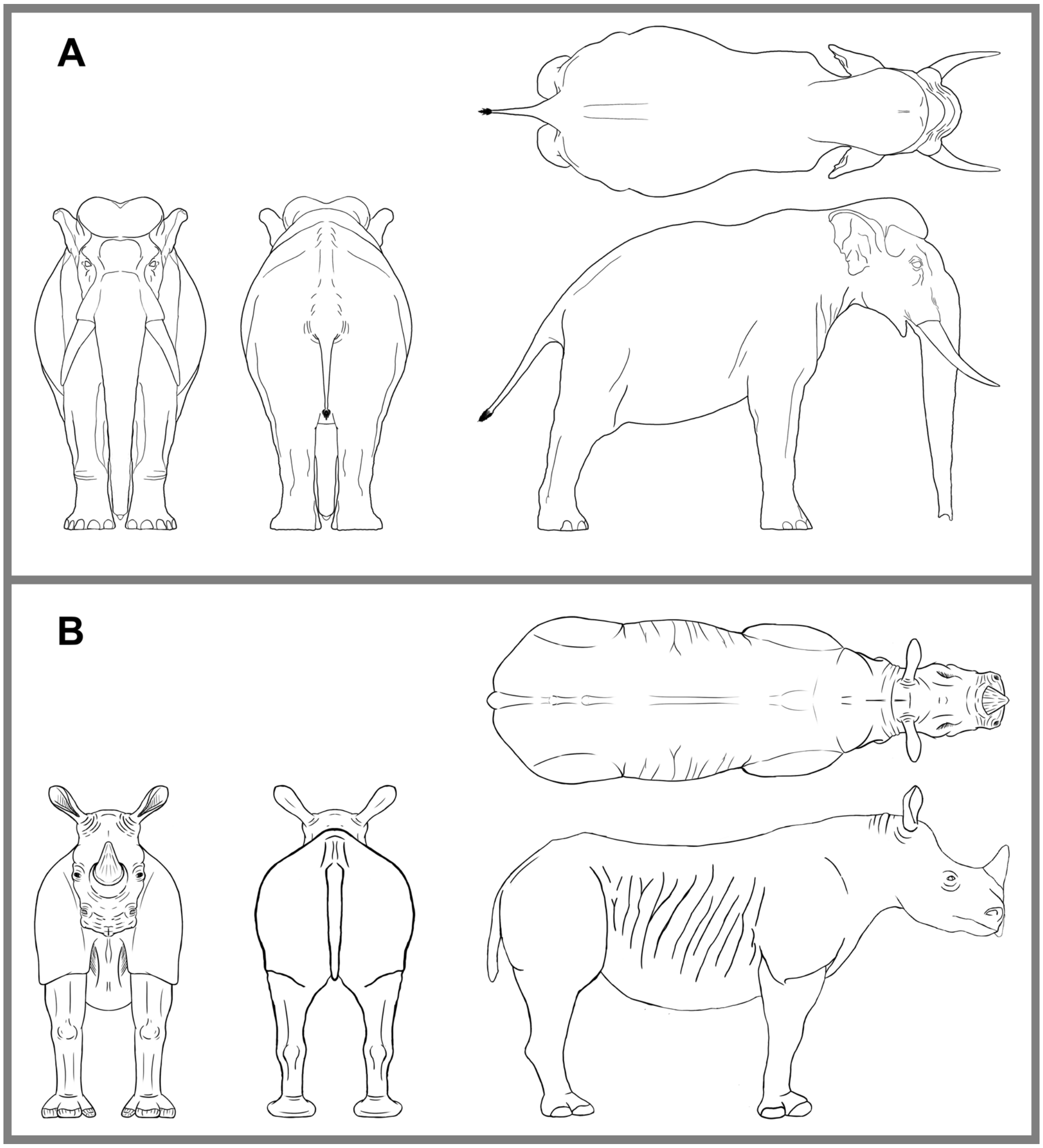

FIGURE 2. Anterior, posterior, lateral, and dorsal image planes as initial modelling reference for: A, *Palaeoloxodon namadicus sinhaleyus*; and B, *Rhinoceros sinhaleyus*.

the creation of an animation rig. A rig comprises a system of joints and a hierarchical set of animation controls that allow a 3D artist to manipulate the model while deform its underlying geometry in a predictable manner. In the present context, rigging was necessary not for character animation as an end in itself but for testing and selecting anatomically credible poses prior to rendering. Deformation quality therefore had a direct bearing on the believability of the final reconstruction.

Because none of the artists collaborating on this project were specialist riggers, an automated modular rigging workflow was used to create the foundational quadrupedal rigs (Roy, 2014). In this case, the workflow was implemented through Rapid Rig: Modular 2, a third-party automated rigging system for Autodesk Maya (Nelson, 2016). These rigs were then customised for each species to accommodate differences in proportion and articulation (Figure 8A-B). Following rig generation, each rig was bound to the surface geometry through a skinning process. Each mesh, composed of thousands of vertices arranged primarily into quadrilateral faces (Figures 4A and 5A), was assigned weighted influence values linking each vertex to one or more joints within its corresponding rig (Figure 9). Effective skinning ensured that movement and deformation occurred smoothly and

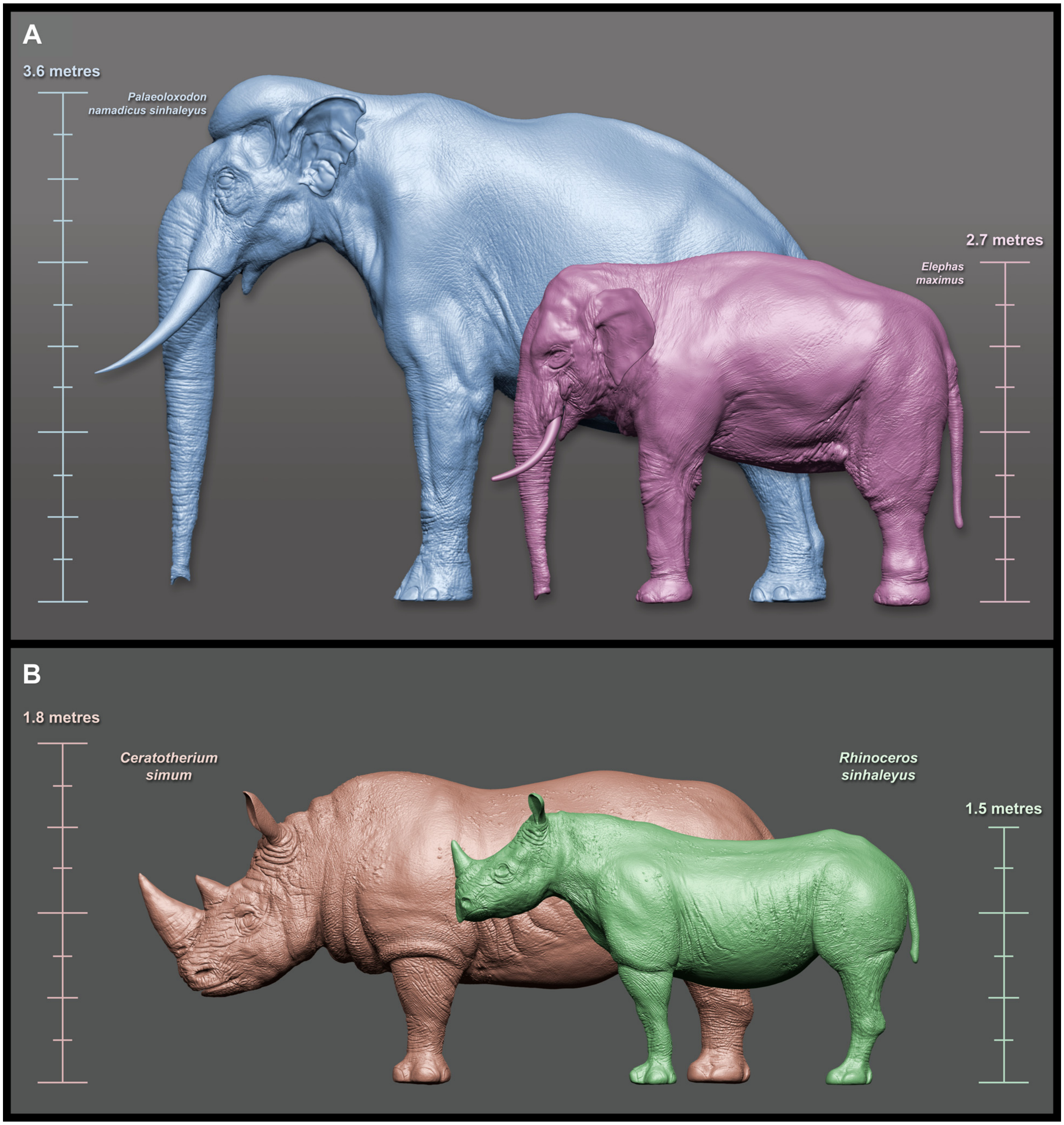

FIGURE 3. Comparison between original stock 3D models and revised digital sculptures developed in this study. A, *Palaeoloxodon namadicus sinhaleyus* (blue) derived from the model of *Elephas maximus* (pink); B, *Rhinoceros sinhaleyus* (green) derived from the model of *Ceratotherium simum* (orange).

plausibly across the model (Kennedy, 2021), allowing the animals to be posed in anatomically credible configurations.

Posing within the environment. Once a 3D asset has been fully modelled, textured, and rigged, it can be posed. In a moving-image context, this would involve a sequence of poses to generate animation; however, in the present project, a single pose was required for each final image.

