RETHINKING THE EVOLUTION OF TEMPORAL FENESTRAE IN TURTLES: AN INTERACTIVE APPLICATION FOR COMPARATIVE ANATOMY AND PHYLOGENETICS

by
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Abstract

The question of turtle origins is among the oldest and most debated problems in vertebrate systematics. A key factor in this debate is the pattern of temporal fenestration in the skull, which has long been central to amniote evolutionary hypotheses. Recently, there has been robust evidence supporting turtles as having evolved within the diapsid radiation, which includes all other living reptiles. This requires that the anapsid skull in turtles is secondarily derived. 'Transitional' fossils that support this theory were elusive until the Middle Permian reptile *Eunotosaurus africanus* was re-examined using computed tomography (CT) in 2015. *Eunotosaurus* exhibits features that help reconcile the gap between turtles and other reptiles, but how it does so is still misunderstood. This misconception is attributed to the complexity of the evolutionary concepts involved and a need for more intuitive visuals describing the complex architecture of the *Eunotosaurus* skull.

This thesis communicates the importance of *Eunotosaurus* to the study of turtle origins through a novel digital reconstruction and a 3D interactive web application. The first of its kind, this reconstruction utilizes best practices for restoring a fossil's antemortem shape. It is then implemented in an application focused on contextualizing this taxon in the 'tree of life.' This application provides a valuable learning resource for students and investigators as it contributes to virtual paleontology, evolutionary science pedagogy, and functional morphology.

Chairpersons of the Supervisory Committee

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Introduction

Where do turtles come from? This is one of the oldest and most debated questions in vertebrate evolutionary biology (Cox, 1969; Rieppel & Riesz, 1999; Zardoya & Meyer, 2001; Lyson *et al*. 2010, Lee 2013; Field *et al.* 2014; Schoch & Sues, 2016, 2019; Lyson & Bever, 2020). At the center of this conflict is the turtle body plan, which represents an extreme form of evolutionary 'experimentation' through which we can gauge the potential of developmental pathways among reptiles and ourselves. Resolving this mystery would provide new insights into the nature, timing, and order of character transformations that gave modern turtles their unique anatomy. One morphological area that has long held sway in the phylogenetic classification of amniotes (the clade comprising mammals, reptiles, birds, their respective lineages, and shared ancestor) is the temporal region of the skull, which enjoys a substantial diversity of form across the evolutionary history of this group (Cope, 1892; Williston, 1917; Werneburg, 2019).

Turtles exhibit a lack of temporal fenestration, giving them an anapsid skull that encases the adductor chamber completely in bone. They have this in common with many early (stem) reptiles and crown amniotes (Laurin & Reisz, 1995). Historically, this similarity was regarded as the conservation of the ancestral amniote form, assigning turtles as the sole survivors of a stem lineage that diverged long before the other crown reptiles (living tuatara, snakes, lizards, crocodilians, birds, and their closest fossil relatives) (see Joyce, 2015). However, recent morphological and molecular studies reject this hypothesis and conclude that turtles evolved within the diapsid radiation – which includes all living reptiles and is broadly defined by a skull with upper and lower temporal fenestrae (Bhullar & Bever, 2009; Schaffer *et al*. 2013; Wang *et al.* 2013; Bever *et al.* 2016).

This would mean that the anapsid skull in turtles is secondarily derived, an ancestral callback built around a diapsid evolutionary scaffold (Rieppel & deBragga, 1996). Yet, despite the theory of secondary anapsidy enjoying strong genomic support, recognizable 'intermediate' fossils that evidenced this trajectory from diapsid to anapsid remained elusive (Field *et al*. 2014). For years, the most significant stem turtle identified in the fossil record was the Late Triassic *Proganochelys quenstedti*, which had an anapsid skull (Gaffney, 1990). Where was this distant turtle relative with a *diapsid* skull?

The year 2015 brought *two* fossils fitting this description (Bever *et al.* 2015; Schoch and Sues, 2015). The oldest and most phylogenetically stem-ward of the two is *Eunotosaurus africanus* Seeley, a 260-million-year-old South African reptile that shares a striking number of unique post-cranial features with modern turtles (Gaffney, 1990; Gow, 1997; Li *et al.* 2008; Bever *et al*. 2015). While it had been discovered in 1892, it was not until 2015 that the enigmatic cranial morphology of *Eunotosaurus* – initially thought to lack an upper temporal fenestra (UTF) – was examined using computed tomography (CT) for the first time. This study by Dr. Gabriel Bever and colleagues found several cranial similarities with turtles, and most importantly, a hidden UTF. This opening was superficially covered by an anterior elongation of the supratemporal bone. This, coupled with a recognizable UTF and LTF (diapsid condition) in juvenile *Eunotosaurus* means that the expansion of the supratemporal occurred later in its ontogeny or life history. This ontogenetic change could very well explain the eventual anapsid condition in more crown-ward turtles, as changes in developmental histories have been known to contribute to major evolutionary novelties in other groups, or taxa (McNamara, 2012; Tokita *et al.* 2013; Haridy *et al*. 2016).

To summarize, *Eunotosaurus africanus* is an organism with both parareptile-like and turtle-like features that not only precedes the next fossil turtle relative (*Pappochelys)* by 20-million years but also displays a developmental shift in its temporal fenestration. Not only is it the diapsid 'intermediate' turtle form hypothesized by the genomic data, but its unique life history suggests a mechanism by which later turtles could have lost their temporal fenestrae. *Eunotosaurus* exhibits features that help reconcile the gap between turtles and other reptiles, but the evolutionary concepts involved in understanding this link can be complicated and are often misunderstood.

Interactive Learning in Academia

Advances in computational and graphic technologies – and the increasing ubiquity of their use – have opened the door for a wave of educational and investigative innovations. Information-rich multimedia applications support self-managed learning by responding to user interaction and leveraging the full spectrum of human processing capabilities, providing an alternative to the inefficiencies of rote memorization (Dembo & Seli, 2012). The applications in research are also significant: from 3D modeling technology revolutionizing how morphological data is collected, analyzed, and disseminated to interactive simulation applications dramatically improving surgical planning and medical training (van de Kamp *et al*. 2014; Smith *et al.* 2016; Sánchez-Margallo *et al.* 2021; Viglialoro *et al.* 2021). Overall, 3D interactive media are accessible, effective in communicating complex spatial relationships, and increase user enjoyment and knowledge retention (Raffan et al. 2017).

Existing Resources. The last two decades have brought a wave of new efforts concerning the teaching of evolutionary biology (Wei *et al*. 2012). Growing recognition of the interrelatedness of evolution in the life sciences has fueled several initiatives. Among them are the American Association of Medical Colleges' *Scientific Foundations for Future Physicians* which establishes evolutionary understanding as a key competency for students in medical disciplines, and *Vision and Change in Undergraduate Biology Education*, a teaching campaign backed by the National Science Foundation (NSF), National Institutes of Health (NIH), and the American Association for the Advancement of Science (AAAS). Outside of academia, the movement to bring scientific literacy to a wider audience has leveraged the digital age to produce a wealth of resources and platforms for teaching and learning evolutionary science. However, to the average user, much of this knowledge is difficult to attain either because it is locked behind a paywall, is intended to be accessed in the context of a lesson plan, and/or creates a high cognitive load with long-form text and difficult-to-read diagrams. A table of these resources can be found in **Appendix A**.

The best interactive online tools dealing with phylogenies and teaching macroevolutionary concepts are the Understanding Evolution project (https://evolution.berkeley.edu) run by the University of California Museum of Paleontology (UCMP) and the Evolution Lab (https://www.pbs.org/wgbh/nova/labs/lab/evolution/) run by NOVA Labs and the Biogen Foundation. Both projects do well to introduce tree-thinking, though the former is a generalized teaching aid designed for educators and the latter relies on outdated phylogenetic models and a staggeringly large tree diagram without any annotations on cladistics. Moreover, none of these digital resources go into detail on current findings in turtle phylogeny, much less use 3D morphological data for comparative analysis.

Teaching Evolutionary Biology. A proper understanding of key evolutionary concepts is crucial to appreciating the role that *Eunotosaurus* plays in the discussion of turtle evolutionary history. Furthermore, a foundational understanding of macroevolutionary processes and inferences has broad implications for humankind. Consider how animal studies implicitly integrate evolutionary thinking by exploiting our shared ancestry with model organisms. A key concept in this discipline is tree-thinking, which involves using cladograms – also called phylogenetic trees – that depict the evolutionary relationships between groups based on common ancestry.

While it may be expected that any individual who has taken an introductory biology course would be familiar with these concepts, research routinely finds that even students with extensive secondary-level and collegiate science coursework retain misconceptions and deficits in understanding evolution (Alters & Nelson, 2002). This knowledge gap is credited to persistent experiential, intuitive, myth-based, or vernacular biases that misappropriate the science (González Galli & Meinardi, 2011). Among these misconceptions are a tendency to ascribe intentionality to evolution, thinking in terms of evolutionary progress or advancement, the idea of "higher" and "lower" organisms, and an overall lack of key tree-thinking skills (Meir *et al.* 2007, Novick & Catley, 2007; Young *et al.* 2013).

To combat this problem of poor knowledge retention and misinformation, award-winning evolutionary biologist David A. Baum writes "what is needed are more resources:

computer programs, educational strategies, and accessible presentations of current phylogenetic knowledge" (2005). Fulfilling this need was the impetus for creating a novel interactive web application that not only communicates the findings of *Eunotosaurus'* cranial morphology in the context of turtle evolution but also clarifies the macroevolutionary concepts that underpin this work.

Didactic Considerations. The workflow for developing the web application design was informed by Jesse James Garrett's Elements of User Experience, onto which the following learning theories were applied:

- *Mezirow's Transformative Learning Theory* – provides opportunities for identifying, questioning, and revising student assumptions (Mezirow, 1997)
- *Sweller's Cognitive Load Theory* – champions reducing strain on learners' working memory by avoiding information overload (Sweller, 1988)
- *Mayer's Cognitive Theory of Multimedia Learning* – a set of principles for optimizing instructional design (Mayer & Moreno, 1998; Mayer, 2005, 2019)

Project Objectives and Scope

This project aims to design a 3D (three-dimensional) interactive progressive web application (PWA) that will detail and compare the cranial anatomy of *Eunotosaurus* against multiple taxa in their evolutionary contexts, clarify relevant phylogenetic relationships and inferences, and review cladistic principles in an interactive learning environment. Overall, this will communicate the significance of *Eunotosaurus* in the phylogenetic story of turtle evolution. Current images of *Eunotosaurus* and the proposed evolutionary change from diapsid to anapsid are limited to static reconstructions found only in scientific literature. They do not allow for full detail of the complex cranial anatomy involved and are designed with the assumption that a viewer will not project any of the common misconceptions seen in students of evolutionary science. Didactic efforts will focus on macroevolutionary patterns and phylogenetic inference, as these concepts are not only relevant but also usually under-represented in evolutionary biology curricula (González Galli & Meinardi, 2011).

The development of this application will continue to be an iterative process over the long term, and will change as stakeholder input, future user testing, and platform constraints come into play. The chosen format, PWA, leverages the speed, native media playback, and offline capabilities of a mobile app with the standalone cross-platform functionality of a web page. My goal here is to set the stage for further development of the final, functional end-user product. The scope of this project involves creating the following:

a) Digital 3D reconstruction of a *Eunotosaurus africanus* skull for comparative analysis
b) Design for the overall information architecture of the web application
c) Prototype of a specific user path that highlights key navigational, didactic, and customization functions of the final product
d) Several 2D reconstructions of fossil and extant representatives of the reptiles being compared to *Eunotosaurus africanus*
e) A reproducible workflow documenting the user experience and pedagogic principles that guided the design of the application, CT data acquisition, and digital reconstruction process.

Audience

The primary audience for this application will be scientific investigators, graduate, and undergraduate students who study organismal and evolutionary biology. The secondary audience includes hobbyists and lay individuals with interests in turtles, paleontology, evolution, and/or systematics. A potential tertiary audience would be educators interested in incorporating multimedia science applications into their lesson plans.

Significance

This project will not only produce a novel reconstruction of a *Eunotosaurus africanus* skull but an innovative approach for teaching and clarifying phylogenetic evolutionary hypotheses. Interactive 3D visualizations are a powerful tool for promoting understanding of complex ideas and will continue to revolutionize the field of biological communication. This application and methods will serve as a model for digital skull reconstructions across multiple disciplines, from virtual paleontology to functional morphology and craniofacial surgical planning. The user interface design methods will also model the assimilation of pedagogic and user experience principles in interactive biocommunication.

Methods

This section provides an overview of two aspects of the project. The first part deals with the techniques involved in the novel fossil reconstruction of *Eunotosaurus africanus*. The second covers design principles, didactic considerations, and details of the progressive web application. To put it another way, the first part centers on the discovery portion of the thesis, and the second part focuses on visual storytelling and interactive learning design.

Part 1. Novel Fossil Skull Reconstruction

The most influential contribution to evolutionary science comes from the study of fossils, which provide dated records of the morphological changes that occurred across evolutionary history (Scotland *et al.* 2003; Schoch & Sues, 2019). However, they are usually discovered bearing not only the marks of lifetime trauma and wear, but also post-mortem deformation over eons of geological compaction, chemical changes, and tectonism. These deformations can include flattening, bending, warping, shearing, erosion, or breakage. Reconstructions aim to achieve as close to an antemortem shape as possible to inform comparative analyses.

Several fossil taxa were reconstructed: a 3D skull of *Eunotosaurus africanus*, and seven 2D iconographic representations of relevant taxa including *Eunotosaurus*, *Captorhinus aguti*, *Youngina capensis*, *Sphenodon punctatus*, *Mesosuchus browni*, *Proganochelys quenstedti,* and *Chelydra serpentina*. The 2D reconstructions were based on previous work in primary sources (detailed later), two-dimensional shear correction from CT data, and specimen photography. The novel 3D reconstruction was more complicated, and so had to be broken down into two major stages. The first stage included reorientation of preserved bones, addressing deformations, and restoration of bilateral symmetry. The second was the extrapolation of missing data and global restoration of smooth contours. The former was done first in Cinema4D® (Maxon Computer GmbH), and the latter will be completed in ZBrush (Pixologic).

CT Data Acquisition. A detailed micro-CT scan and volume render of *Eunotosaurus africanus* was provided by the Center for Functional Anatomy and Evolution (FAE), at the Johns Hopkins University School of Medicine. While the surface details of the cranial anatomy could be observed on the original specimen, there was a limit to how much of the surrounding matrix could be extracted without endangering the integrity of the fossil (**Fig. 1**). Since the advent of minimally invasive computed tomography (CT), virtual segmentation and reconstruction have become standard practice because it allows investigators to work with fossils without harming valuable original materials.

The specimen (M777) had already been segmented from volumetric CT data using Amira®, and each bone was exported as a surface mesh. Initially, the data set was compressed and incomplete, so further recovery of surface meshes from Amira® was needed.

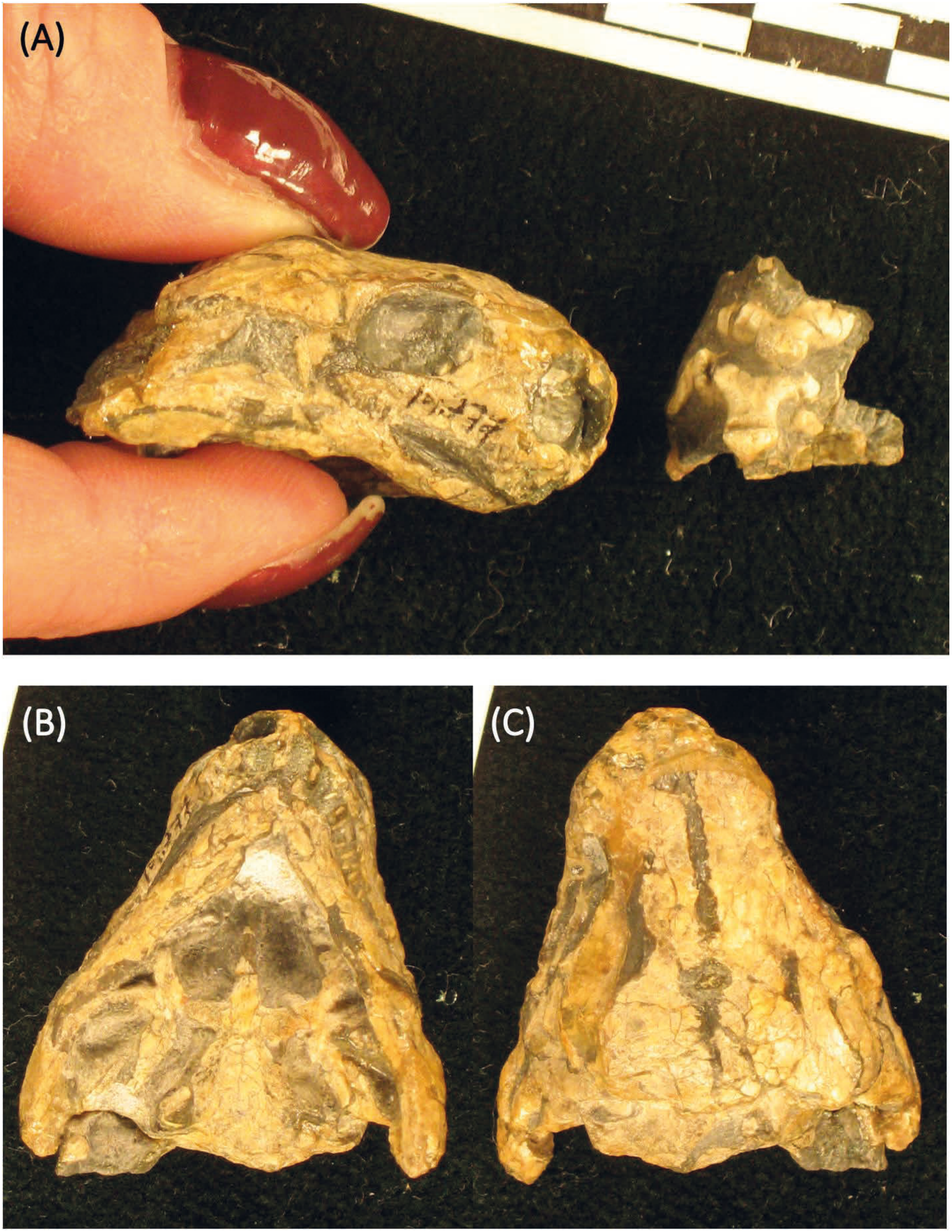


Figure 1a-c. Photographs of the *Eunotosaurus africanus* specimen, M777. **(A)** Lateral view, nose pointing to the right. **(B)** Ventral view. **(C)** Dorsal view. The nose is oriented towards the top in the last two photos.

Fossil Data Recovery. To accommodate for the older technology that the data and Amira® software were natively located on, any bones or meshes that were missing details after compression in the provided .STL files were pulled from Amira® in batches. Structures that were not in contact, like the nasal and the pterygoid bones, were exported in the same .OBJ file for later separation in ZBrush®. This batch method also helped direct the placement of bones that were missing in the original data set, as existing bones could be used as touchstones for placing new data.

This process began in Amira®, where the segmentation was completed before this project. A surface mesh needed to be generated from the volumetric data for later transfer to modeling programs like Cinema4D®. With the segmentation data object already generated in the Project Viewer, all that was needed was to right-click the object and Generate Surface. This created a new generator module called SurfaceGen. Clicking Apply in the Properties panel spawned a surface object titled segmentation.hx.surf. In the button menu, a Surface View module was then formed.

In the initial file setup, Dr. Bever had assigned a different material name to each bone. Therefore, the Properties > Material menu could be used to select the desired bone surface render. The viewer was cleared of previously selected data points (Properties > Action > Clear), and the desired material was loaded in the 3D viewer (Properties > Action > Add). Afterward, the Surface View > Extract Surface function generated an Extract Surface module. Clicking Apply in the Properties panel created an Extracted Surface object (**Fig. 2a**). This object could be selected and exported under Files > Export Data As > Wavefront (*.obj). Once each batch was saved, the Extracted Surface and Extract Surface objects were deleted, the Surface View cleared (Properties > Action > Clear), and a new Material (bone) could be chosen for export (**Fig. 2b**).

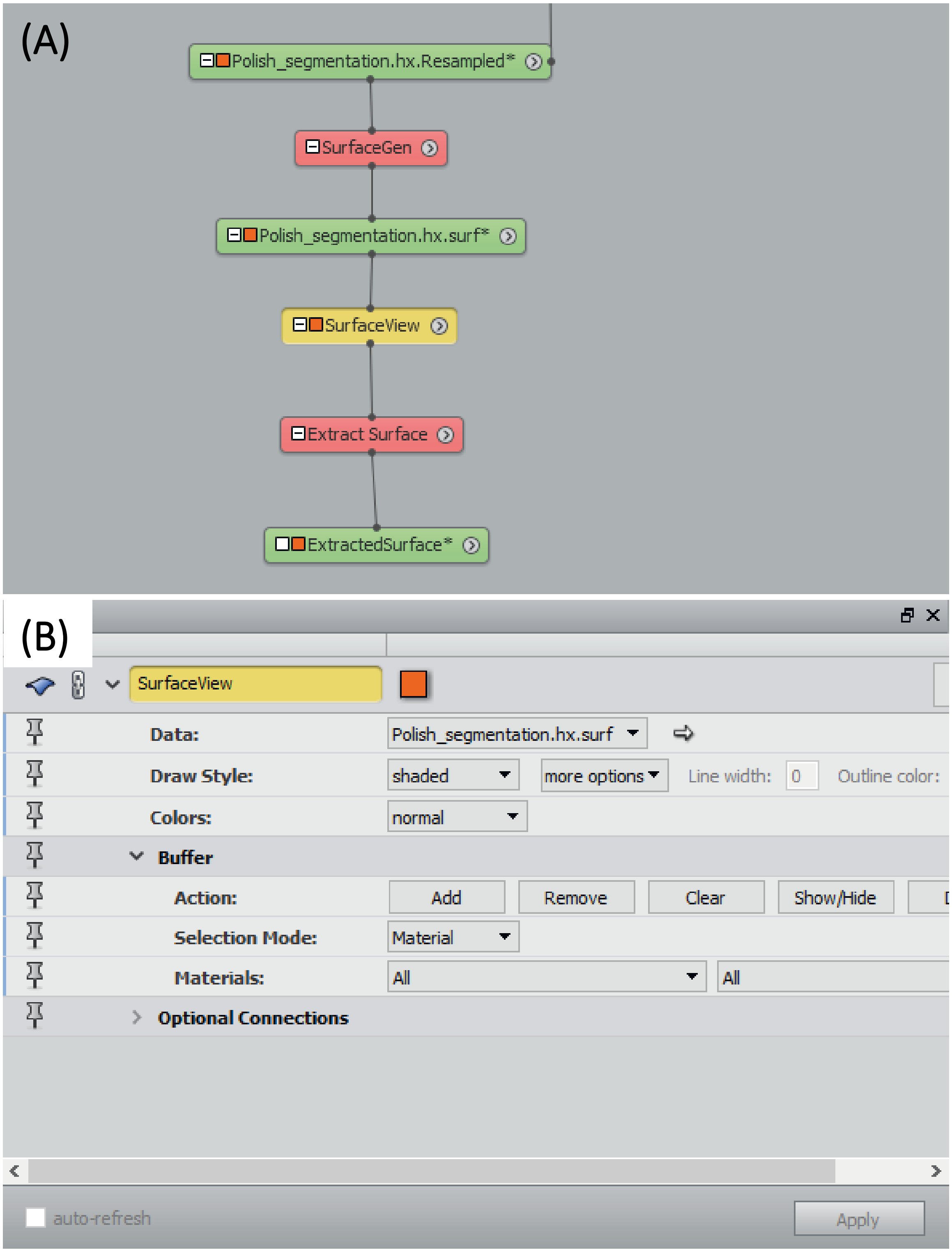


Figure 2a-b: Amira Workspace. **(A)** Workspace with generators. **(B)** Properties manager.

After these bundled .OBJ files were imported in ZBrush®, individual bones were isolated by using the SelectLasso tool (CTRL + SHIFT + Drag). Everything captured in the shape made by the cursor appeared filled in green. Everything outside the shape was hidden and then deleted using the Delete Hidden function (Tools > Geometry > Modify Topology > Delete Hidden). This feature was so useful it was added to a custom interface for a more efficient workflow. The isolated bone mesh was exported from ZBrush as a separate .OBJ file. Using the Undo function, the hidden and deleted mesh could be restored, and the isolation process repeated, as necessary.

The recovered high-fidelity bone mesh was then imported to Cinema4D® (C4D) and placed onto the segmented skull by matching the coordinates of the new .OBJ to the original bone being replaced. When needed, recovered meshes with a rough surface were augmented to desired smoothness with the Polygon Reduction and Subdivisions Surface generators (Subdivision Surface > Object Properties > Type = OpenSubdiv Loop, Subdivision Editor = 1, Subdivision Renderer = 1). To reduce strain on the graphics card, these generated forms were then converted to a single mesh using Object > Current State to Object.

For bundled meshes that included missing bones, no processing was done in ZBrush®. Rather, the .OBJ files were opened in C4D directly and the coordinates of an existing mesh were used to guide the placement of the previously missing one. For example, when placing the left exoccipital bone, which was missing in the file provided for this project, a mesh containing the left and right exoccipital –whose coordinates in space were preserved during export from Amira – was placed using the existing right exoccipital as a guide. Then, in Point

Mode (Modes > Points) the redundant right exoccipital bone was selected (Select > Selection Filter > Lasso Selection) and deleted.

Housekeeping

***Cleaning* the *Mesh*.** As artifacts and unidentified fragments were removed during the rearrangement portion of the restoration, holes were sometimes created in the mesh. To patch these holes in the geometry, the mesh selection was changed from Object Mode to Polygon Mode (Modes > Polygons) so that the edges of the holes were visible. Normally, the workflow for fixing holes is using the Close Polygon Hole (Mesh > Add> Close Polygon Hole) function, but the density and irregular topology of the mesh interfered with the calculations required for this to work properly. Instead, a Voronoi Fracture object (MoGraph > Voronoi Fracture) was added to the Object Manager and made the parent of the mesh being repaired. With the Voronoi Fracture object selected and attention turned to the Attributes Manager, the default point generator was deleted to avoid fracturing the object (Sources > Sources > Point Generator-Distribution > Press 'Delete'). Then, the holes were closed (Object > Object Properties > Optimize and Close Holes). For clarity's sake, I also unchecked Colorize Fragments in the Object Properties tab so the color-coding for textures was preserved. The Voronoi Object and optimized mesh were then made into a single object (Object > Current State to Object).

Tracking Changes. Materials were used as a color-coded visual record of the retrodeformation process. As new adjustments were made, a new material corresponding to the nature of the change would be applied to the object. The order of colored materials in the object manager tags would then provide information on the sequence of changes any single element has undergone. In this project, the following color code was established:

- White = No Change
- Pink = Recovered from Amira
- Blue = Original Element in Need of Repositioning
- Yellow = Reflected Across Sagittal Plane
- Red = Repositioned
- Green = Counter-deformed
- Orange = Superimposed

With each round of changes, the file was saved incrementally so that mistakes or missteps could be resolved without loss of information (File > Save Incrementally…). This meant that each new save would create a numbered snapshot of the reconstruction. By the end of the first stage of this project, there were 80 incremental save files.

