Received: 28 June 2021 | Revised: 30 September 2021 | Accepted: 10 October 2021

DOI: 10.1002/jmor.21421

RESEARCH ARTICLE

JOURNAL OF morphology WILEY

# Virtual and augmented reality: New tools for visualizing, analyzing, and communicating complex morphology

Robert L. Cieri[1,2] | Morgan L. Turner[3,4] | Ryan M. Carney[5] | Peter L. Falkingham[6] | Alexander M. Kirk[5] | Tobias Wang[7] | Bjarke Jensen[8] | Johannes Novotny[9] | Joshua Tveite[10] | Stephen M. Gatesy[3] | David H. Laidlaw[10] | Howard Kaplan[11] | Antoon F. M. Moorman[8] | Mark Howell[1] | Benjamin Engel[12] | Cole Cruz[13] | Adam Smith[13] | William Gerichs[13] | Yingjie Lian[13] | Johanna T. Schultz[2] | C. G. Farmer[1]

[1]School of Biological Sciences, University of Utah, Salt Lake City, Utah, USA

[2]School of Science and Engineering, University of the Sunshine Coast, Maroochydore, Queensland, Australia

[3]Department of Ecology, Evolution, and Organismal Biology, Brown University, Providence, Rhode Island, USA

[4]Department of Computer Science and Engineering, University of Minnesota, Minneapolis, Minnesota, USA

[5]Department of Integrative Biology, University of South Florida, Tampa, Florida, USA

[6]School of Biological and Environmental Sciences, Liverpool John Moores University, Liverpool, UK

[7]Department of Biology, Zoophysiology, Aarhus University, Aarhus, Denmark

[8]Department of Medical Biology, Amsterdam Cardiovascular Sciences, Amsterdam University Medical Centres, Amsterdam, the Netherlands

[9]VRVis Zentrum für Virtual Reality und Visualisierung Forschungs-GmbH, Vienna, Austria

[10]Department of Computer Science, Brown University, Providence, Rhode Island, USA

[11]Advanced Visualization Center, University of South Florida, Tampa, Florida, USA

[12]School of Dentistry, University of Utah, Salt Lake City, Utah, USA

[13]School of Computing, University of Utah, Salt Lake City, Utah, USA

**Correspondence**
Robert L. Cieri, School of Biological Sciences, University of Utah, Salt Lake City, UT 84112, USA.
Email: bob.cieri@gmail.com

**Funding information**
Company of Biologists; National Geographic Society, Grant/Award Number: W340-14; National Science Foundation, Grant/Award Numbers: 1929637, EAR-1452119, EAR-0917538, IOS-0925077

## Abstract

Virtual and augmented reality (VR/AR) are new technologies with the power to revolutionize the study of morphology. Modern imaging approaches such as computed tomography, laser scanning, and photogrammetry have opened up a new digital world, enabling researchers to share and analyze morphological data electronically and in great detail. Because this digital data exists on a computer screen, however, it can remain difficult to understand and unintuitive to interact with. VR/AR technologies bridge the analog-to-digital divide by presenting 3D data to users in a very similar way to how they would interact with actual anatomy, while also providing a more immersive experience and greater possibilities for exploration. This manuscript describes VR/AR hardware, software, and techniques, and is designed to give practicing morphologists and educators a primer on using these technologies in their research, pedagogy, and communication to a wide variety of audiences. We also include a series of case studies from the presentations and workshop given at the

  

2019 International Congress of Vertebrate Morphology, and suggest best practices for the use of VR/AR in comparative morphology.

**KEYWORDS**
anatomy, collections, comparative, education, visualization

## 1 | INTRODUCTION

It is intriguing to contemplate the cosmic journey of matter through its various natural and artificial transmutations. Billions-of-years-old "star stuff" makes up the genetically encoded building blocks of morphology in living organisms (in vivo), developing and evolving into "endless forms most beautiful," with some organic structures chemically transformed into fossils (in situ). By harnessing electromagnetic radiation such as X-rays, we can render such matter into the pixels and voxels of the digital world (in silico), including virtual reality (VR) (Figure 1). These bits of data can then be returned to the analog world, through augmented reality (AR) ("in holo") or 3D printing.

Modern imaging technologies, such as computed tomography (CT), magnetic resonance imaging (MRI), and traditional as well as stereo scanning electron microscopy (SEM), have revolutionized the study of morphology by providing scientists accurate digital versions of biological structures to measure, analyze, enhance, or modify. The power of this technology, however, has been significantly limited by the interface—exploring 3D morphology on a 2D screen with a mouse and keyboard is unwieldy, and much more awkward than interacting with real anatomy. The rise of VR/AR, which enables 3D interaction with increasingly realistic virtual morphology, promises to solve this challenge by giving researchers and educators an analog interface with digital data. Early pioneering work utilizing VR/AR to visualize morphology has included various medical applications (Azuma, 1997; Eckhoff et al., 2003) as well as "augmented paleontology" (Bimber et al., 2002, 2003). For systematic reviews of VR in education, see (Pellas et al., 2021; Radianti et al., 2020).

Here, we review the current state-of-the-art in VR/AR, describe the advantages and disadvantages of current hardware/software configurations and web-based tools, introduce a new environment for "multiplayer VR analysis," cover a few case studies in research and teaching, as well as suggest best practices and future directions for VR/AR in morphology. A few detailed workflows for loading volumetric, surface, and simulation data into common VR environments are included as Supporting Information.

## 2 | METHODS

As morphologists, much of our digital 3D models of biological structures originate from CT, photogrammetry, or other scanning modalities. These models can be created de novo, or obtained from repositories like MorphoSource, DigiMorph, Sketchfab, GitHub, Blend Swap, or Thingiverse, where 3D models can be shared and downloaded. Common file types for 3D files are OBJ, X3D, FBX, or STL, although these differ in the information they include about the 3D model. While STL files only describe the surface geometry and are mainly used in 3D manufacturing, X3D and FBX files also include information about colors, materials, textures, and even animation.

Typically, such 3D models are geometrically dense, and thus too computationally expensive for smoothly rendering in real-time computer graphics environments. For complex models, scenes, and custom apps, it is often necessary to optimize models for VR/AR via remeshing and texture mapping techniques (see case study on *Digital Dinosaurs*; Kirk et al., 2018). Depending on the morphological complexity and questions driving the analysis, a spectrum of VR/AR software tools are possible—from readily available and easy-to-use viewers of static 3D models, to fully custom applications that can take years and large collaborations to develop.

### 2.1 | Virtual reality (VR)

More advanced and expensive VR headsets, like the HTC Vive or Oculus Rift, require a computer with a proper processor, GPU, and enough RAM, as well as certain ports to connect the VR headset. Other options are all-in-one VR headsets, which have a GPU, a processor, and RAM inbuilt, but are therefore limited in processing power (Table 1). VR devices come with controllers, which allow the user to navigate and operate in the virtual world. Depending on the headset, base stations can track the movement of the headset in a certain area; therefore, the user's movement in the real world is copied in the virtual world. The easiest and cheapest quick start option is Google Cardboard, a platform encouraging VR usage and development for anybody, because it works with a smartphone and a VR viewer made from cardboard and lenses. Google Cardboard provides a software development kit (SDK) to develop applications, which is available for Android, Unity, and iOS. The following are the minimum computer specifications required for work in VR: *HTC Vive*: Intel ® Core™ i5-4590 or AMD FX™ 8350 equivalent or better, NVIDIA ® GeForce ® GTX 970 4GB, AMD Radeon™ R9 290 4GB equivalent or better VR Ready graphics card, 4GB RAM or more; *Oculus Rift*: Intel Core i3-6100 or better; AMD Ryzen 3 1200 or FX-4350, or better, Nvidia GeForce GTX 1050 Ti or better; AMD Radeon RX 470 or better, 8GB RAM or more; *Pimax 5K*: Intel i5-4590 or above, NVIDIA ® GeForce ® GTX 1070 or above, 8GB RAM or more.

### 2.2 | Augmented reality (AR)

Augmented reality is defined as the real-time projection of virtual objects in a real-world environment. It is a type of mixed reality on a continuum between entirely real and entirely virtual (Milgram & Kishino, 1994). This blending of analog and digital worlds into a unified experience is the key difference—and advantage—of AR compared to VR. Augmented reality enables us to emerge from the allegorical cave of VR and project the digital "shadows" into the realm of true forms instead—providing new opportunities for scientific exploration in research and pedagogy.