A central aim of this research was the believable integration of each reconstructed species into a photographic environment representing the type of habitat in which the taxon is inferred to have lived. To support this integration, photographic references depicting closely related extant species in

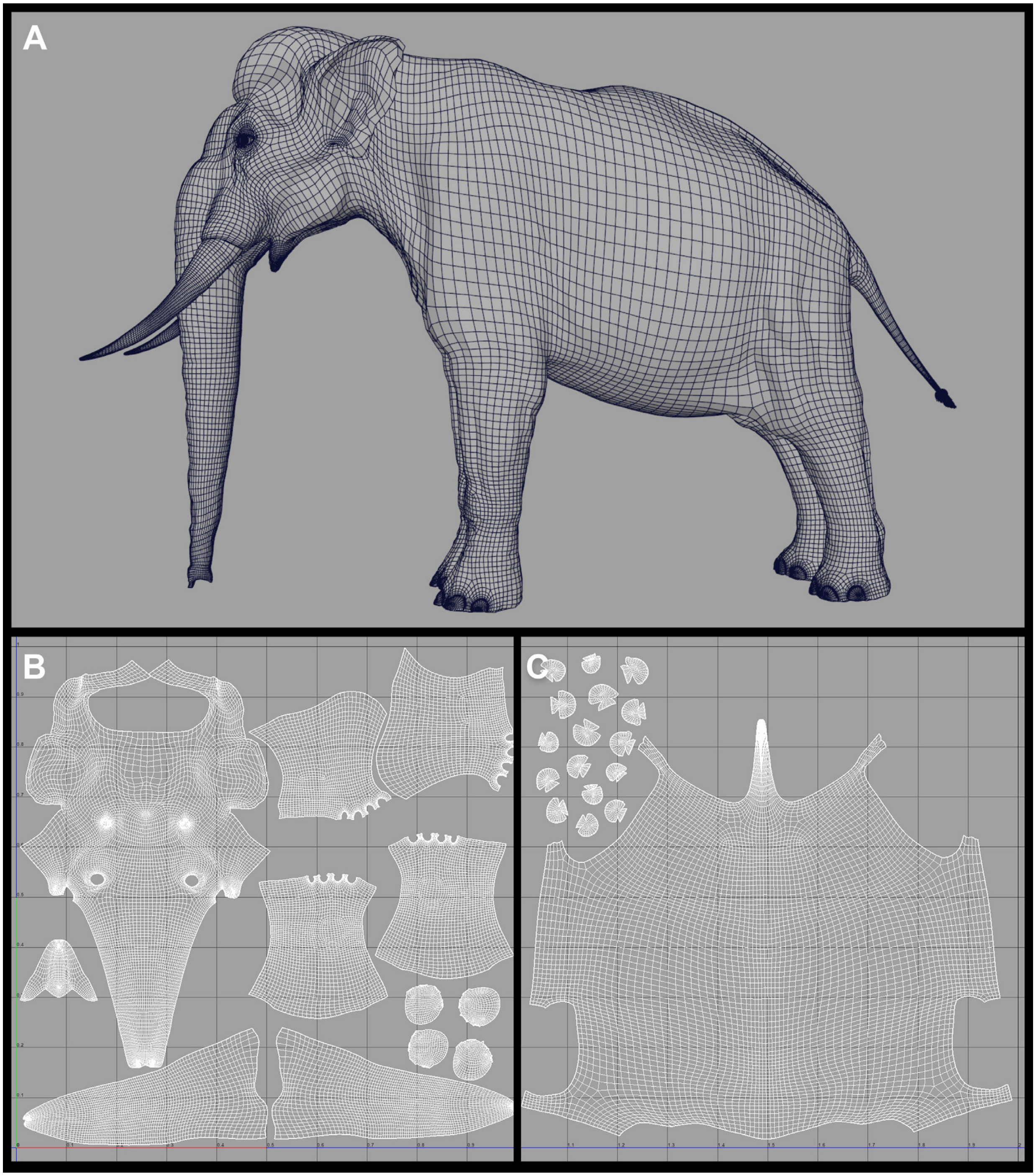

FIGURE 4. A, low-resolution model of *Palaeoloxodon namadicus sinhaleyus* represented in 3D (X-Y-Z) space. B, UV layout of the *P. namadicus sinhaleyus* model projected in 2D (U-V) space corresponding with the head, trunk, legs, tusks, footpads, and oral cavity. C, 2D-projected UV layout of *P. namadicus sinhaleyus* corresponding with the main torso, tail, and toenails.

ecologically analogous settings were selected. These images provided reference for plausible body posture, lighting conditions, and surface reflectance.

For *Rhinoceros sinhaleyus*, a photograph of *Rhinoceros unicornis* taken in Kaziranga National Park by Diganta Talukdar (2017) was used as a primary pose and lighting reference (Figure 10). The wet grassland setting is broadly analogous to

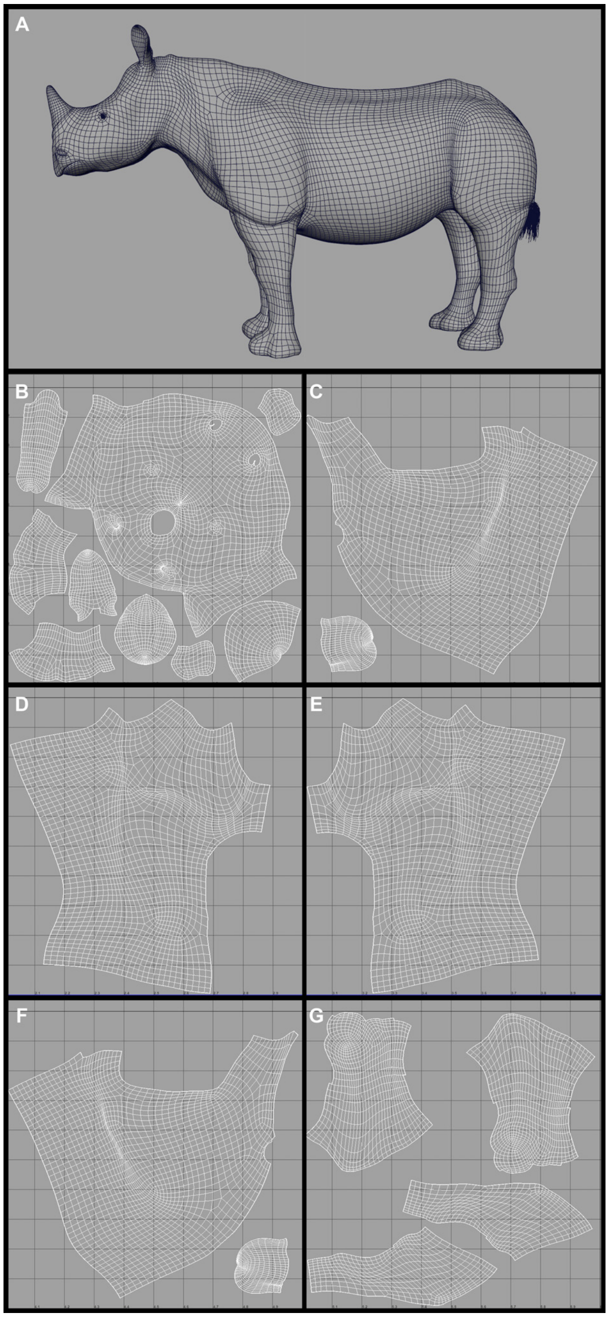

FIGURE 5. A, low-resolution model of *Rhinoceros sinhaleyus* represented in 3D (X-Y-Z) space. B, UV layout of the *R. sinhaleyus* model projected in 2D (U-V) space corresponding with the head, oral cavity, and front feet. C & F, UV layout for the posterior body, upper hind legs, and ear (left and right sides, respectively). D & E, UV layout for the anterior body and upper forelegs (left and right sides, respectively). G, UV layout for the lower hind legs and neck.

floodplain environments of the Sabaragamuwa Basin. The image depicts *Rhinoceros unicornis* in a dynamic stance with two small birds perched on its back. This pose was selected because it produced a clear silhouette that emphasised distinguishing morphological features relevant to *R. sinhaleyus*, particularly its proportionally longer limb structure. The inclusion of birds was retained in the final composition because it enhanced environmental integration without introducing additional speculative anatomical detail.

Because the creative team was based in New Zealand throughout production, direct photographic documentation of Sri Lankan environments was not feasible. Instead, licences were obtained for a range of royalty-free stock photographs, including the image of *Rhinoceros unicornis* shown in Figure 9. In each case, the reference animal was digitally removed and its pixels replaced with surrounding image data to produce a clean background plate suitable for compositing. These extractions were performed through digital inpainting and image repair techniques in Adobe Photoshop. The resulting plates preserved lighting, colour balance, and environmental texture consistent with the original photographs, enabling the seamless integration of rendered 3D assets.

Lighting, rendering, and compositing. An important factor in believably integrating a 3D creature into a photographed environment is the replication of the scene's lighting conditions. In VFX practice this is commonly achieved using high dynamic range (HDR) imaging, which retains a broader range of luminance values than standard photography. HDR capture typically involves photographing a chrome sphere from a fixed position using multiple exposure values, which are then combined to produce a single HDR image suitable for image-based lighting (Okun and Zwerman, 2020).

When imported into 3D software such as Autodesk Maya, an HDR image functions as a spherical image-based lighting source, allowing the digital scene to be illuminated using light data derived from the photographed environment. This enables the direction, colour, and relative intensity of incoming light to be reproduced across the full sphere surrounding the model, providing a coherent lighting context for rendering prior to compositing.

Creating a location-specific HDR image requires on-site capture under the same lighting conditions as the photographed scene. Because the creative team was not physically present in Sri

FIGURE 6. Example texture maps applied to the *Palaeoloxodon namadicus sinhaleyus* model and spread across UV tiles. The diffuse colour map for: A, head, trunk, legs, tusks, footpads, and oral cavity; and B, torso, tail, and toenails. Roughness map for: C, head, trunk, legs, tusks, footpads, and oral cavity; and D, torso, tail, and toenails.

Lanka during this research, it was not possible to generate HDR images directly from the target environments. This geographic displacement is the same constraint that necessitated the use of licensed stock photography for background plates. As HDR lighting information cannot be recovered from standard single-exposure photographs, alternative sources of environmental lighting were required.

To address this limitation, third-party HDR image libraries commonly used in visual effects production were consulted. Platforms such as PolyHaven provide high-quality HDR images suitable for approximating real-world lighting conditions. Multiple HDR images were tested for each scene to identify the closest match to the photographic backdrop, with particular attention to overall light intensity, dominant directionality, colour temperature, and atmospheric diffusion caused by cloud cover or haze, all of which influence shadow softness and contrast. An HDR image taken at Klötzle Blei, Germany by Andreas Mischok (2020)

FIGURE 7. Diffuse colour maps applied to the *Rhinoceros sinhaleyus* model and spread across the six UV tiles described in Figure 5.