Restoration Approach

With the virtual fossil assembled, the next step of the reconstruction was "**retrodeformation**," or identifying and reversing the postmortem deformations of the skull data (**Fig. 3-4**). A more specific operation universally used in retrodeformation is restoring bilateral symmetry, known as "**symmetrization**." Symmetrization is usually undertaken early on in vertebrate reconstruction, with the choice of technique often determining the shape of the outcome (Ogihara *et* al. 2006, Gunz et al. 2009). This is because, in the absence of a perfectly preserved control, all reconstructions take on a margin of error associated with the infinite possibilities for fragments to move in three-dimensions assumptions about the level and nature of deformation. The more heterogeneous the deformation, the more interpretation is introduced (Lautenschlager, 2016; Perez-Ramos, 2020). Despite the risk of interpretation error, digital restoration can provide great insights into the functional morphology of a fossil specimen, invite educational outreach, and lay the groundwork for further research (Molnar *et al.* 2012; van de Kamp *et al.* 2014).

To begin, analysis of the deformations in specimen M777 built upon previously published work (see Gow, 1997 and Bever *et al.* 2015) and changed as new observations were made along the reconstruction process. Among the distortions noted were:

- Broken skull roof that had been re-adhered with epoxy cement
- Some dorsoventral crushing and torsion across the rostrum, incomplete maxilla and mandible, broken right vomer, and twisted pterygopalatine and basicranial complexes
- Dorsally displaced palate (vomer and anterior pterygoid)
- Medially displaced left jugal and missing right jugal
- Damaged facial region with significant loss of nasal information
- Displaced quadrate ramus on the right pterygoid
- Medially displaced right epipterygoid between the prootic and laterosphenoid suture
- Severely damaged exoccipital bones

The methods used here follow the current standard known as the 'reflection and averaging' technique: landmarks on preserved structures were reflected across the sagittal plane, average position values were calculated against their corresponding reflection, and then the original shape was adjusted to the calculated average point. While this approach is not without its faults, namely that it does not fully reverse the effects of profound compression, bending, or symmetrical deformation, it is effective (a) when the deformation is not severe and (b) in tandem with other restoration methods (Tallman *et al*. 2014). Given the complex distortions and bone loss that specimen M777 had undergone, other methods such as superimposition of partially preserved structures, repositioning of disturbed fragments, and extrapolation based on morphological constraints also had to be employed in the reconstruction process. Moreover, the incomplete and uneven state of preservation across each side of the skull called for extensive mirroring of missing components from one side to the other.

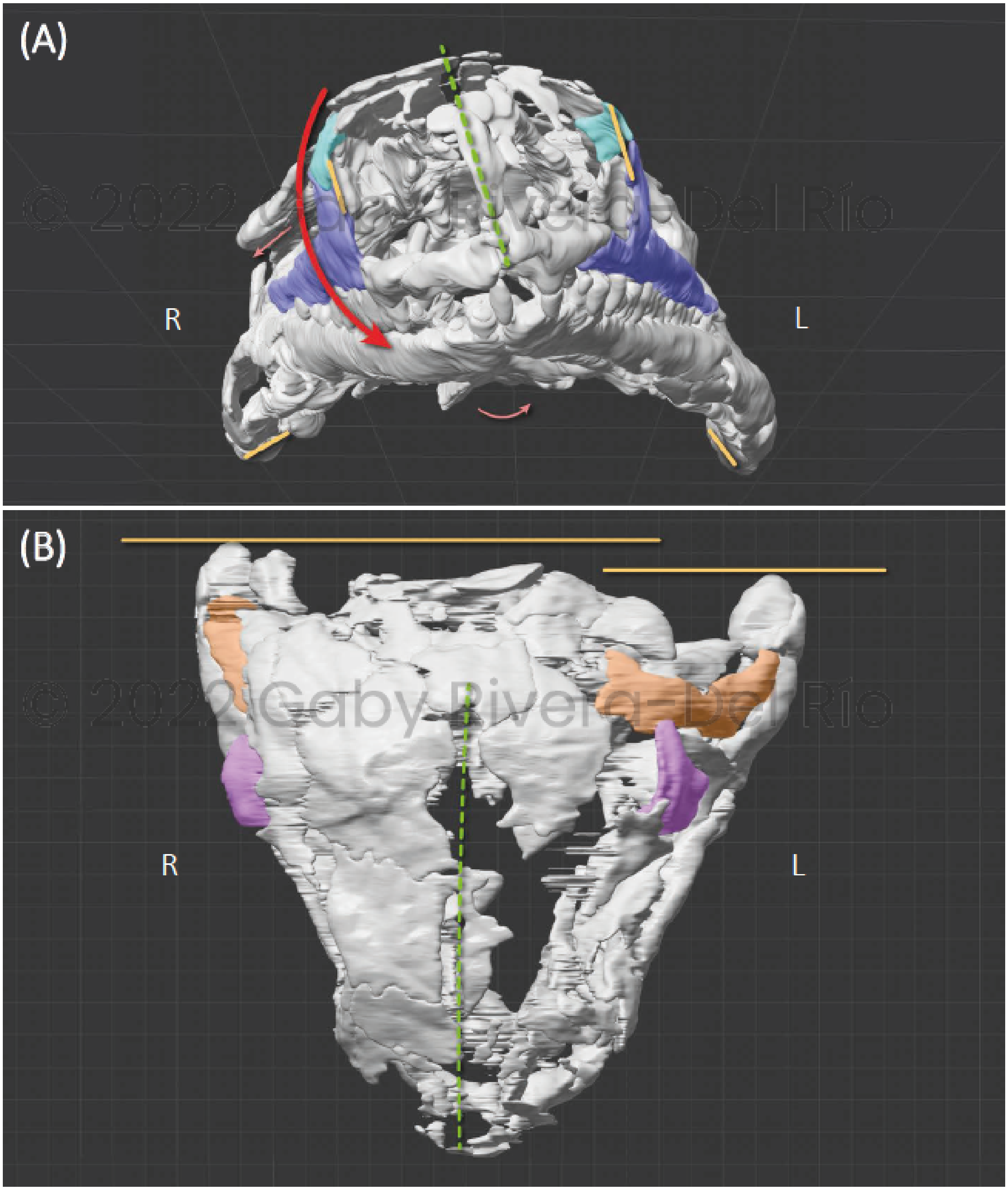


Figure 3a-b: Annotated *Eunotosaurus* segmentation. Markings reflect the taphonomic deformations from an **(A)** anterior-inferior view and **(B)** superior view. Note the twisting of the snout that deviated from the midsagittal plane (green dotted line). Yellow lines and highlighted bones are used to compare the displacement of symmetrical structures. The prefrontal bones (light blue) and maxilla (dark blue) are affected by the torsion on the snout (A). Below are the postorbital (purple) and squamosal (orange) bones which were shifted by asymmetrical compression (B).

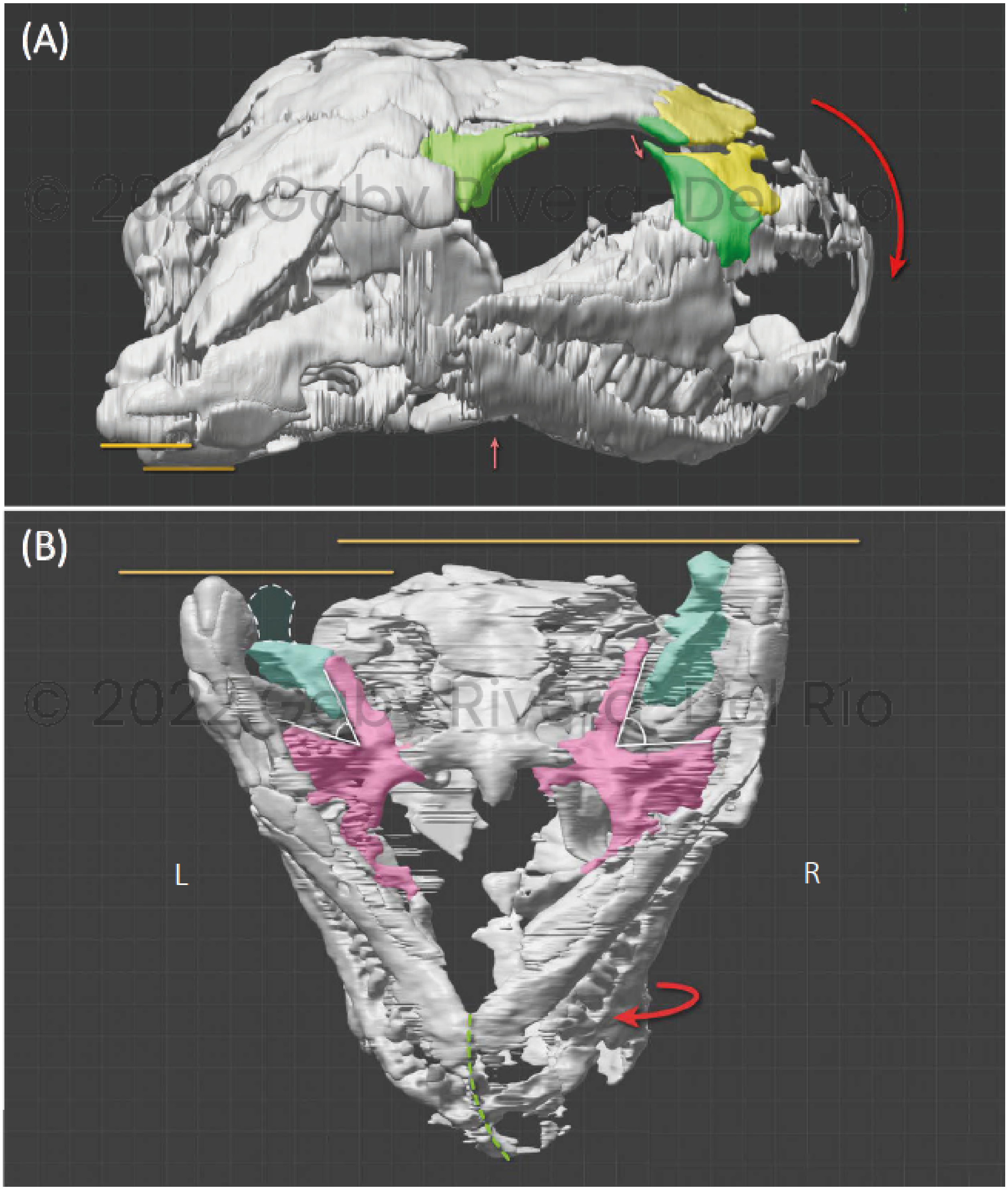


Figure 4a-b: Annotated *Eunotosaurus* segmentation continued. Markings reflect the taphonomic deformations from an **(A)** right lateral view, and **(B)** inferior view. Note the breaks that divide the green and yellow periorbital region (A) and allow the rostrum to be rotated inferiorly. In (B) the deformations of the pterygoid and quadrate bones can be appreciated. Compression has not only displaced the entire masticatory apparatus on one side but changed the angle between the pterygoid bone's lateral and posterior rami. The left quadrate is also missing a posterior projection.

Stage 1. Assembly and Retrodeformation

The ‘reflection and averaging’ technique was crucial to the reconstruction and underpinned all subsequent efforts of restoring the specimen. An imaginary midsagittal plane was placed on the skull and used as a guide for reflecting the bones that were best preserved across that plane. For example, much of the left side of the skull roof was either destroyed or deformed while the right side was intact, necessitating a mirroring of the preserved elements to the left to restore bilateral symmetry.

Establishing the Sagittal Plane. To determine the midsagittal plane, the basioccipital and nasal bones were used as landmarks. This could be done thanks to the lack of lateral bending across the snout of the specimen. The axis of the Null object containing all the skull bones, which was offset to one side, was set along this imaginary midsagittal plane (Modes > Enable Axis or Shortcut L). Once placed, the axis was re-tethered to the mesh (Shortcut L) and moved to the 0,0,0 world coordinates in C4D (Tools > Reset PSR). To test this placement of the sagittal plane, the bones whose bilateral relationship was least affected by diagenetic factors – the articular, angular, surangular, and prearticular bones of the lower jaw – were reflected and compared to one another. There had been a shift along the z-axis but the reflections across the perpendicular plane were well matched. This would sufficiently serve as a reference point for the reconstruction.

Mirroring. Mirroring, or reflection, is a particularly useful technique when one side of the fossil is well-preserved and the other side is not, for example, due to weathering and erosion on the exposed side. Moreover, this technique sets up the process of averaging out components that have been transformed over time.

Normally, a user would mirror objects in C4D by entering Point Mode (Modes > Points) and going to Mesh > Clone > Mirror. However, while this does produce a second mesh that is reflected along the object axis, the mirrored object is (1) not separate, and (2) often overlaps the original mesh at certain points. Transforming the mirrored mesh created from this action would pull the overlapping polygons apart like taffy.

Instead, the desired bone mesh was selected in Object Mode (Modes > Object), then duplicated using Copy (CTRL/CMD + C) + Paste (CTRL/CMD + V). In the Coordinates Manager, the Position was set to World and the middle value to Scale. Then using the viewport compass as a reference to find the perpendicular axis across the midsagittal plane (in this case the x-axis), the appropriate value was 'flipped.' This meant turning the positive scale coordinates in the x-axis negative.

Figure 5: Mirroring of Skull Roof Elements. Dorsal view. In red are the original components which were repositioned medially, and in yellow are the mirrored copies where the skull roof was missing.

Elements that had been transformed before reflection needed their Rotation values reset to 0,0,0 (Shortcut L > Coordinates Manager > Rotation) for this method to work properly, as doing so without zeroing out the Rotation values would yield a reflection across the sagittal plane that was off kilter.

Averaging. Averaging the landmarks of deformed elements is the usual next step after mirroring, particularly for structures that are away from the midline. This is because deformation can create a significant deviation of these elements from their original position. When reflected, corresponding elements can be some distance apart, thus necessitating averaging of landmark structure positions to produce a symmetrical reconstruction.

As each bone was imported to the C4D file, they were all consistently placed in space relative to the original data because they all had the same axis. After the establishment of the midsagittal plane, the reference axis for every bone was changed to the 0,0,0 position. This made mirroring quick and easy, as converting the Scale in the Coordinates Manager from positive to negative produced a perfect reflection. For averaging the position of the reflected element and its counterpart, the axes were adjusted to a specific landmark by first releasing it (Modes > Enable Axis) and manually setting it in the viewer or Coordinates Manager. Re-enabling the axis ensured that once it was set the elements could then be moved. In Object Mode, the two elements were selected together (hold SHIFT while clicking), and C4D's Coordinates Manager would set the axis of the two objects at the average point between their positions. The averaged value was then plugged into the Coordinates Manager for each bone, and the reflected element (now re-positioned) could be mirrored again to return to its native side of the specimen.

Superimposition. While mirroring was instrumental to replacing the missing or eroded elements of the fossil, it was limited by the necessity for a complete source component on the well-preserved side to create the reflected counterpart. Fossils can present with uneven or distinct states of preservation on either side of the symmetrical plane, with no single component fully preserved. In these instances, elements that are incomplete on both sides but retain different information can be superimposed to make a single complete element.

The need for superimposition was determined with the reflection of a particular element to its corresponding side and observing that the preservation was inconsistent. After averaging the positions of these bones, rotating to match their planes, determining their fit to surrounding anatomy, and considering morphological constraints, the two surface meshes would be overlapping to some extent. C4D's Volume Builder (Volume > Volume Builder) and Volume Mesher (Volume > Volume Mesher) generators were then used to remesh the parts into a single element (**Fig. 6**). The Volume Builder needs to be made the child of the Volume Mesher and the elements that need to be superimposed must then be made the children of the Volume Builder. The resolution of the voxels used to calculate the new mesh can be set in the Volume Builder's Properties Panel (Object Properties > Voxel Size). In this case, the voxel size was set between 1.5 – 2 cm. The result is a more complete surface mesh object built from the combined volumes of the superimposed parts. This new composite could then be mirrored to the other side to maintain bilateral symmetry. Note: if any trimming needed to be done to remove extraneous information, any resultant holes in the surface mesh would need to be closed (see *Housekeeping* above) before superimposition can occur, as the Volume Builder cannot properly calculate an open mesh.

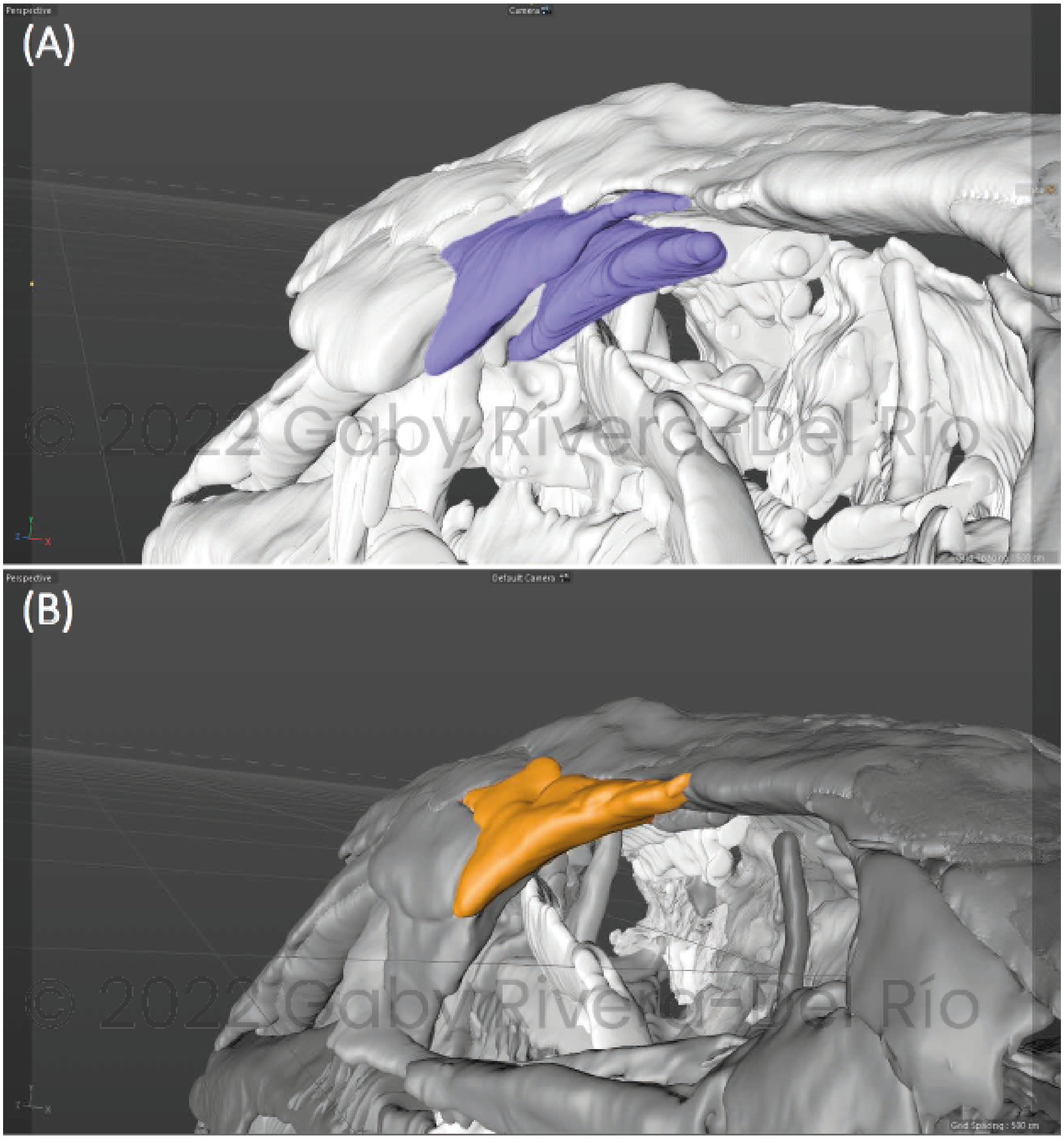


Figure 6a-b: Superimposition of postfrontal bones. Anterolateral view of the orbit and skull roof. **(A)** Purple shows the split parts of the postfrontal, with both the original right element missing some anterior mass and a mirrored complete left element. (B) Orange shows the product of superimposing these parts.

Repositioning. Broken or disarticulated elements were a frequent encounter in this reconstruction. Distinct from the repositioning part of the averaging technique, this involved manually adjusting elements in space without the limitations imposed by averaging. This is necessary if a break separates large fragments of the same element, superimposition cannot be readily done due to lack of overlap, and for articulating elements that have been recognizably separated. Because this was done manually, great care was taken to stay as anatomically plausible as possible by using a landmark-based approach, keeping the morphological constraints, and known relationships with other bones consistent with the literature (Gunz *et al.* 2009). It should be noted that because the articulations in three-dimensional space can vary, this step does introduce more uncertainty into the restoration than reflecting and averaging alone. Even so, this was to be expected with the level of deformation in the original data. To allow greater control of the repositioning, the axis of each mesh was changed as needed (Shortcut L). This was particularly useful when one point of an element was in position, but rotation was still required to move the rest of it into place. Moving the axis to the contact point ensured it was not disturbed.

Plastic Retrodeformation. Taphonomic distortion was another major hurdle in this reconstruction. This occurs when elements warp, bend, shear, or stretch without breaking, which can have deleterious effects on the useful morphological information retained in the fossil (White 2003). This makes it by far the most challenging postmortem change to accurately address in reconstructions. Extreme care had to be taken to maintain the integrity of important morphological characters. For example, intense observation and attention had to be paid during the retrodeformation of the pterygoids, as their intimate sutures with the quadrate, prootic, and laterosphenoid bones have significant implications to the relationship between Pan-testudines (the clade inclusive of *Eunotosaurus* and all stem-ward turtles) and archosaurs (Bhullar. *et al.* 2009; Bever *et al*. 2015).

It was apparent from first glance that the ventral elements of the mandible and skull would need some manner of plastic retrodeformation beyond what mirroring and averaging could accomplish, as the twisting of the snout also extended to the lateral projections of the parabasisphenoid, pterygoid, prootic, and basioccipital bones. In other places, such as the left pterygoid, there was the matter of counteracting compression forces that acted along the length of the bone. While the same approach was taken here to average out the positions of corresponding landmarks, simple position transformations would not be enough to undo the distortion.

To address this problem, deformer objects (Create > Deformer) were employed in this portion of the reconstruction. Among the most used were the Bend, Twist, and Freeform Deformation (FFD) objects. The amount of correction was determined by eye, with results checked against existing components and known sutures with other bones. All these deformers are independent of the object they are affecting, making them non-destructive means of controlling mesh shape.

Firstly, Bend and Twist deformers were instrumental in correcting the torsion of the snout and basicranial region. The paired maxilla and prefrontal bones were more displaced than stretched, but midline structures like the nasal, mandibular, premaxillary, vomerine, and basicranial components required some amount of counter-twisting to restore bilateral symmetry (**Fig. 7**). This was especially the case for the paired dentary bones in the mandible, which had suffered multiple distortions over the millennia (**Fig. 8**). Because of their independence from the mesh, multiple deformers were layered onto the parent mesh to precisely control retrodeformation. Effects could also be double-checked by individually toggling each deformer on and off when needed.

Given that the skull is a fully articulated structure, it was often necessary to apply a single deformer across multiple bones that contacted one another. To do this, the desired meshes were selected and dropped into a Null Object (Create > Null). Then a chosen deformer was made a child of that Null object, allowing all the child meshes to be manipulated together, reflecting the ripple effects of applied forces across intimately connected bones.

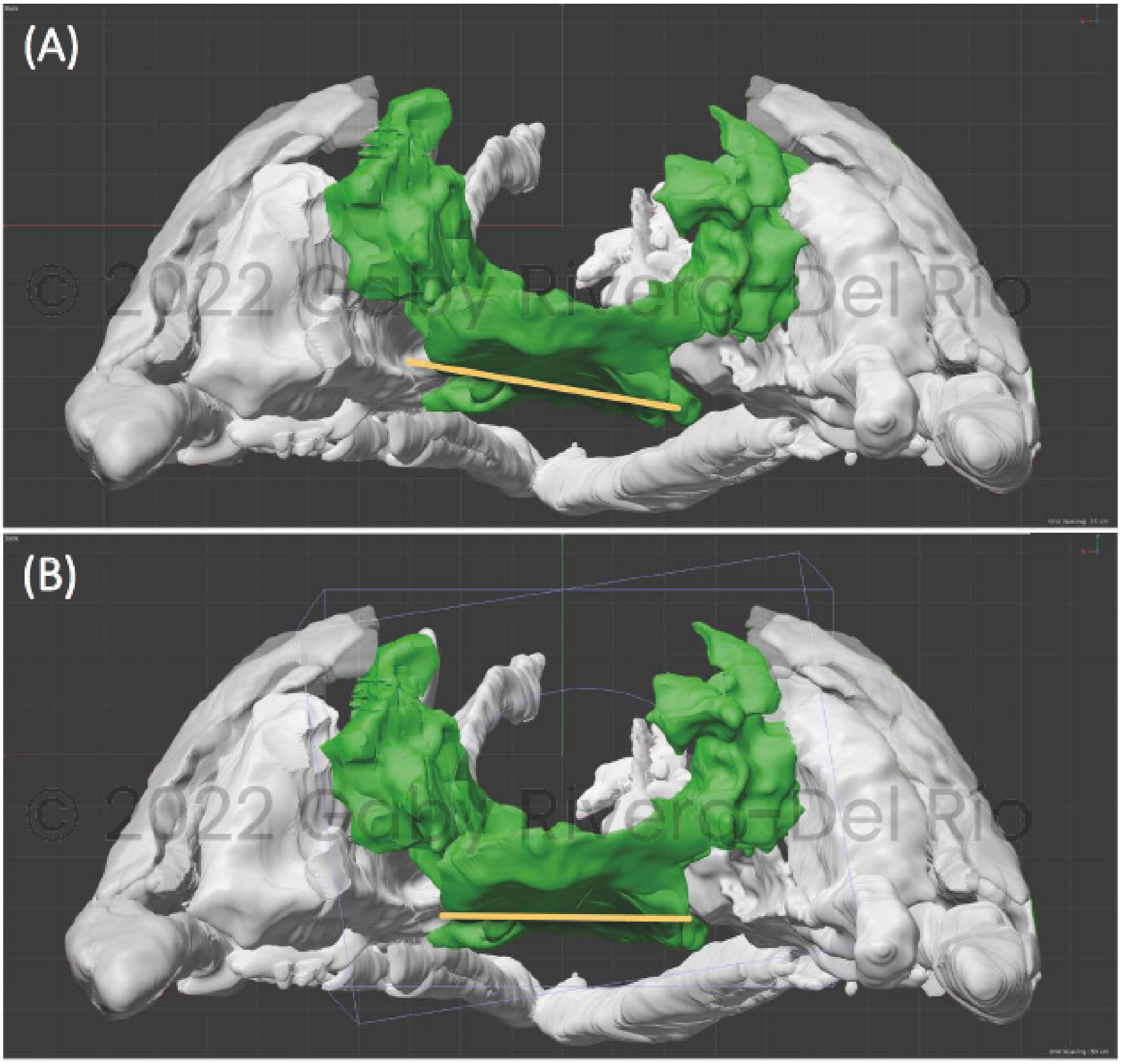


Figure 7a-b: Twist Retrodeformation of the Basicranium and Prootic Apparatus. Posterior view, with external rostrum, skull roof, and, the rear wall of the endocranium removed for visibility. The yellow line illustrates the change in the tilt of before **(A)** and after **(B)** retrodeformation. Note the blue box which visibly denotes the deformer's bounds in the after image.