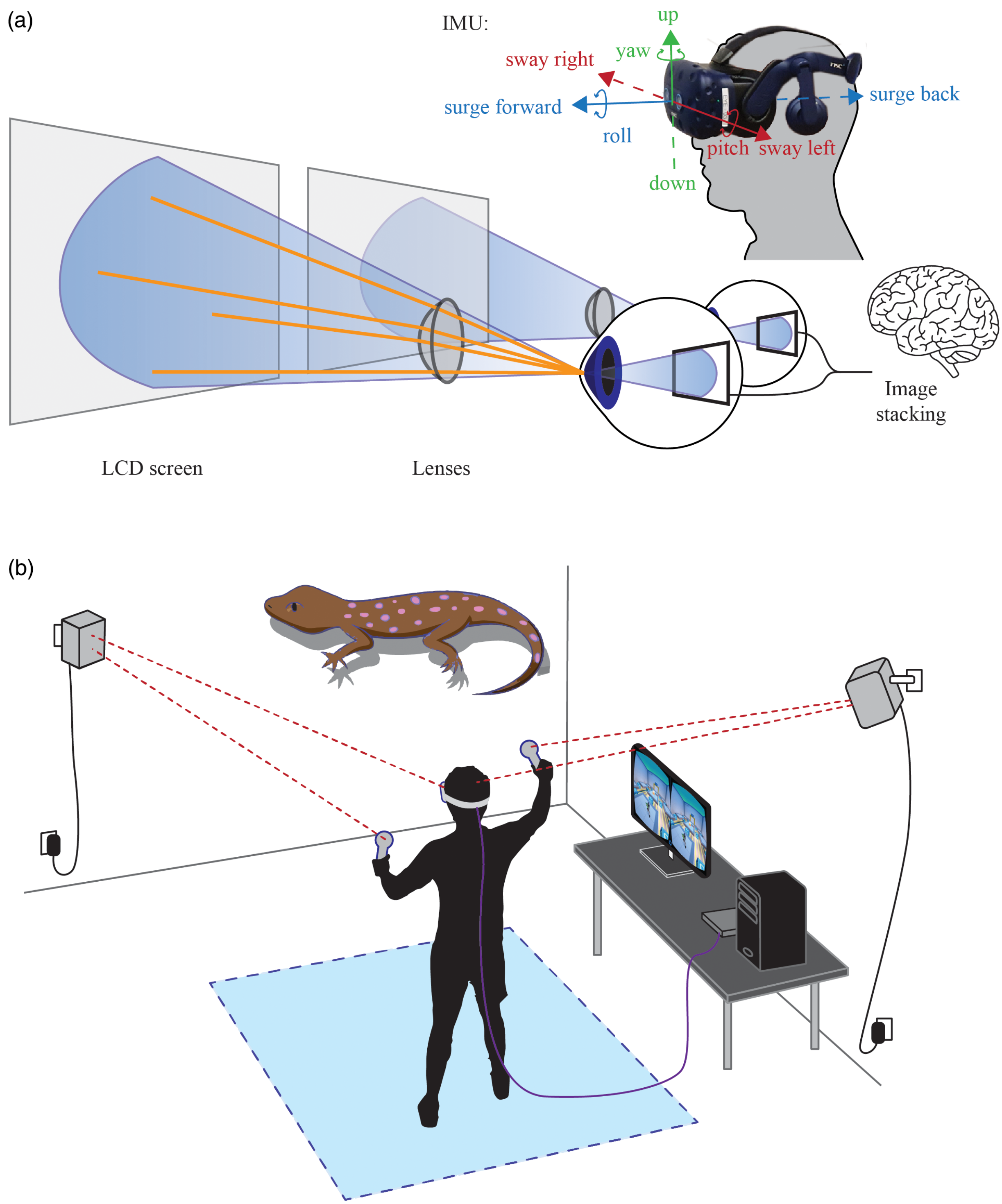


FIGURE 1 How virtual reality works. Virtual reality works by projecting a stereoscopic display in front of a headset (a) that changes in real time depending on the relative rotation and orientation of the head detected by an inertial measurement unit (IMU), and the relative translation of the head through the environment using fixed infrared (IR) emitters and rotating lasers contained within one or more base stations. The headset contains an array of IR detectors which read both signals from the base station(s) to triangulate its position in 3D space (b). The user can also interact with the virtual reality environment using handsets, which also contain arrays of IR detectors which read the signals from the base station(s)

**TABLE 1** Important parameters for different virtual reality hardware options

| Model (first release) | Set | Resolution, screen size | Field of view (FOV) | Refresh rate |
|---|---|---|---|---|
| HTC Vive Pro (2016): Tethered or wireless | Headset (6DOF), 2× controllers, 2× base stations (IR) | 2880 × 1700, 3.4″ | 110° | 90 Hz |
| Oculus Rift (2016) | Headset (6DOF), 2× touch controllers, 2× IR sensors | 2160 × 1200, 3.4″ | 110° | 80 Hz (S)–90 Hz |
| Oculus GO (2018): all-in-one headset | Headset (3DOF), 1× controllers | 2560 × 1440, 5.5″ | 95° | 60–72 Hz |
| Oculus Quest: all-in-one headset (2019) | Headset (6DOF), 2× controllers | 1440 × 1600 per eye | 95° | 72 Hz |
| HP Reverb (2019) | Headset (6DOF), 2× controllers | 2160 × 2160 | 114° | 90 Hz |
| Pimax 5 K Plus (2018) | Headset (6DOF), 2× controllers | 2560 × 1440 per eye | 200° | 144 Hz |
| Google Cardboard VR + SDK (2014) | VR platform for the Google Cardboard "headset" for phones | Screen size up to 6″ | | |

Abbreviations: DOF, degrees of freedom; IR, infrared; SDK, software development kit.

Mobile AR via smartphones and tablets (monoscopic video; Supplementary Video) is the most ubiquitous form of AR, which also includes other handheld devices, as well as headsets (below) and projection displays (spatial AR sensu Bimber & Raskar, 2019; Azuma et al., 2001). Mobile AR has become globally popularized through social apps (Snapchat's Lenses, Facebook's Spark AR) and gaming apps (Pokémon GO, Jurassic World Alive), and to a lesser extent, innovative products such as AR coloring books for inspiring budding biologists. Other apps such as Sketchfab (below) offer AR functionality for 3D models, and various AR apps exist for education (e.g., Augment, CoSpaces Edu, JigSpace), including anatomy (e.g., Human Anatomy Atlas, Complete Anatomy Platform, Froggipedia). Another notable recent example is the custom AR app Insects3D for ant morphology and biogeography (Sarnat et al., 2019).

Smartphone-based AR headsets are more immersive (stereoscopic optical) and include a variety of devices from the Mira Prism to various Google Cardboard-esque adapters (e.g., Aryzon, HoloKit, ZapBox). Dedicated AR headsets include the first-mover Google Glass smartglasses, which were released in 2013 but never crossed the chasm to broad adoption. However, development and production are still ongoing for the Google Glass Enterprise Edition. Most of the other AR headsets are in either experimental and development stages (e.g., Apple Glass), or have not received substantial traction (e.g., Magic Leap). Currently, Microsoft HoloLens has proven to be the top AR headset, as many organizations are utilizing the HoloLens for research, training, and commercial purposes. HoloLens software includes the 3D Viewer app for viewing simple models and animations in file formats such as FBX, OBJ, and STL.

Various software development kits exist for AR (Rokhsaritalemi et al., 2020). The top three currently include Apple's ARKit for iOS apps, Google's ARCore for Android apps, and Microsoft's Windows SDK along with Visual Studio for HoloLens apps. While web browser-based AR and the "immersive web" are currently in their infancy, recent standards include WebXR (https://www.w3.org/TR/webxr/), which supports both AR and VR.

## 2.3 | Quick start for viewing 3D models in VR/AR

For a complete beginner, the most straightforward path to getting your data into VR or AR is by importing into Sketchfab, which accepts most 3D data formats (https://help.sketchfab.com/hc/en-us/articles/202508396-3D-File-Formats). Users can then view models in VR via the Sketchfab app or WebGL-enabled web browser on smartphones (using Google Cardboard, or equivalent) or VR hardware (see *Hardware*). Models can also be viewed in AR using the mobile app, or natively by downloading the *USDZ* version of the model in iOS or through an enterprise account. The free Sketchfab account allows multiple uploads, and it is possible to link to Sketchfab in research papers (e.g., Cieri & Farmer, 2020). Without VR hardware, Sketchfab still allows traditional 3D viewing.

## 2.4 | New open-source software for 'multiplayer' virtual reality analysis

Open-source software packages provide more complex viewing and analysis options but require more setup and working knowledge of specific software (Table 2). StreamlineVR is a stand-alone, interactive, real-time, VR, 3D simulation file viewer built in Unity. It allows users to import all of their X3D files representing their simulations at runtime of our application, to view their entire simulation play out in an uninterrupted VR experience. Useful tools are provided to the user for coloring, translating, and scaling meshes to improve efficiency while studying data. Users are also able to save their work to come back to in the future and are able to send their projects to other potential collaborators.

StreamlineVR was created to address a critical issue present in other similar applications, whereby users are restricted to viewing a single *.X3D* file at a time within a VR environment. Only being able to view a single file at a time without interfacing back with the computer terminal prevents the users from being able to view simulations play

**TABLE 2** Software commonly used in virtual reality applications

| Software | About | Programming language | OS | Cost |
|---|---|---|---|---|
| Unreal engine | Complete suite for real-time technology development, over visualization and real-time rendering to high-quality game design for PCs, consoles, mobiles, VR, AR | C++, blueprints; Supports Python-scripting | Mac, Linux, Windows | Creator (free) and publisher version |
| Unity | Creation of interactive 3D content for games for a wide range of platforms (more options in the pro version) | C#, UnityScript, Boo | Mac, Linux, Windows | Free and pro version |
| Sketchfab (online platform) | Publish, find, or buy 3D models and VR/AR content, online 3D visualization (similar to YouTube but for 3D files) | | Mobile app and browser, desktop browser, VR headset | |
| Autodesk Maya | 3D modeling, animation, rendering, and visual effects | Maya Embedded Language (MEL), Python | Mac, Linux, Windows | License (free for academics) |
| Cinema 4D | 3D modeling, animation, rendering, and visual effects | COFFEE, Python | Mac, Linux, Windows | License or student/ educator version |
| Blender | Open-source 3D creation suite including 3D modeling, animation, rendering, visual effects, motion tracking, video editing, and native VR capability | Python | Mac, Linux, Windows | Free |

out in VR without constantly exiting and restarting the visualization. Constantly exiting and entering the VR space to control the playback of simulation is greatly hindering, limiting the efficiency at which users can glean information from their data. StreamlineVR addresses this issue by allowing users to import every time-step (every X3D file) all at once when creating a new project. After that, every time-step is available to the user within VR, which allows the application to quickly play through the files to recreate the simulation in VR. Users will need to be equipped with the StreamlineVR application, VR hardware, and the X3D files they want to view to fully utilize the app. More information including brief tutorials is available at: https://adamjsmith117.github.io/streamlinevr-webpage/. The project can be downloaded for use at: https://github.com/bobcieri/StreamlineVR.

Commercial software with multiplayer capacity is also available and suitable to view, analyze, and teach anatomy. Several examples are Elucis® and syGlass® are two examples that have been recently used create a virtual classroom to teach anatomy during the COVID-19 pandemic. A video example of the virtual classroom interaction can be viewed at the following url: https://farmer.biology.utah.edu/movies/utah_vid_1.mp4.