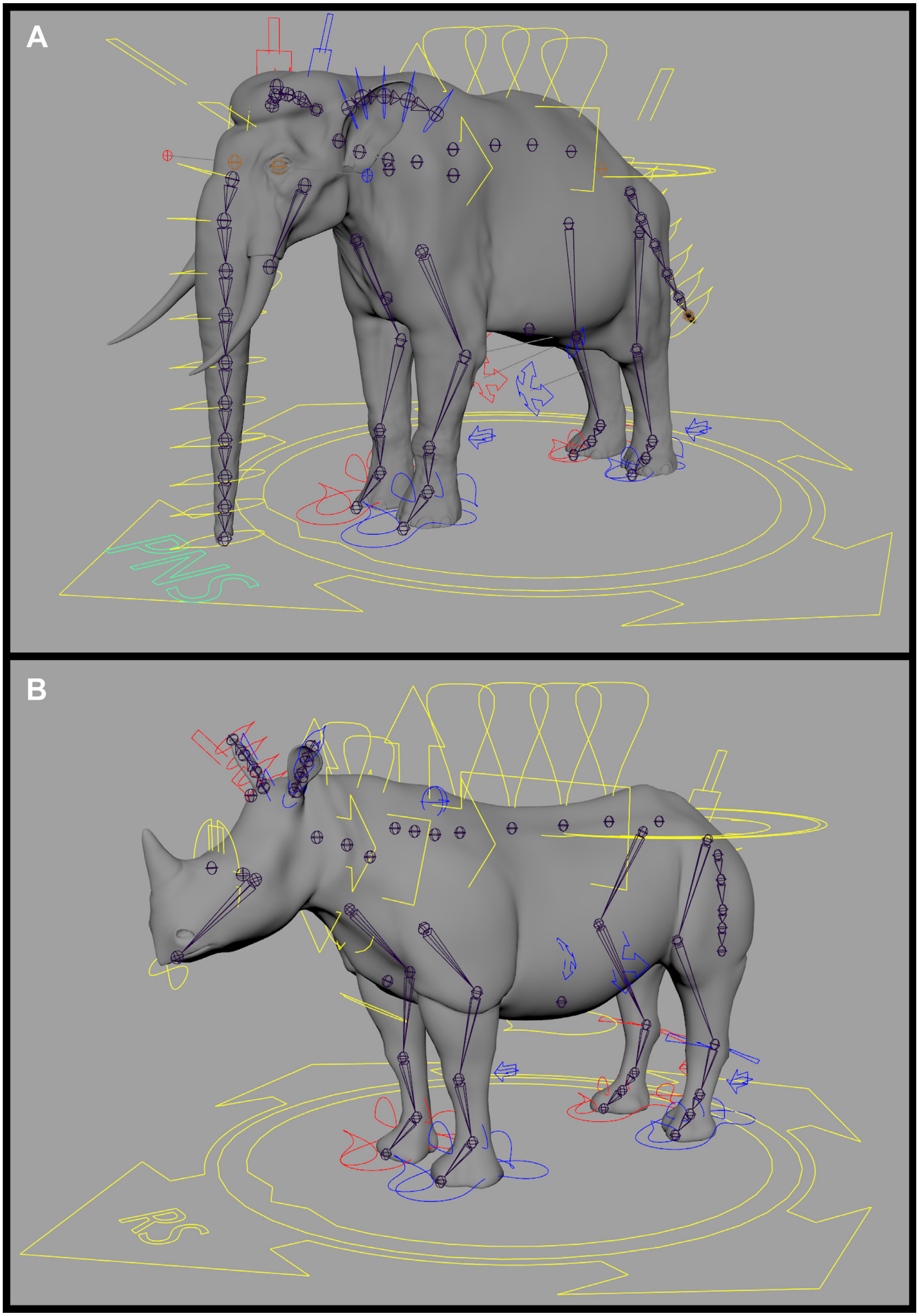

FIGURE 8. A, the joint-based rig with animation controls for *Palaeoloxodon namadicus sinhaleyus*; B, the rig for *Rhinoceros sinhaleyus.*

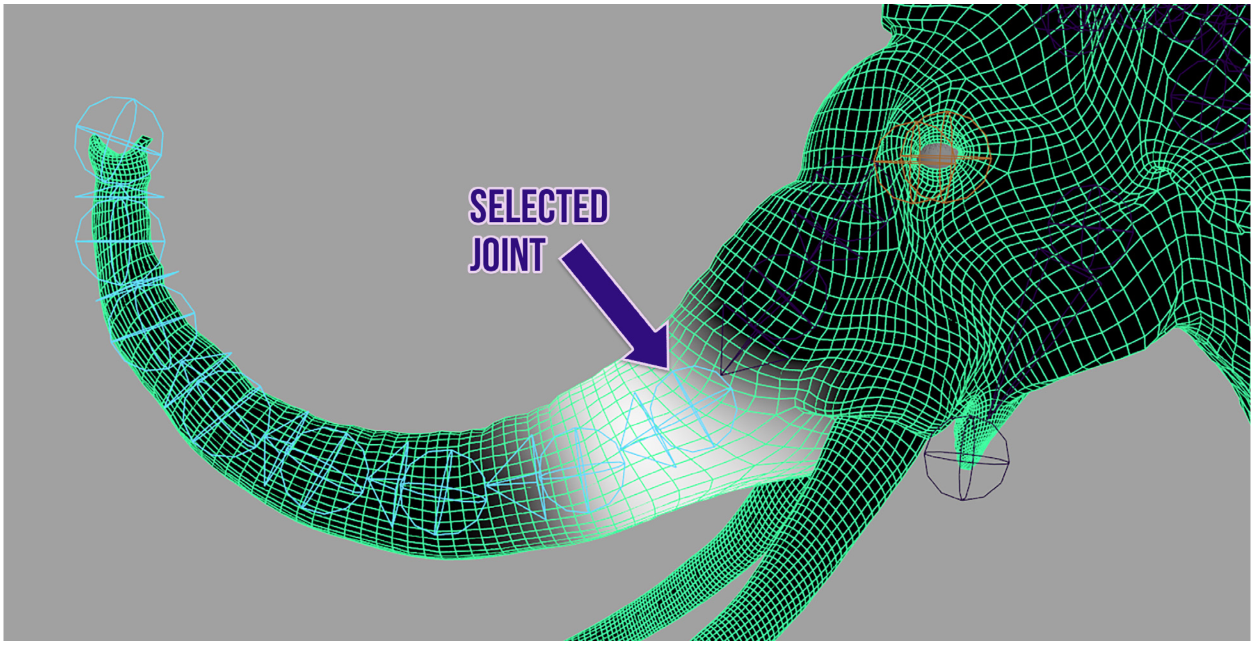

FIGURE 9. Skinning the joint-based rig to the 3D model. In this image, the influence of the selected joint on the surrounding geometry is represented in greyscale, ranging from black (0% influence) to white (100% influence), with proportional gradations in between. Individual vertices are located at the intersections of the green edge lines on the model's surface.

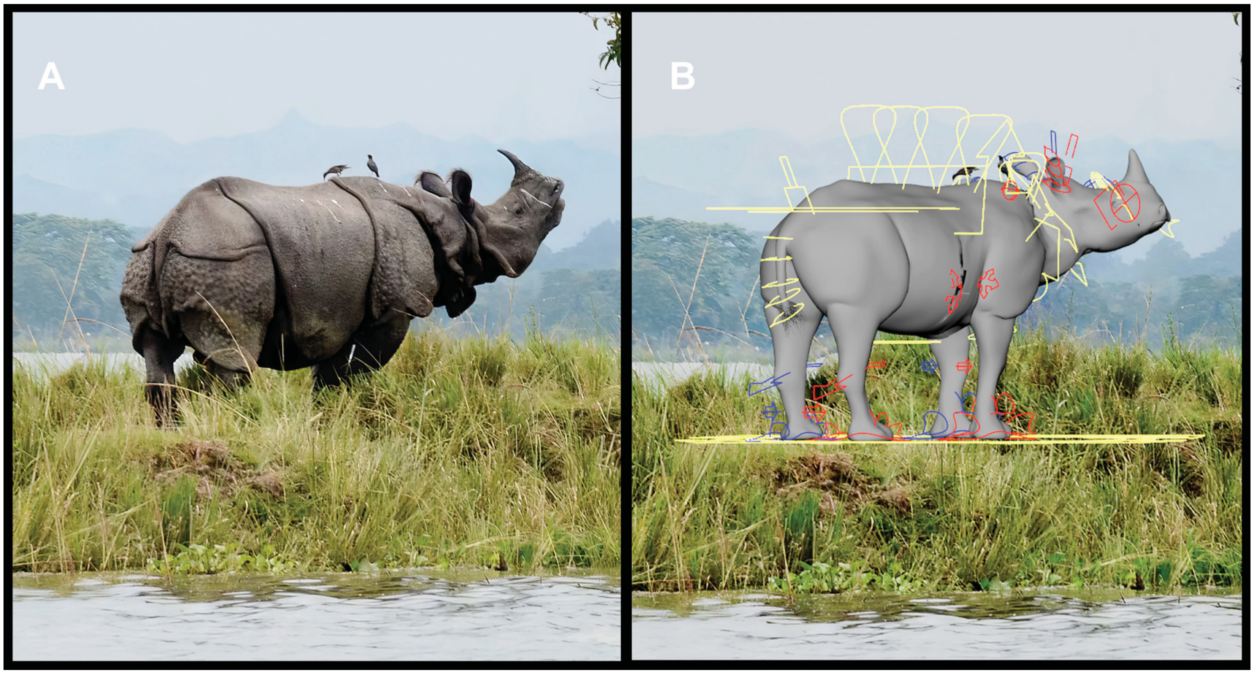

FIGURE 10. Side-by-side comparison with the original reference photograph. A, *Rhinoceros unicornis*; B, the posed 3D reconstruction of *Rhinoceros sinhaleyus* composited into the same image after digitally removing *R. unicornis*. The scene simulates a palaeoenvironment analogous to the Sabaragamuwa Basin during the Late Pleistocene, incorporating landscape elements associated with Adam's Peak and the Kuruwita region, Sri Lanka (often locally referred to as "Paradise"). Original photograph: Diganta Talukdar, "Beauty of Kaziranga National Park" (2017), Wikimedia Commons, licensed under CC BY-SA 4.0.

FIGURE 11. A, high dynamic range (HDR) image used as the baseline source of environmental illumination for the scene featuring *Rhinoceros sinhaleyus*. The rectangular HDR image is mapped onto a spherical dome encompassing the 3D scene, from which illumination is cast onto all scene assets. Although the HDR was photographed at Klötzle Blei, Germany, rather than within a floodplain environment, it was selected because its overcast sky produced a pattern of diffuse illumination closely matching the lighting conditions visible in the source photograph. B, the HDR image was used solely for lighting information and does not appear in the final rendered background. C, additional directional and fill illumination was provided using digital light sources within the scene (white rectangles). HDR image: Andreas Mischok, “Kloetzle Blei” (2020), PolyHaven, licensed under CC0.

was used in the *Rhinoceros sinhaleyus* composition (Figure 11).