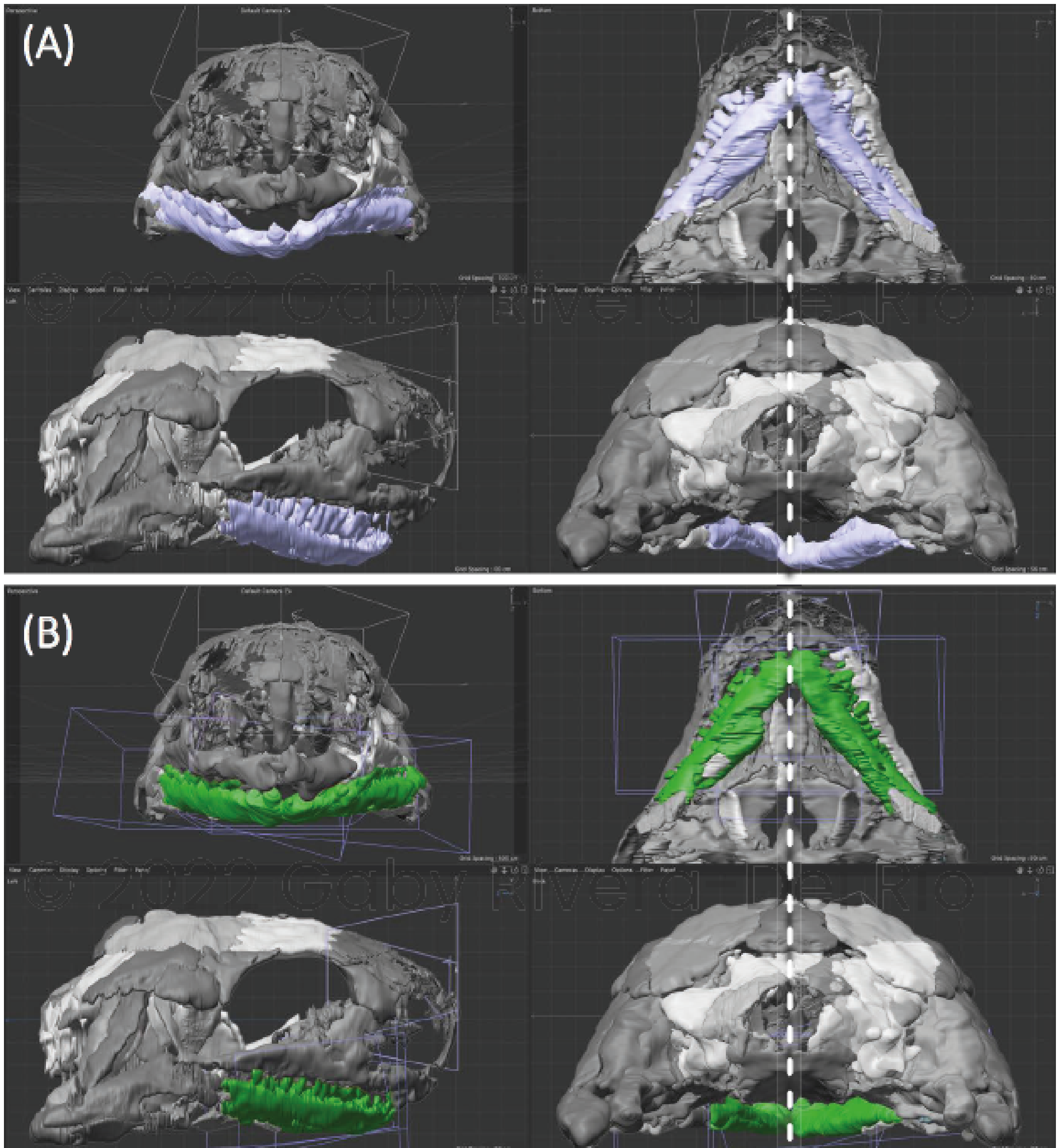


Figure 8a-b: Complex Retrodeformation of the Mandible. Orthogonal views from top left to bottom right: anterior, inferior, right lateral, and posterior. Before **(A)** and after **(B)** retrodeformation. In this case, two twist deformers and one bend were used to straighten out the mandibular profile, align the teeth with the maxilla, and align the midline suture with the sagittal plane (white dashed line).

After correcting the twist in the midline structures came the issue of undoing the effects of compression. This was by far the most complex portion of the reconstruction, as the affected structures – namely the pterygopalatine, pterygoquadrate, and masticatory apparatus – shared multiple sutures with numerous bones. Because of the many articulation points of these cascades, displacement along the lengthwise axis had consequences for all surrounding elements. This was made apparent through the pterygoid bones, which could not be mirrored, displaced, or otherwise manipulated in a manner that would restore bilateral symmetry. The left side was compressed along its entire length. The right side was unevenly stretched and broken from the torsion that affected the snout. Moreover, the left masticatory apparatus was compressed such that the quadrate was rotated superiorly and the right pterygoquadrate was pushed outward such that it was disarticulated from the right prootic (**Fig. 10a**).

For this, the answer was FFD, or Freeform Deformation, which creates a grid-like scaffold that can be fitted to the bounds of a given mesh object (Object Manager > FFD Generator > Properties Manager > Object > Fit to Parent). When the FFD is made the child of an object, each point along the generated cube lattice corresponds to a parameterized portion of the parent object (**Fig. 9**). These points can be manipulated in Point Mode (Modes > Points). Any deformations to the lattice structure create associated changes to the parent mesh, regardless of its complexity or point density. Moreover, the ability to reset this deformer allowed revisions to be made as new information came in or fresh eyes were laid on the model.

Still, this deformer was used sparingly as its capacity to preserve volume was limited. In cases where the deformation was consistent throughout the element, or the FFD would otherwise be too complicated to apply, the Bend and Twist deformers were preferred. Every time the Bend deformer was used, it was adjusted to preserve the volume of the parent object (Bend Object > Properties Manager > Object > Keep Length).

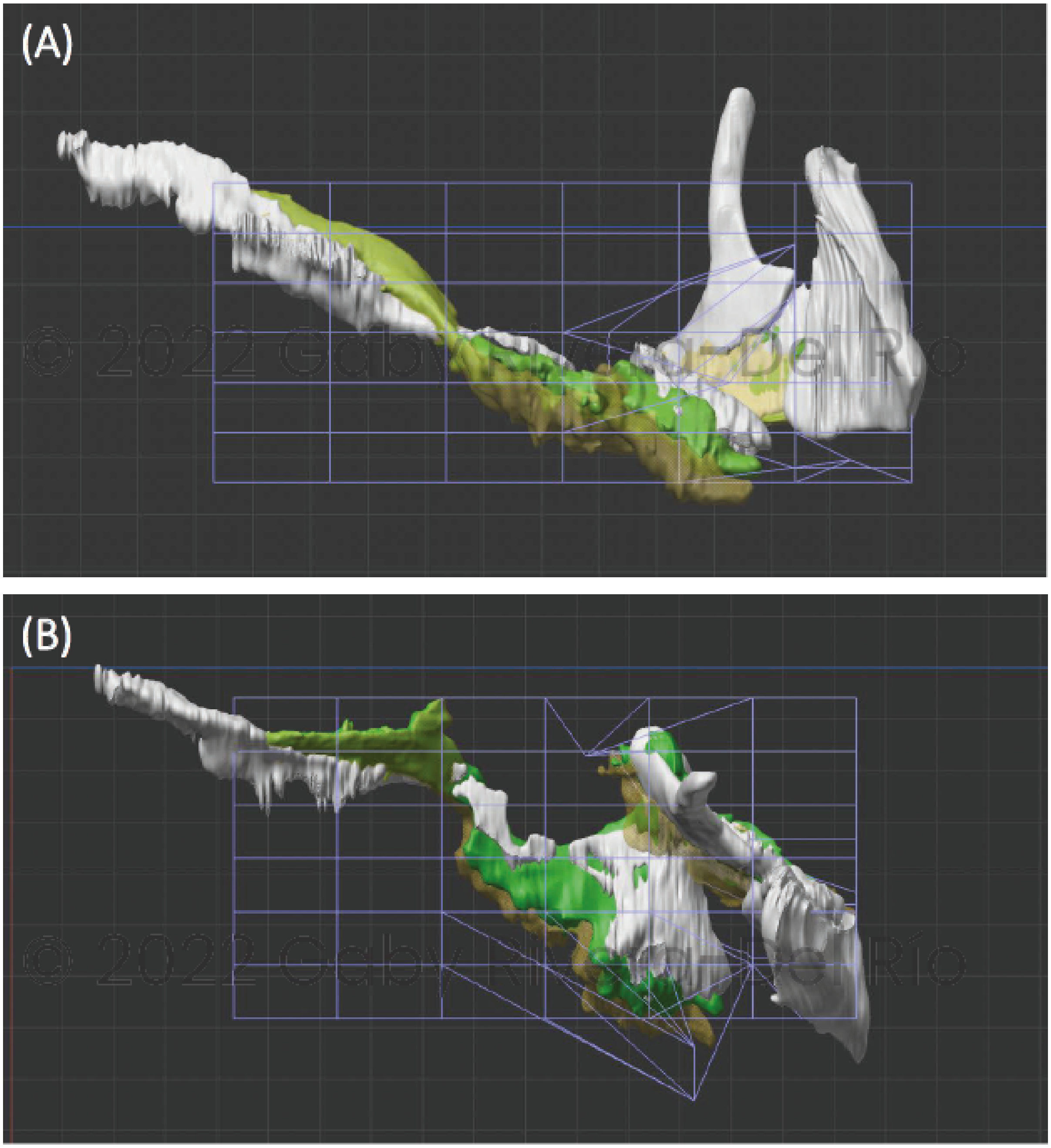


Figure 9a-b: Freeform Deformation of the Pterygoid Bones. Seen from the **(A)** left lateral perspective and **(B)** superior view. In white is the left pterygoid, epipterygoid, and quadrate bones. In yellow is the right pterygoid mirrored across the sagittal plane. The two structures have previously been deformed to a uniform length using FFD. In green is a superimposed pterygoid composite made from the complete data on each side. In both images, the prominent landmarks of the amalgam pterygoid are being deformed to the midpoints in three-dimensional space between those of the left and right pterygoid bones. This creates a structure that can be reflected to restore bilateral symmetry.

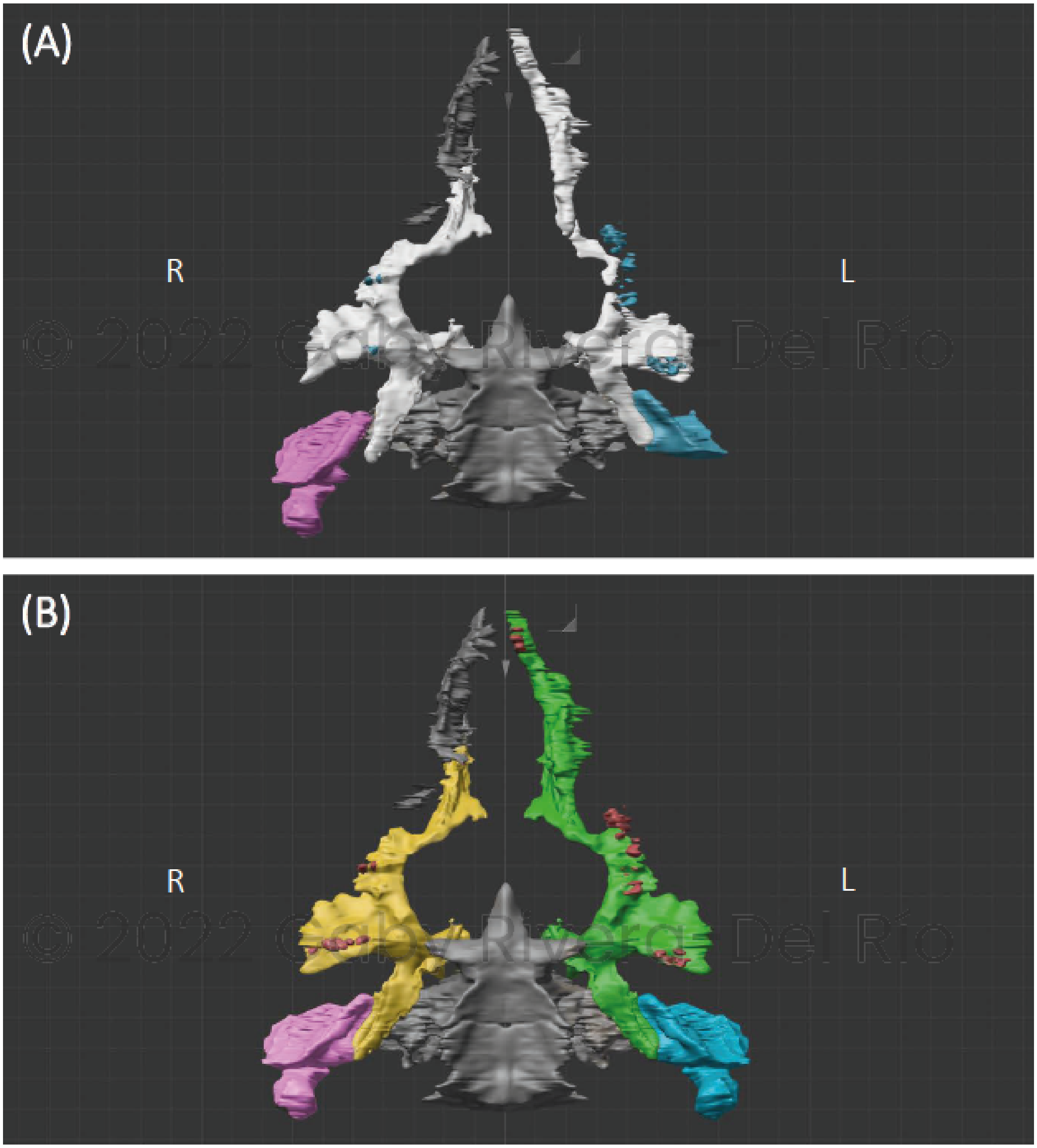


Figure 10a-b: Retrodeformation of the Pterygoquadrate Apparatus. Before **(A)** and after **(B)** superimposition, retrodeformation, and mirroring. Some elements that were missing on the left pterygoid were superimposed before manipulation via FFD.

Extrapolation. While the previously mentioned methods can do a lot to restore useful morphological information from fossil data, there are times when no amount of reflecting, duplicating, or other means of exploiting bilateral symmetry can recover the missing original form. In those cases, extrapolation is the last recourse. Often this is done by using other specimens – either of the same species or a close relative – as reference for retrodeformation or estimating missing parts. This could not be done here, however, as like with other paleontological work, this specimen represents the most complete adult *Eunotosaurus* skull in the fossil record. Even if another specimen was available, the potential for interspecific variation, sexual dimorphism, or the age of the specimen to introduce more error is too high. The only available options were to compare across distantly related taxa stem-ward and crown-ward in evolutionary time to extrapolate the variability that could exist. This approach, while not perfect, meets the needs of creating a workable model for biomechanical analysis. This was helped by the fact that the extrapolated changes in question – such as correcting the displacement of the palate and introducing a bend– held little phylogenetic signaling value (**Fig. 12**).

In all cases where extrapolation had to be used it was paramount to maintain known sutural contacts, assess morphological constraints, and preserve the volume of the mesh. When deciding what alterations could fall within the biological potential of the specimen, the chief references used were papers describing the cranial morphology of other turtle relatives (**Fig. 11**) like *Proganochelys quenstedti* and *Pappochelys*, and descriptions of various *Euntosaurus* specimens (Cope, 1892; Gow, 1997; Bever *et al*. 2015; Schoch & Sues, 2017).

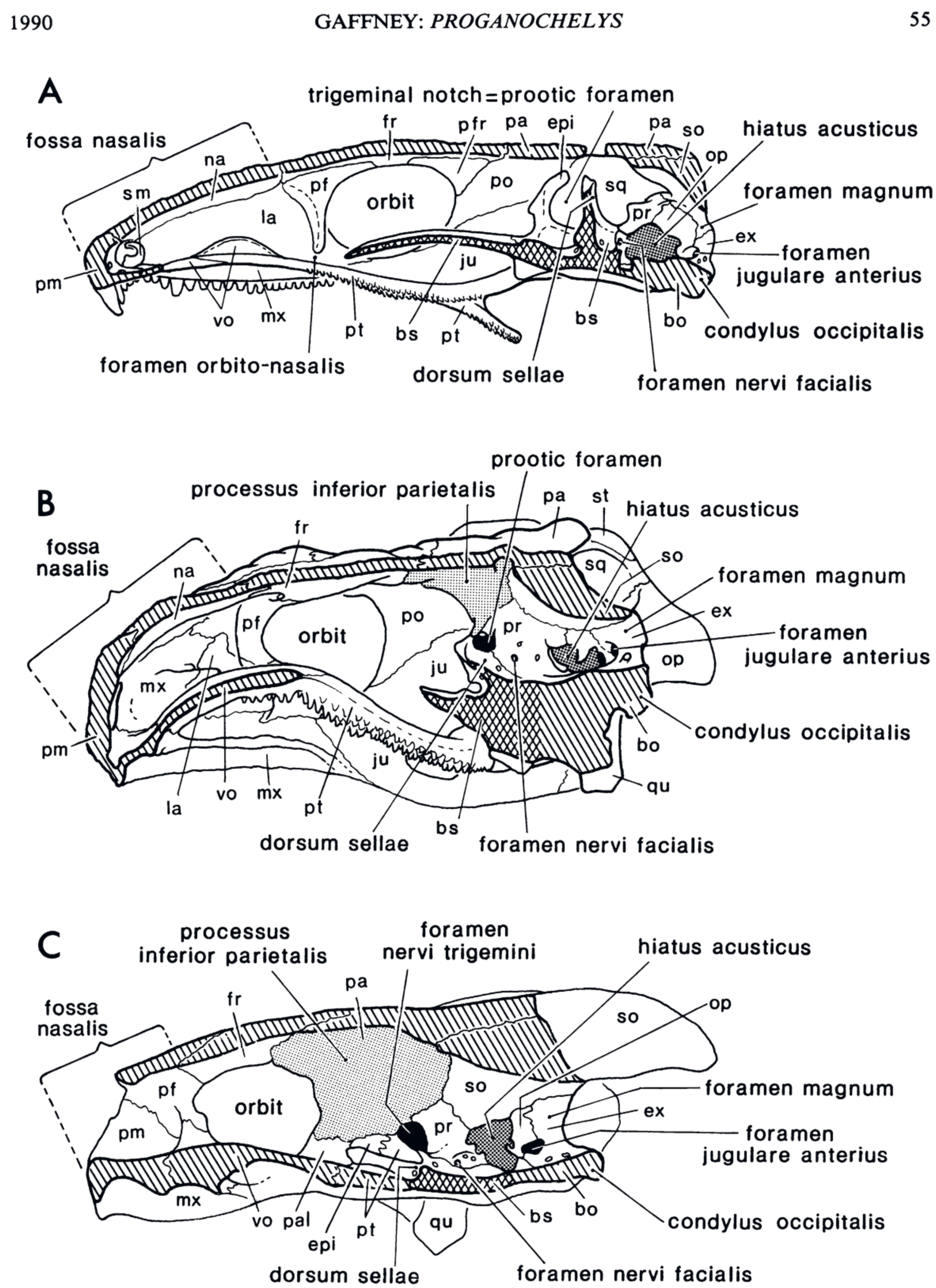


Figure 11: Comparison of Sagitally Sectioned Skulls. Figure from Gaffney (1990). Shown from top to bottom are *Captorhinus, Proganochelys,* and *Chelydra.* Images such as these were used in tandem with written morphological findings to extrapolate the palatal deformation needed to restore its anterior contact with the premaxillae, seen in Figure 11. Text not meant to be read.

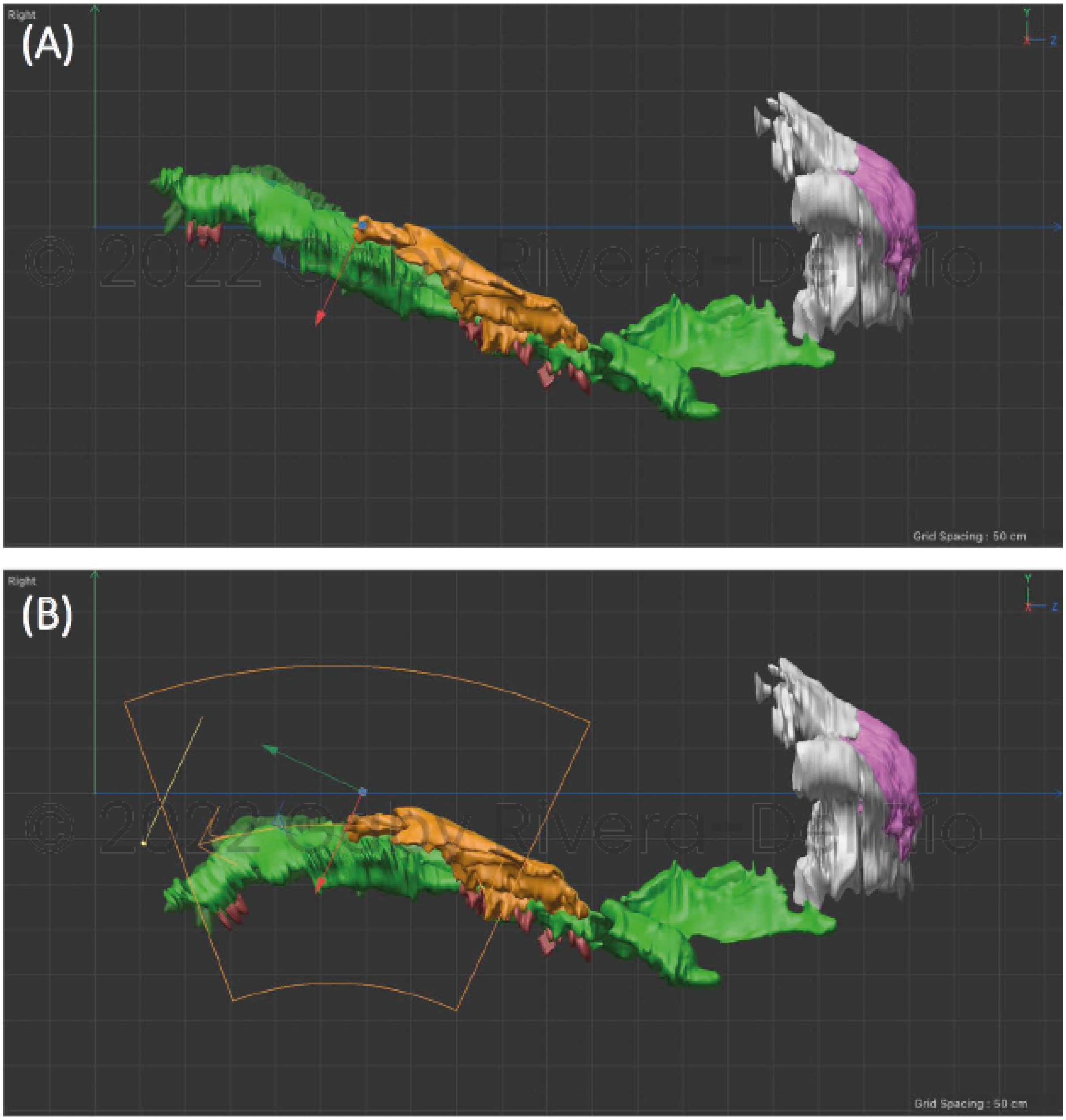


Figure 12a-b: Bend Deformation of the Dorsally Displaced Palatal Structures. Seen from the right lateral perspective. The axis of the bend deformer was matched to the direction of the bone **(A)** to further preserve its volume after bending **(B)**. Note that because the palatine and pterygoid bones maintain strong sutural contact across the posterior length of the vomer, they too were affected by the dorsal deformation.

Part 2. User-Centered Design Framework

The next step in this project was to build a web application that would house and contextualize the reconstructed *Eunotosaurus* skull.

In the user experience (UX) industry, few books have had as wide an impact as Jesse James Garrett's *Elements of User Experience* (2010). In it, he organizes the foundational principles of UX design into a five-plane framework: **strategy**, **scope**, **structure**, **skeleton**, and **surface**. Each plane, or tier, sets the stage for the next, with early goal setting and planning (abstract) informing the structure and content of the final product (concrete). The end-user experience reflects every decision made along each plane of this framework.

Moreover, the entire framework can be further subdivided into two approaches. Depending on the vision for a given interactive product, one can look at issues that arise as a functional problem or an information dissemination problem. These approaches hinge on the purpose of a given system as either a platform for functionality, an information resource, or – more commonly – a mix of both. The functional approach is concerned with tasks, which not only encompass the steps of a given procedure but also how users think through them. The informational approach is concerned with meaning, which entails helping users to find and understand the information provided. The guiding principles behind this application balance the two approaches.

The **Strategy** encompasses the *overall objective* of the application, incorporating the user's needs and creator's goals for the final product. The **Scope** encompasses the specific functions, features, and content that will deliver on the project's strategic goals, defined here through *enabling objectives*. The **Structure** determines how these functions are organized, mapped in the *information architecture,* and defined through the interaction design of the application. The **Skeleton** plane is a concrete expression of the more abstract structural concerns of the UX design. It takes the form of *prototypes* that are designed to facilitate understanding, define key user interface (UI) elements, and arrange navigational components for maximum efficiency and impact. This is where the point of contact between the user and the system takes shape. Overlying all of these is the **Surface** plane which comprises the finalized interactive application. This is where visual design elements tie the entire conceptual framework into a functional end-user experience. In all, this workflow builds from a conceptual foundation to increasingly specific functional and sensory design work (**Fig. 13a**).

It should be noted that thinking of these planes as discrete steps that are set in stone once completed can result in a stilted product (**Fig. 13b**). Decisions made at each phase naturally define and restrict the available options further up the framework, but sometimes implementing an idea can reveal the need to go back to the drawing board. As such, the workflow should be adaptable and deliberate. Changes will come as new information is attained and prior decisions are revised accordingly.