## 2.5 | Developing custom applications

Custom applications provide endless analysis possibilities but can be time-consuming to create. The two most popular developer tools for getting 3D models into VR/AR are the Unreal (Epic Games) and Unity (Unity Technologies) engines. Both offer a free version and come with a similar toolkit, therefore the choice between the two is mainly influenced by user preferences or the supported programming languages. Unreal Engine is based on C++, but also includes visual scripting in the form of nodes, called blueprints, and Python. Unity is based on C#, and additionally offers UnityScript and/or Boo. The newest releases of Unity now also include visual scripting, called Bolt. A similar feature of both engines is the ability to build the scene once and deploy it to different platforms, simplifying the final deployment process. Both development tools provide support for a wide range of platforms, PCs, mobiles, consoles, and VR/AR devices. For enabling real-time computer vision capabilities—recognizing and tracking images and objects in the real world for AR—the Vuforia plugin for Unity has more tutorials available than the Unreal4AR plugin for Unreal, allowing for a slightly easier learning curve for new developers. A common opinion is that Unity is more beginner friendly, whereas Unreal is a professional's game engine with better graphical fidelity. Unreal Engine also includes DataSmith, which allows for easy file conversion, which is an advantage because often this step can be very tricky with proprietary computer-aided design (CAD) file formats of different CAD software. Both platforms described above take 3D models as input. With custom applications, time-based data can be addressed in several ways, based on available computational power and needs of the research. Custom applications can range substantially in complexity. Users are recommended to collaborate with computer scientists who specialize in VR/AR development.

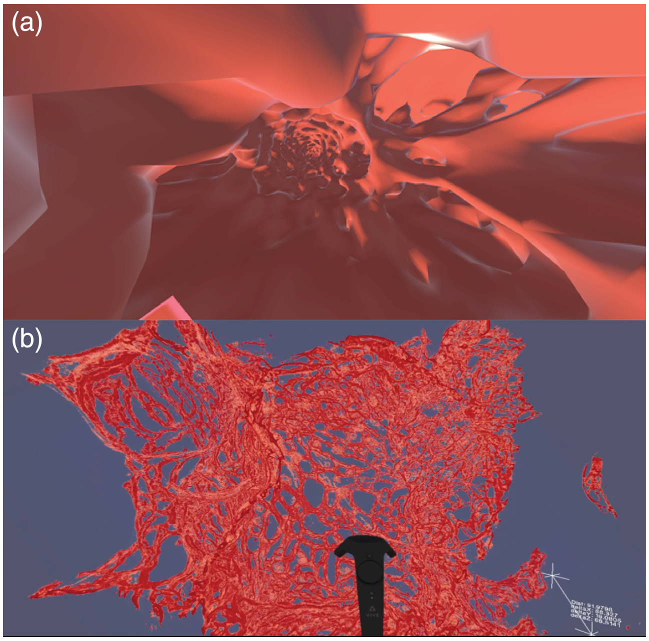


**FIGURE 2** Complex anatomy in virtual reality. (a) Inside view of one of a large conducting airway in an American alligator that has been modified to be a surface file, created using Elucis. (b) Human alveolar capillary net immunostained for VE-cadherin (data courtesy of Astrid Gillich and Ross Metzger). Data were obtained using confocal microscopy and imaged in VR using ParaView. Faithful measurements are possible (e.g., bottom right of the screen)

## 3 | DISCUSSION

### 3.1 | Case studies: Virtual reality and augmented reality in action in organismal morphology

Seven examples of how morphologists are currently using VR/AR are detailed below. The first and second case studies describe pulmonary anatomy and airflow simulations, respectively, from vertebrate lungs studied using VR. The third case study describes the use of virtual reality to investigate simulations of track formations in paleontology. The fourth and fifth case studies describe the use of 3D imaging techniques to investigate and communicate cardiac structure and function. The sixth case study details how VR/AR has been taught in the college classroom and used to visualize paleontological reconstructions such as the flying dinosaur, *Archaeopteryx*. The final case study describes how VR can be used in place of, or to augment, traditional hands-on training with dental patients.

#### 3.1.1 | Virtual reality for the study of complex morphology

Nearly a 100 years ago, August Krogh made a plea in the Silliman Memorial Lectures for the study of anatomy to be more quantitative, and lamented that much of our understanding of form and function is superficial or incomplete due to inadequate methodologies (Krogh, 1922). Some 40 years later, the development of electron microscopy, stereology, and improvements in X-ray technologies revolutionized the ability of scientists to approach the study of anatomy quantitatively, but these methods lose 3D information, either because slices of tissue need to be very thin to be imaged, or the X-rays project the absorption data onto 2D films. With advances in computer technology and software, slices or sections of tissues can be reconstructed into mathematically faithful 3D representations of the original object, but these 3D data generally suffer loss of information because they are visualized using 2D screens. Virtual reality allows the scientific quest of understanding and quantifying anatomy to come full circle, where 3D data can be reduced to sections so that extraordinarily detailed information can be gleaned from each section, reconstructed into a mathematical 3D representation, and then visualized and quantified in fully 3D form. One of the most remarkable things about this advancement in technology is that it is possible to project the object in such a way that the viewer looks at it from the inside out, regardless of the scale of the original object, and can command the software to make structures that are obstructing the view simply vanish from sight, through manipulations of the transfer function. An example of this process on the anatomy of an American alligator (*Alligator mississippiensis*) can be viewed here: https://youtu.be/NVLDizeCMBA.

Figure 2 provides an example of pulmonary data collected using two different techniques and at two different scales and visualized in VR using two different software packages. In (a), CT was used to obtain a stack of data from an American alligator. Each slice of this stack provides information on the density of the structures in a plane of tissue that was 300 μm. A screenshot of a projection into VR of this stack of data shows an inside view of an alligator lung. It is as if one were looking at the lung through an endoscope, or as though one were literally standing in the lung having a look around. Figure 2b shows a screenshot of the projection into VR of a human alveolus where the capillaries were immunostained for VE-Cadherin (white). The image was reconstructed from a stack of 133 sections, with a total thickness of 164.21 μm. Resolution of each image is as follows: $x$: 1024 pixels, $y$: 1024 pixels, $z$: 133 slices, channels: 1, 16-bit. Scaling: $x$: 0.554 μm, $y$: 0.554 μm, $z$: 1.244 μm. Image size: $x$: 566.74 μm, $y$: 566.74 μm, $z$: 164.21 μm. Both sets of data can be projected and magnified in VR so that the 3D relationships can be observed, and measurements can be made.

The ability to make measurements in VR and to "see" the topography as though one were standing inside the structure has been important in advancing comparative studies of pulmonary form and function. Lungs are highly compliant and deflate when excised from the body and opened for inspection. Thus, understanding their 3D topography has been challenging. Virtual reality helps to overcome these difficulties in several ways. Because the topography can be captured readily, even in living animals using CT, structures can be reconstructed and studied as they are in the intact animal. By contrast, traditional dissection requires some destruction or distortion of the morphology of interest. This is an advantage furthermore when preparing for surgical implantations because the internal topography of the structure can be related to landmarks on the animal's surface in its original configuration.

### 3.1.2 | Virtual reality for studying pulmonary anatomy and airflow patterns

Recent advances in VR enable researchers to interact with fully immersive, affordable, interactive digital environments, and have revolutionized our study of pulmonary airflow patterns (Cieri & Farmer, 2020). Unidirectional pulmonary airflow, a condition where lung gases travel in the same direction through most of the airways throughout the respiratory cycle, has recently been shown to be present beyond Aves, including crocodilians (Farmer, 2015; Farmer & Sanders, 2010; Schachner, Hutchinson, & Farmer, 2013), green iguanas (Cieri et al., 2014), and monitor lizards (Cieri & Farmer, 2020; Schachner, Cieri, et al., 2013), and has raised new questions about the underlying fluid dynamical phenomena occurring in unidirectional lungs. Direct measurements of airflow can be difficult because lungs are complex, delicate organs (Figure 3a,b) and many portions of the respiratory system are inaccessible with conventional instruments (Cieri et al., 2014). Computational fluid dynamics (CFD) modeling, which can be visualized in VR, provides a new avenue to investigate how anatomical structure gives rise to fluid flow. To be accurate, the models must be based on anatomically faithful digital meshes but assessing the accuracy of these meshes is difficult on traditional 3D computer displays. Virtual reality substantially enhances this technique in terms of inspecting and validating model meshes, as well as visualizing and interpreting simulated flow data (Figure 3).

First, VR facilitates the creation of accurate meshes because it allows us to inspect these virtual structures' quality and accuracy before we run simulations. Second, VR displays flow simulation data in a more intuitive way than 2D screens. Using the VR plugins available in ParaView (www.paraview.org, Kitware), users can navigate through the simulated flow fields, getting a "molecule's eye view" of flow phenomena (Figure 3b), and can watch flow patterns change over time in the StreamlineVR software, improving our ability to communicate the results of fluid dynamics simulations in a more intuitive manner. In this study, CT scans were segmented into a detailed computational mesh, accurately representing the major and minor airways of monitor lizards, *Varanidae*. The surface of the computational meshes expanded and contracted to simulate lung motion during ventilation and provided the boundary conditions for flow. During both phases of ventilation in the model, air moves caudally through the intrapulmonary bronchus and cranially through the secondary bronchi, moving between secondary bronchi through intracameral perforations.

### 3.1.3 | Developing virtual reality visualizations to explore substrate flow during dinosaur track formation

Fossil footprints, or tracks, are purely sedimentary structures that preserve a record of substrate flow around a moving foot (Falkingham et al., 2020; Falkingham & Gatesy, 2014; Gatesy & Falkingham, 2020). During the period of foot-ground interaction, both the original surface and deeper layers are deformed. For extinct theropod dinosaurs, experiments with living birds offer valuable reference, yet substrate and foot opacity hinders direct observation of subsurface foot movement and sediment flow. X-ray imaging can be combined with 3D animation to reconstruct skeletal motion through X-ray Reconstruction of Moving Morphology (Brainerd et al., 2010; Gatesy et al., 2010). XROMM has enabled track formation in a chicken-like bird, the guineafowl, to be elucidated across a spectrum of substrates (Falkingham & Gatesy, 2014; Turner et al., 2020). Viewing sediment motion is more difficult in X-rays, though a limited number of metal particles within the substrate have been traced using this method (Ellis & Gatesy, 2013).