In practice, HDR images alone rarely provide complete or sufficiently directed illumination for a 3D scene, particularly when they are not captured under the same conditions as a reference photograph (Figure 11B). Consequently, additional virtual light sources were introduced to refine the lighting so that the rendered model more closely matched the observed pattern of illumination in the photographic plate. These lights were used to reproduce key lighting cues present in the source image, including dominant light direction, relative shadow placement, and highlight falloff across the animal’s form (Figure 11C). Rather than overriding the HDR-based environmental illumination, these supplementary lights were applied selectively to reconcile discrepancies between generic HDR lighting and the specific lighting conditions visible in the photograph.

Rendering refers to the process of converting the assembled 3D scene into a bitmap image incorporating geometry, materials, textures, and lighting. For this project, rendering was performed using the Arnold renderer within Autodesk Maya. Producing a believable result required iterative adjustment of rendering parameters through testing and refinement. Although the final image appears singular, the scene was rendered as multiple discrete passes representing different visual components. These passes were subsequently recombined during compositing, providing fine-grained control over the final image and allowing targeted adjustments without re-rendering the entire scene (Okun and Zwerman, 2020).

In this project, the rendered image was divided into a series of discrete render passes, each containing a specific arbitrary output variable (AOV), including diffuse colour, subsurface scattering colour, specular colour, and ambient occlusion. The background photograph was retained as a separate image. These passes were recombined in Adobe After Effects to reconstruct the final image, allowing localised adjustment of individual visual components without re-rendering the entire scene. A cryptomatte pass was also generated to enable precise isolation of specific regions of the render, such as the main body, eyes, and hair (Figure 12). The solid colour identifiers within the cryptomatte were converted into selection masks in After Effects and used to target adjustments during compositing.

Following compositing, the resulting image was refined in Adobe Photoshop to finalise integration between the rendered asset and the photographic background. For the *Rhinoceros sinhaleyus* scene, this included painting foreground vegetation over portions of the feet to restore correct depth relationships, as well as applying targeted colour correction to improve coherence between the rendered lighting and the photographic plate (Figure 13). These adjustments are representative of the finishing processes applied across all images produced in this research.

SPECIES ACCOUNTS

Throughout the Pleistocene, fluctuating sea levels periodically exposed a land bridge across the Palk Strait, linking northern Sri Lanka with the southern tip of the Indian peninsula (Figure 14). This connection facilitated the movement of terrestrial fauna between the two regions (Chauhan,

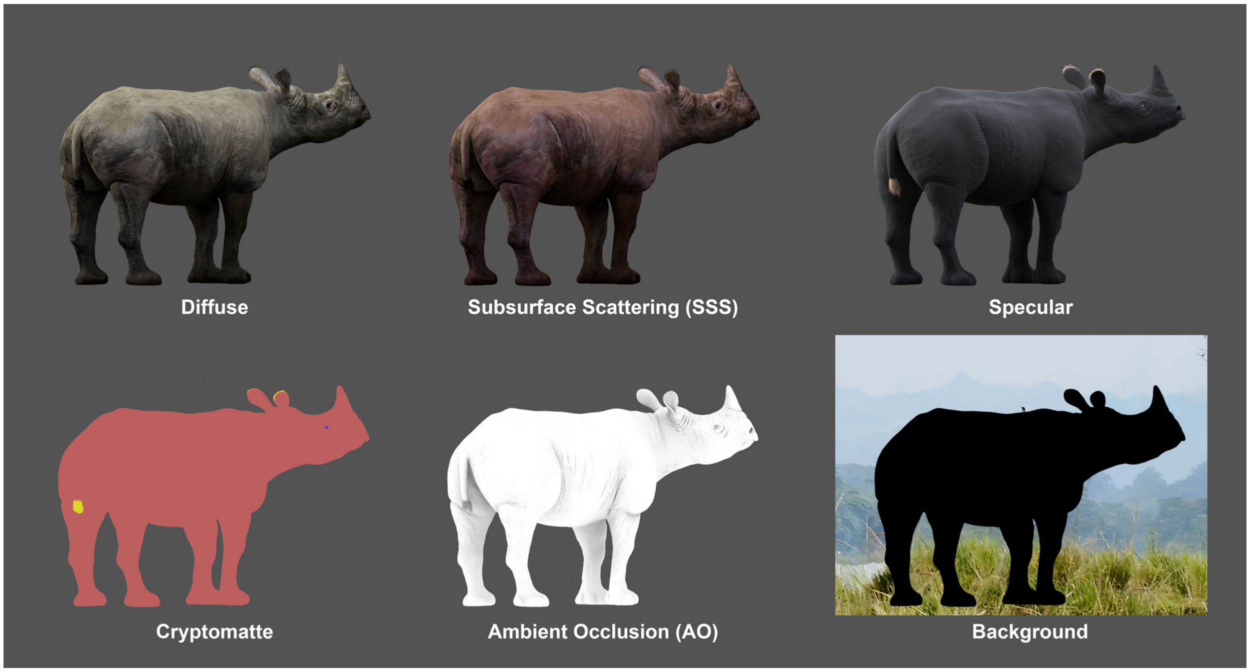

FIGURE 12. The render of *Rhinoceros sinhaleyus* separated into various arbitrary output variables (AOVs).

FIGURE 13. A, the background photographic plate; B, the reconstructed render of *Rhinoceros sinhaleyus* created by compositing individual render passes (AOVs) over the background plate; C, the final integrated image following colour correction and foreground paint work, including grass elements painted over the feet to restore depth relationships.

2007). Within Sri Lanka, the Sabaragamuwa Basin has yielded the greatest concentration of fossil remains from the island's extinct Quaternary megafauna (Sumanarathna et al., 2021). The species discussed in this article were recovered primarily from the vicinity of Ratnapura and are collectively referred to as the "Ratnapura Fauna".

These fossils occur within the gem-bearing gravels of the Ratnapura Beds. Deraniyagala (1958) noted extensive redeposition of these gravels had disrupted their original stratigraphic context, making it difficult to establish reliable chronological frameworks. Building on this issue, Deraniyagala (1988) proposed that, if redeposition had not substantially altered the original stratigraphic relationships, *Palaeoloxodon namadicus sinhaleyus* and *Rhinoceros sinhaleyus* were likely contemporaneous. It was emphasised, however, that resolving this question would require detailed and systematic chronological investigation of the Ratnapura Beds (Chauhan, 2007).

Despite these uncertainties, multiple lines of evidence indicate that past ecological conditions within the Sabaragamuwa Basin were broadly comparable to those of the present day. Palaeoenvironmental data suggest a heterogeneous landscape comprising forested uplands, savannah, and extensive freshwater systems (Roberts et al., 2015; Sumanarathna et al., 2016).

Below, we present rendered reconstructions of two extinct taxa examined in this study – *Palaeoloxodon namadicus sinhaleyus* and *Rhinoceros sinhaleyus*. Each reconstruction is accompanied by a discussion of the scientific and aesthetic considerations informing its development. These discussions address external morphology (appearance) as well as inferred aspects of environment and behaviour where relevant. Given the fragmentary nature of the fossil record for both species, the reconstructions necessarily involve degrees of informed speculation; however, all interpretive decisions are grounded in available evidence and supported by comparative data from closely related taxa.

Sri Lankan Straight-Tusked Elephant

Order: PROBOSCIDEA Illiger, 1811
Family: ELEPHANTIDAE Gray, 1821
Genus: PALAEOLOXODON Matsumoto, 1924
Species: *Palaeoloxodon namadicus* (Falconer and Cautley, 1846)
Subspecies: *Palaeoloxodon namadicus sinhaleyus*

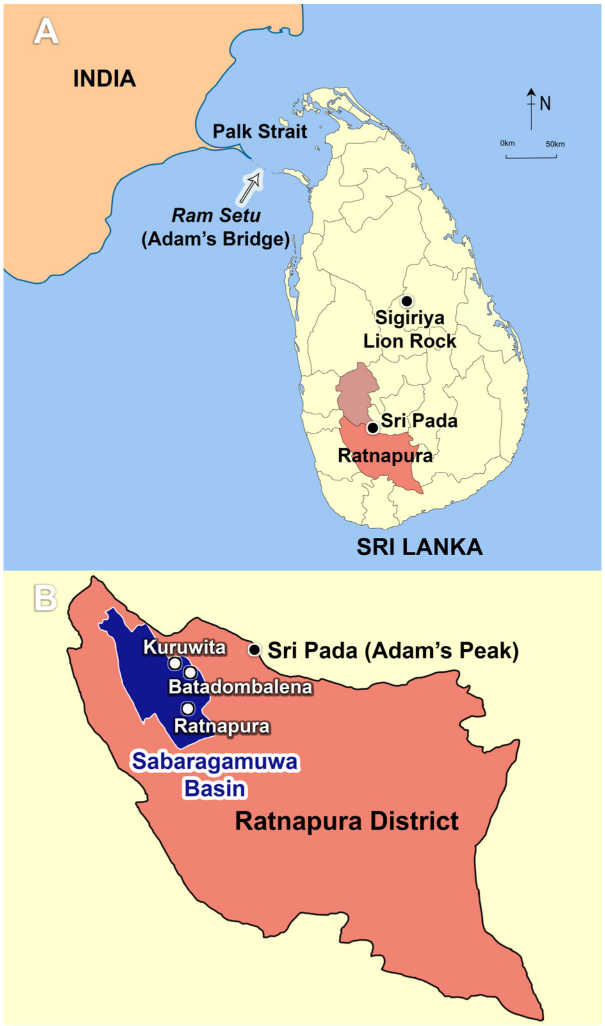

FIGURE 14. Map of Sri Lanka showing the Palk Strait and the submerged limestone shoals known as Ram Setu (Adam's Bridge). The Sabaragamuwa Province comprises two districts (highlighted in red), including the Ratnapura District in the south, within which the Sabaragamuwa Basin is located (highlighted in dark blue). Base map of Sri Lanka adapted from "Sri Lanka Sabaragamuwa locator map.svg" by Jeroen (2007), Wikimedia Commons, licensed under CC BY-SA 2.5. Modifications by the authors include the addition of the neighbouring Indian coastline, labelling of Sri Lankan provinces and key localities, and colour changes to distinguish between the Sabaragamuwa Province and Ratnapura District.