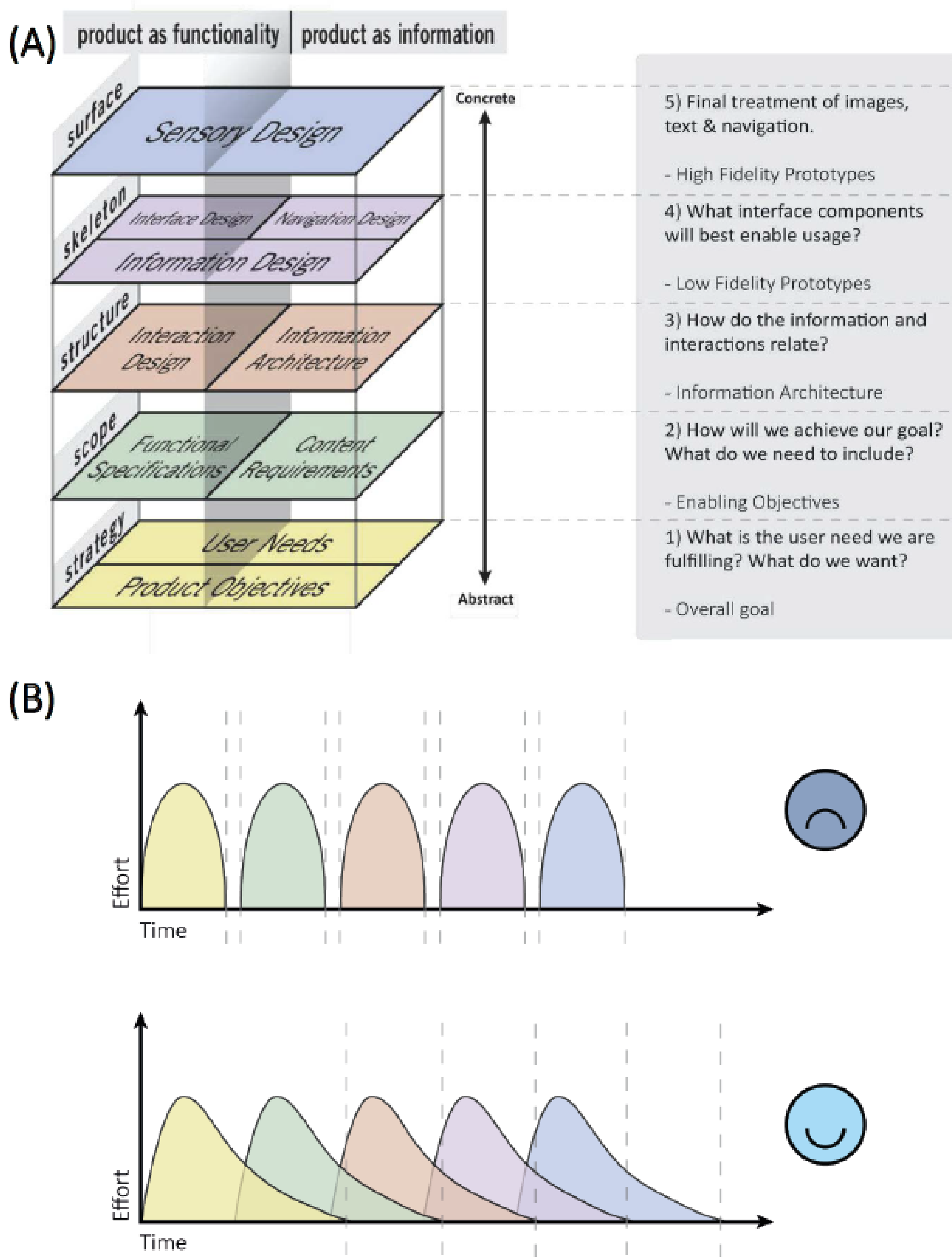


Figure 13a-b. The Five Planes of User Experience Design. They are split to convey the dual approaches to interactive media and broken down by related questions and actions **(A)**. Below is a diagram of the workflows for iterating through these planes. They are best approached in a continuous rather than discrete fashion **(B)**. Figure adapted from *Elements of User Experience* (Garrett 2010).

Strategy: Objectives and User Needs

It was important to establish a shared communication goal with Dr. Bever. The motivations behind this novel reconstruction and web application were to not only provide a visual resource for cranial support of a *Eunotosaurus* – turtle clade but to do so in a manner that tackled common intuitive biases and misunderstandings.

Overall Objective. This application will accessibly communicate the morphological and phylogenetic insights *Eunotosaurus africanus* contributes to the still-debated question of turtle origins. It was determined that the **primary users** are investigators, graduate, and undergraduate students of evolutionary biology and paleontology. Once these core aspects of the application strategy were defined, the work of validating the approach and conducting the research could begin.

Research and Identified User Needs. At the start, preliminary research was carried out to contextualize the existing communication challenges and identify user needs. This initial phase of research covered the following:

Information-Oriented Exploration

- Web search for key terms: *Eunotosaurus africanus*, early turtle relatives, turtle evolution, learn evolution, evolution misconceptions, reading cladograms, and others
- Existing learner resources: online learning modules like the NOVA Evolution Lab, images, videos, and science news articles
- Existing teacher resources: online lesson plans, educational primers, pedagogic content, design guides, and primary literature on science education
- Relevant existing interactive resources: anatomical model viewers, learning apps

- Reviewing knowledge gaps and information needs from the educator perspective
- Review of the existing body of scientific literature on *E. africanus* to identify the core concepts in the story that need communicating

Function-Oriented Exploration

- Review of basic user interface design principles, navigation, and conventions
- Market research on web application layouts
- Informal stakeholder interviews

Key Research Findings. The first round of research focused on identifying any resources that touched on the same ideas as this novel application. Several assets for teaching, informing the public, and fighting misconceptions about evolutionary science were identified throughout this phase of development. Among these were educator references for building lesson plans, scientific articles, short videos, and interactive web tools aimed at a lay audience. Again, a table of these resources can be found in **Appendix B**. While there is plenty of information online, some major problems were quickly apparent: information overload, difficulty in separating trustworthy sources from misinformation, and high saturation of educator-focused materials over student-facing ones. Moreover, no online resources outside of primary literature specifically covered turtle phylogeny or discussed cranial evidence of a *Eunotosaurus*– turtle clade. In all, this preliminary work confirmed the dearth of web-based applications focused on demystifying phylogenetic concepts or communicating new data in turtle systematics.

To help inform the content curation and design process, there was also a need to identify the major obstacles to communicating phylogenetic research. It would be difficult, for example, to try and convey how *Eunotosaurus* adds to our understanding of evolutionary byproducts, or exaptations – traits that served one function and were then co-opted to serve another – if they believe evolution is a purpose-driven, teleological process. Among the greatest obstacles to learning evolutionary biology, even among academics, is the persistence of intuitive biases and value judgments on scientific understanding. Some of the most common preconceptions are:

- Vernacular misconceptions, which arise from words having disparate meanings in a scientific context and everyday use. Examples include seeing evolution as "only" a theory or using *fitness* to describe a given individual's vitality and health rather than reproductive success (Alters & Nelson, 2002). The adjustment for this is to include plain-language descriptions of these terms and make definitions easily accessible.
- Reductionist biases that atomize organisms into discreet traits which have been optimally forged by natural selection to fulfill their purpose. This view considers an organism's traits as a function of being "for" a specific purpose, rather than the result of the circumstances that *caused* it to arise (Gould & Lewontin, 1979). This mode of thought makes prescriptions about a trait existing to meet a need or fulfill the "intentions" of an external force… forgetting that traits can be developmental or physiological byproducts or be non-adaptive altogether. Counteracting this requires acknowledging the role that multiple factors play in an organism's morphology – be they genetic, developmental, or phylogenetic – and avoiding the use of design-oriented terms in pedagogy. Additionally, the conceptualization of phylogenetics (shared ancestry) helps by placing morphology in a broader historical context.

- Progressionist notions of evolution as a linear process that gradually produces "higher" or more "advanced" forms. These ideas often underlie further misconceptions that see evolutionary change as following a "mainline" leading to a distinct endpoint (usually humans) and all other species as derivative of "sidetracks" along that main lineage (O'Hara 1992). These biases can be disrupted by rotating nodes on a tree diagram to avoid a ladder-like appearance, particularly ones that contain humans as a terminal taxon.
- Mistaking sister taxa for ancestors. This misconception is quite common, often taking the form of the question "If we humans descended from chimps, why are there still chimps?" The reality is that while chimps and humans share a recent common ancestor, this ancestor was neither chimp nor human. The misconception stems from a mistaken idea that speciation is a process by which one entire species gradually morphs into another, or "anagenesis" (Gregory, 2008). The answer is to stress the existence of common ancestry from which species *diverge*, rather than *emerge*. Rotating nodes in a tree can interrupt linear thinking in this intuitive bias.
- Biases of common reading convention that cause observers to glean several incorrect things about a phylogenetic tree, or cladogram (Meir *et al*. 2007; Gregory, 2008):
    - That taxa at the far right on a tree represent the more "advanced" groups, or conversely, that the outgroup taxon on the far left is more "basal" or similar to the root ancestor of all others on the tree. While the structure of certain trees may appear to coincide with this reading, assuming so is fallacious, especially when the terminal taxa on a tree are all extant or living. All living

taxa that share common ancestry have been evolving for just as long as one another. This thinking can also be disrupted by rotating the nodes of a tree, as well as explicitly recognizing that any given cladogram represents an incomplete sample of life to communicate only relationships.

- That a long branch on a phylogeny indicates a lineage that has changed very little over time. This can be combatted by either signaling towards the true diversity of a given terminal taxon or adding more representatives to "balance" the tree out.
- A tendency to read relatedness between taxa by "counting nodes," or judging their physical distance in the diagram. As a reading error, this can be addressed by clearly signaling how grouping works in the diagram.

While this list is by no means exhaustive, it does provide a solid foundation for guiding the subsequent phases of development, particularly in terms of information dissemination. It could also be revisited whenever needed throughout the design process as new questions of pedagogic concern arose. From this grasp of the barriers to understanding, the content curation and design could take shape.

Scope: Content Curation and Functional Specifications

The Scope plane translates the overall objective into specific requirements for functionality and content. Defining these requirements is key to an efficient workflow, as new ideas often come up throughout the iterative process. Being able to compare them against these baselines helps in evaluating whether ideas fit into the project's end goals. This also extends to ideas that cannot be executed within the deadline but can form the basis of the next milestone in future development. In this methodology, defining the requirements begins with *enabling objectives.*

Enabling Objectives. Enabling objectives are supporting players in the execution of the overall goal of the application. They inform the functional and content requirements of the app by breaking down the broader main objective into specific goals. Goals to bridge the major knowledge gaps identified in the research phase (see *Key Research Findings*) and a list of the key tasks for carrying them out was organized into **Table 1**.

User Personas. User personas are archetypal representations of the user population. They serve as touchstones for building empathy towards user perspectives, facilitating discussion with stakeholders, and anticipating user needs throughout the design process. In all, they are useful for defining the scope of the project and prioritizing features. Each persona consists of a name and photo, key demographics, their frustrations (or "pain points"), a quote that encompasses their personality, and their goals.

The name and photo (downloaded copyright-free from Unsplash.com) help in reinforcing empathy for the personas, with key demographics used to cover the range of potential users and inform their needs. Frustrations and personality cues help structure later information and surface design. These personas were based on preliminary research, input from stakeholders and educators, personal experience with teaching evolutionary biology to post-secondary students, and observation of hobbyist circles in the paleobiology community. All personas can be viewed in **Appendix C**.

Content and Functional Specifications. Following the preliminary research data, user persona data, and stakeholders like Dr. Bever, the content requirements for the project were defined. Among them was a directive to make terminology accessible through plain-language text and linked definitions. Moreover, there was careful consideration for word usage, necessitating multiple rounds of stakeholder feedback on text alone. This is because incautious use of terminology has, in the past, reinforced vernacular misconceptions about evolutionary processes (Schoerning, 2014). Another specification was deciding that while evolutionary biology represents a vast discipline, the contents in the application would focus on macroevolution and tree-thinking only. This would keep the focus on the big-picture of turtle phylogeny and address the most neglected and misunderstood facets of evolution pedagogy.

Functionally, a few things were deemed important. First was the ability for users to observe three-dimensional skull data and isolate bones, as it would allow for close observation of landmarks and features. This would set up understanding and appreciation for the host of characters used in comparative analysis. Next on the list of functions was the ability for users to interact with a cladogram. In the teaching of cladistics, five core tree-thinking skills have been named (1) identifying characters (or synapomorphies), (2) knowing which taxa on a tree exhibit or do not exhibit a character, (3) understanding clades as a concept, (4) evaluating relatedness of groups in a tree, and (5) using deductive reasoning based on most recent common ancestry (Novick & Catley, 2013). While most college students with some background in biology have enough knowledge to reason through skills 1-2, they lack skills 3 and 4, which deal with diagram structure. Therefore, users need to be able to affect and observe the structure of the cladogram, be it to rotate nodes or expand the available information.

With these content and function requirements in mind, the Key Tasks identified earlier could be translated into features for the final product (Table 2). These specifications, while prone to change as design constraints were introduced, allowed the project to move in a more concrete direction.

Users will be able to…	Key Tasks
Understand why *Eunotosaurus* is considered a stem turtle	▪ Observe the cranial sutures and structures that support a turtle affinity for *Eunotosaurus* ▪ Know post-cranial evidence for a *Eunotosaurus*-turtle clade ▪ Distinguish between the crown, stem, and total clades
Understand how comparative morphology can inform evolutionary relationships	▪ Make detailed observations of cranial morphology ▪ Make comparative inferences based on ancestral, recent, or unique traits ▪ Use evidence of most recent common ancestry to make inferences
Understand how *Eunotosaurus*, a stem turtle, adds to our knowledge of crown-ward turtle evolution	▪ Understand how fossils let us make inferences about the past relating to modern species ▪ Distinguish between the crown, stem, and total clades ▪ Understand relative relatedness of taxa in a tree ▪ Use evidence of most recent common ancestry to make inferences ▪ Learn about the contribution of *Eunotosarus* to turtle origins
Recognize their current knowledge gaps in evolutionary biology, if any	▪ Reflect on their intuitive biases surrounding evolution ▪ Be able to rotate nodes in an interactive tree diagram ▪ Be able to add taxa onto an unbalanced tree diagram ▪ Review terminology that they may be misinterpreting

Table 1. Summary of enabling objectives and key tasks for those objectives.

Users will be able to…	Associated App Features
Understand why *Eunotosaurus* is considered a stem turtle	***Morphology***: ▪ Comparative Morphology Tab ▪ Taxon Overview ***Phylogeny***: ▪ Information Panel ***Resources***: ▪ Discussion
Understand how comparative morphology can inform evolutionary relationships	***Morphology***: ▪ Comparative Morphology Tab ▪ Mini Cladogram ***Phylogeny***: ▪ Interactive Cladogram ▪ Appearance > Filter by Major Trait ▪ Fundamentals > Phylogenies and Deductive Reasoning
Understand how *Eunotosaurus*, a stem turtle, adds to our knowledge of crown-ward turtle evolution	***Phylogeny***: ▪ Information Panel ▪ Fundamentals > Crown vs. Stem ▪ Fundamentals > Form and Function in Phylogeny ***Resources***: ▪ Discussion
Recognize their current knowledge gaps in evolutionary biology, if any	***Phylogeny***: ▪ Fundamentals ▪ Information Panel ▪ Terminology Links ***Resources***: ▪ Discussion

Table 2. Summary of enabling objectives and associated app features.

Structure: Information Architecture

The Structure plane defines the activities, interactions, and information that the user will navigate. Where the Scope defines requirements, the Structure tangibly influences the final product. Part of this is outlining an *information architecture*, a flexible structure that organizes the components of the application and how users can move through it efficiently and effectively. Tied into the information architecture is *interaction design*, which anticipates user queries and behaviors, then designates how the system will accommodate them.

Information Architecture. The information architecture is expressed through *flowcharts*, which organize the component features and content into a navigable framework. The program used to put together the first iteration of a flowchart, found in **Appendix D**, was the draw.io webtool (https://app.diagrams.net). The polished version was created using Lucidchart (**Fig. 33**).

As described in **Table 1**, three major parts of the application were planned to help address the enabling objectives: **Morphology**, **Phylogeny**, and **Resources**. The **Morphology** houses the 3D models of *Eunotosaurus* and other taxa, allowing users to not only appreciate the intricate cranial anatomy that supports a *Eunotosaurus*-turtle clade but compare how the bony relationships change across taxa. 3D models were chosen because cranial bone relationships are so complex that a familiarity with the architecture in space is usually needed to fully understand 2D representations. This is why it is the first module users encounter. Next is the **Phylogeny** section. It places *Eunotosaurus* within its most-relevant evolutionary context, visually tells the story of secondary anapsidy in turtles, and serves as a platform through which users can brush up on their phylogenetic knowledge. Lastly, the

Resources section ties the interactive experiences from the previous sections into concise didactic material. It contains two subheadings: Articles and Appendix. In Articles, users can access multimedia learning modules related to turtle evolution and *Eunotosaurus*. The Appendix holds additional information that more knowledgeable users will be interested in, such as the character matrix used to create the **Phylogeny** section's cladogram and a link to Dr. Bever's lab website.

Initially, the information architecture chart was made to act as a point for discussion with Dr. Bever and stakeholders regarding information hierarchy and functions that would meet the enabling objectives. For example, users might still need help connecting the dots between the distinct morphological and cladistic information found in the first two sections, so the Articles tab – which summarizes the major takeaways – was prioritized as the landing page for the Resources section. Where the information architecture organizes content, the functions that support it are defined by the interaction design.

Interaction Design. Together with the informational components of this design comes the functional element of the Structure plane, known as interface design. This is the axis upon which the rest of the UI design process revolves. It is the dialogue between the user and the product or service. In other words, it is how the user will communicate with the system and how the system will respond. This dialogue was expressed in four domains:

- **Words.** The word choice in the interactive components, like button labels, needed to be at once clear, meaningful, and effective. The goal is to impart as much information as possible without overwhelming or confusing the user. For example, ambiguous language such as a simple "More" to describe the entire supplementary information section for the application warranted stakeholder input and consultation with a thesaurus. This tab was then renamed "Resources." In the same vein is the capacity for designers to miscalculate the meaning users will take away from a label. Initially, the "Articles" subheading was called "Modules" to reflect the presence of organized educational content, but stakeholders expressed concerns about the term having too many definitions to be clear, as well as a negative emotional association with standardized testing.

- **Visual representations.** This covers the use of images, graphics, typography, and icons that convey meaning or help in user navigation. Part of the interaction considerations here was to ensure ease of use. Simple, intuitive design language such as using radio buttons that denote mutually exclusive selections (as opposed to checkboxes, which users associate with enabling multiple selections) set expectations for what an interaction entails. Typography was also used to impart meaning, with type conventions such as underlined blue text to signal the presence of a link. This is also where visual feedback comes into play (see Navigation Design for an example).
- **Space.** This aspect of interaction design exploits the human tendency to think in terms of physical space, not just the devices they use to access digital systems. In practice, this means a few things: keeping physical metaphors in mind (think about how modern systems utilize them; there is a *desktop*, *folders*, a *trash bin,* and *windows*, to name a few), exploiting user skills for physical interaction with objects, and – more mundanely – device capabilities.

Incorporating a 3D model that users can manipulate through intuitive mouse or touch-based gestures was the first idea to meet this consideration. Beyond that were the decisions to include an interactable cladogram designed to be explored, rather than creating an animation that would deliver the same information. The choice to add visible nodes, turn them into buttons and make their dimensions touch-friendly were all functional design choices relating to the information-dissemination goals outlined earlier.

- **Time.** This relates to media on a time axis, such as music or video. Another way to look at it is how the user may want to spend their time. For those who want to achieve a thorough understanding, the first two sections (Morphology and Phylogeny) provide a rich didactic landscape for exploration and discovery. For those who want to cut to the chase, the Resources portion provides clear, informative articles and videos that synthesize the background and supporting information they need to understand the '*Eunotosaurus* hypothesis' (see Joyce *et al. 2015).*

Skeleton: Interface, Information Design, and Navigation

The Skeleton plane is all about creating a user-friendly layout that enables the easy completion of desired tasks. Whereas the structure concerned itself with the broader architectural and interactive components, this plane refines the level of detail.

The Skeleton is defined through the interface, navigation, and information designs. The *interface design* connects users to the system's various functions. The *navigation design* allows the user to see and move through the system's Structure. The *information design* draws on and incorporates the other two elements to communicate ideas to the user. *Prototypes* bring these three parts of the skeleton together in a cohesive reference for the final product's visual polish.

Interface Design. Creating a serviceable interface design is about selecting the right elements for the task at hand. While deciding which functions appear on a given screen falls within the plane of Structure, how they are realized and refined is the bread and butter of interface design. For example, it was determined early on in prototyping that a dropdown menu should be placed in the Morphology screen. While the first interaction a user would attempt when given a 3D model viewer is to click on the model itself, a list would also allow users to see their options before committing to a selection. A dropdown is the only space-saving medium for including the total list of bones and bony landmarks available. However, the execution of that dropdown menu was the subject of much debate. In the end, the desire to reduce cognitive strain led to the adoption of a standard menu with a hover effect over a multi-level dropdown with subheadings (**Fig. 14**). This back-and-forth between functional requirements and user-friendliness was a constant throughout the iterative process.

Figure 14a-b. Iterations of dropdown menu designs. The multi-level dropdown menu **(A)**, while used to break down the major components of the articulated skull, hides information under a second level of navigation. It also relied on clicks for making selections, which can drag out the exploration process. The standard hover menu **(B)** is more intuitive and requires less thinking on the user's part.

Navigation Design. Navigation design allows users to get around within the system. Therefore, it must accomplish the following:

1) Provide the means to get from point A to point B on the site or application.
2) Communicate the relationship between the elements on each page.
3) Orient the user to the relationship between the contents of the navigation and the page the user is currently viewing.

The first was achieved through incorporating a persistent global navigation bar that linked to all the major sections of the application. To orient the user to which section they are currently viewing, the sharp contrast between a near-black background and white text is used as a modern take on the button press metaphor (**Fig. 15**). This is an example of how feedback supports navigation and interaction design.

At each section, local navigation provided users with access to “nearby” functions related to the available tasks. On this same page, the lower local navigation bar is colored using a light blue that was consistently used throughout the application for local navigation components. When an option is selected, it too uses a ‘pressed button’ design to orient the user to their last action.

Contextual navigation – which was incorporated into the content itself – took the form of in-text hyperlinks and “See Also” links that allow users to clarify unfamiliar or confusing vocabulary and draw associations between concepts. Here, the contextual navigation also includes the use of instructional color and changes in line weight to help the user keep track of their place in the cladogram and impart meaning.

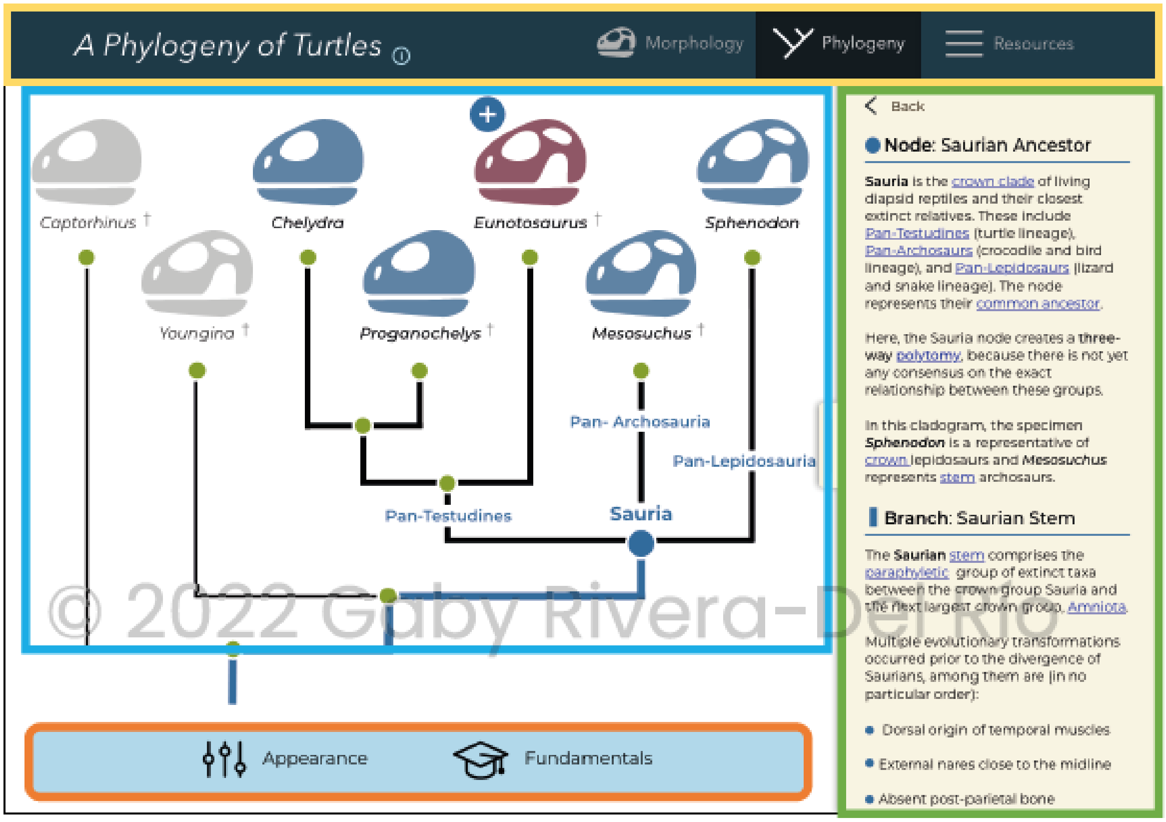


Figure 15. Annotated navigational design in the Phylogeny section. Highlighted are the global navigation bar (yellow), the local navigation bar (orange), the information panel full of contextual hyperlinks for key terminology (green). In blue is the cladogram itself, which is meant to orient the viewer across the diagram and uses instructional color and shapes to make connections between the text's subheadings and the diagram. Text not intended to be read.

Information Design. Information design incorporates the two previously discussed elements to optimize the presentation of information to the user. It involves not only deciding on the visuals that will accompany the text and impart meaning but also curating the way information is grouped. Given the project aim for this system as a didactic tool, this was by far the most important design component to the success of the application. This was the domain through which the misconceptions and pedagogic challenges identified earlier needed to be addressed.

Because the interpretation of phylogenetic trees is central to the way evolutionary relationships are interpreted and discussed, and many intuitive biases that form around them are visually related, the Phylogeny section's cladogram required considerable time and effort to design (**Fig. 16-18**) (Dees, 2014; Novick & Catley, 2012). The following design choices were made to reduce potential misinterpretation of the phylogenetic tree:

- Adding an Info button that alerts users not only to the specific purposes of a cladogram but links to a primer module, "Cladograms 101."
- Adding dots at the nodes and ends of the tree to signify that the elements are interactable, draw a visual parallel between the end taxa and the nodes which represent common ancestors (unknown taxa whose evolutionary divergence yielded the ancestral species beyond that point in the tree), and reaffirming the importance of nodes in the interpretation of a phylogeny (Catley, 2006)
- The vertical line style of the phylogenetic tree was chosen because the horizontal splitting at the nodes fights the intuitive bias that there is an evolutionary "mainline," like a long diagonal backbone may suggest (Novick *et al*. 2007, 2010, 2012)
- Including as much plain language as possible and adding clarifying links to important terms (Schoerning 2014)
- Tree loads with already-rotated nodes and group of interest not on the far right to avoid a "ladderized" appearance, which discourages intuitive notions of evolutionary progress or advancement (Meir *et al.* 2007; Gregory, 2008)

- The user is given the option to expand the branches to give a more complete view of the diversity within, dispelling the perception that the groups outside of the taxon of interest are not as complex (Catley, 2008)
- When a node is selected, labels appear that explicitly name the groups terminal taxa to represent, as not all are the sole representative of their clades like *Eunotosaurus* (Sweller 1988)
- Option to add taxa like synapsids and mammals to the tree as an amniote outgroup, simultaneously fighting notions of mammalian forms as "higher" and the assignment of outgroups as more "basal" or "primitive." Note: this could not be fully addressed because of constraints on the size of skulls for use in morphological analysis, but future development plans include an open workspace that can be zoomed into and out of that will address the issue of an unbalanced phylogenetic tree.