To see detailed dynamic interactions between substrate and foot as track features form throughout the entire track volume, we use Discrete Element Method (DEM) simulations. Foot motion based off CT scans of Early Jurassic fossil tracks and guineafowl XROMM data serve as inputs for dynamic DEM substrate simulations made up of millions of particles (Falkingham & Gatesy, 2014). Unfortunately, the large particle numbers required for high-resolution simulations (>2,000,000) make observation of subsurface patterns difficult due to occlusion and visual similarity between elements (Figure 4a).

To explore the dense time-varying volumes of 3D data generated from these methods, we turned to an immersive VR room, Brown's Yurt Ultimate Reality Theater (YURT) (Figure 4b). Virtual reality provides significant advantages for spatially complex data (Novotny et al., 2019; Schuchardt & Bowman, 2007). Both stereo and motion parallax, particularly for close-up data exploration, allows for particle location, movement, and depth to be easily perceived relative to neighboring particles. Color is no longer needed to represent depth and can be used to represent other variables. Off-the-shelf data analysis tools were unable to adequately visualize the spatial complexity of our unsteady flow datasets, leading us to design our own VR visualization application.

Through an iterative visualization development process spanning 4 years, we created a custom application to view the interactions and flow patterns of interest in the challenging datasets. Introducing our visualization problem to students in a VR visualization design course using the scientific sketching method (Keefe et al., 2008; Novotny et al., 2019) at the start of our collaboration rapidly moved visualizations through sketching, prototyping, and implementation phases, exposing the subject scientists to a range of possible visualizations. Following each course offering, weekly meetings were held in the YURT, immersing the visualization experts and domain scientists in the newest application features (Figure 4c,d). These frequent and hyper-focused meetings maintained continuous feedback between the learning of data and the direction of visualization development.

Our custom application now creates interactive visualizations that allow us to synthesize substrate flow at the particle (Figure 4d, e), particle cluster (Figure 4e,f), surface (Figure 4e,g,h), and volumetric scale (Figure 4e–h) while maintaining anatomical context—providing a dynamic perspective on the 3D formation of dinosaur track morphology. A video showing these visualizations is found at

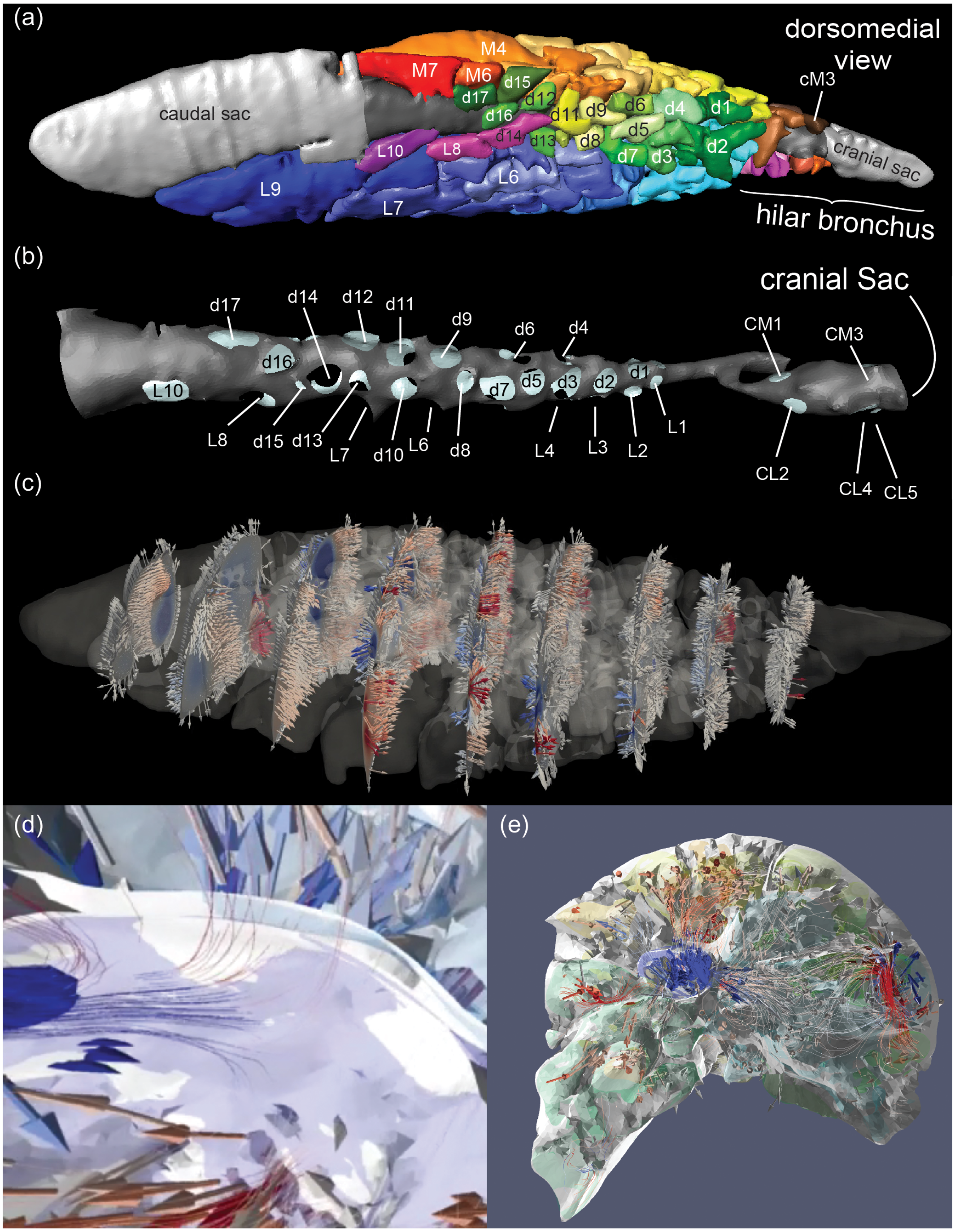


**FIGURE 3** Virtual reality aids in interpreting results from computational fluid dynamics (CFD) simulations. Both the external (a) and internal (b) anatomy of varanid lungs (*Varanus exanthematicus* figured) are complex, with multiple chambers branching off a long intrapulmonary bronchus and connected via fillagrated walls. This complex anatomy leads to even more complex pulmonary airflow patterns (c) that are difficult interpret using traditional 3D analysis techniques such as slices with glyphs indicating flow direction and magnitude. Virtual reality environments give a "particle's eye view" (d), allowing for a more intuitive appreciate of local flow environments. It is also possible to follow streamlines through the simulation (e) to visualize where flow paths diverge from the main streams while maintaining a broad perspective. (a–c) Adapted from Cieri and Farmer (2020)

https://www.youtube.com/watch?v=TWz5gqV0X3w. For more detail on the features, process of development, and insight gained from these visualizations, see Novotny et al. (2019). The DinoYURT application is available on GitHub (https://github.com/jonovotny/DinoVR) for time-varying point cloud or polygonal model data.

### 3.1.4 | Dynamic imaging techniques to understand functional morphology of the heart

While the heart serves the common function of delivering blood flow into the arteries of all vertebrates, there are large differences in the

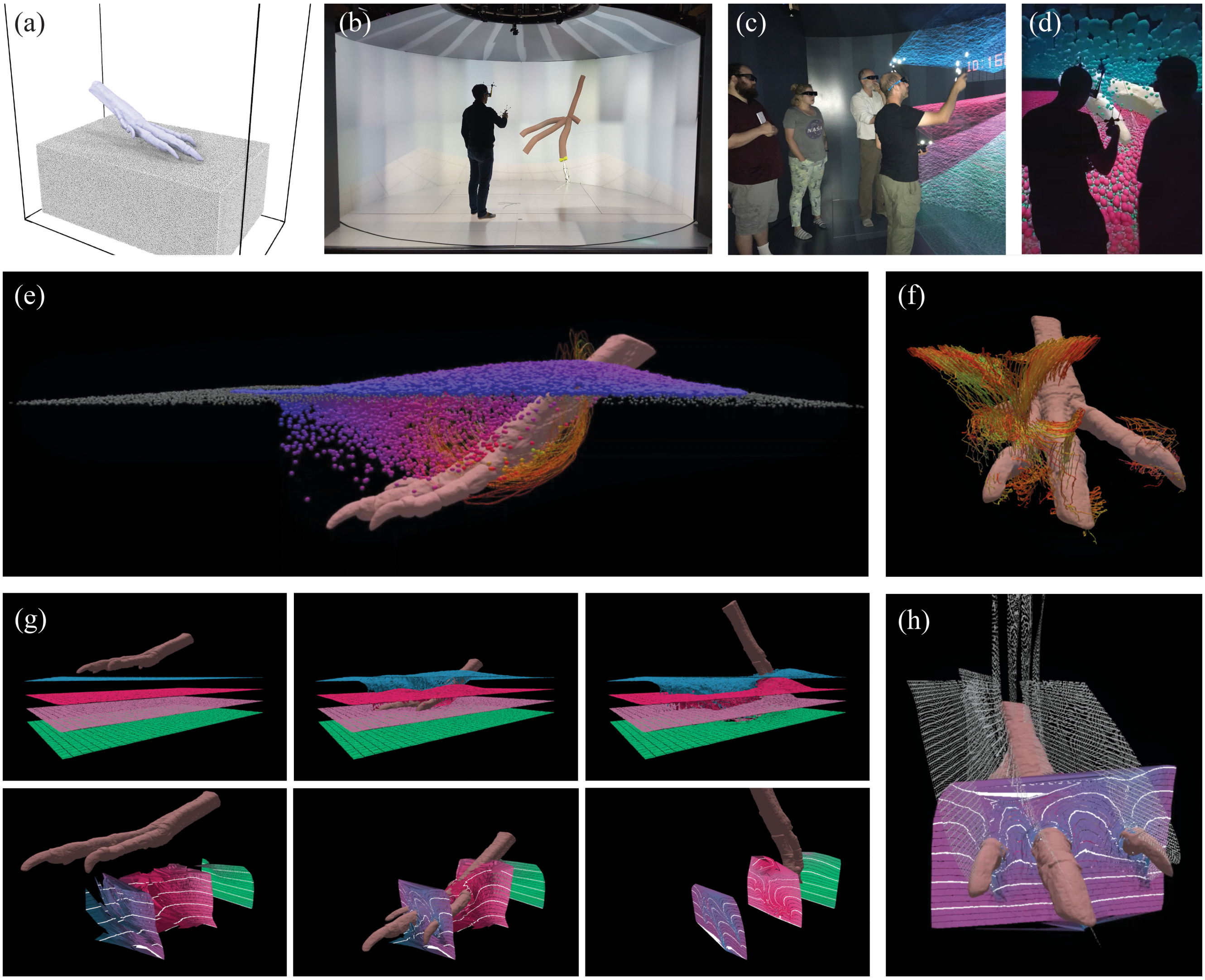


**FIGURE 4** Visualizing substrate flow in DEM-simulated dinosaur track formation using the DinoYURT application. (a) Starting frame of an animated dinosaur foot indenting a DEM simulated substrate volume. (b) The YURT ultimate reality theater (YURT) at Brown University. (c, d) Collaboration meetings in the YURT showing scale and immersion of data. (e) A lateral view of a deforming surface. (f) Example of clustered pathlines of particle movement, anterior view. (g) Example DinoYURT time surface visualizations. (h) Comparison of foot motion and simulated layer deformation