(Deraniyagala, 1944)
(Figure 15)

Appearance. *Palaeoloxodon* is a genus of extinct straight-tusked elephants that dispersed from Africa to Europe and across Asia by the Middle Pleistocene (MPT: 780-129 ka). Although the genus is represented by a substantial fossil record, the number of distinct species it comprises remains unresolved. *Palaeoloxodon namadicus* is well documented within the Indian subcontinent, with cranial material recovered from sites including Hathnora and Narmadapuram (Madhya Pradesh), Nandur Madhmeshwar (Maharashtra), and the broader Narmada Valley region (Larramendi et al., 2020).

Evidence for *Palaeoloxodon namadicus* in Sri Lanka was reported by Deraniyagala (1955), who proposed that isolated molars recovered from gem pits in Kuruwita were sufficiently distinct to justify designation as the subspecies *Palaeoloxodon namadicus sinhaleyus*. This distinction was based solely on dental material that he described as smaller than that of the *forma typica*. Deraniyagala (1958) further noted that these remains were associated with hippopotamus fossils uranium-dated to the Upper Pleistocene (11.7–129 ka). More recent radiocarbon dates from the Narmada and Son Valleys indicate that *P. namadicus* persisted until approximately 20-32 ka, extending well into the late Pleistocene megafaunal extinction interval (Turvey et al., 2021). In the absence of contradictory evidence, it is therefore plausible that a Sri Lankan population, if taxonomically distinct, may have survived into a similar period and become extinct no earlier than c. 20 ka.

Owing to the absence of a complete skeleton, estimates of body size for *Palaeoloxodon namadicus* are necessarily uncertain and vary depending on the skeletal elements used for extrapolation. Larramendi (2016) reports individual fossil measurements that imply shoulder heights ranging from approximately 400 to 450 cm. Deraniyagala (1958) inferred a smaller overall stature for *P. namadicus sinhaleyus* based on reduced molar size; however, this inference remains speculative. Dental size alone can vary due to multiple factors, including individual variation, ontogeny, and sexual dimorphism, and no additional anatomical evidence was provided to support subspecific differentiation. Compounding this limitation, the fossils referenced by Deraniyagala (1955; 1958) have since been lost, precluding reanalysis using contemporary comparative methods.

One of the most distinctive features of the subfamily Palaeoloxodontinae is the parieto-occipital crest (POC), a cranial apomorphy that is characterised by an "anterior projection of the skull roof that is formed by the forward bending and subsequent overhang of the occipital surface" (Larramendi et al., 2020, p. 2). Among palaeoloxodont taxa, this feature is most strongly developed in

FIGURE 15. Three-dimensional reconstruction of an extinct male Sri Lankan straight-tusked elephant (*Palaeoloxodon namadicus sinhaleyus*) wading through shallow wetland terrain. The scene uses the environment of Sigiriya Lion Rock as an ecological analogue and depicts *P. namadicus sinhaleyus* at an estimated shoulder height of 360 cm for comparative scale. Background plate: stock photograph by Paul Prescott (2014).

Palaeoloxodon namadicus, extending anteriorly from near the external nasal aperture and overhanging much of the frons (Larramendi et al., 2020). Deraniyagala (1955, Plate 13) illustrated the POC of *P. namadicus sinhaleyus* using broad strokes rather than fine anatomical details. As depicted, the crest may be read as either an exposed bony structure or one covered by limited soft tissue. While Deraniyagala (1955) described the morphology of the POC, he did not propose a functional explanation. This is relevant primarily as historical context, because earlier interpretations of palaeoloxodont species (Osborn, 1931) treated the crest chiefly as a conspicuous cranial feature, whereas more recent work (Larramendi et al., 2020) has instead emphasised its biomechanical significance as a site of muscular attachment and head support. The reconstruction presented here, however, did not derive the dimensions or form of the crest from Deraniyagala's figure, but from recent comparative research on Palaeoloxodon cranial morphology, as discussed below.

Following more recent fossil discoveries, Larramendi et al. (2017) proposed that the POC served a functional role as an attachment area for enlarged dorsal neck musculature in palaeoloxodont species. As individuals matured, the POC may have provided increased leverage to counterbalance the growing anterior mass of the head and elongated tusks. Support for this interpretation comes from the notably broad occiput characteristic of *Palaeoloxodon*, and from well-defined intermuscular markings on the skull roof of *P. namadicus*. These markings are divided by a pronounced median channel along the nuchal surface, extending from the nuchal fossa to a mid-sagittal depression at the cranial vertex, a configuration interpreted as indicating the presence of paired splenius muscles (Larramendi et al., 2020). Taken together, these features provide strong anatomical support for interpreting the POC as a musculoskeletal adaptation associated with head and tusk support (Figure 16). However, functional demands alone do not fully account for the degree of intra-

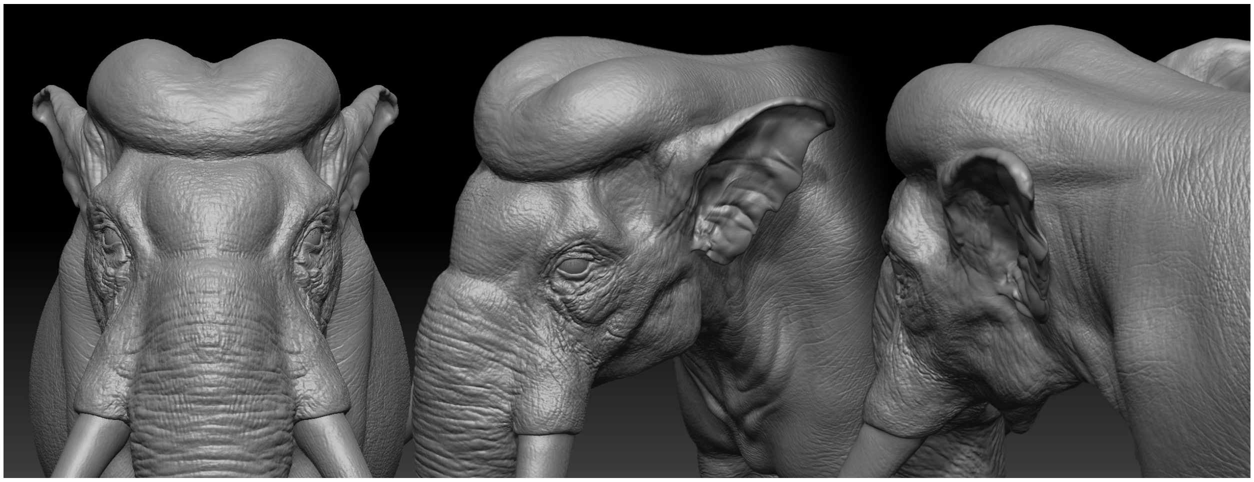

FIGURE 16. Close-up view of the parieto-occipital crest (POC) in the reconstruction of *Palaeoloxodon namadicus sinhaleyus* produced within this study. Following Larramendi et al. (2020), the crest is shown as the attachment site for enlarged dorsal neck musculature (including the splenius and supersplenius), contributing to structural support for the head and tusks in adult individuals.

specific variability observed in POC development (Larramendi et al., 2020).

This study incorporates the limited morphometric data derived from fossil material attributed to *Palaeoloxodon namadicus sinhaleyus* recovered from the Sabaragamuwa Basin, Sri Lanka (Sumanarathna et al., 2021), together with earlier published material described by Deraniyagala (1955; 1958). However, the Sri Lankan remains are extremely sparse and consist only of isolated dental material, providing support primarily for taxonomic attribution and the plausibility of reduced body size rather than for detailed cranial or postcranial reconstruction. Accordingly, anatomical reconstruction was informed chiefly by established morphological characteristics of mainland *P. namadicus* and by comparative osteological and functional studies of *Palaeoloxodon antiquus*. Soft-tissue reconstruction followed an extant phylogenetic bracketing approach, using osteological correlates as primary indicators of muscle origin and insertion. Muscle placement and relative mass were inferred from features of the nuchal surface, intermuscular lines, and occipital breadth, drawing on comparative dorsal neck musculature reconstructions of *Palaeoloxodon antiquus* and *Elephas maximus* presented by Larramendi et al. (2017).

Recent studies suggest that *Palaeoloxodon namadicus* differed from *Palaeoloxodon antiquus* in possessing a more hypertrophied POC, consistent with a proportionally larger and heavier head and tusks (Larramendi, 2016; Larramendi et al., 2017; Larramendi et al., 2020). Although *P. namadicus* is described as taller and more gracile in overall body proportions than *P. antiquus*, it nonetheless appears to have supported a substantially more massive cranial structure (Larramendi, 2018). On this basis, *P. antiquus* – which is represented by more complete skeletal material, including articulated specimens from sites such as Neumark-Nord 1 (Larramendi et al., 2017) – provides a suitable anatomical proxy for reconstructing the fragmentary remains attributed to *P. namadicus sinhaleyus*.

For the purposes of soft-tissue reconstruction, the two species are treated as functionally analogous. Both occupied broadly similar ecological niches as temperate to semi-arid grazers or mixed feeders, and likely shared comparable muscular and integumentary adaptations (Larramendi et al., 2017; Sumanarathna et al., 2017). These characteristics were translated into volumetric form by extrapolating proportional relationships observed in extant elephants, with allowances made for increased dorsal neck musculature consistent with the enlarged POC. Additional soft tissues, including connective tissues and skin thickness, were estimated from comparative anatomical data on living elephants (Mikota, 2006; Marchant and Shoshani, 2007) and modified only where osteological correlates indicated specific mechanical or postural requirements. In practice, this chiefly involved conservative augmentation of the dorsal neck musculature and adjacent soft-tissue volume in areas where the nuchal surface, occipital breadth, and enlarged POC indicate increased demands associated with head and tusk support. The resulting external morphology therefore rep-

FIGURE 17. Three-dimensional reconstruction of an extinct male Sri Lankan straight-tusked elephant (*Palaeoloxodon namadicus sinhaleyus*) depicted within a landscape near the Batadombalena prehistoric cave site, used here as an environmental analogue. Original photograph: lexiks, "Elephant goes through jungle" (2013), iStock photo ID 177590574 (standard license).

resents a conservative synthesis of osteological evidence, extant analogues, and documented muscle-scar interpretations, rather than speculative embellishment (Figure 17). Variation in POC development among *Palaeoloxodon namadicus* individuals appears to be correlated with both age and sex, with the most pronounced crests observed in fully mature, M3-bearing males (Larramendi et al., 2020). The observed range of variation suggests a degree of sexual dimorphism, although current interpretations remain constrained by limited sample sizes. Assuming sexual dimorphism was present, two non-exclusive explanations have been proposed: first, that pronounced POC development functioned as a secondary sexual characteristic; and second, that increased prominence in adult males reflects allometric scaling associated with greater overall mass, particularly heavier and more robust tusks, relative to females (Larramendi et al., 2020).