Though this was not the only area where information design was applied, the cladogram provides the most robust example of its use in this methodology. Other decisions of information design included how topics were to be grouped, how much information to display – in this case, it was making the tradeoff between a more complete tree and having skull figures large enough for the user to appreciate the differences between taxa.

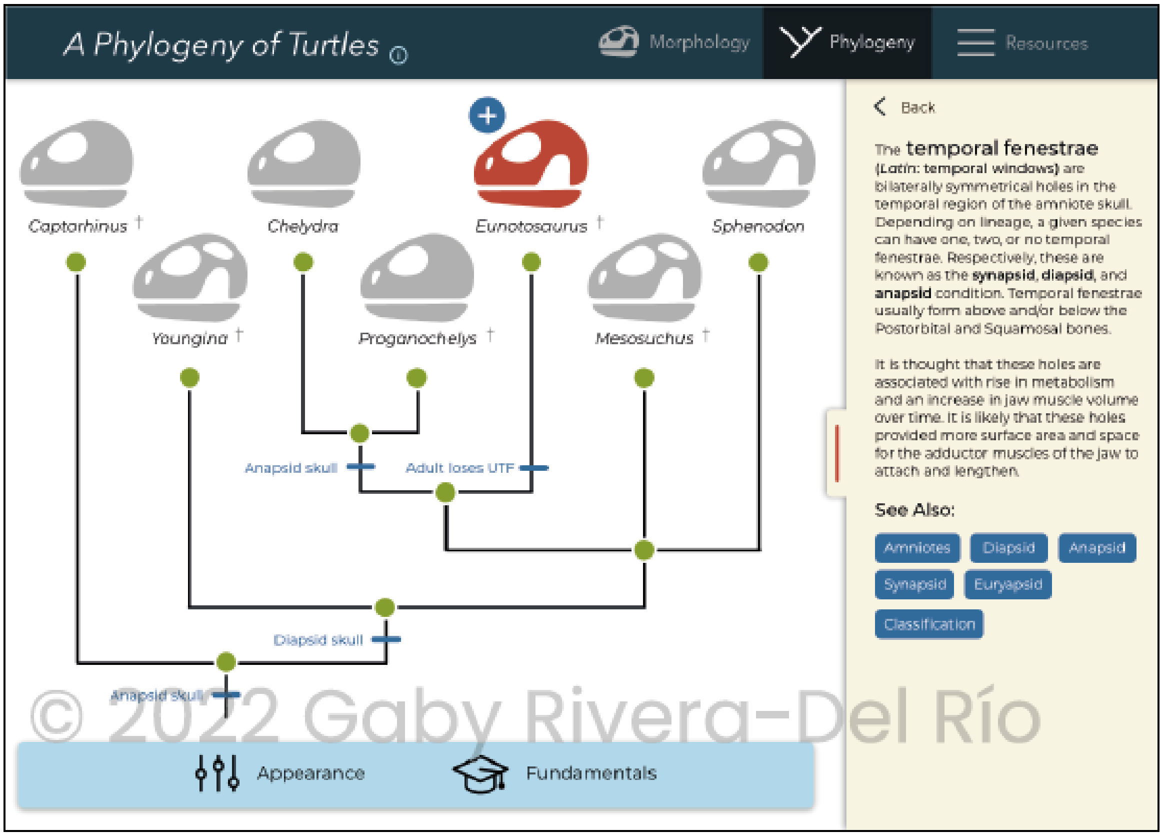


Figure 16. Example of information design. In this interaction, opening the information link to a character or trait, such as temporal fenestrae, not only opens an information panel with contextual navigation links (see Navigation Design) but also maps that trait on the cladogram. The royal blue color of both elements creates a visual link between them. Text not intended to be read.

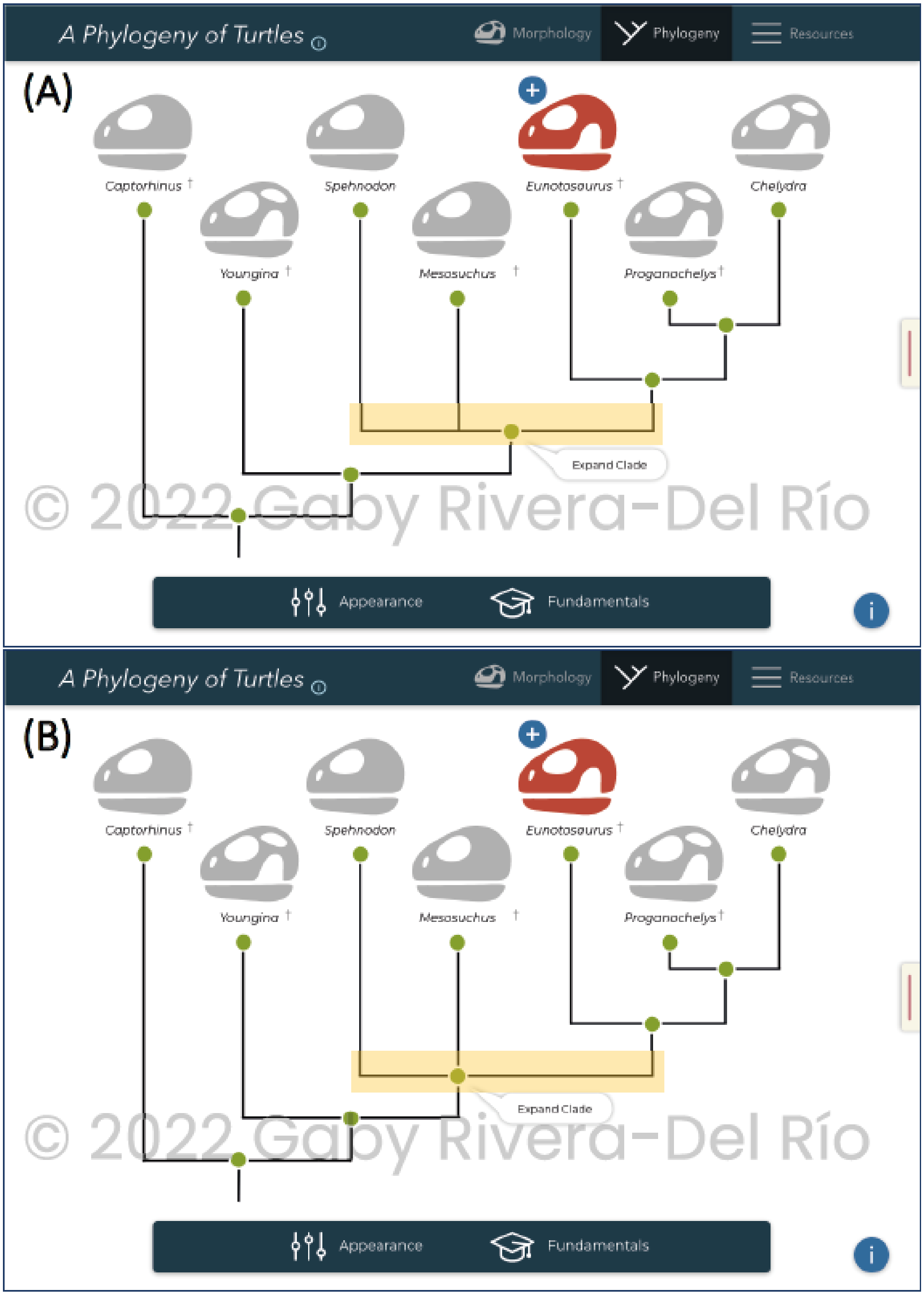


Figure 17a-b. Iterations of cladogram information design. Note that the multifurcation, or polytomy, is highlighted in each image. The design choice to center nodes along the bifurcations created an offset multifurcation **(A)** where the left side held two descendant lineages and the right had one. This was adjusted **(B)** to avoid the potential misconception that the left two taxa were more closely related to each other than to the right one. Text not intended to be read.

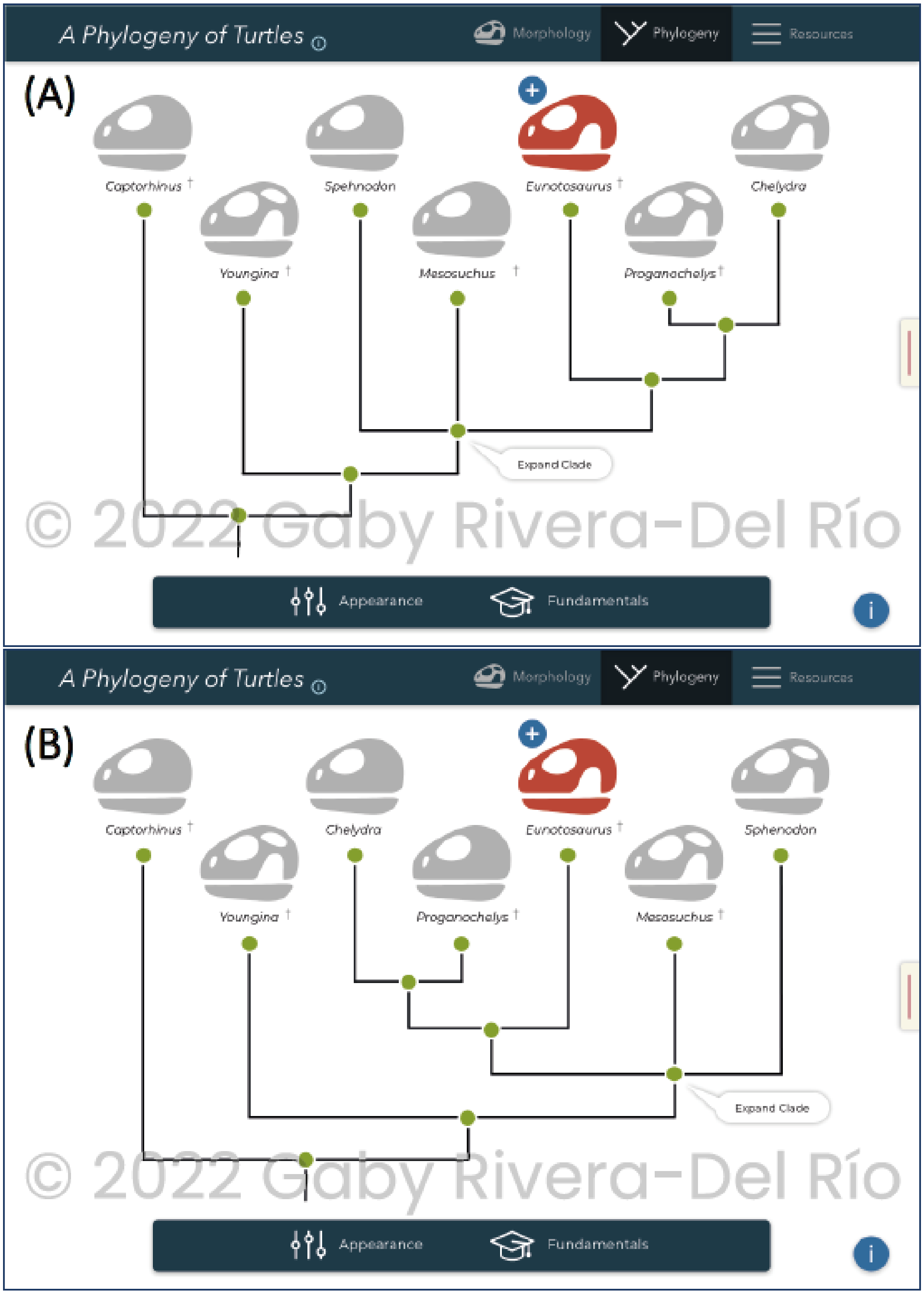


Figure 18a-b. More iterations of cladogram information design. The top image (A) shows a "ladderized" cladogram that has the group of interest at the far right. While accurate, it promotes thinking that evolutionary progress is successive and/or linear. The bottom image **(B)** shows the same information but with terminal taxa rotated at their nodes, disrupting this thinking, and moving the group of interest, Pan-Testudines, to the center. Text not intended to be read.

Surface: Visual Design

Design Principles. The surface design for this application focused on four major principles: Consistency, Discoverability, Feedback, and Accessibility.

Consistency. The Consistency principle leverages the human tendency to find and adhere to patterns. In practice, this means limiting the number of ways actions and elements are represented so users do not have to learn new representations for each task they want to complete. One avenue for consistency is visual design, for which a *style guide* is often used (**Appendix E**). One way to achieve unity in design is through instructional or meaningful color. For example, elements of the application that allow users to associate or interpret didactic content were colored royal blue. Likewise, explanatory text is accompanied by an unsaturated sandy yellow color, and highlights isolating bony structures are in goldenrod. This visual consistency not only reduces cognitive load and increases predictability but allows for meaning to be applied when elements break that consistency. Outside of serving as a reference to the colloquial phrase 'tree of life,' this was the reason for using green on the nodes of the phylogenetic tree diagram.

It is not just internal consistency that is useful, however. External consistency entails using well-established conventions of user interface design in each system. According to Jakob's Law of Internet User Experience, users spend most of their time on sites other than yours and will bring their expectations from previous experience to your system. As such, it is imperative to design patterns to which users are accustomed. This application does so in multiple cases, from the use of "ⓘ" for pop-ups that provide additional information, to using carrot symbols for dropdown menus (**Fig. 19**). Layout elements are also borrowed from conventional design practices, such as placing search bars and exit buttons at the top right, and nesting titles and back buttons on the top left. These elements come together to make a product that meets user expectations.

Discoverability. The Discoverability principle ensures users can see everything they need to accomplish a task without redundant or extraneous information. This can be inverted to remind designers that components that are hidden or hard to see will be under-utilized. Designing for discoverability takes many forms. It can refer to the establishment of visual hierarchy with font weights, color contrast, and size of elements cueing the user onto what is important in each page. The use of multiple tools for establishing hierarchy is used in the Morphology section, which leverages the stark contrast between the off-white bone model and the dark background of the 3D viewer. A second method for establishing hierarchy was the use of drop shadows which place the local navigational content as more important than the appearance tools on the bottom left of the 3D viewer (Fig. 19).

Another way to design for discoverability is through affordances or visual cues that signal an element's capabilities. A physical example of this would be the inclusion of a metal plate at doorknob height for doors that need to be pushed. The visual design of this app, translated to the inclusion of scroll bars whenever possible and cutting off certain elements, such as text or buttons, within a given window to let the user know that they can scroll to see more. Hover effects are another form of affordance, letting users know that an element is interactable. The inclusion of distinct internal and terminal nodes in the cladogram was another affordance added to the design, serving both an interactive element for users to afford working with the tree through its nodes, and to reinforce node-based cladistic analysis.

Feedback. Where discoverability cues users to how they can interact, what happens once they do so is where feedback comes into play. This facet of visual design is directly tied to the interaction and navigation design by providing cues to the user about what action has been taken, what they have accomplished by it, and what their options are for the next steps. It was previously noted that the use of a spatial metaphor for a pressed button (by darkening the background of a selection) was the visual cue for global and local navigation. Another example is the change in dot size and color when Landmarks are selected in the Morphology section (Fig. 19). Feedback signifiers also include error messages, loading screens (like the one present at the application open), animations (like a slide-out animation for the Information Panel), and any other means of reducing user uncertainty.

Accessibility Principles. Building on the prior three principles is the accessibility principle. This requires setting design constraints aimed at creating an inclusive product. One way to do this is the adhere to the Web Content Accessibility Guidelines (WCAG) published by the Web Accessibility Initiative of the World Wide Web Consortium. Some of the constraints utilized throughout the production of this application are:

- Conforming to minimum AA-AAA level contrast for graphic and text elements
- Not relying solely on color to imbue meaning, but shape, context, and size as well
- Redundancy of affordances for navigation and interaction design
- Creating the design for a small viewport (iPad Pro 11-inch) that can be scaled up

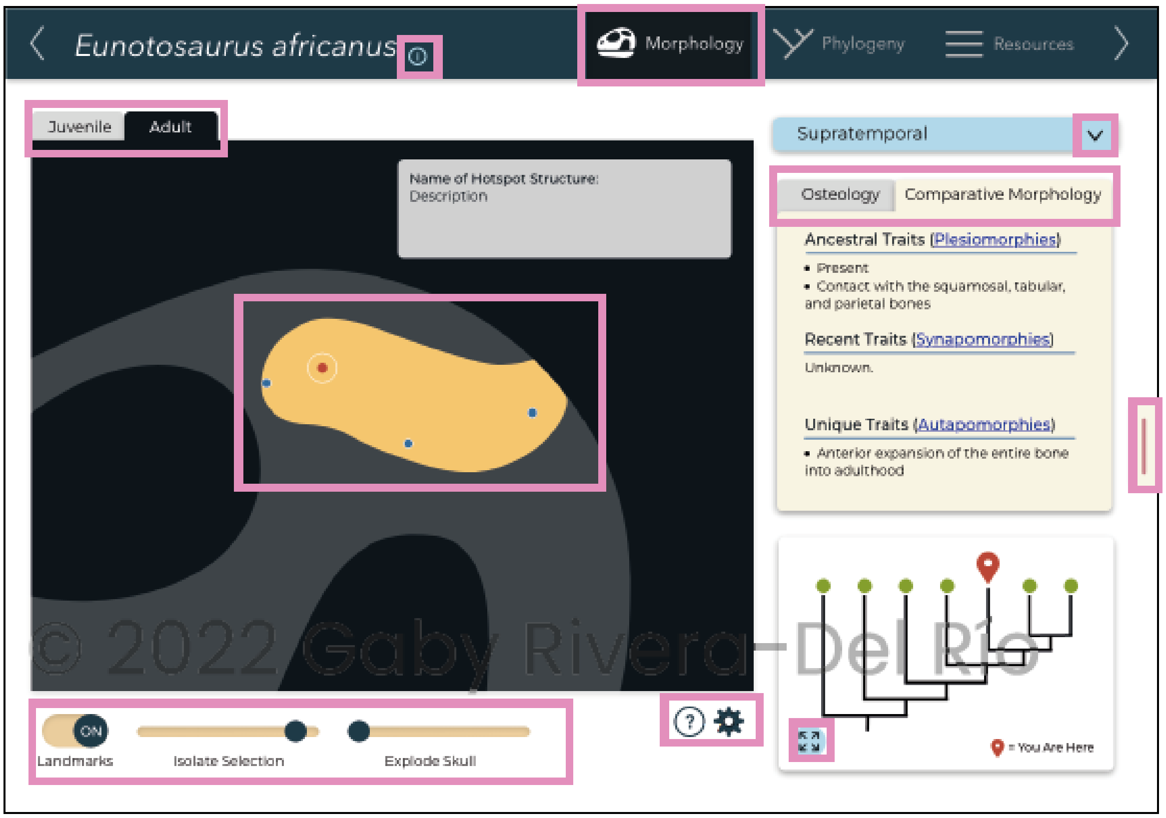


Figure 19. Prototyped morphology section with landmarks enabled. Here, the visual design principles can be observed in action. Some examples of feedback and consistency are in pink. Text not intended to be read.

Results

Project Objectives and Scope

The goal of this project was to design a web application that will enable users to analyze the cranial morphology of *Eunotosaurus africanus* how it informs the origination of the turtle body plan. Central to executing this goal was creating an accurate cranial reconstruction that can contribute to comparative and biomechanical analyses.

Novel 3D Reconstruction. A novel digital fossil reconstruction of the largest and most complete *Eunototsaurus* skull (M777), both crucial to the didactic goals of the project and necessary for finite element analysis (see Discussion), was created in Cinema4D® (**Fig. 20-25**), with a refinement process undertaken in ZBrush®.

This first stage was conducted using best practices for retrodeformation and validated by expert feedback from Dr. Bever and his lab. It filled the missing anatomy via extensive mirroring and superimposition of existing elements, as well as restoring the silhouette of the skull. In all, the segmented data comprised over 70 bones and bone fragments, all of which were repositioned, retrodeformed, superimposed, or mirrored at some point in the process.

2D Reconstructions. Several illustrated skull reconstructions were generated to populate the cladogram. For the extinct taxa, they represent novel reconstructions which include the braincase and pterygopalatine structures which are often omitted from figures in the primary literature (**Fig. 26-32**).

User Interface Design. The UI design portion of the project underwent the entirety of its first development cycle, culminating in the generation of the following assets:

A flowchart (**Fig. 33**) was created to organize the structural components of the web application. Some of the media that comprise this include text, images (.png), animation (.mp4), 3D models (.obj), and computed tomography stacks (.tif).

A series of medium- and high-fidelity wireframes were created as mock-ups of the end-user product (**Fig. 34-48**). For the written content of informational wireframes, see **Appendix A**.

These prototypes were built using best practices for pedagogic user interface design, and their completion marks the first round of development for the application. Throughout the process, design principles laid out in the Understanding Evolution project by the University of California at Berkeley's Museum of Paleontology were incorporated for optimizing the understanding and retention of macroevolutionary concepts. The small blue numbers on the flowchart reflect the image on the storyboard.

Additionally, the information architecture and overlying design were built to accommodate future revisions and additions.

Didactic Illustrations and Diagrams. Among the assets created to supplement didactic text in the user interface were:

- A pedagogically designed phylogenetic tree (**Fig. 39-46**)
- Supplementary graphic elements, i.e., simplified schematic reptile skulls

o Figure. Direct comparison between original volume and reconstruction

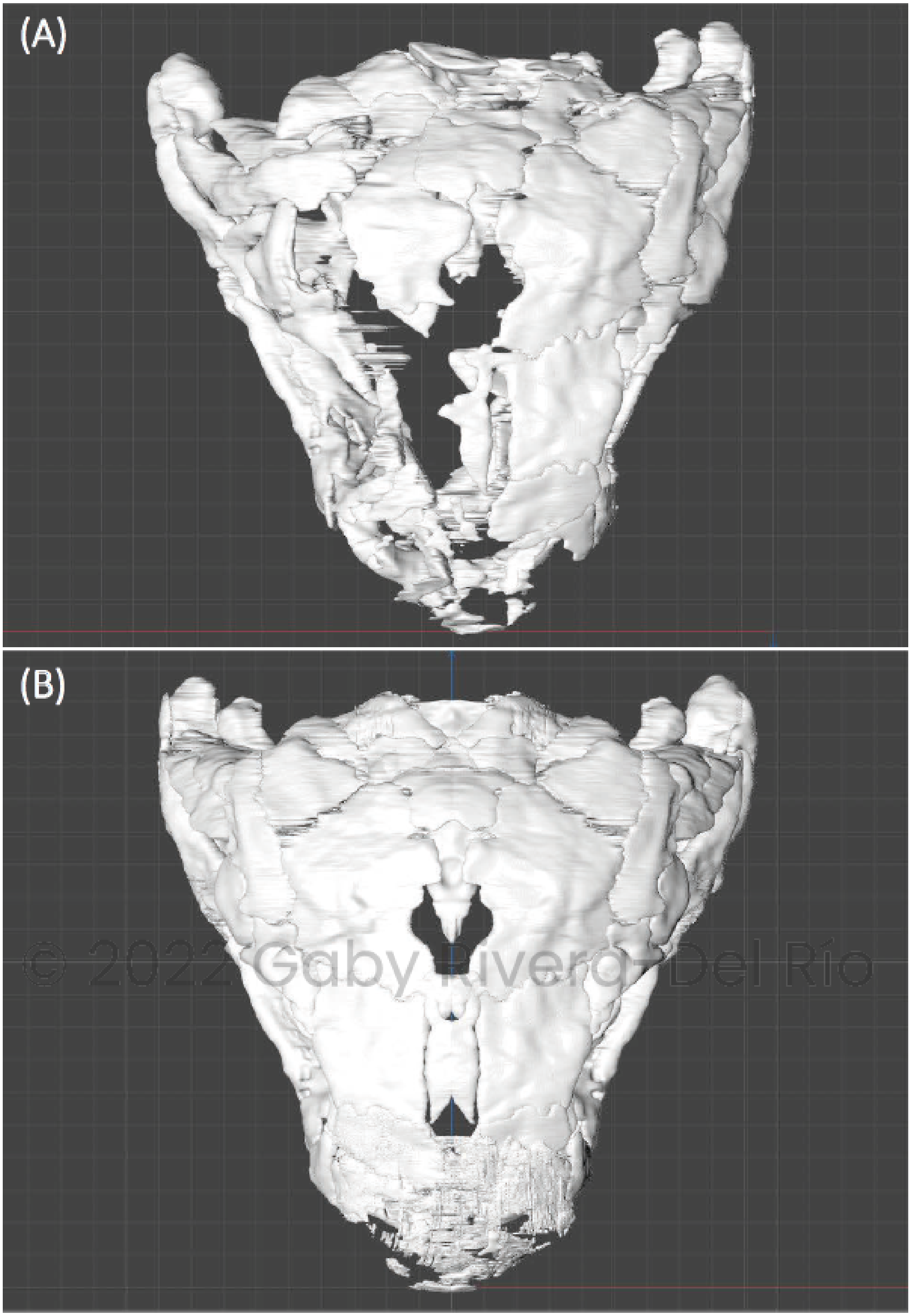


Figure 20a-b. *Eunotosaurus africanus* 3D reconstruction. Dorsal View. **(A)** Before. **(B)** After.

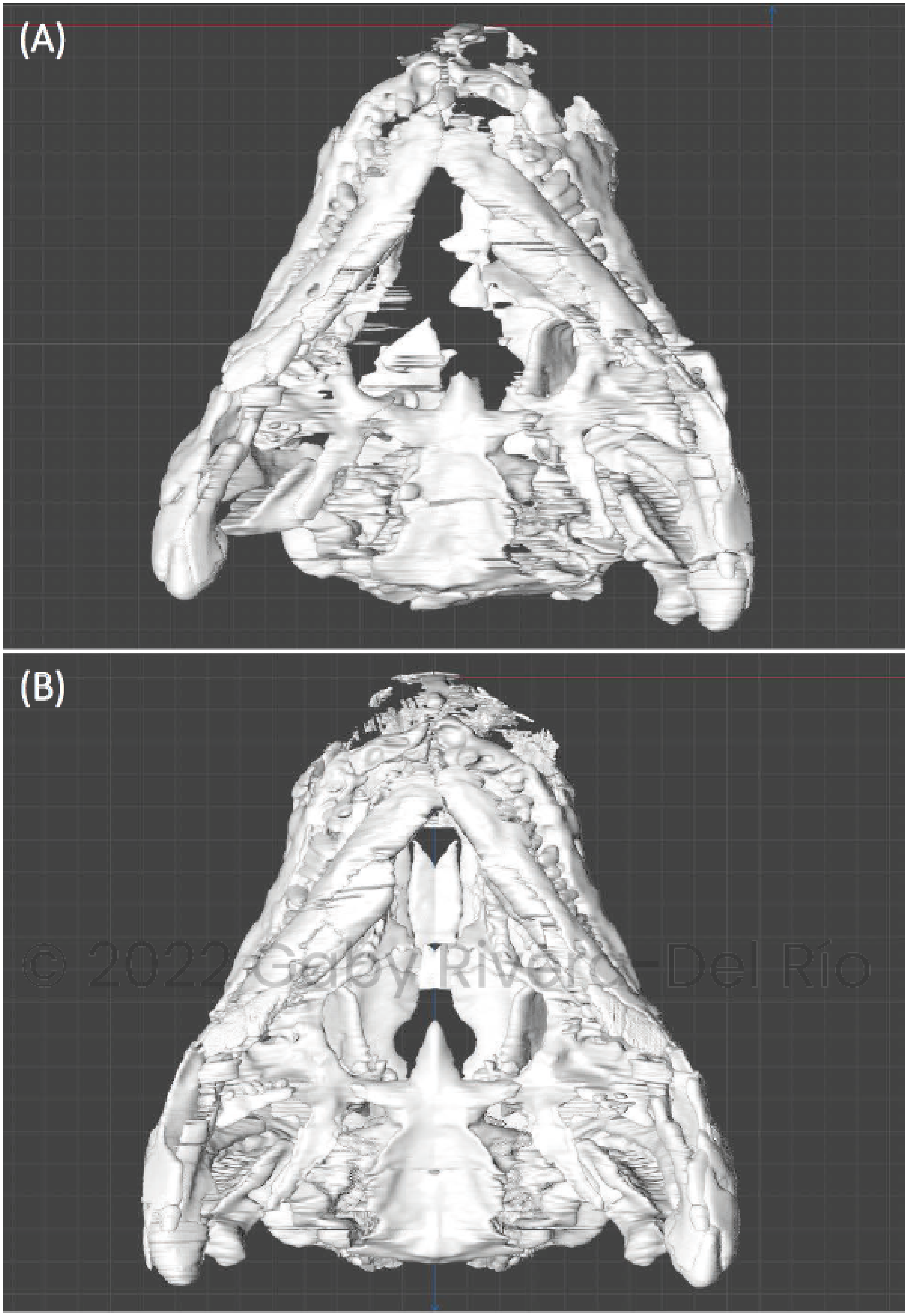


Figure 21a-b. ***Eunotosaurus africanus*** **3D reconstruction.** Ventral View. **(A)** Before. **(B)** After.