cardiac anatomy amongst the different vertebrate groups. The major evolutionary changes were associated with the appearance of a pulmonary circulation in air-breathing vertebrates providing a separate venous inflow and the complete separation of the left and right ventricles in crocodilians, birds, and mammals (Kardong, 2014). In this context, the cardiac ventricles of lizards, snakes, and turtles have an unusually complex 3D anatomy by being partially divided into three chambers by septa, one of which is in the sagittal plane and the other spirals from the horizontal plane cranially to approximately the sagittal plane caudally. Further complicating matters is that the atrial inflow is on the left of the ventricular midline and all arteries arise to the right of the midline because this necessitates that the oxygen-rich blood will have to cross from the ventricular left side and through part of the lumen that contains oxygen-poor blood in order to reach the systemic arteries. No wonder, then, that many of us have experienced a frustrating mismatch between the two-dimensional pictures or drawings of textbooks, reviews, and primary papers and the actual hearts we are investigating. As an additional complication, the heart is in constant motion, and the structural basis for cardiac function must therefore account for the motion of the relevant structures through the entire contractile process, including cardiac filling in diastole and emptying in systole.

To improve our understanding of movement of tissues and flow of blood beyond the limitations of static 2D figures, we have spent substantial efforts to move towards 3D descriptions. This has relied on dynamic imaging, which can be achieved by imaging techniques, such as ultrasound, nuclear magnetic resonance, or CT. We have used imaging on various species of reptiles to clarify the role of various cardiac structures. In many cases, the new dynamic images confirm the predictions made earlier on basis of classic dissections, but their didactic values are not to be underestimated, and a future goal would be to develop 3D and dynamic images that could be used for VR. For example, ultrasound served to clarify the contractile nature of the sinus venosus that actually constitute an additional cardiac chamber (Jensen et al., 2014, 2017) and showed the dynamic nature of atrioventricular valves and their importance in separating blood flows during cardiac filling (Jensen et al., 2010, 2014).

Ultrasound can be combined with injection of contrast (e.g., water with tiny air-bubbles) to follow the path that the blood follows through the beating heart. We used this approach to address the continuing debate on the position of the major septum dividing the reptilian ventricle (the vertical septum; [Jensen et al., 2011, 2014]). In this case, the visualization of blood flows revealed a sharp boundary along the vertical septum, supporting the view that blood flow separation can be ascribed to a thin aggregate of trabecular muscle.

Because the reptilian ventricle is non-spherical and highly trabeculated, it has been very difficult to estimate ejection fraction based on end-systolic and end-diastolic volumes. Here, MRI recently proved useful in generating dynamic visualizations of the entire cardiac cycle in tortoises, and verified the notion of very high ejection fractions in ectotherms (Williams et al., 2019). Magnetic resonance imaging (MRI) is a more cumbersome and expensive technique than ultrasound, and suitable images often require that the acquisition is triggered on the basis of the electrocardiogram (e.g., Williams et al., 2019).

As a practical problem, the imaging techniques require that the experimental animals are either physically restrained or immobilized with anesthetics during the imaging procedure. Even mild restraint, for example, for ultrasound, has profound influence of cardiac function. Some species, for example, crocodilians, at least under some circumstances, can react with bradycardia that is likely to increase end-diastolic volume. However, most reptiles react to constraint with a tachycardia and increased sympathetic tone that also increases contractility and lowers end-diastolic volume. The effects of anesthetics are also complicated because they act both centrally in the brain causing withdrawal of vagal tone on the heart (resulting in tachycardia).

### 3.1.5 | 3D models for communicating cardiac structure and function

The human heart develops four chambers, veins, and arteries from a linear heart tube, and between vertebrates there is much variation in heart morphology. To better understand these differences, we have generated more than 70 3D models in the last decade. Here, we discuss two aspects of 3D modeling. First, the workflow and in-house use. Second, we observe that our published models are almost never used, and that 3D PDFs are generally much under-used (Newe & Becker, 2018)—even though 3D PDFs may facilitate teaching (Chekrouni et al., 2020) and 3D models facilitate the preparation of surgery (Bartel et al., 2018). If models are adapted to VR, perhaps their communal use will be greater.

Our 3D modeling starts from an image series based on MRI or histology visualized with conventional histology stains or in-situ hybridization for mRNA or immunohistochemistry for protein. The image series is then imported to the software Amira (see [De Bakker et al., 2016] for details) and each image is then labeled for the items that are to be visualized in 3D, such as the whole organ, tissue-type, structure, domain of mRNA or protein expression, etc. A key aspect of the workflow is that precise labelling requires that each image is labeled. Time expenditure therefore increases with the number of images and items to be labeled and this increase, we suspect, is greater than linear. For 'crude' in-house analysis, modeling based on approximately 50 images labeled for 3–5 items has often been enough for analyses of the data and such 3D modeling can be done within a couple of days. For publishing, we spend additional time to simplify the models by reducing the size of artifacts (typically from sub-optimal alignment of images) and by 'smoothing' and/or 'interpolation' of labels to make surfaces less irregular. This makes the models easier to understand. Such work, however, pushes the time expenditure from number of days to weeks or even more when a great number of images and labeled items are used (see De Bakker et al., 2016 for details).

Using 3D modeling, we have shown that embryonic lizard, chicken, mouse, and human hearts are remarkably similar in structure and in expression patterns of transcription factors such as *Tbx3*, which in turn allowed us to predict similarity in electrical activation of the hearts (Jensen et al., 2012). Using 3D modeling again (Jensen et al., 2014), this time of the formed hearts of four species of squamate reptiles, we harmonized the description of reptile heart anatomy which has a notorious complexity (Kardong, 2014; Webb et al., 1971) that is augmented by a heterogeneous literature in terms of analysis and terminology (Webb et al., 1974). Additionally, similar 3D modeling has been used to show spatial differences in proliferation (de Boer et al., 2012), to quantify the area of connection between two molecularly identified tissues (Mohan et al., 2020), and more.

### 3.1.6 | *Digital Dinosaurs*: VR/AR in the college classroom

> It took about 25 years to progress from drawing stick figures on a screen to the photorealistic dinosaurs in "Jurassic Park." Within another 25 years, we should be able to wear a pair of AR glasses outdoors to see and interact with photorealistic dinosaurs eating a tree in our backyard. (Azuma, 1997)

These final words of Azuma's classic survey of AR truly augured our current technological age. Subsequent advances in cameras, sensors, and displays, along with the steady march of Moore's Law, have ushered in an adaptive radiation of new AR devices, particularly the georeferenced computers we now carry around in our pockets—smartphones. The recent advances in AR as well as VR technologies have also opened up novel pedagogical opportunities for STEAM curricula—not just as powerful tools to *communicate* complex 3D data and concepts to students, but also as a fertile new medium that empowers students to *create* their own immersive and interactive scientific visualizations.

Such technical skills training is integrated into the labs and lectures of *Digital Dinosaurs*, an annual undergraduate biology course at the University of South Florida (USF). Through their weekly computer-based labs, 24 students follow a sequential and integrated pipeline of scanning and processing 3D data, creating and animating models, and then deploying and visualizing them in VR/AR. The students' "real-world" exams consist of (1) a take-home midterm: writing a four-page NSF pre-proposal on a digital morphology research project (which they are encouraged to submit to external funding opportunities), and (2) a final project that involves scanning and modeling their own digital and 3D-printed creature (either real or imaginary), along with a conference-style presentation and dissemination on the course's VR/AR-capable Sketchfab page (https://sketchfab.com/digitaldinosaurs).

Data acquisition techniques include photogrammetry, structured light, and laser scanning. Synergistically, most materials for the final projects are sourced from the skeletal collection of the concurrent *Comparative Vertebrate Anatomy* course, in turn preserving these specimens as digital models available as morphology teaching assets for VR/AR and 3D printing. During the Autodesk Maya labs, students learn modeling and animation skills by creating a virtual museum exhibit, along with various objects and an animated *Deinonychus* specimen. Some students have difficulty orienting and navigating within the 3D space, so it is useful to preemptively explain the difference between rotating an object and rotating the user's view within the scene (as well as to have them enable the viewport grid as a frame of reference). In a subsequent lab, the scenes are exported as .FBX files and brought into Unity, which the students use to prepare their creations for VR/AR.

During the VR/AR lab co-hosted by the USF Advanced Visualization Center, students rotate through stations where they use various VR (Vive, Rift/Quest/Go, Cardboard) and AR (HoloLens, Aryzon, Mira, ZapBox) headsets and related devices (iPad, iPhone, Leap Motion sensor) (Figure 5c–f). Students are able to view and interact with the 3D scenes that they and their classmates created in the previous labs, as well as various anatomical apps and models (e.g., HoloAnatomy, Sketchfab).