Reconstruction. Fossil remains of *Palaeoloxodon namadicus* are less complete than those of the European straight-tusked elephant, *Palaeoloxodon antiquus*. As a result, the reconstruction of *P. namadicus sinhaleyus* necessarily draws on large-scale morphological characteristics established for *P. antiquus*, modified to reflect traits associated with South Asian populations.

Although the available fossil material is insufficient to definitively distinguish *Palaeoloxodon namadicus sinhaleyus* from the *forma typica*, this study accepts the plausibility of a geographically isolated Sri Lankan subspecies that was modestly smaller than its mainland counterparts, potentially as a result of incipient insular dwarfing (Baleka et al., 2021). Accordingly, *P. namadicus sinhaleyus* is depicted here as morphologically equivalent to *P. namadicus* but scaled to approximately 80% of the maximum shoulder height (360 cm) estimated for the largest mainland individuals (Larramendi, 2016).

This scaling choice is informed by Deraniyagala's (1955) original suggestion that the Sri Lankan population was of reduced stature, together with comparative dwarfing patterns documented for insular palaeoloxodont taxa. Baleka et al. (2021) quantified dwarfing rates in *Palaeoloxodon cf. mnaidriensis*, a descendant of *P. antiquus* from Sicily, identifying height reductions ranging from 0.15 to 41.49 mm per generation (assuming a 31-year generation time), and mass reductions between 0.79 and 200.95 kg per generation. These estimates reflect a wide range of possible evolutionary trajectories, contingent on colonisation timing and isolation duration, and ultimately indicate that the island form underwent an overall mass reduction of approximately 85% relative to the ancestral mainland form, leaving it at roughly 15% of the mainland ancestor's mass.

However, the ecological and biogeographic conditions governing dwarfing on Sicily differ substantially from those of Sri Lanka. Sri Lanka is approximately 65,610 km² in area – roughly 2.5 times larger than Sicily (25,711 km²) – and island size is generally correlated with greater resource availability and more complex ecological interactions (Faurby and Svenning, 2016). While no direct mathematical relationship exists between island area and dwarfing rate, smaller and more isolated islands tend to promote stronger ecological release and reduced predation pressure, accelerating body size reduction, whereas larger islands typically constrain these effects through sustained competition and predation (Faurby and Svenning, 2016; Sumanarathna et al., 2017).

During the Quaternary, Sri Lanka supported a suite of large predators, including *Panthera leo sinhaleyus*, *Crocodylus sinhaleyus*, and *Homo sapiens* (Sumanarathna, 2018; Sumanarathna et al., 2021). The continued presence of such predators would have limited ecological release and moderated selective pressures toward extreme dwarfism, in contrast to smaller islands such as Sicily, where comparable predators were absent Baleka et al. (2021).

Geological and bathymetric evidence further suggests that Sri Lanka experienced repeated periods of connectivity with the Indian mainland. The limestone shoals of Adam's Bridge (Ram Setu), spanning approximately 48 km, would have been partially or fully emergent during glacial sea-level regressions exceeding 3–10 m (Dandabathula et al., 2024; Sumanarathna, 2018). Multiple regressions greater than 10 m occurred between approximately 200 and 40 ka (Lambeck and Chappell, 2001), potentially enabling recurrent migration and gene flow in megafaunal populations such as *P. namadicus*. Fossils recovered from the Ratnapura gravels fall broadly within this temporal window (Deraniyagala, 1992).

Taken together, these factors support a hypothesis of moderate, rather than extreme, size reduction in *Palaeoloxodon namadicus sinhaleyus*. Conditions favouring limited dwarfing include prolonged but intermittent isolation, altered resource availability relative to mainland environments, partial ecological release constrained by predation, and periodic genetic exchange facilitated by land-bridge connectivity (Baleka et al., 2021). In contrast to the pronounced dwarfing observed in Sicilian palaeoloxodonts, the larger landmass of Sri Lanka, its predator regime, and the likelihood of repeated recolonisation events argue for a more conservative reduction in body size. On this basis, our scaling of *P. namadicus sinhaleyus* to approximately 80% of the maximum size of the *forma typica* represents a cautious and scientifically defensible reconstruction given current ecological, geological, and palaeontological evidence.

Integumentary traits are not preserved for *Palaeoloxodon* material from Sri Lanka; consequently, external appearance was reconstructed using nearest-living-relatives and functionally supported elephant skin models, while remaining conservative where phylogenetic and ecophenotypic signals are ambiguous. Skin texture follows the well-documented condition in extant elephants, in which the integument is strongly sculptured by wrinkles and crevices arranged in geometric patterns that retain water and slow dehydration, thereby supporting evaporative cooling during periodic wetting and wallowing (Lillywhite & Stein, 1987). Recent biomechanical and developmental studies further demonstrate that elephant skin wrinkling arises through an interaction of form and function rather than as a purely superficial feature, particularly along the trunk where wrinkle density and depth vary with mechanical use (Martins et al., 2018; Schulz et al., 2024). Hair coverage was reconstructed as very sparse, consistent with expectations for extremely large-bodied elephants inhabiting warm climatic conditions; Larramendi et al. (2017) argue that the high body volume-to-surface-area ratio of straight-tusked elephants implies reduced insulation and enhanced heat transfer, paralleling extant elephants with sparse hair distributions (Myhrvold et al., 2012).

Colouration and visible patterning were treated as ecologically plausible approximations rather than diagnostic traits. Comparative observations indicate clear differences in skin tone and texture between Asian and African elephants, with Asian elephants typically exhibiting lighter, sometimes pinkish pigmentation and smoother trunk skin, and African elephants showing darker grey coloration with more deeply cracked epidermis (Schulz et al., 2024). Given the close phylogenetic relationship between *Palaeoloxodon* and *Elephas*, and the aim of remaining within the known range of extant elephant integument phenotypes, the reconstruction adopts pigmentation broadly comparable to *Elephas maximus* as a conservative baseline, acknowledging that apparent colour in living elephants is strongly influenced by mud, dust, hydration, and sun exposure.

Colouration and visible patterning were treated as ecologically plausible approximations rather than diagnostic or phylogenetically prescriptive traits. While *Palaeoloxodon* has historically been grouped with Asian elephants (*Elephas maximus*) based on morphological characters, recent genomic analyses indicate a closer evolutionary relationship between *Palaeoloxodon antiquus* and extant African forest elephants (*Loxodonta cyclotis*), suggesting a more complex evolutionary history for straight-tusked elephants than previously assumed (Meyer et al., 2017).

Importantly, integument colour in extant elephants shows substantial overlap across lineages and is strongly influenced by environmental factors such as habitat, substrate, hydration, sun exposure, and behaviour, including dust- and mud-bathing. Comparative observations indicate broad differences in average skin tone and texture between Asian and African elephants, with Asian elephants often exhibiting lighter, sometimes pinkish pigmentation and smoother trunk skin, and African elephants tending toward darker grey tones with more deeply cracked epidermis (Schulz et al., 2024). Given the humid, wet-zone environments inferred for *Palaeoloxodon namadicus sinhaleyus*, and the aim of remaining within the documented phenotypic range of extant elephant integument while avoiding over-specific phylogenetic claims, the reconstruction adopts a moderately light grey baseline with subtle mottling, compatible with both Asian and African forest elephant analogues. This approach reflects ecological plausibility rather than taxonomic certainty, acknowledging that apparent colour in living elephants is highly variable and often dominated by extrinsic factors.

Ear size and morphology were reconstructed conservatively. Larramendi et al. (2017) note that ear dimensions in elephants correlate more strongly with body size and thermoregulatory demands than with phylogeny and therefore cannot be inferred directly from extant relatives alone. For *Palaeoloxodon*, relatively large ears are tentatively inferred as a thermoregulatory adaptation consistent with its exceptional body mass and warm-climate context, but their exact shape and proportional extent remain uncertain. Recent genetic evidence indicating a closer evolutionary relationship between *Palaeoloxodon* and *Loxodonta cyclotis* complicates earlier assumptions of a purely Asian-elephant-like morphology (Meyer et al., 2017) but does not in itself provide direct constraints on ear form. Accordingly, ear morphology in the reconstruction reflects a generalised large-elephant condition rather than a close analogue drawn from any single extant species. This approach is consistent with Larramendi (2016), who proposed that *Palaeoloxodon antiquus* likely possessed robust, intermediate-sized ears broadly comparable to those of *Elephas maximus*, rather than the extreme enlargement seen in *Loxodonta africana*.

Trunk morphology presents similar inferential limits. Larramendi et al. (2017) emphasise that the form of the trunk tip is not reliably linked to dietary behaviour and cannot be reconstructed with confidence for extinct elephants. In the absence of fossil evidence constraining trunk-tip anatomy in *Palaeoloxodon* and given the high functional plasticity of the elephant trunk across extant taxa, the reconstruction adopts a single dorsal finger configuration. This choice reflects a conservative modelling decision that avoids introducing additional anatomical specialisation unsupported by direct evidence, rather than a definitive claim about trunk morphology. As such, it should be understood as an illustrative approximation within the known range of extant elephant variation.

Tusk morphology in *Palaeoloxodon namadicus sinhaleyus* was informed by comparative anatomy, palaeoecological context, and historical reconstructions. Whereas *Palaeoloxodon antiquus* is characterised by extremely long, largely straight tusks associated with open temperate woodland and savannah-like environments in Europe (Larramendi et al., 2017), *P. namadicus sinhaleyus* is known from markedly different habitats. Fossil and environmental evidence places this subspecies within the wet-zone landscapes of the Sabaragamuwa Basin, which during the Late Pleistocene were dominated by dense tropical vegetation (Amano et al., 2023). In such environments, very long, forward-projecting tusks would likely have imposed mechanical constraints on locomotion through thick undergrowth, favouring reduced tusk elongation. On this basis, we reconstructed *P. namadicus sinhaleyus* with predominantly straight, medium-length tusks, a decision consistent with Deraniyagala's (1955, Plate 13) reconstruction of the taxon.