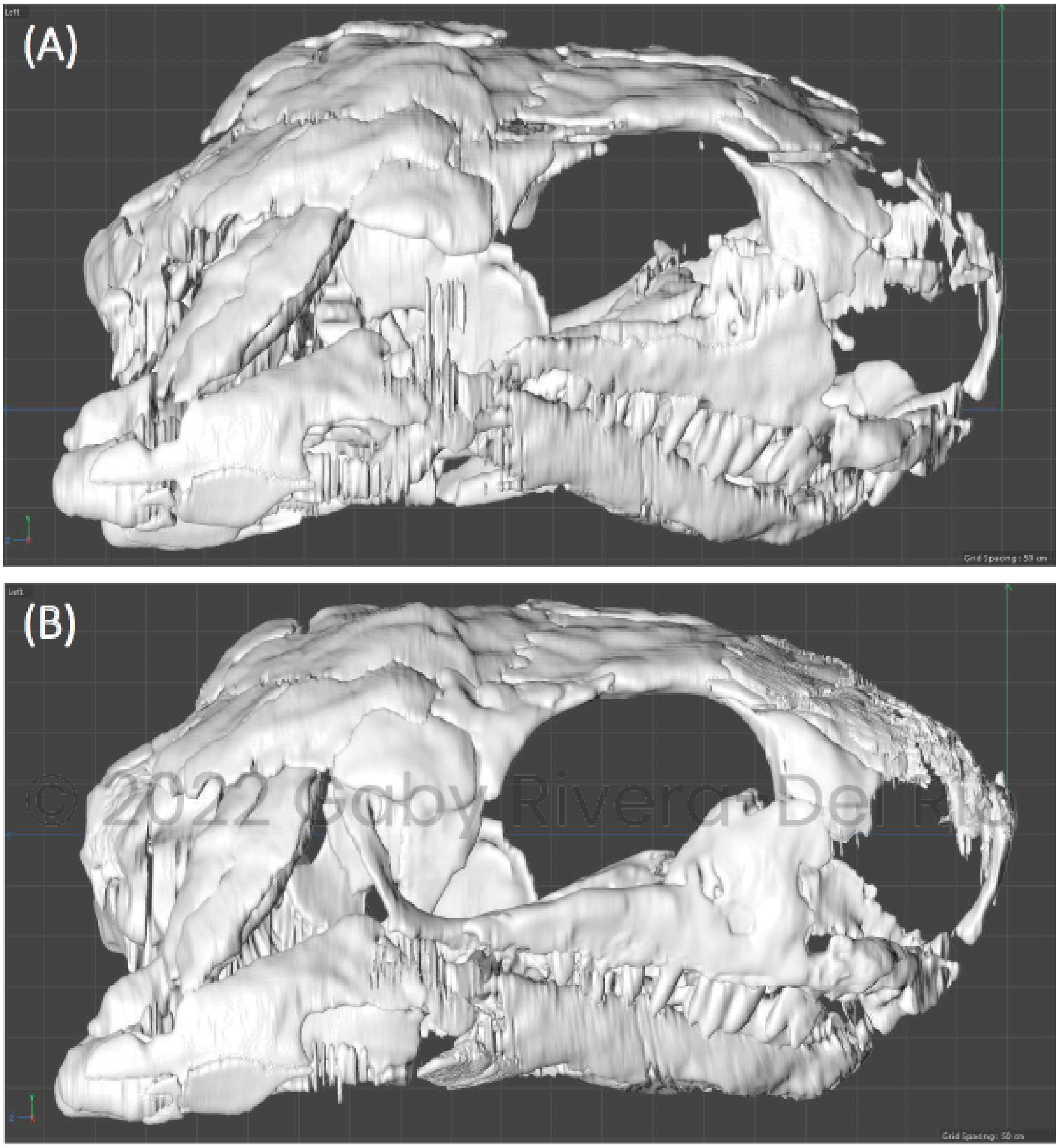


Figure 22a-b. ***Eunotosaurus africanus*** **3D reconstruction.** Right Lateral View. **(A)** Before. **(V)** After.

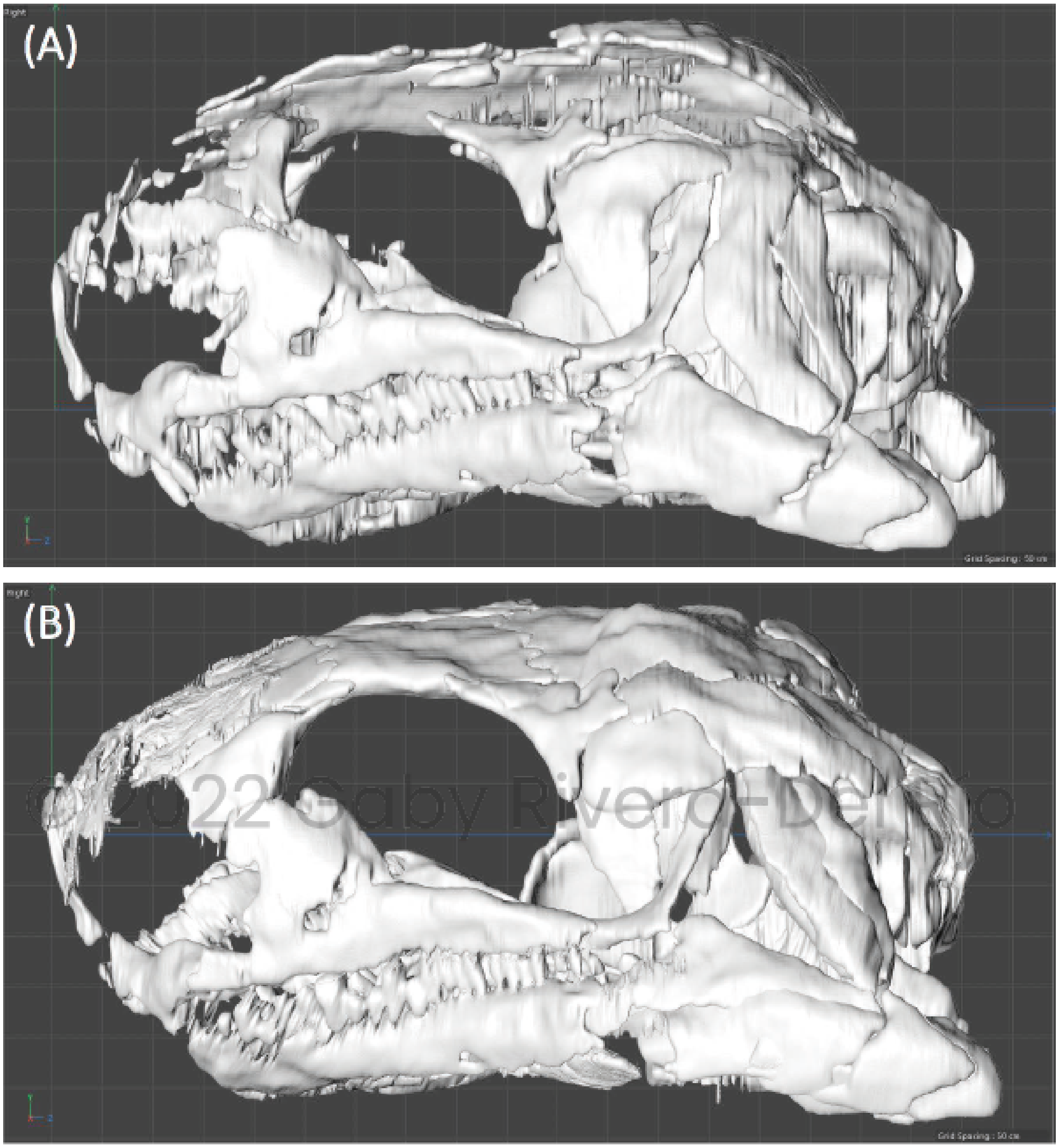


Figure 23a-b. *Eunotosaurus africanus* 3D reconstruction. Left Lateral View **(Top)** Before. **(Bottom)** After.

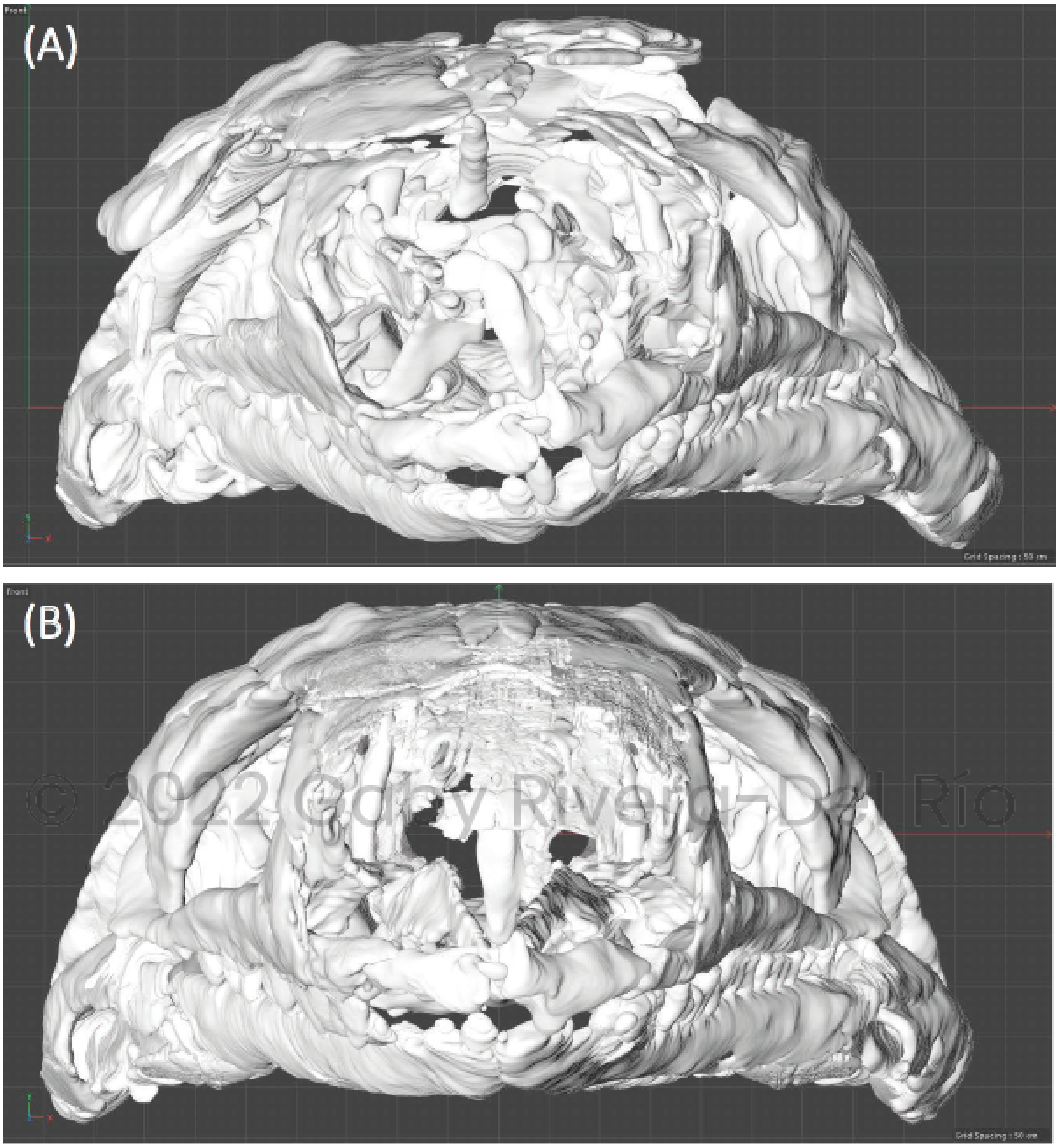


Figure 24a-b. ***Eunotosaurus africanus*** **3D reconstruction.** Anterior View **(Top)** Before. **(Bottom)** After.

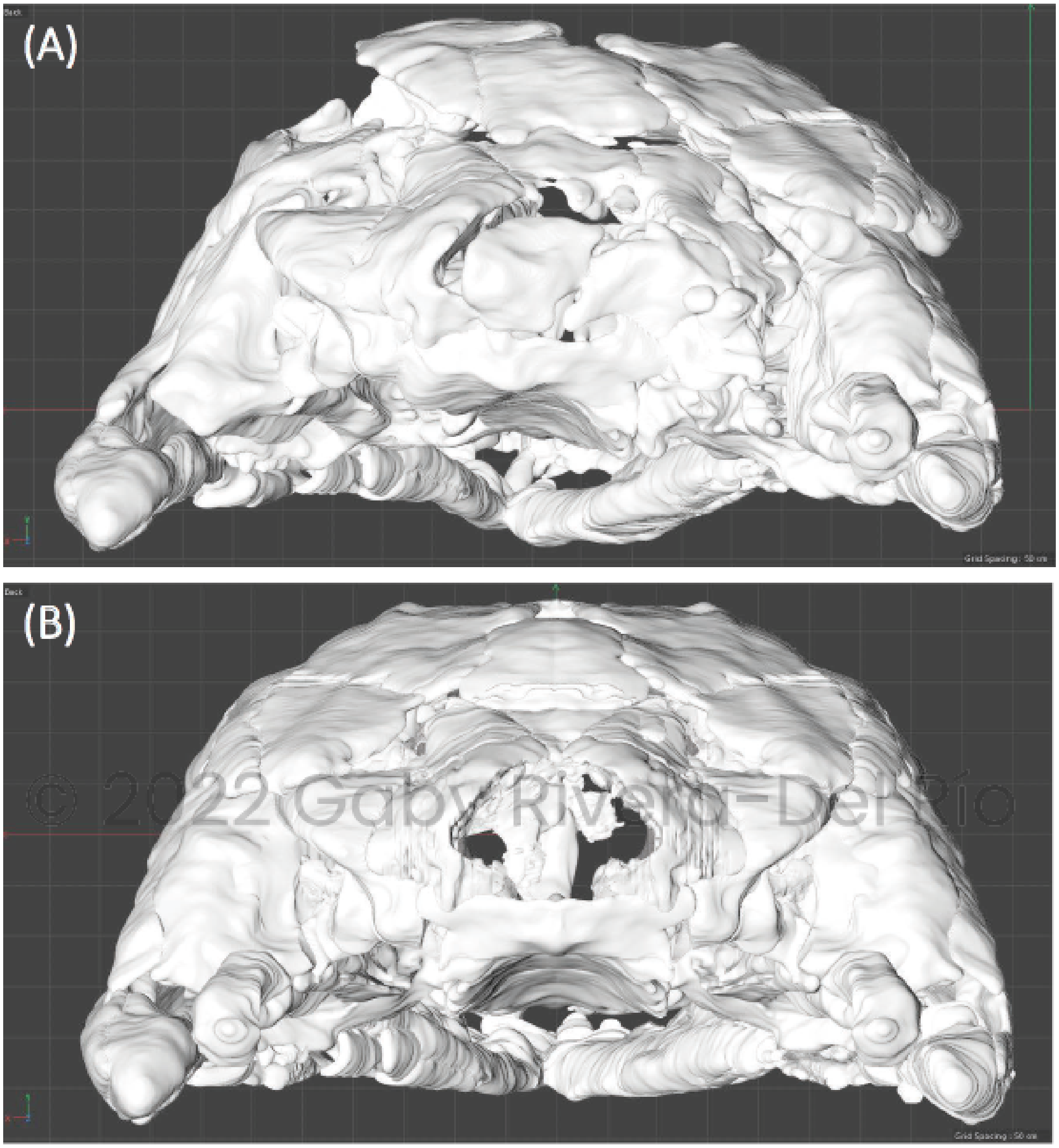


Figure 25a-b. *Eunotosaurus africanus* 3D reconstruction. Posterior View **(Top)** Before. **(Bottom)** After.

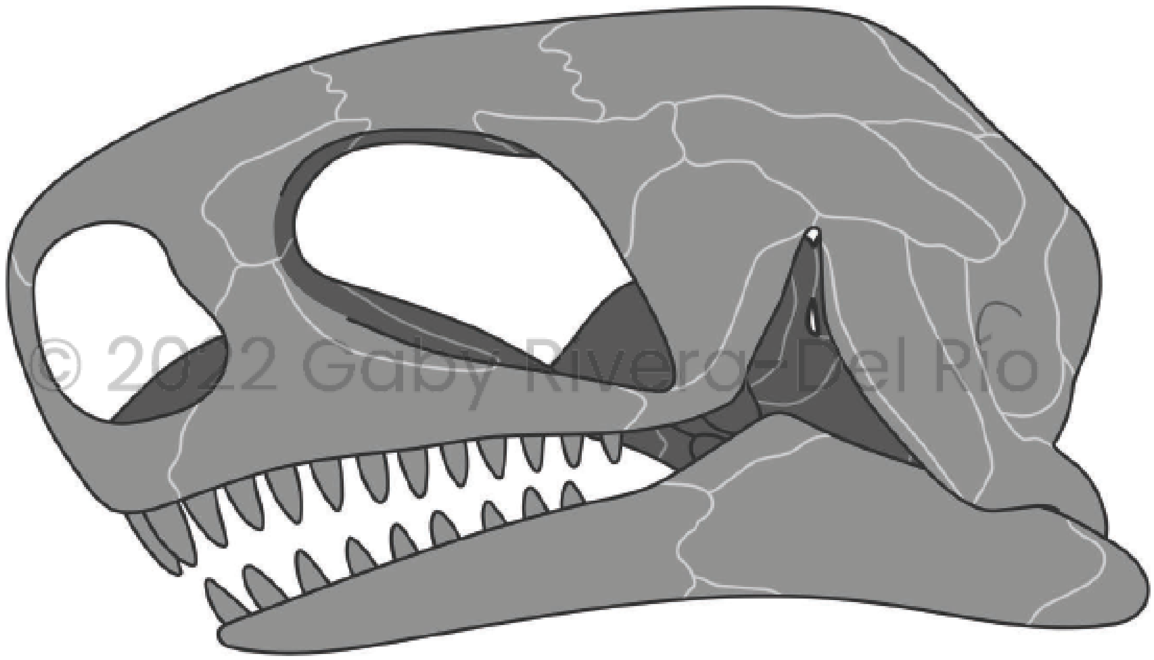


Figure 26. ***Eunotosaurus africanus*** **2D reconstruction.** Image initially referenced and adjusted from Bever *et al*. (2015, 2016). This incorporates the 3D reconstruction performed in the project.

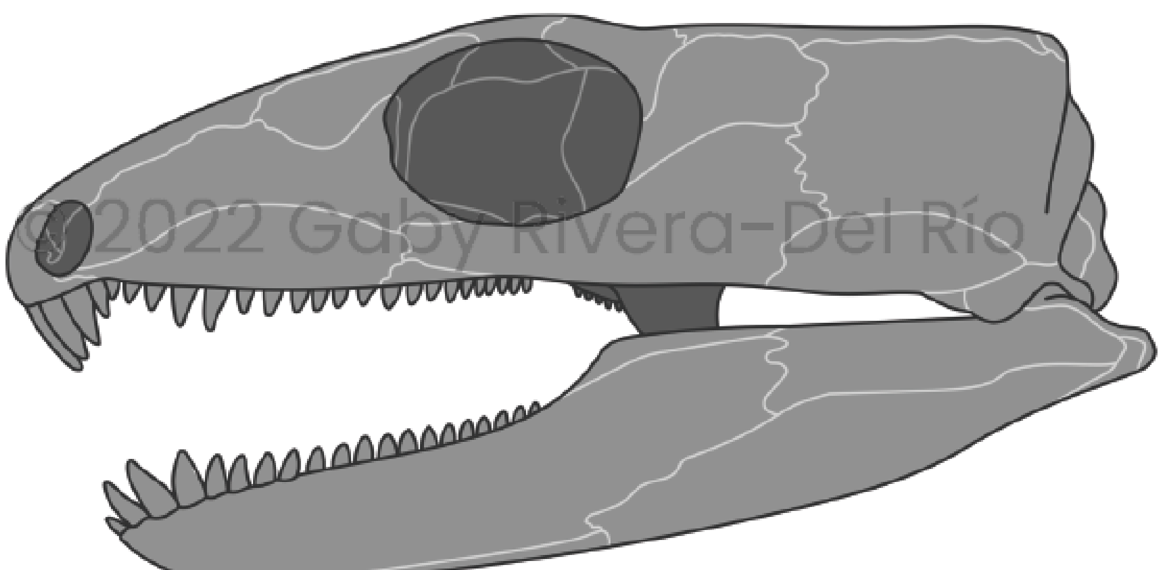


Figure 27. ***Captorhinus aguti*** **2D reconstruction.** Image referenced and adjusted from LeBlanc & Reisz (2015), and Reisz *et al*. (2020). This one was reconstructed from several sources to include braincase and pterygopalatine elements.

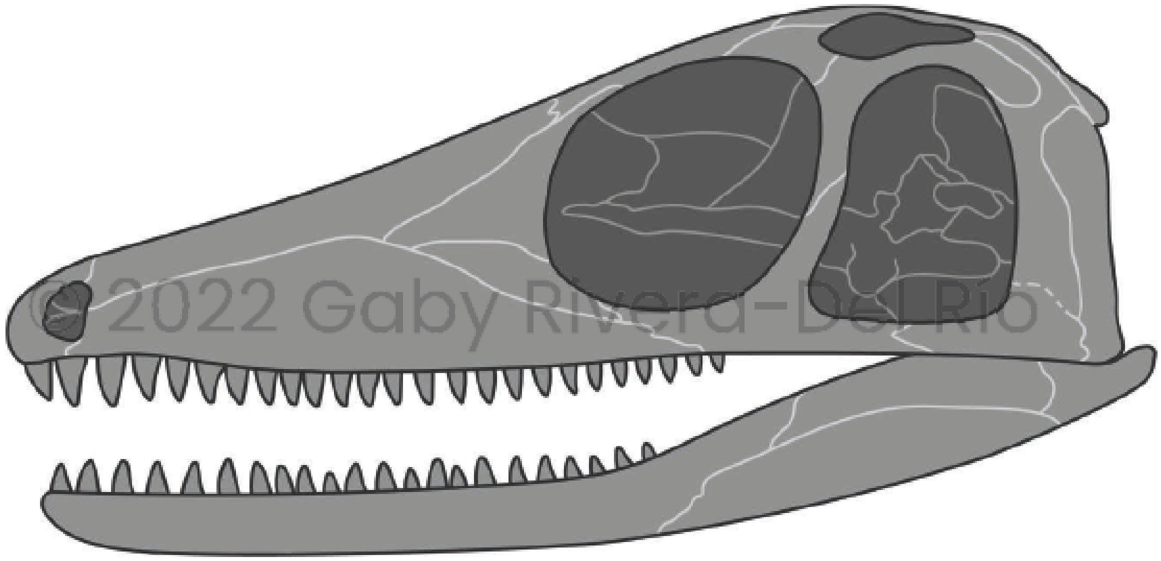


Figure 28. *Youngina capensis* 2D reconstruction. Image referenced and adjusted from Carroll (1981), and Gardner *et al.* (2010). This one was reconstructed from several sources to include braincase elements.

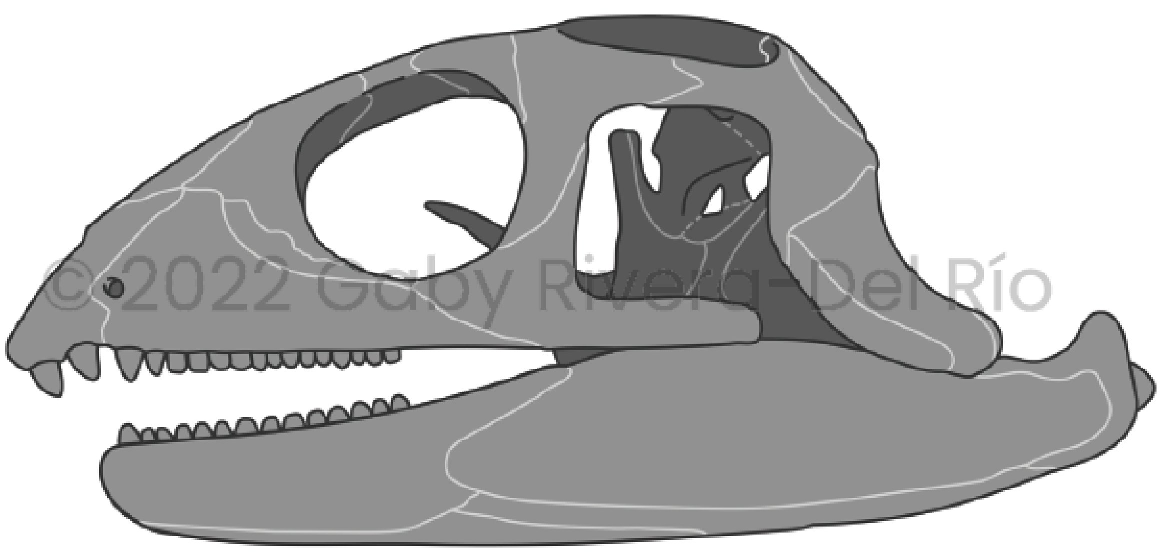


Figure 29. *Mesosuchus browni* 2D reconstruction. Image referenced and adjusted from Dilkes (1998), and Sobral & Müller (2019). This was reconstructed from several sources to include braincase and pterygopalatine elements.