One of the centerpieces of the lab experience is our interactive "ARchaeopteryx holographica" skeletal reconstruction of the Thermopolis specimen of *Archaeopteryx lithographica* (WDC-CSG-100). This 3D model was the product of multiplanar X-ray microtomosynthesis and marker-based XROMM kinematics research projects (Carney, 2016), efforts which also serve as instructional examples throughout the *Digital Dinosaurs* lectures. Led by the course's former student-turned-teaching assistant, we also generated photorealistic bone textures via macrophotogrammetry (Figure 5a), for compositing with each high-resolution, X-ray scanned bone model (Kirk et al., 2018). These assets, along with a photogrammetric reconstruction of the in situ fossil's limestone slab and hand-modeled wing feathers (both normal mapped), were then optimized for VR/AR through UV unwrapping in ZBrush (Pixelogic), followed by mesh retopology, texture transfer, and atlas generation in Maya (Figure 5b). Also using Maya, the full skeleton was assembled, rigged, and then animated using scientific motion transfer of in vivo kinematics from extant archosaurs—a flapping chukar and a walking alligator—to drive the glenohumeral joint (Carney, 2016). Finally, the in silico models and various animated sequences were developed into three custom AR app prototypes using Unity, and then demonstrated *in holo* using iOS and HoloLens devices during the VR/AR lab (Figure 5c–f; Video S1). Bringing this Digital Dinosaur "back to life" in an immersive and interactive AR environment allowed students to better visualize and comprehend the complex 3D morphology and motion of the flight stroke.

A student feedback assignment on the VR/AR lab illustrated that the HoloLens was the favorite device, specifically given the *immersion* and ability to blend realities, the *interactivity* with 3D objects, and the *visualization* of morphology that is otherwise difficult to see. However, students also mentioned the device's limited field of view as a detriment. The integrated nature of this VR/AR lab within the context of the course was noted by students as well: "It was also interesting to see the different ways that what we've been learning to do in Maya in class, and what was described at the Unity talk, can be applied!"

Such connection to the other labs is important for demonstrating that these VR/AR devices are not simply fun toys but functional tools. It is also quite evident that creating their own digital content not only allows students to gain a better understanding and appreciation of these technologies, but also fosters substantial intrinsic motivation throughout the assignments and final project. Ultimately, VR/AR can serve as an integral pedagogical component of undergraduate curricula, helping to engage, instruct, and inspire the next generation of biologists—as well as equip them with the digital skills to become innovators in the 21st century workforce.

#### 3.1.7 | Virtual reality for dental education

VR/AR may present partial solutions to the problems of extremely high cost and lack of standardization in dental education. First, the average dental student in 2017 incurred \$287,000 of education debt according to the American Dental Education Association (ADEA), an increase of 165% from the class of 2002 (Durham et al., 2019). Traditional dental education requires a great deal of expensive materials such as impression and filling materials for such procedures as making impressions of people's mouths and filling cavities. To take one example, impression materials cost between \$18 and 35 per procedure, and students are expected to do around 20 impressions on dummy patients for an implant or prosthodontics course.

Second, teaching in VR enables the standardization of information across multiple classes and/or institutions. Information from one school's experience of practicing dental implants was used in the VR teaching module in another institution that had limited access to dental implants and patients ready or able to receive dental implants. This kind of transfer can help to level the playing field in dental education. Even though the limited-access school will probably never have

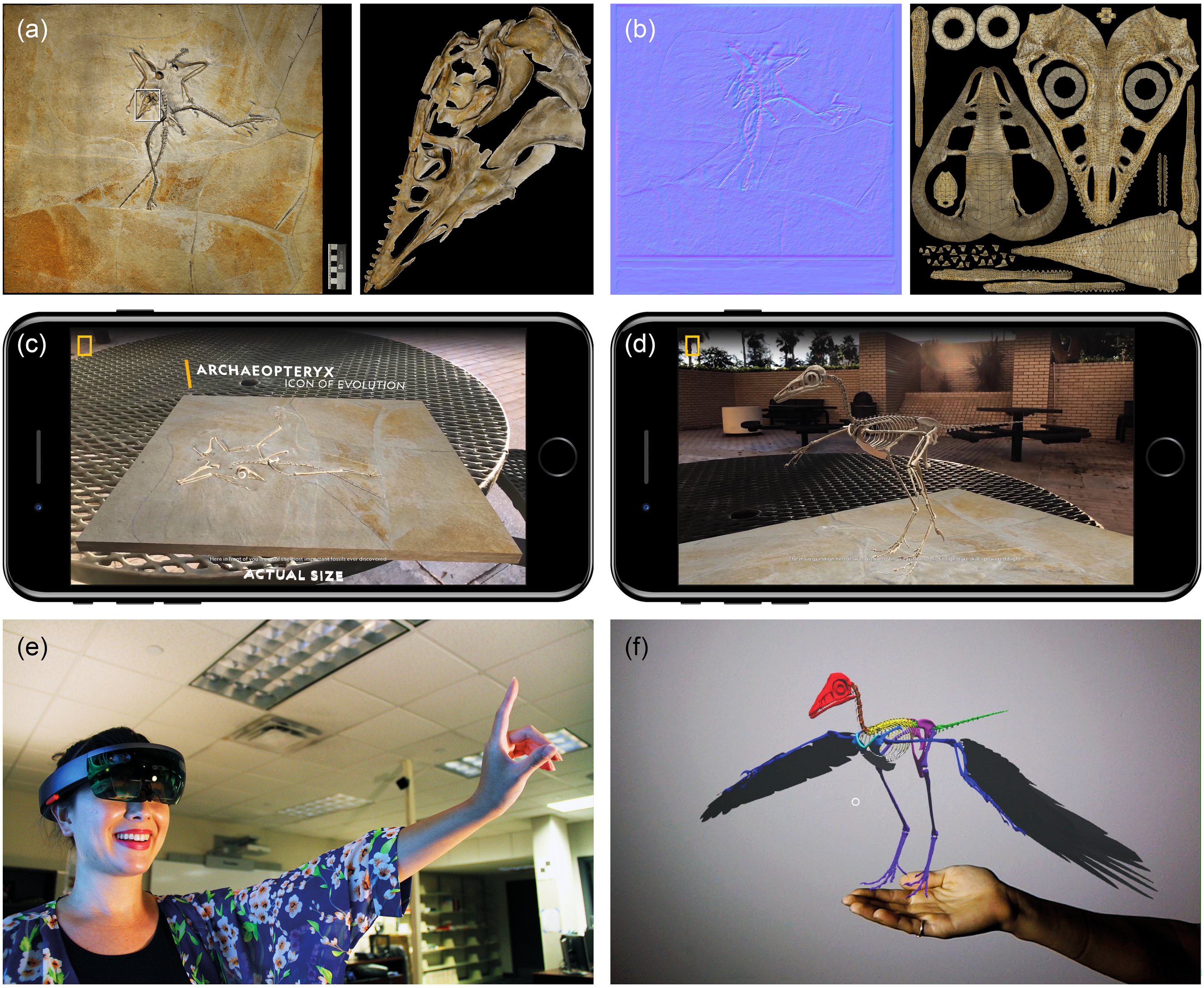


**FIGURE 5** Bringing *Archaeopteryx* "back to life" using two augmented reality platforms. (a) High-resolution photogrammetric reconstruction of the fossil slab (left) and close up of in situ cranial elements (right, from white box) of the Thermopolis specimen of *Archaeopteryx lithographica* (WDC-CSG-100). Scale bar: 8 cm. (b) Normal map of fossil slab top and sides (left). Texture atlas of cranial elements (right), generated after UV unwrapping, 3D assembly, retopology, and texture transfer of photogrammetry data (a, right). Maya UV snapshot is overlaid to illustrate the retopologized polygons (black lines). Map and atlas are 4096x4096 .PNG images. (c and d) Frames from iPhone screen recording of interactive AR app prototype, illustrating reconstructions of the textured slab and skeleton (see Video S1). (e) Student using a HoloLens AR headset to visualize and interact with the ARchaeopteryx model, and demonstrating the "air tap" finger gesture. (f) Student's view of the model, captured by the HoloLens as a mixed reality photo

students learn hands-on with implants during their education, the VR implant module will give them a virtual hands-on experience that they can use in their future practice.

We have developed several VR modules for dental education including a restorative implant dental module, a dental anatomy module, and a dental radiology module. The restorative implant module simulates the placement of dental implants for the students, with five subunits that give students virtual hands-on experience planning implantations and implanting dental products in different locations in the mouth. The exact location of missing teeth, the resorption or geometry of bone, as well as the medical history and allergy of the patients can be customized, such that hundreds of unique clinical situations can be simulated. The dental anatomy module familiarizes students with the complex anatomy associated with root canals at real and larger-than-life size. The dental radiology module is a 3D, fully interactive scan of the human head that allows students to view the CT scan data from any angle or plane, as if they were holding a human head in their hands.

### 3.2 | Best practices

The uses of VR/AR discussed above have been made possible through the rapid increase of digital imaging and modeling techniques applied to morphological studies. In recent years, guidelines have been presented for sharing and archiving such data (e.g., Davies et al, 2017), and we reiterate the most pertinent points here:

- All data required to replicate/verify a published study should be made publicly available upon publication, either as supplemental data hosted by the respective journal, or in a public repository (e.g., Figshare, MorphoSource, etc.) linked from the paper.
- Data archived in this way should include both the reconstructed models and original input data; that is, CT reconstructions should include surface models and original image stacks; photogrammetric data should include reconstructed models and original photo sets.
- Data files should be published/archived in accessible formats, ideally lossless, and open.