No cranial material is currently known for *Palaeoloxodon namadicus sinhaleyus*, and as a result the morphology of the parieto-occipital crest remains unknown. Among palaeoloxodonts, the development and expansion of the POC is generally interpreted as a response to increased cranial and ante-cranial loading, including the mass and leverage of large tusks and associated trunk musculature (Larramendi, 2016). Following the hypothesis advanced by Larramendi et al. (2020) that the POC also functioned as an attachment site for enlarged splenius and supersplenius musculature, this reconstruction explicitly visualises that functional relationship (Figures 15–17). Given that *P. namadicus sinhaleyus* is reconstructed here with intermediate-length tusks rather than the exceptionally long and robust tusks of its *forma typica*, it is reasonable to speculate that selective pressure for extreme POC enlargement may have been reduced in this subspecies. However, there is no direct evidence to constrain the degree of variation that may have existed in the POC itself, nor in associated splenius and supersplenius musculature. While previous illustrations of *Palaeoloxodon namadicus* and *Palaeoloxodon antiquus* depict varying degrees of soft-tissue mass surrounding the POC (Deraniyagala, 1955; Uchytel, 2012; Larramendi et al., 2017), the present reconstruction is, to our knowledge, the first to clearly articulate the anatomical relationship between the POC and dorsal neck musculature in palaeoloxodonts. Any inferred reduction in these structures should therefore be understood as a modelling assumption made for biomechanical plausibility rather than a definitive anatomical reconstruction.

Environment context. In this research, *Palaeoloxodon namadicus sinhaleyus* is depicted within wetland marsh and open grassland environments (Figures 15 and 17). The grassy field setting was photographed in an environment analogous with the Sabaragamuwa Basin, a documented fossil locality for this species (Sumanarathna et al., 2021). The wetland environment was photographed near Sigiriya Lion Rock in north-central Sri Lanka and is used here as an ecological analogue rather than a site-specific reconstruction. Although no fossil material of *P. namadicus sinhaleyus* has been recorded from the Sigiriya area, this absence more likely reflects uneven patterns of palaeontological recovery than demonstrated exclusion from that region. The majority of Sri Lanka's Quaternary megafaunal fossils have been recovered incidentally through gem mining in the Sabaragamuwa Basin, whereas other regions have not been investigated with comparable intensity (Sumanarathna et al., 2021). Paleoenvironmental evidence from Late Pleistocene Sri Lanka indicates the persistence of humid tropical conditions alongside habitat mosaics that included forest, wetlands, forest-edge settings, and more open areas, rather than a wholly different environmental regime from that of the present (Wikramanayake, 2004; Roberts et al., 2017; Amano et al., 2023). This interpretation is also consistent with Acavidae evidence from Batadombalena, where environmentally sensitive land snails show broad continuity between fossil and extant assemblages in the island's wet zone over approximately 30,000 years (Sumanarathna et al., 2016). The inclusion of the Sigiriya landscape is therefore illustrative, intended to evoke one plausible expression of this broader environmental range, rather than to imply fossil occurrence at that specific locality.

Sri Lankan Rhinoceros

Order: PERISSODACTYLA Owen, 1848
Family: RHINOCEROTIDAE Gray, 1821
Genus: RHINOCEROS Linnaeus, 1758
Species: *Rhinoceros sinhaleyus* (Deraniyagala, 1936)
(Figure 18)

Nomenclature. The nomenclatural history of the Sri Lankan rhinoceros material is complex and remains unresolved. P.E.P. Deraniyagala (1938) applied the previously suggested subspecific name *sinhaleyus* to several extinct Ceylonese forms, including *Rhinoceros sivalensis sinhaleyus,* while noting that differences between the extinct faunas of India and Ceylon appeared generally subspecific, although more complete material might demonstrate specific distinction. Deraniyagala later used the combination *Rhinoceros sinhaleyus* in the monograph "The Pleistocene of Ceylon" (1946). S.U. Deraniyagala subsequently referred to the Sri Lankan form as *Rhinoceros sinhaleyus* and distinguished it from *R. sivalensis* on dental grounds, while also noting similarities with *Rhinoceros unicornis* and the limited nature of the available evidence (Deraniyagala, 1988, 1992). The present article does not seek to resolve the taxonomic status of this material. Instead, *Rhinoceros sinhaleyus* is used here in a historical and operational sense to refer to the fossil rhinoceros traditionally identified under that name in Sri Lankan palaeontological literature. The reconstruction should therefore

FIGURE 18. Three-dimensional reconstruction of the extinct Sri Lankan rhinoceros (*Rhinoceros sinhaleyus*) standing on a grassy island within an extensive wetland environment. The scene is intended to evoke palaeoenvironmental conditions inferred for the Sabaragamuwa Basin during the Late Pleistocene. The background incorporates the Adam's Peak massif and surrounding landscapes near Kuruwita, Sri Lanka, used here as a regional environmental analogue rather than a precise locational reconstruction.

be understood as a visualisation of this historically recognised form, rather than as a systematic reassessment of its species-level validity.

The fragmentary nature of the Sri Lankan rhinoceros record is compounded by the loss, poor documentation, or uncertain present location of some historically reported material. For this reason, the reconstruction relies primarily on published descriptions, historical figures and photographs where available, and comparison with extant and fossil rhinoceros species. This limitation is not treated as grounds for taxonomic certainty, but as part of the methodological problem the visualisation addresses: how to responsibly reconstruct historically documented but incompletely preserved Sri Lankan Quaternary fauna.

Appearance. Rhinocerotidae is a family of large, heavy-bodied herbivorous mammals typically exceeding one tonne in mass and characterised by one or more keratinous nasal horns. Members of the family possess thick, protective skin with sparse hair coverage, and extant species occupy a wide range of habitats across sub-Saharan Africa and South and Southeast Asia, including grasslands, savannahs, shrublands, tropical forests, and wetlands (Laurie et al., 1983; Groves and Leslie, 2011; Sumanarathna et al., 2021). The earliest members of family Rhinocerotidae diverged approximately 4.3 million years ago (Bai et al., 2020).

The genus *Rhinoceros* is defined by the presence of a single nasal horn (Groves, 1983) and is represented today by two extant examples: *Rhinoceros unicornis* and *Rhinoceros sondaicus*. In Sri Lanka, *R. unicornis* persisted into the Holocene, but during the Middle to Late Pleistocene, at least two additional rhinocerotid taxa were present in the Sabaragamuwa region: *Rhinoceros sinhaleyus* and *Rhinoceros kagavena*. Both taxa are primarily known from dental material, although *R. sinhaleyus* is additionally represented by a partial mandible with a pronounced gonial prominence and a proximal fragment of a scapula (Deraniyagala, 1958; Sumanarathna et al., 2021).

Dentition provides the principal basis for distinguishing these species. *Rhinoceros sinhaleyus* exhibits brachyodont, relatively square molars, whereas *R. kagavena* is characterised by hypsodont dentition, suggesting differing feeding strategies (Deraniyagala, 1939). Deraniyagala (1958, p. 116) described *R. sinhaleyus* as "somewhat smaller than the living *R. unicornis*" and associated it with swampy environments (Chauhan, 2007). On this basis, Deraniyagala (1988) later speculated that the species may have possessed shortened limbs adapted for soft, waterlogged substrates.

However, subsequent fossil discoveries complicate this interpretation. Fossils of *R. sinhaleyus* recovered from gem pits in the Kuruwita region of the Sabaragamuwa Province – a mountainous area whose present terrain closely resembles that inferred for the Late Pleistocene – indicate that the species was not restricted to lowland swamps (Sumanarathna et al., 2021). Moreover, *R. sinhaleyus* shares close affinities with fossil rhinoceroses from the Shivalik Hills of northern India, including *R. unicornis* and *R. sivalensis* (Deraniyagala, 1958; Sumanarathna et al., 2021). Dental morphology aligns *R. sinhaleyus* with the *R. unicornis* lineage through the presence of a crista, while the low crown height and square tooth profile suggest a relatively primitive condition and a smaller-bodied form, potentially closer to *R. sivalensis* or the extant *R. sondaicus* (Deraniyagala, 1958). Groves and Leslie (2011) have argued for a close – possibly conspecific – relationship between *Rhinoceros sinhaleyus*, *Rhinoceros sondaicus*, and *Rhinoceros sivalensis*. Together with the Kuruwita fossil evidence, we interpret this as a broader habitat range for *R. sinhaleyus* encompassing swampy lowlands, floodplains, and more rugged or elevated terrain, which would suggest that extreme limb shortening is unlikely.

Integumentary features are not preserved in the fossil record of *Rhinoceros sinhaleyus*, and no skin impressions or soft tissue remains are known. Consequently, the external appearance of this species was inferred using a proxy-based framework combining phylogenetic proximity, comparison with extant congeners, and ecological plausibility, following an Extant Phylogenetic Bracket (EPB) approach (Witmer, 1995). Primary analogues were *Rhinoceros unicornis* and *Rhinoceros sondaicus*, both of which have been regarded as closely related to *R. sinhaleyus* and potentially conspecific, although subspecifically destinct (Deraniyagala, 1958; Groves and Leslie, 2011).

Skin texture in the reconstruction follows the general condition observed in extant Asian rhinoceroses: a thick, largely hairless hide with prominent epidermal polygonal patterning. In *Rhinoceros unicornis* and *Rhinoceros sondaicus*, skin thickness ranges from approximately 2.5 to 3.5 cm depending on body region (Sody and Mohr, 1959), and the epidermis is divided into closely arranged, flattened polygons that impart a reticulated surface appearance (Lydekker, 1907; Groves and Leslie, 2011) resembling scales (Harper, 1945). Regional skin folds are a defining feature of the genus, although their development varies between species. *R. unicornis* exhibits deep, armour-like folds, including pronounced cervical and shoulder segmentation (Laurie et al., 1983), whereas *R. sondaicus* shows shallower folds and a diagnostic posterior cervical fold forming an independent nape shield (Grove and Leslie, 2011).

Given the inferred closer affinity of *Rhinoceros sinhaleyus* to *Rhinoceros sondaicus* and its comparatively more primitive morphology relative to *R. sondaicus*, the reconstruction adopts moderately developed skin folds and avoids the exaggerated segmentation and enlarged cervical "bib" characteristic of mature male *Rhinoceros unicornis*. This treatment is consistent with the lighter cranial construction and reduced graviportality observed in *R. sondaicus* and its Pleistocene precursors (Groves and Leslie, 2011).