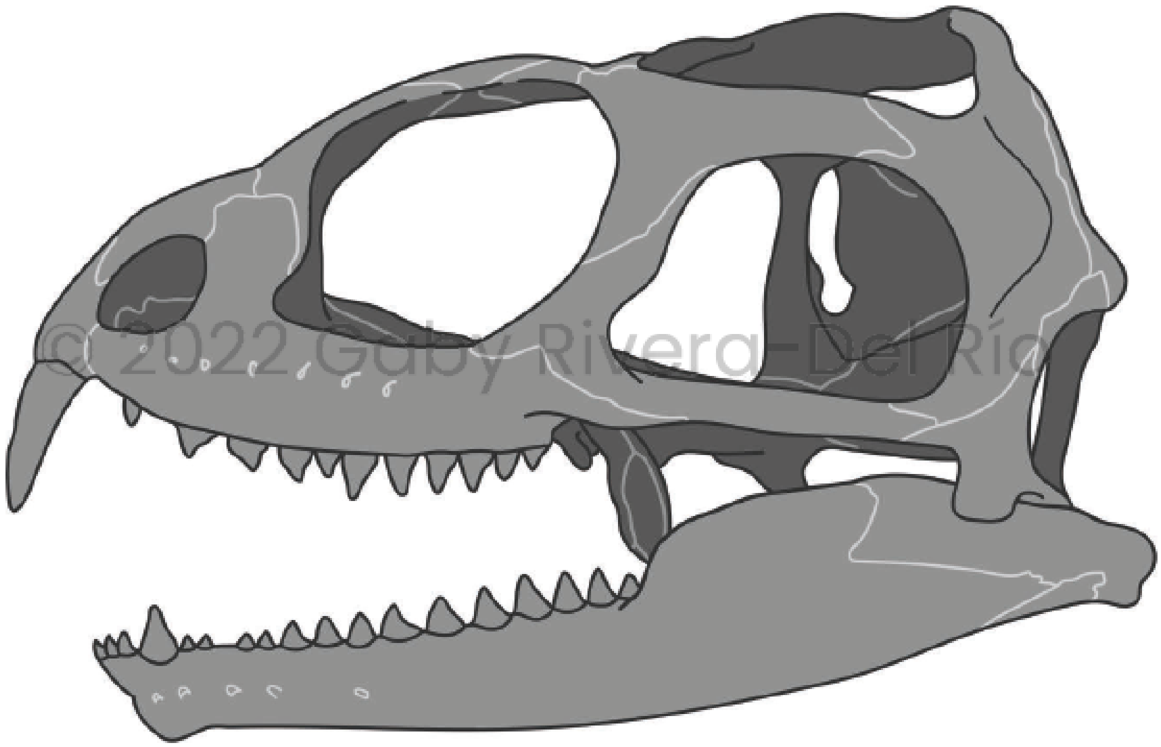


Figure 30. ***Sphenodon*** **2D image.** Image referenced from James *et al.* (2009), and Jones *et al.* (2011). Because this taxon is extant, or living, no reconstruction was needed.

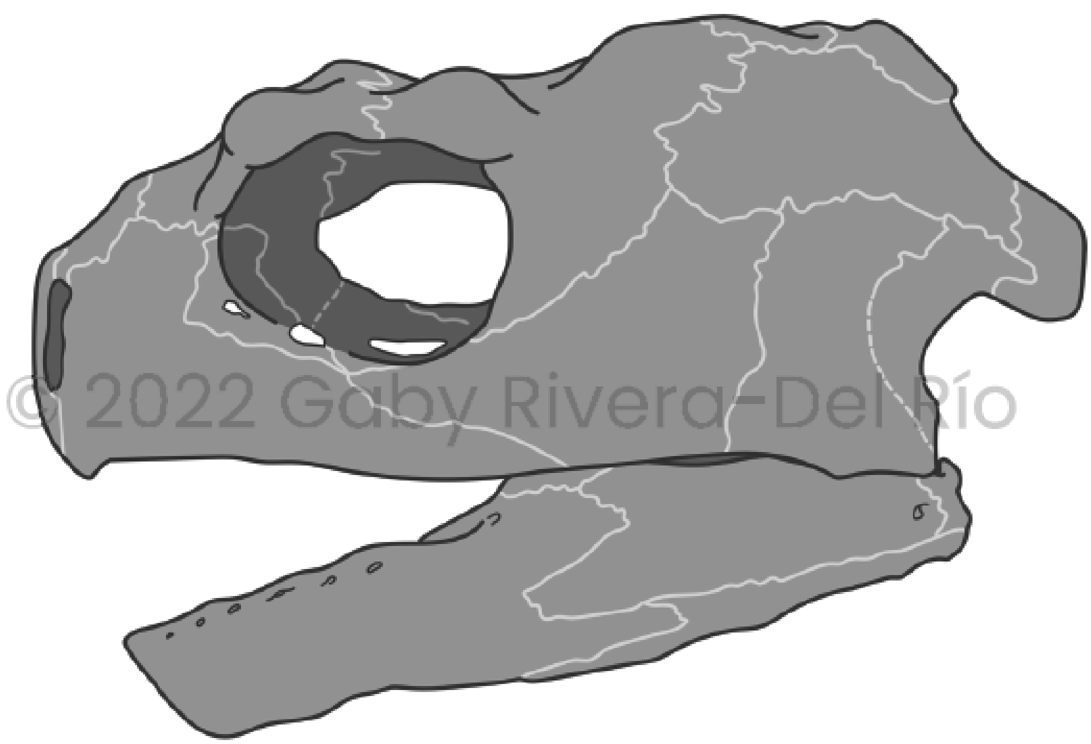


Figure 31. ***Proganochelys quenstedti*** **2D reconstruction.** Image referenced and adjusted from Gaffney (1979, 1990) and Lautenschlager.

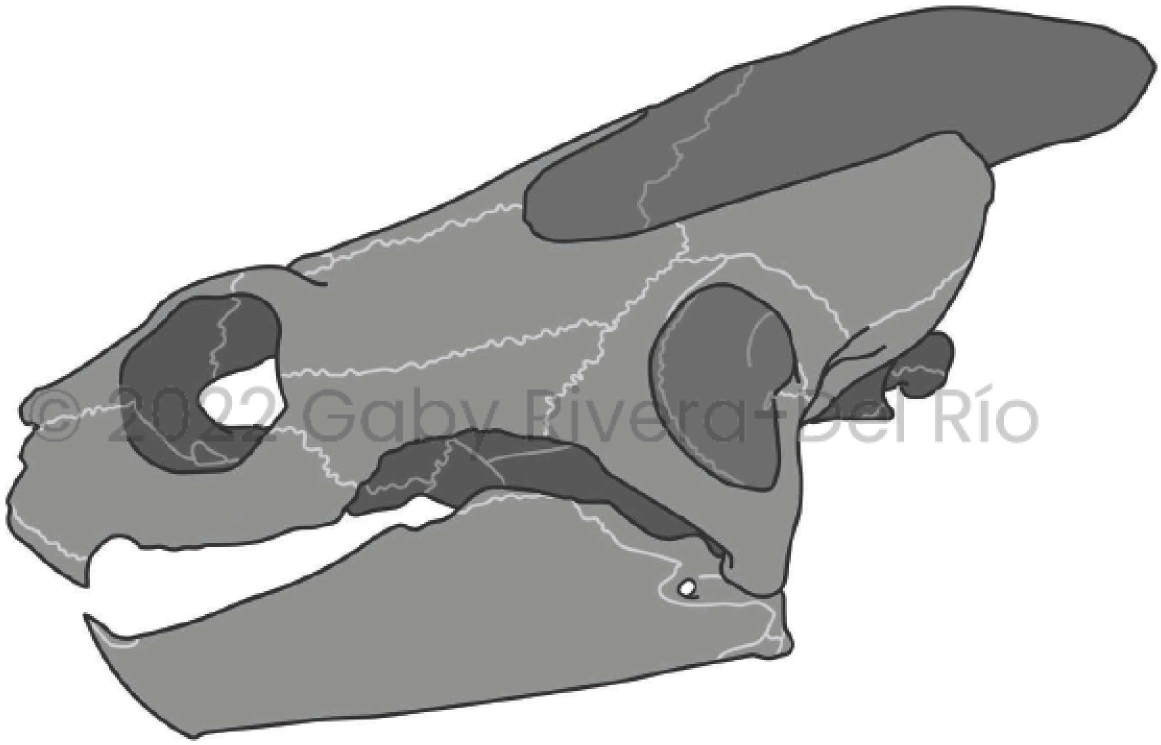


Figure 32. ***Chelydra serpentine*** **2D image.** Image referenced from Werneburg & Maier (2019). Because this taxon is extant, or living, no reconstruction was needed.

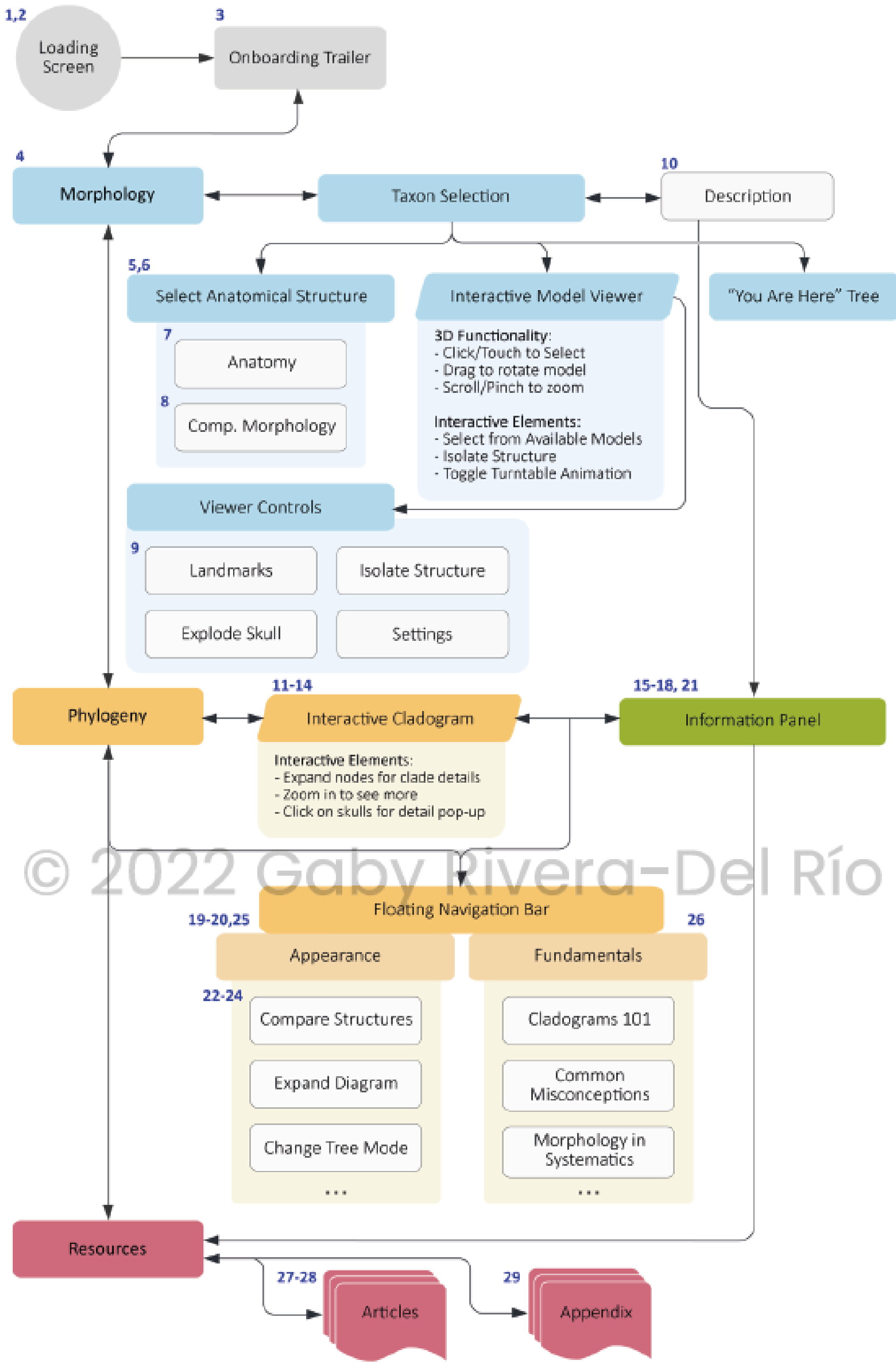


Figure 33. Refined Flowchart. This is the second iteration of the flowchart, with blue annotations coinciding with the order of prototypes in the subsequent **Figures 28-42**.

Figure 34a-b. Application Interfaces. (Top) Splash page. **(Bottom)** Pre-loader.
Text not intended to be read.

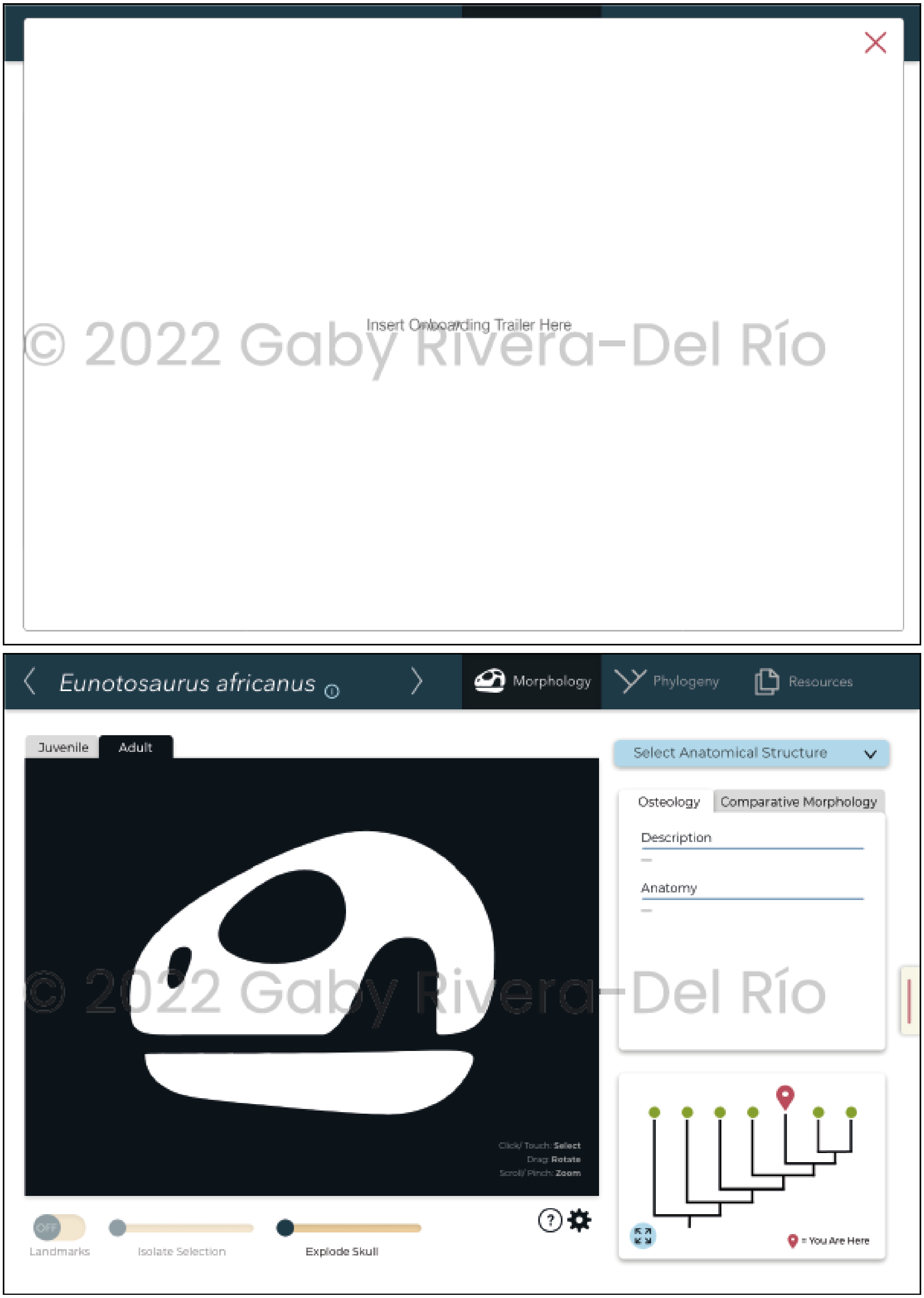
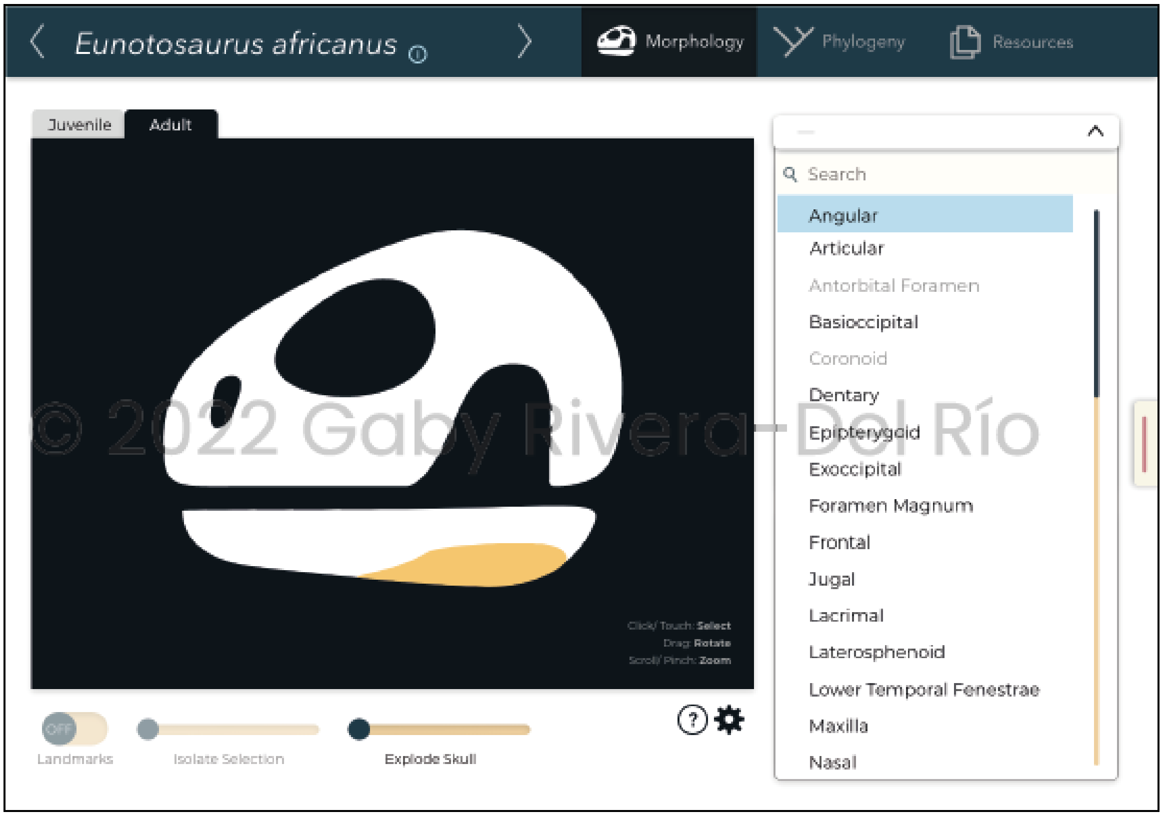


Figure 35a-b. Application Interfaces. (Top) Onboarding dialog box. **(Bottom)** Landing page in Morphology section. Text not intended to be read



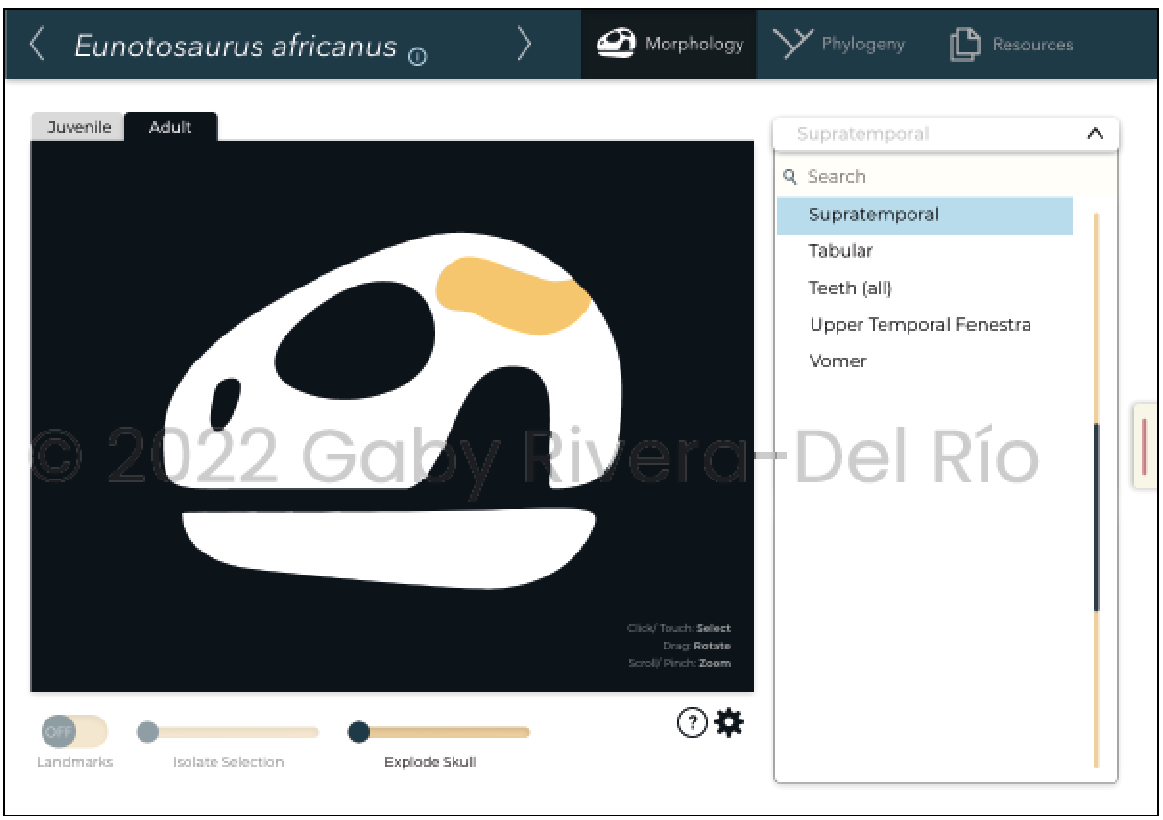


Figure 36a-b. Application Interfaces. (Top and bottom) Selection preview scroll functionality. Text not intended to be read

Figure 37a-b. Application Interfaces. (Top) Post-selection interface changes. **(Bottom)** Push dialog and information navigation. Text not intended to be read.

Figure 38a-b. Application Interfaces. (Top) Landmark mode with annotation dialog. **(Bottom)** Information panel. Living reconstruction by Andrey Atuchin. Text not intended to be read.

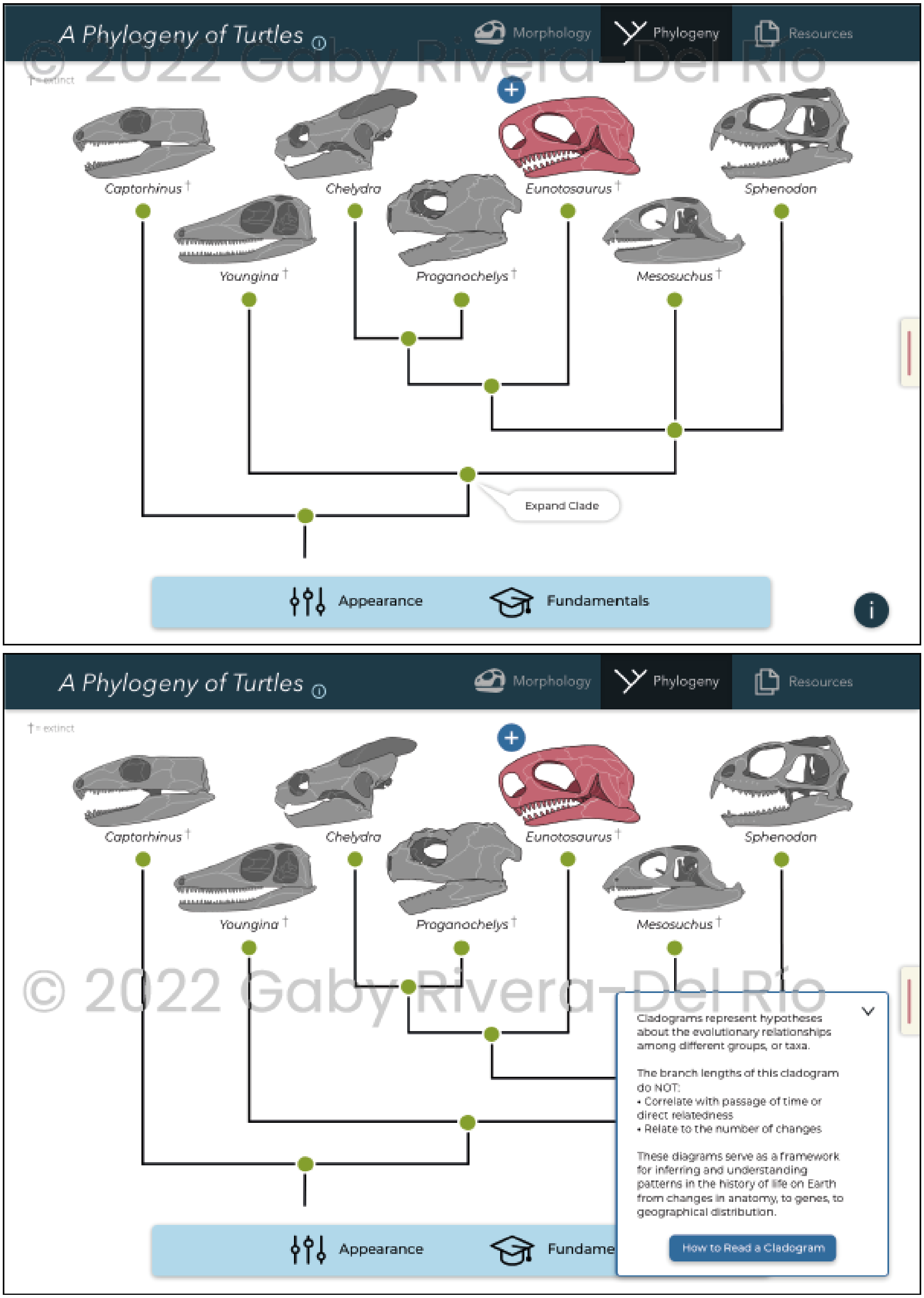


Figure 39a-b. Application Interfaces. (Top) Phylogeny section landing page. **(Bottom)** Information dialog. Text not intended to be read.