Use of such data in VR/AR applications presents additional considerations. While the data itself can be stored or shared in standard formats, the interactive nature of VR/AR means it is the 'experience' of interacting with the data that might be of interest for sharing. A current lack of 'standard' ways of viewing and interacting with VR/AR data makes it difficult to share such experiences. In many cases, including some of those highlighted above, specialist hardware and/or software are required that cannot be easily distributed. This will undoubtedly change in coming years as VR/AR becomes more standard not just in our field, but in other academic fields and beyond, particularly as VR gaming becomes more mainstream. Until such a time that VR interaction becomes standard, however, there are steps which can be taken to facilitate sharing of VR and AR experiences:

- Where possible, use (ideally freely available) existing tools to create the VR/AR experience. For instance, if the experience is built with Unity or Unreal Engine, the scene can be shared and others are able to use the software to view the scene and data. Compatibility with a wide range of VR/AR headsets and controllers are already accounted for by the software, and the range of compatible hardware is maximized. This also offers an opportunity for standardized control schemes across different VR/AR experiences.
- If designing custom software: not all available software is ideal for all use-cases, and it is inevitable that custom VR/AR software will sometimes be required. When this is the case, using common APIs such as SteamVR will maximize compatibility with headsets and controllers. If the software as a whole cannot be made available with the data, consider also producing a 'viewer' application that can ideally be made open source.
- If utilizing specialist hardware: in cases where the VR/AR experience is built around specialist hardware (e.g., the YURT described above), it can be difficult to share that experience. As when using custom software, the answer may be to write a 'viewer' program that maintains compatibility with standard headsets and controllers, and as much functionality of the original software/hardware as possible. This was the case with DinoYURT above, where a separate viewer application was made available allowing visualization and interaction using standard VR headsets.

## 3.3 | Concluding remarks

Over the last few decades, the study of morphology has undergone a digital revolution, whereby computer tools and analyses such as digital imaging (CT, MRI, ultrasound, etc.) and modeling (finite element and CFD) have made the field more quantitative, integrative, and comparative by enabling a big-data approach. Because these techniques bring 3D morphology into a 2D digital environment, however, it is substantially more difficult for analog creatures such as scientists to interact with such data intuitively and collaboratively.

VR/AR promise to close the loop, making 3D morphology and motion more intuitive and accessible. These technologies will only continue to mature, through advances in domains such as optics, haptics, computer vision, and the Internet of Things. Future directions for education and outreach will undoubtedly leverage the accelerating scale and scope of mobile platforms and new breakthroughs in hardware, as well as continue the trend of digitally enhancing or retrofitting analog materials with VR/AR—from 3D models leaping from pages in a textbook, to interactive flesh and motion augmenting specimens in a museum. AR could be useful in the preparation of fossil morphology as well: an X-ray scan could be registered to and projected within the physical specimen and used as a 3D guide for the removal of matrix. Theoretically, CT-scanned bones of living animals could be animated in vivo during marker-based XROMM, for the real-time visualization of moving morphology in VR or perhaps even AR. Looking forward, future breakthroughs in hardware may involve migrating the projected images onto or inside the eyeball itself (e.g., virtual retinal displays). If so, within another 25 years, we should be able to wear a pair of AR contact lenses to see and interact with photorealistic dinosaurs and other virtual morphology in our backyard, classroom, or laboratory.

Until quite recently, access to VR/AR technology has presumably been the main barrier to widespread use of these methods in research, teaching, and outreach. Hardware is becoming much more affordable, more open-source software is being developed, and modern smartphones can enable AR as well as VR when paired with inexpensive cardboard headsets. Advances in VR/AR should also help to make science more open, by better facilitating the sharing of digital data between researchers, labs, and institutions even during periods of restricted travel.

No longer relegated to the realm of science fiction, VR/AR technologies show great potential as a new platform for scientific research. The case studies presented herein demonstrate the utility of and insights gained from applying these various methods to morphological research and pedagogy. VR/AR are not limited to the applications presented, however, and can be used to share, visualize, or analyze any morphological or graphical data, such as paleontological specimens beyond dinosaurs, geometric morphometric data, 3D videos, or the results of finite elements analysis. VR/AR are powerful tools for harnessing new modalities of investigation, collaboration, teaching, and outreach. These emerging avenues can foster interest and intersections across STEAM fields and help inspire future morphologists. Ultimately, we encourage others in the morphology community to adopt this technology in order to fully realize the incredible opportunities of this rapidly evolving digital frontier.

## ACKNOWLEDGMENTS

The authors gratefully acknowledge support from the National Science Foundation (IOS 1929637 to CGF) and the Company of Biologists for financial support of a symposium and workshop hosted by the International Society of Vertebrate Morphology at the 2019 ICVM Congress. We also acknowledge funding support from: National Science Foundation grants EAR-1452119 (SMG and PLF) and IOS-0925077 (SMG); ARCHER Leadership award (PLF); Salomon Faculty Research Award, Brown University (SMG); National Science Foundation grant SGER-0917538 (RMC), National Geographic Society/Waitt Foundation grant W340-14 (RMC), and software donations from Capturing Reality and FEI (RMC). We thank Alec Baines for assisting in the photogrammetric reconstruction, as well as Tina Gagliardo and Hope Bartlin for demonstrating the HoloLens.

## AUTHOR CONTRIBUTIONS

**Robert Cieri:** Conceptualization (lead); data curation (lead); funding acquisition (lead); investigation (lead); methodology (lead); project administration (lead); supervision (lead); visualization (lead); writing – original draft (lead); writing – review and editing (lead). **Morgan Turner:** Data curation (equal); investigation (equal); software (equal); supervision (equal); visualization (equal); writing – original draft (equal); writing – review and editing (equal). **Ryan Carney:** Conceptualization (equal); funding acquisition (supporting); methodology (equal); software (equal); visualization (equal); writing – original draft (equal); writing – review and editing (equal). **Peter Falkingham:** Conceptualization (supporting); methodology (equal); writing – original draft (equal). **Alex Kirk:** Conceptualization (equal); methodology (equal). **Tobias Wang:** Conceptualization (equal); writing – original draft (equal). **Bjarke Jensen:** Conceptualization (equal); writing – original draft (supporting). **Johannes Novotny:** Methodology (equal); software (equal). **Joshua Tveite:** Methodology (equal); software (equal). **Stephen Gatesy:** Conceptualization (equal); methodology (equal); software (equal). **David Laidlaw:** Methodology (equal); software (equal). **Howard Kaplan:** Methodology (equal); software (equal). **Antoon Moorman:** Investigation (equal); methodology (equal); resources (equal); software (equal). **Mark Howell:** Methodology (equal); software (equal). **Benjamin Engel:** Methodology (equal); resources (equal). **Cole Cruz:** Methodology (equal); software (equal). **Adam Smith:** Methodology (equal); software (equal). **William Gerichs:** Methodology (equal); software (equal). **Yingjie Lian:** Methodology (equal); software (equal). **Johanna Schultz:** Methodology (equal); visualization (equal); writing – original draft (equal). **CG Farmer:** Conceptualization (equal); funding acquisition (equal); methodology (equal); project administration (equal); resources (equal); software (equal); writing – original draft (equal).

## PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1002/jmor.21421.

## DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

## ORCID

*Robert L. Cieri* https://orcid.org/0000-0001-6905-9148
*Ryan M. Carney* https://orcid.org/0000-0002-5537-5366
*Bjarke Jensen* https://orcid.org/0000-0002-7750-8035

## REFERENCES

Azuma, R. T. (1997). A survey of augmented reality. *Presence*, *6*(4), 355–385.

Azuma, R.T., Baillot, Y., Behringer, R., Feiner, S., Julier, S., & MacIntyre, B. (2001). Recent advances in augmented reality. *IEEE Computer Graphics and Applications*, 34–47.

Bartel, T., Rivard, A., Jimenez, A., Mestres, C. A., & Müller, S. (2018). Medical three-dimensional printing opens up new opportunities in cardiology and cardiac surgery. *European Heart Journal*, *39*(15), 1246–1254. https://doi.org/10.1093/eurheartj/ehx016

Bimber, O., Encarnação, L. M., & Schmalstieg, D. (2003). The virtual showcase as a new platform for augmented reality digital storytelling. *Proceedings of the Workshop on Virtual Environments, EGVE'03*, 87–95. https://doi.org/10.1145/769953-769964

Bimber, O., Gatesy, S. M., Witmer, L. M., Raskar, R., & Encarnacao, L. M. (2002). Merging fossil specimens with computer-generated information. *Computer*, 45–50.

Bimber, O., & Raskar, R. (2019). *Spatial augmented reality: Merging real and virtual worlds*. AK Peters/CRC Press.

Brainerd, E. L., Baier, D. B., Gatesy, S. M., Hedrick, T. L., Metzger, K. A., Gilbert, S. L., & Crisco, J. J. (2010). X-ray reconstruction of moving morphology (XROMM): precision, accuracy and applications in comparative biomechanics research. *Journal of Experimental Zoology Part A: Ecological Genetics and Physiology*, *313*, 262–279.

Carney, R. M. (2016). *Evolution of the archosaurian shoulder joint and the flight stroke of Archaeopteryx*. Doctoral dissertation, Brown University.

Chekrouni, N., Kleipool, R. P., & de Bakker, B. S. (2020). The impact of using three-dimensional digital models of human embryos in the biomedical curriculum. *Annals of Anatomy*, *227*, 151430. https://doi.org/10.1016/j.aanat.2019.151430

Cieri, R. L., Craven, B. A., Schachner, E. R., & Farmer, C. G. (2014). New insight into the evolution of the vertebrate respiratory system and the discovery of unidirectional airflow in iguana lungs. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(48), 17218–17223. https://doi.org/10.1073/pnas.1405088111

Cieri, R. L., & Farmer, C. G. (2020). Computational fluid dynamics reveals a unique net unidirectional pattern of pulmonary airflow in the Savannah monitor lizard (*Varanus exanthematicus*). *Anatomical Record*, *303*(7), 1768–1791. https://doi.org/10.1002/ar.24293

De Bakker, B. S., De Jong, K. H., Hagoort, J., De Bree, K., Besselink, C. T., De Kanter, F. E. C., Veldhuis, T., Bais, B., Schildmeijer, R., Ruijter, J. M., & Oostra, R. J. (2016). An interactive three-dimensional digital atlas and quantitative database of human development. *Science*, *354*(6315), aag0053. https://doi.org/10.1126/science.aag0053

de Boer, B. A., van den Berg, G., de Boer, P. A. J., Moorman, A. F. M., & Ruijter, J. M. (2012). Growth of the developing mouse heart: An interactive qualitative and quantitative 3D atlas. *Developmental Biology*, *368*(2), 203–213. https://doi.org/10.1016/j.ydbio.2012.05.001

Davies, T. G. (2017). Open data and digital morphology. *Proceedings of the Royal Society B Biological Sciences*, *284*. https://doi.org/10.1098/rspb.2017.0194