Hair coverage is reconstructed as sparse. In extant Asian rhinoceroses, body hair is typically present in juveniles but becomes abraded or lost in adults, with hair consistently retained only as eyelashes, ear fringes, and a terminal tail brush (Laurie et al., 1983). Given the warm, humid environments inferred for *Rhinoceros sinhaleyus* and the absence of evidence for cold-adapted integument, a largely hairless adult phenotype with retained sensory and display hairs is considered the most parsimonious reconstruction.

Colouration is treated as an ecologically plausible approximation rather than a diagnostic trait. Extant *Rhinoceros unicornis* typically exhibits a grey-brown hide that may appear pinkish within skin folds, while *Rhinoceros sondaicus* is generally described as grey to dusky grey (Laurie et al., 1983; Groves and Leslie, 2011). In both species, apparent colour is strongly influenced by wallowing behaviour, mud adherence, and hydration state. Accordingly, *Rhinoceros sinhaleyus* is reconstructed with a neutral grey to grey-brown base tone consistent with extant Asian rhinoceroses inhabiting wetland and forested environments.

FIGURE 19. Sculpture of *Rhinoceros sinhaleyus* by Lalith Wijesinghe (2014), displayed at the Rathnapura National Museum Palaeobiodiversity Museum Park. Photograph by A.R.S.

Other external features follow conditions observed in living members of the genus. The upper lip is depicted as elongated and prehensile, reflecting browsing behaviour associated with brachyodont dentition and paralleling feeding strategies documented in *Rhinoceros unicornis* and *Rhinoceros sondaicus* (Laurie et al., 1983; Groves and Leslie, 2011). A single nasal horn is included, consistent with the defining characteristic of *Rhinoceros*, with size and curvature kept conservative to avoid overstating sexual dimorphism or horn hypertrophy in the absence of direct fossil evidence. Ear morphology, including a fringe of marginal hairs, and a terminal tail brush are also retained, as these features are consistently present across extant rhinocerotids.

Reconstruction. Drawing on inferred morphology from Shivalik rhinoceroses and closely related Asian taxa adapted to environments ranging from wetlands to upland and mountainous terrain, *Rhinoceros sinhaleyus* is reconstructed with longer-than-average limb proportions (Figure 17). This treatment reflects phylogenetic and morphological affinities with Shivalik *Rhinoceros* species and supports limb proportions suited to mobility across heterogeneous landscapes rather than specialisation for persistently waterlogged substrates. A sculptural reconstruction by Lalith Wijesinghe displayed at the Palaeobiodiversity Museum Park of the Rathnapura National Museum (Figure 19) likewise depicts a long-limbed *R. sinhaleyus*, providing independent visual support for this interpretation.

In the scene depicted, an adult male *R. sinhaleyus* stands above tall grass on a temporary floodplain island. When reconstructed alongside *Rhinoceros unicornis* within a comparable environmental context (Figure 10), *R. sinhaleyus* is portrayed with a more gracile overall build. This reflects Deraniyagala's (1955) description of the species as somewhat smaller than the living Indian rhinoceros and avoids assuming the robust, heavily armoured proportions characteristic of mature male *R. unicornis*. While this comparison does not yield definitive measurements, it provides a relative frame of reference grounded in extant morphology.

In *Rhinoceros unicornis*, documented shoulder heights range from approximately 147 to 193 cm (Laurie et al., 1983), establishing a practical upper bound for body size within the genus. Although a partial proximal scapula of *Rhinoceros sinhaleyus* has been recovered from Kuruwita, the fragmentary nature of this postcranial material precludes reliable estimation of body size or shoulder height. As a result, overall proportions were contextualised using extant Asian rhinoceroses, with *R. unicornis* treated as an upper dimensional limit rather than a direct analogue.

In the absence of limb material suitable for quantitative scaling, shoulder height for *Rhinoceros sinhaleyus* was estimated through comparative allometry with its closest extant analogue, *Rhinoceros sondaicus*. This comparison is supported by close phylogenetic affinity and shared aspects of general limb bone morphology between *R. sondaicus* and *R. unicornis*, which are broadly similar despite differences in robustness (Mallet et al., 2019). Although dental dimensions are not isometrically linked to body size, the brachyodont, relatively square molars of *R. sinhaleyus* align it with smaller browsing rhinoceroses rather than larger grazing forms (Deraniyagala, 1939). Given the documented shoulder height range of *R. sondaicus* (150–170 cm), evidence for subspecific size reduction in peripheral populations (Groves and Leslie, 2011), and Deraniyagala's (1958) characterisation of *R. sinhaleyus* as a more primitive taxon, a conservative shoulder height estimate of approximately 150 cm places the species at the lower end of the *Rhinoceros* size spectrum without overstating its stature.

Environmental context. The landscape depicted for *Rhinoceros sinhaleyus* is informed by both the geological and palaeoecological context of the Sabaragamuwa region and the comparative ecology of closely related Asian rhinoceroses. As skeletal morphology alone does not permit precise habitat discrimination in rhinocerotids, ecological inferences must remain broad and be treated cautiously (Mallet et al., 2019). Closely related species may share similar limb morphologies while occupying distinct but overlapping environments, particularly where access to water and dense vegetation is a common constraint.

Late Pleistocene evidence from Sri Lanka, particularly from the island's wet zone and adjoining regions, indicates humid tropical conditions with heterogeneous habitat structure, including forested environments, wetlands, forest-edge settings, and more open grassland components (Wikramanayake, 2004; Roberts et al., 2017; Amano et al., 2023). This broader environmental framework is consistent with the geological context of the Sabaragamuwa Basin, from which *R. sinhaleyus* fossils have been recovered (Sumanarathna et al., 2017). Comparative evidence from extant Asian rhinoceroses further supports the plausibility of such habitat mosaics. For example, *Rhinoceros unicornis* is most often associated with semi-open floodplains, riverine grasslands, and swampy alluvial environments, whereas historical accounts of *Rhinoceros sondaicus* indicate use of a broader range of habitats, including lowland forests, fertile floodplains, open glades within forest, and hilly or mountainous terrain prior to its modern range contraction (Laurie et al., 1983; Groves and Leslie, 2011). Both species retain a strong affinity with water but differ in the degree of openness and vegetation structure they preferentially exploit.

Fossil evidence places *Rhinoceros sinhaleyus* within the Sabaragamuwa Basin, including the Kuruwita region (Deraniyagala, 1958; Sumanarathna et al., 2017), an area characterised during the Pleistocene by heterogeneous landscapes encompassing wetlands, floodplains, forested lowlands, and adjacent upland terrain (Wikramanayake, 2004; Roberts et al., 2017; Amano et al., 2023). Taken together, these lines of evidence suggest that *R. sinhaleyus* was ecologically flexible rather than restricted to a single narrowly defined habitat type (Sumanarathna et al., 2021). Accordingly, the reconstruction situates *R. sinhaleyus* within a temporary floodplain bordered by tall grasses and wetland vegetation. This setting is presented as one plausible ecological context within the inferred environmental range for the species, rather than as an exclusive or definitive habitat reconstruction.

The scene also includes small passerine birds perched on the body of *Rhinoceros sinhaleyus*. These birds were present in the original reference photograph of extant *Rhinoceros unicornis* and were intentionally retained in the reconstruction to preserve a documented behavioural context. In living *R. unicornis*, birds such as mynahs (*Acridotheres tristis*) are known to forage opportunistically on invertebrates associated with the rhino's skin (Laurie et al., 1983). However, owing to their small size and lack of diagnostic detail in the source image, the birds depicted here cannot be identified to species level. Their inclusion therefore indicates a generalised interaction between rhinocerotids and small insectivorous passerines, rather than implying the co-occurrence of any specific bird taxon with *R. sinhaleyus*. This choice reflects a behaviourally plausible ecological association rather than a taxonomic claim.

CONCLUSION

This study presents the first integrated three-dimensional palaeoart reconstructions of *Palaeoloxodon namadicus sinhaleyus* and *Rhinoceros sinhaleyus* grounded explicitly in Sri Lankan fossil, geological, and palaeoecological contexts. By synthesising fragmentary fossil material with comparative anatomy, extant phylogenetic bracketing, palaeoenvironmental evidence, and documented ecological analogues, the reconstructions offer updated visual hypotheses for two poorly known Quaternary megafaunal taxa. These images do not claim to represent definitive appearances, but rather articulate current, evidence-informed interpretations that can be revised as new data emerge.

A key contribution of this research lies in the explicit documentation of reconstruction decisions. Anatomical assumptions, scaling choices, soft-tissue inferences, and environmental contexts are made transparent, with clear distinction between fossil-supported constraints and areas of informed speculation. This includes the treatment of insular size reduction in *Palaeoloxodon namadicus sinhaleyus*, limb proportions and habitat flexibility in *Rhinoceros sinhaleyus*, and the functional interpretation of the parieto-occipital crest in palaeoloxodonts. By rendering these decisions visible rather than implicit, the reconstructions function not merely as illustrations, but as testable syntheses of current knowledge.

Methodologically, this study demonstrates how contemporary 3D animation and visual effects workflows can be integrated into palaeontological research without sacrificing scientific rigour. The use of modular digital assets, anatomically constrained deformation, and explicitly defined ecological analogues allows reconstructions to be interrogated, updated, or repurposed as new evidence becomes available. In this respect, the models are not static endpoints but adaptable research artefacts, capable of supporting future visualisation, comparative analysis, and public-facing interpretation.

The reconstructions presented here also represent the first palaeoart produced using 3D animation methodologies to directly support Sri Lankan palaeontological research and constitute the first substantial visual revisions of *Palaeoloxodon namadicus sinhaleyus* and *Rhinoceros sinhaleyus* in several decades. By situating these taxa within plausible environmental contexts drawn from the Sabaragamuwa Basin and ecologically comparable regions elsewhere in Sri Lanka, the study highlights the ecological diversity of Sri Lanka’s Quaternary landscapes and underscores the scientific value of a fossil record that remains largely understudied.

Finally, this work emphasises the importance of transparency as reconstructions become increasingly realistic and persuasive. As palaeoart continues to move toward higher visual fidelity, the risk of conflating interpretive imagery with settled fact increases. Explicitly communicating uncertainty, assumptions, and alternative interpretations is therefore not ancillary to the reconstruction process but central to its scientific credibility. In this sense, the reconstructions presented here are intended not only to visualise extinct species, but to model an approach to palaeoart that treats visualisation as a rigorous, accountable component of palaeontological research.

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