Durham, M., Engel, B., Ferrill, T., Halford, J., Singh, T. P., & Gladwell, M. (2019). Digitally augmented learning in implant dentistry. *Oral and Maxillofacial Surgery Clinics of North America*, *31*(3), 387–398. https://doi.org/10.1016/j.coms.2019.03.003

Eckhoff, D. G., Bach, J. M., Spitzer, V. M., Reinig, K. D., Bagur, M. M., Baldini, T. H., … Humphries, S. (2003). Three-dimensional morphology and kinematics of the distal part of the femur viewed in virtual reality: Part II. *Journal of Bone and Joint Surgery—Series A*, *85*(SUPPL. 4), 97–104. https://doi.org/10.2106/00004623-200300004-00012

Ellis, R., & Gatesy, S. (2013). A biplanar X-ray method for three-dimensional analysis of track formation. *Palaeontologia Electronica*, *16*(1) 1T, 16p-1T, 16p, 1–16. http://palaeo-electronica.org/content/pdfs/324.pdf

Falkingham, P. L., & Gatesy, S. M. (2014). The birth of a dinosaur footprint: Subsurface 3D motion reconstruction and discrete element simulation reveal track ontogeny. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(51), 18279–18284. https://doi.org/10.1073/pnas.1416252111

Falkingham, P. L., Turner, M. L., & Gatesy, S. M. (2020). Constructing and testing hypotheses of dinosaur foot motions from fossil tracks using digitization and simulation. *Palaeontology*, *63*(6), 865–880. https://doi.org/10.1111/pala.12502

Farmer, C. G. (2015). Similarity of crocodilian and avian lungs indicates unidirectional flow is ancestral for archosaurs. *Integrative and Comparative Biology*, *55*(6), 1–10.

Farmer, C. G., & Sanders, K. (2010). Unidirectional airflow in the lungs of alligators. *Science*, *327*(5963), 338–340.

Gatesy, S. M., Baier, D. B., Jenkins, F. A., & Dial, K. P. (2010). Scientific rotoscoping: a morphology-based method of 3-D motion analysis and visualization. *Journal of Experimental Zoology Part A: Ecological Genetics and Physiology*, *313A*, 244–261.

Gatesy, S. M., & Falkingham, P. L. (2020). Hitchcock's Leptodactyli, penetrative tracks, and dinosaur footprint diversity. *Journal of Vertebrate Paleontology*, *40*(3), e1781142. https://doi.org/10.1080/02724634.2020.1781142

Jensen, B., Larsen, C. K., Nielsen, J. M., Simonsen, L. S., & Wang, T. (2011). Change of cardiac function, but not form, in postprandial pythons. *Comparative Biochemistry and Physiology—A Molecular and Integrative Physiology*, *160*(1), 35–42. https://doi.org/10.1016/j.cbpa.2011.04.018

Jensen, B., Moorman, A. F. M., & Wang, T. (2014). Structure and function of the hearts of lizards and snakes. *Biological Reviews of the Cambridge Philosophical Society*, *89*(2), 302–336. https://doi.org/10.1111/brv.12056

Jensen, B., Nielsen, J. M., Axelsson, M., Pedersen, M., Löfman, C., & Wang, T. (2010). How the python heart separates pulmonary and systemic blood pressures and blood flows. *The Journal of Experimental Biology*, *213*(Pt 10), 1611–1617. https://doi.org/10.1242/jeb.030999

Jensen, B., Boukens, B. J. D., Postma, A. V., Gunst, Q. D., van den Hoff, M. J. B., Moorman, A. F. M., Wang, T., & Christoffels, V. M. (2012). Identifying the evolutionary building blocks of the cardiac conduction system. *PLoS One*, *7*, 1–13.

Jensen, B., Vesterskov, S., Boukens, B. J., Nielsen, J. M., Moorman, A. F. M., Christoffels, V. M., & Wang, T. (2017). Morpho-functional characterization of the systemic venous pole of the reptile heart. *Scientific Reports*, *7*(1), 1–12. https://doi.org/10.1038/s41598-017-06291-z

Kardong, K. V. (2014). *Vertebrates: Comparative anatomy, function, evolution (seventh)*. McGraw-Hill.

Keefe, D. F., Acevedo, D., Miles, J., Drury, F., Swartz, S. M., & Laidlaw, D. H. (2008). Scientific sketching for collaborative VR visualization design. *IEEE Transactions on Visualization and Computer Graphics*, *14*(4), 835–847. https://doi.org/10.1109/TVCG.2008.31

Kirk, A., Baines, A., Kaplan, H., & Carney, R. M. (2018). Macrophotogrammetric reconstruction of Archaeopteryx. *Journal of Vertebrate Paleontology: Program and Abstracts*, 159.

Krogh, A. (1922). *The anatomy and physiology of capillaries*. Yale University Press.

Milgram, P., & Kishino, F. (1994). A taxonomy of mixed reality visual displays. *IEICE Transactions on Information Systems*, *E77-D*(12), 1–15.

Mohan, R. A., Bosada, F. M., Weerd, J. H. V., Van Duijvenboden, K., Wang, J., Mommersteeg, M. T. M., Hooijkaas, I. B., Wakker, V., de Gier-de Vries, C., Coronel, R., & Boink, G. J. (2020). T-box transcription factor 3 governs a transcriptional program for the function of the mouse atrioventricular conduction system. *Proceedings of the National Academy of Sciences of the United States of America*, *117*(31), 18617–18626. https://doi.org/10.1073/pnas.1919379117

Newe, A., & Becker, L. (2018). Three-dimensional portable document format (3D PDF) in clinical communication and biomedical sciences: Systematic review of applications, tools, and protocols. *Journal of Medical Internet Research*, *20*(8), e10295. https://doi.org/10.2196/10295

Novotny, J., Tveite, J., Turner, M. L., Gatesy, S., Drury, F., Falkingham, P., & Laidlaw, D. H. (2019). Developing virtual reality visualizations for unsteady flow analysis of dinosaur track formation using scientific sketching. *IEEE Transactions on Visualization and Computer Graphics*, *25*(5), 2145–2154. https://doi.org/10.1109/TVCG.2019.2898796

Pellas, N., Mystakidis, S., & Kazanidis, I. (2021). Immersive virtual reality in K-12 and higher education: A systematic review of the last decade scientific literature. *Virtual Reality*, *9*, 835–861. https://doi.org/10.1007/s10055-020-00489-9

Radianti, J., Majchrzak, T. A., Fromm, J., & Wohlgenannt, I. (2020). A systematic review of immersive virtual reality applications for higher education: Design elements, lessons learned, and research agenda. *Computers and Education*, *147*(July 2019), 103778. https://doi.org/10.1016/j.compedu.2019.103778

Rokhsaritalemi, S., Sadeghi-Niaraki, A., & Choi, S. M. (2020). A review on mixed reality: Current trends, challenges and prospects. *Applied Sciences (Switzerland)*, *10*(2), 1–26. https://doi.org/10.3390/app10020636

Sarnat, E. M., Hita Garcia, F., Dudley, K., Liu, C., Fischer, G., & Economo, E. P. (2019). Ready species one: Exploring the use of augmented reality to enhance systematic biology with a revision of Fijian Strumigenys (hymenoptera: Formicidae). *Insect Systematics and Diversity*, *3*(6), 1–43. https://doi.org/10.1093/isd/ixz005

Schachner, E. R., Cieri, R. L., Butler, J. P., & Farmer, C. G. (2013). Unidirectional pulmonary airflow patterns in the savannah monitor lizard. *Nature*, *506*, 367–370. https://doi.org/10.1038/nature.12871

Schachner, E. R., Hutchinson, J. R., & Farmer, C. G. (2013). Pulmonary anatomy in the Nile crocodile and the evolution of unidirectional airflow in Archosauria. *PeerJ*, *1*, e60–e60.

Schuchardt, P., & Bowman, D. A. (2007). The benefits of immersion for spatial understanding of complex underground cave systems. *Proceedings of the ACM Symposium on Virtual Reality Software and Technology, VRST*, *1*(212), 121–124. https://doi.org/10.1145/1315184.1315205

Turner, M. L., Falkingham, P. L., & Gatesy, S. M. (2020). It's in the loop: Shared sub-surface foot kinematics in birds and other dinosaurs shed light on a new dimension of fossil track diversity: Looping tridactyl foot kinematics. *Biology Letters*, *16*(7), 27–32. https://doi.org/10.1098/rsbl.2020.0309rsbl20200309

Webb, G., Heatwole, H., & Bavay, J. D. (1971). Comparative cardiac anatomy of the Reptilia. I. the chambers and septa of the varanid ventricle. *Journal of Morphology*, *134*, 335–350. http://onlinelibrary.wiley.com/doi/10.1002/jmor.1051340306/abstract

Webb, G. J. W., Heatwole, H., & Bavay, J., de. (1974). Comparative cardiac anatomy of the reptilia. II. A critique of the literature on the Squamata and Rhynchocephalia. *Journal of Morphology*, *142*, 1–20. http://onlinelibrary.wiley.com/doi/10.1002/jmor.1051420102/abstract

Williams, C. J. A., Greunz, E. M., Ringgaard, S., Hansen, K., Bertelsen, M. F., & Wang, T. (2019). Magnetic resonance imaging (MRI) reveals high cardiac ejection fractions in red-footed tortoises (Chelonoidis carbonarius). *Journal of Experimental Biology*, *222*(18), 1–6. https://doi.org/10.1242/jeb.206714

## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

**How to cite this article:** Cieri, R. L., Turner, M. L., Carney, R. M., Falkingham, P. L., Kirk, A. M., Wang, T., Jensen, B., Novotny, J., Tveite, J., Gatesy, S. M., Laidlaw, D. H., Kaplan, H., Moorman, A. F. M., Howell, M., Engel, B., Cruz, C., Smith, A., Gerichs, W., Lian, Y., … Farmer, C. G. (2021). Virtual and augmented reality: New tools for visualizing, analyzing, and communicating complex morphology. *Journal of Morphology*, *282*(12), 1785–1800. https://doi.org/10.1002/jmor.21421