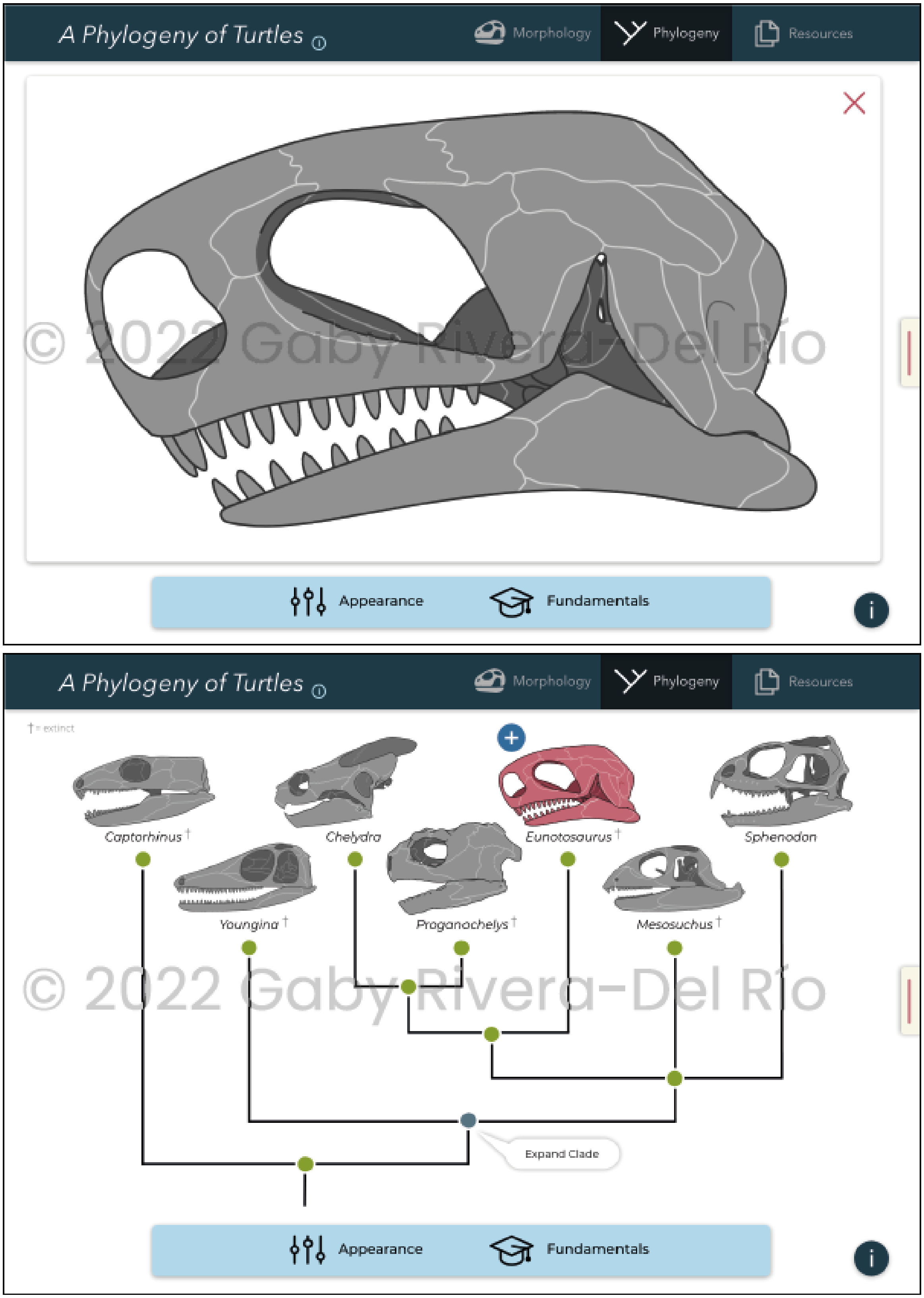


Figure 40a-b. Application Interfaces. (Top) Click skull for detail function. **(Bottom)** Hover feedback over a node, and push dialog for interaction. Text not intended to be read.

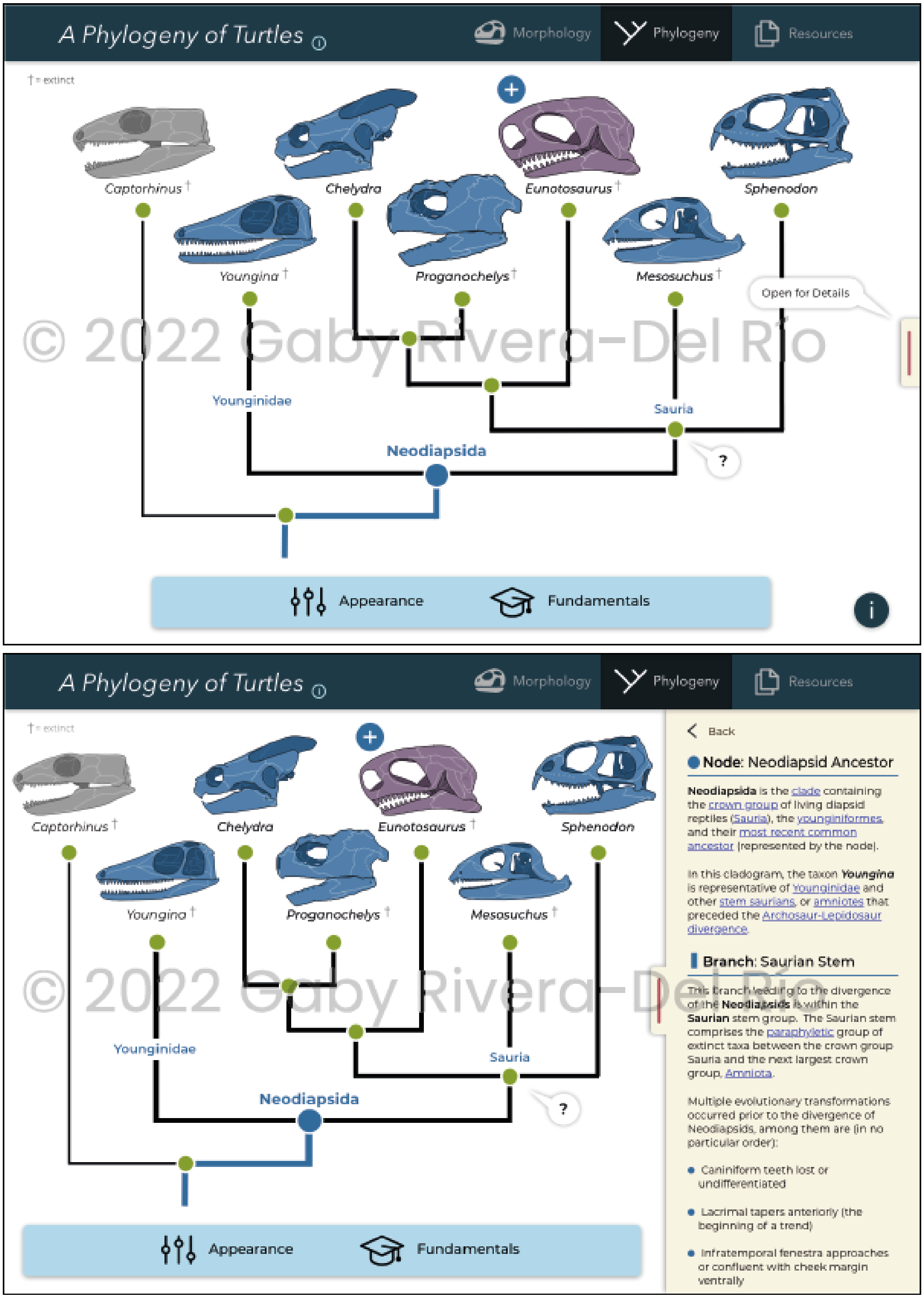


Figure 41a-b. Application Interfaces. (Top) Clade detail function and push to open Information Panel. **(Bottom)** Information Panel function. Text not intended to be read.

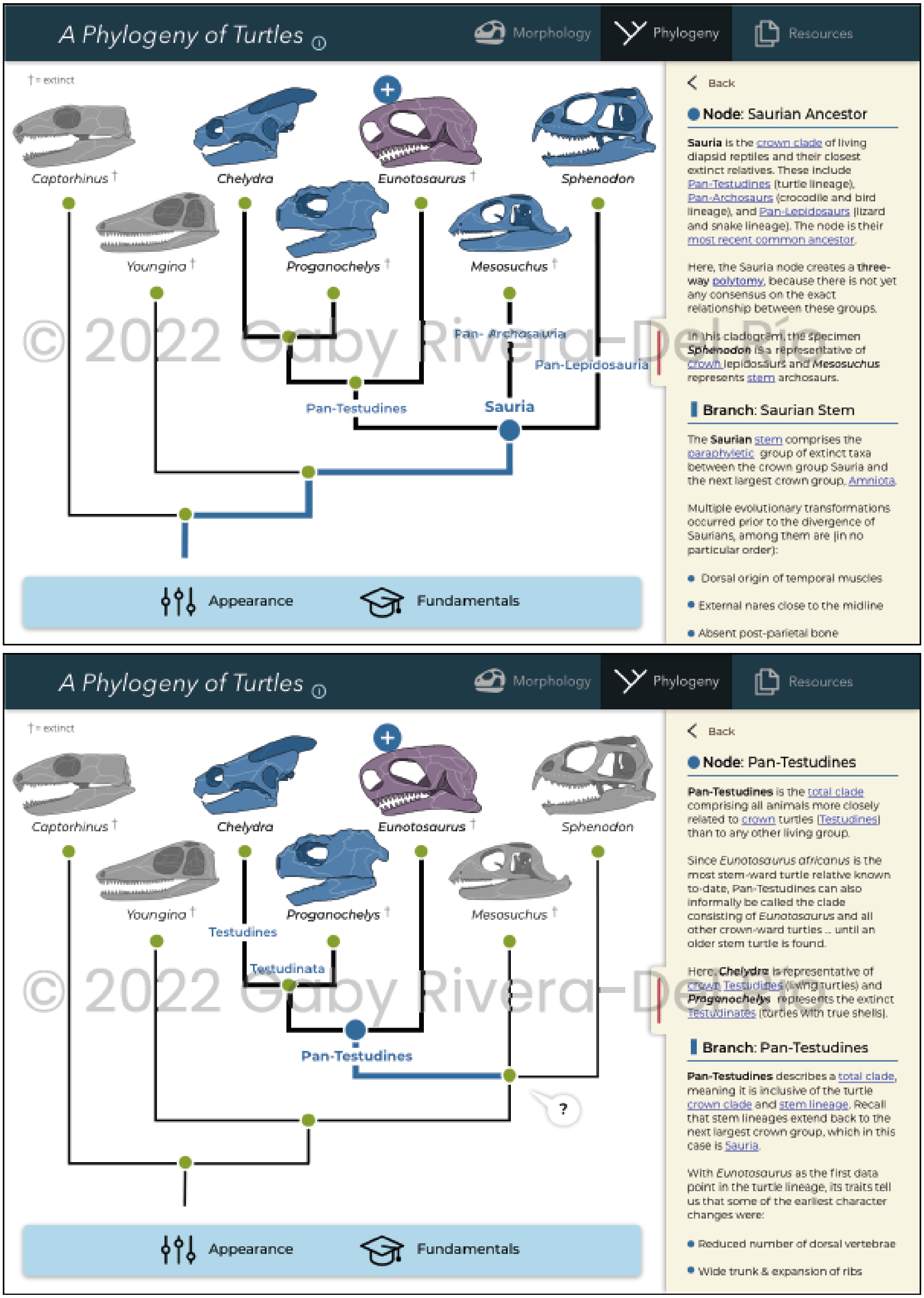
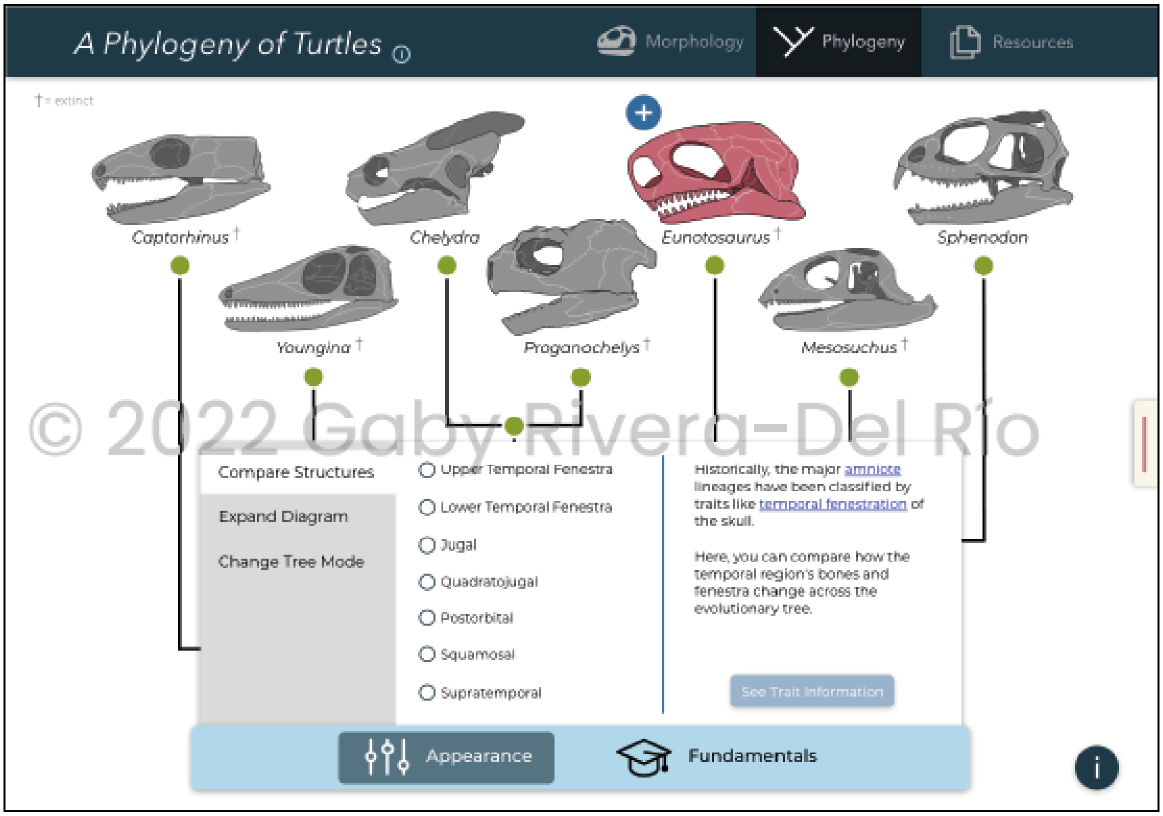


Figure 42a-b. Application Interfaces. (Top and Bottom) Specificity of clade detail function and visual feedback. Text not intended to be read.



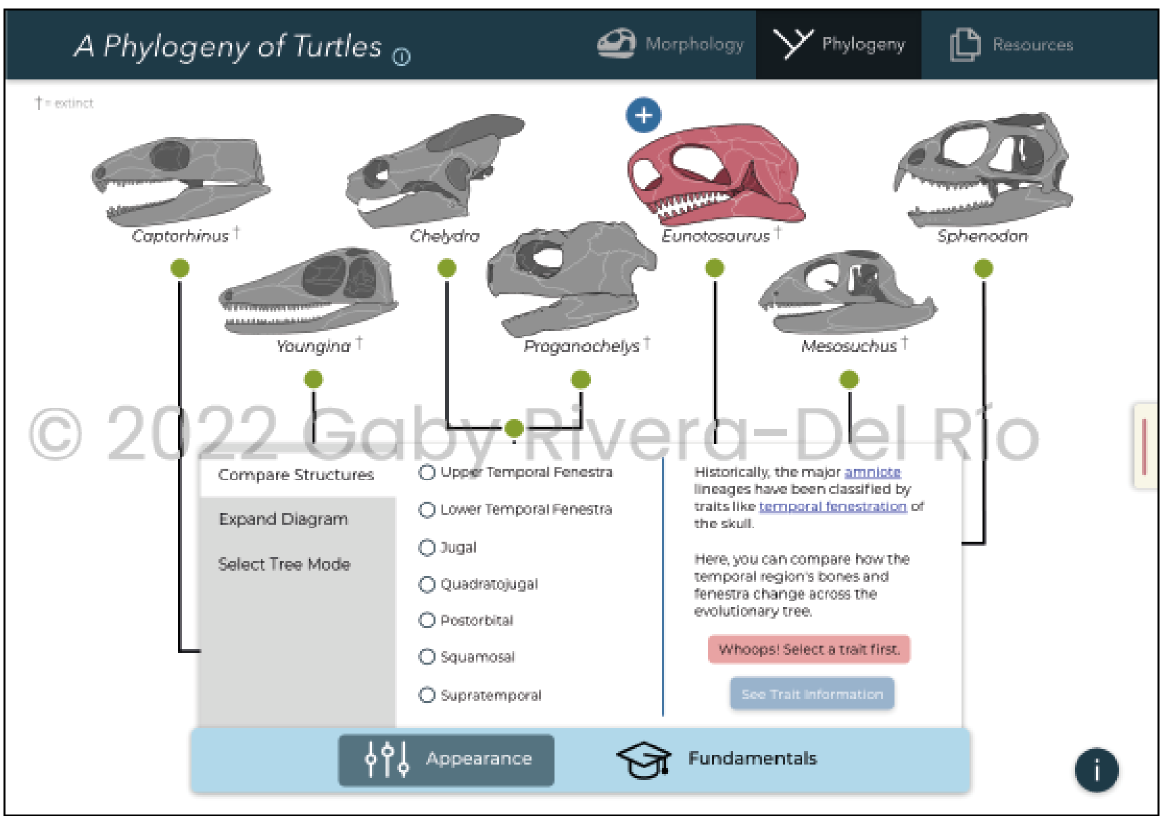
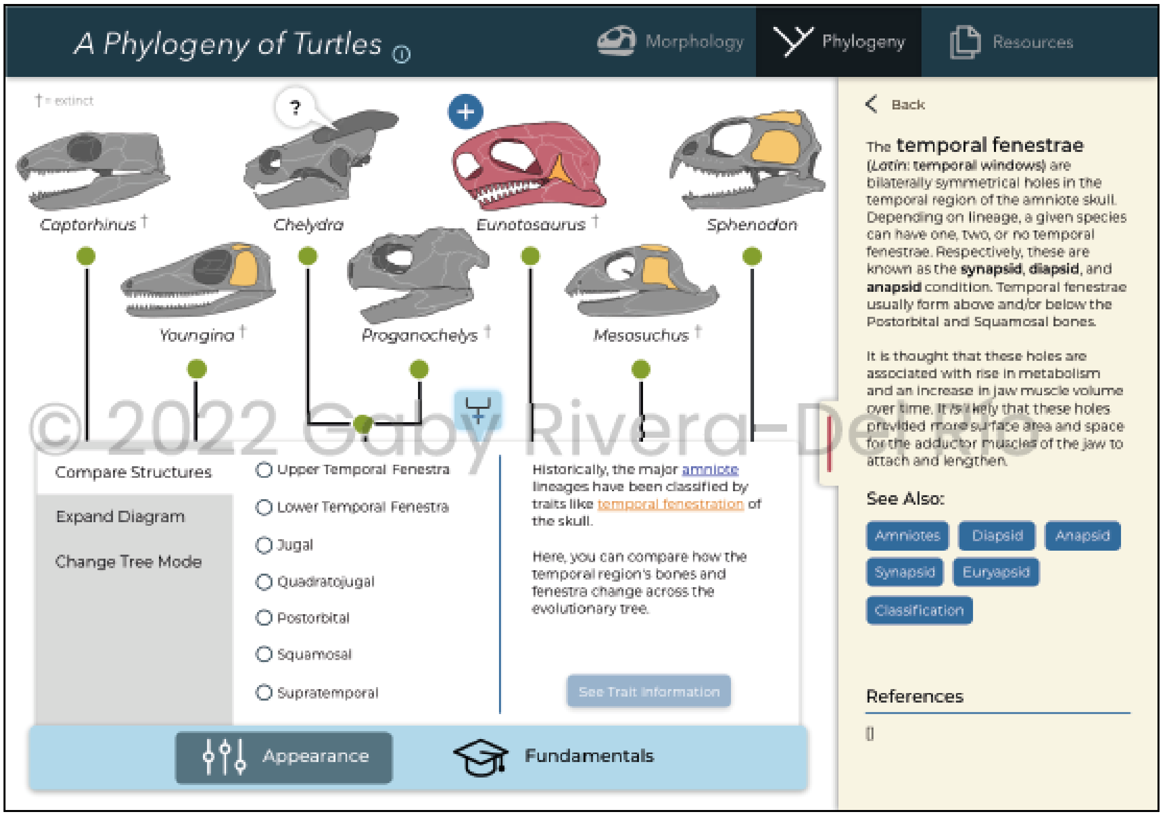


Figure 43a-b. Application Interfaces. (Top) Bottom navigation, Appearance panel. **(Bottom)** Error message feedback. Text not intended to be read.



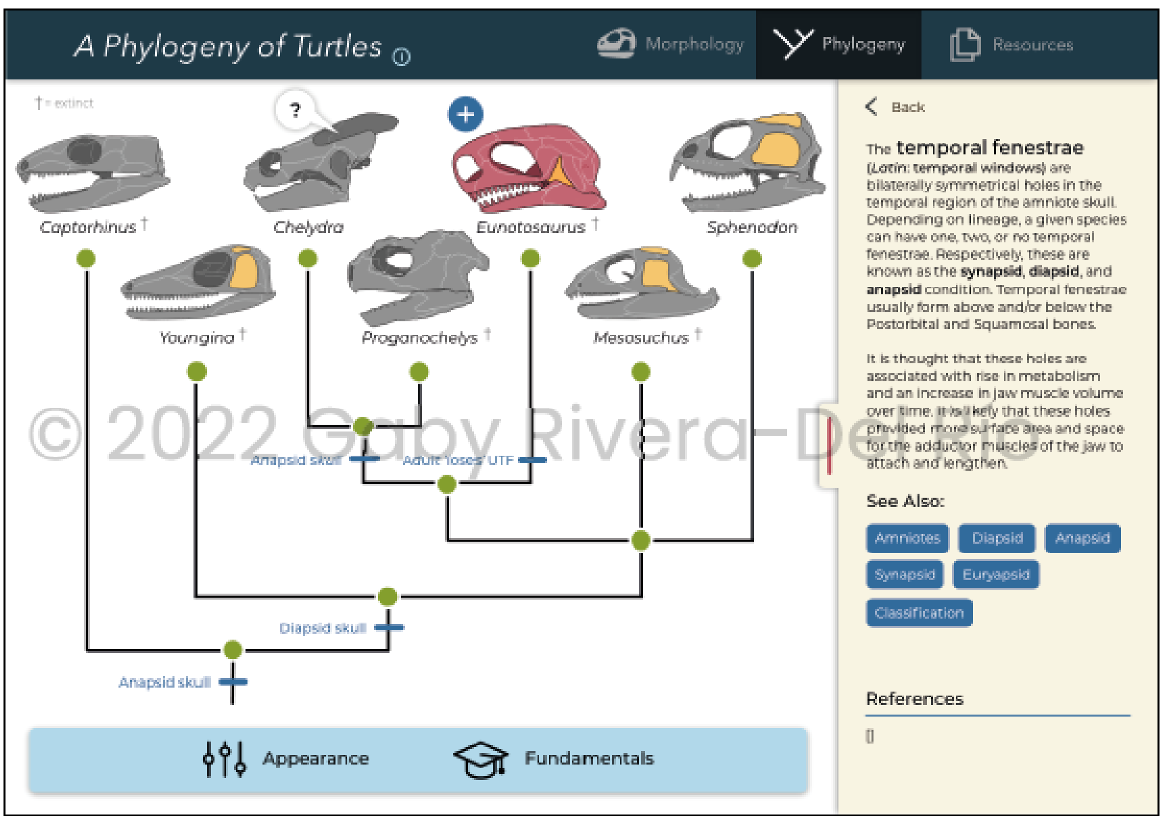


Figure 44a-b. Application Interfaces. (Top) Information panel interaction with in-text definition link, and notification of changes. **(Bottom)** Mapping of tree characters. Text not intended to be read.

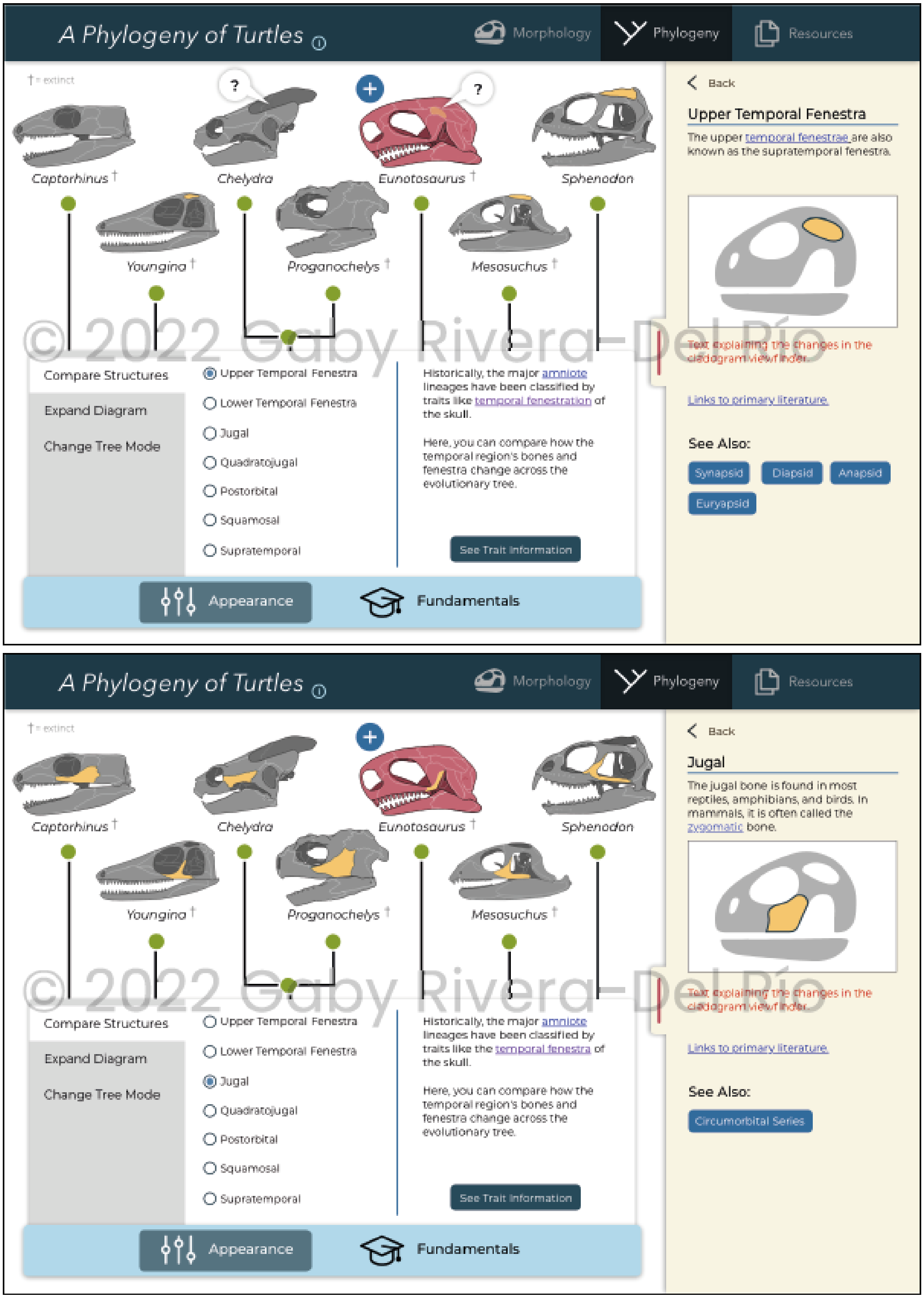


Figure 45a-b. Application Interfaces. (Top and Bottom) Comparison of structures across taxa function. Text not intended to be read.

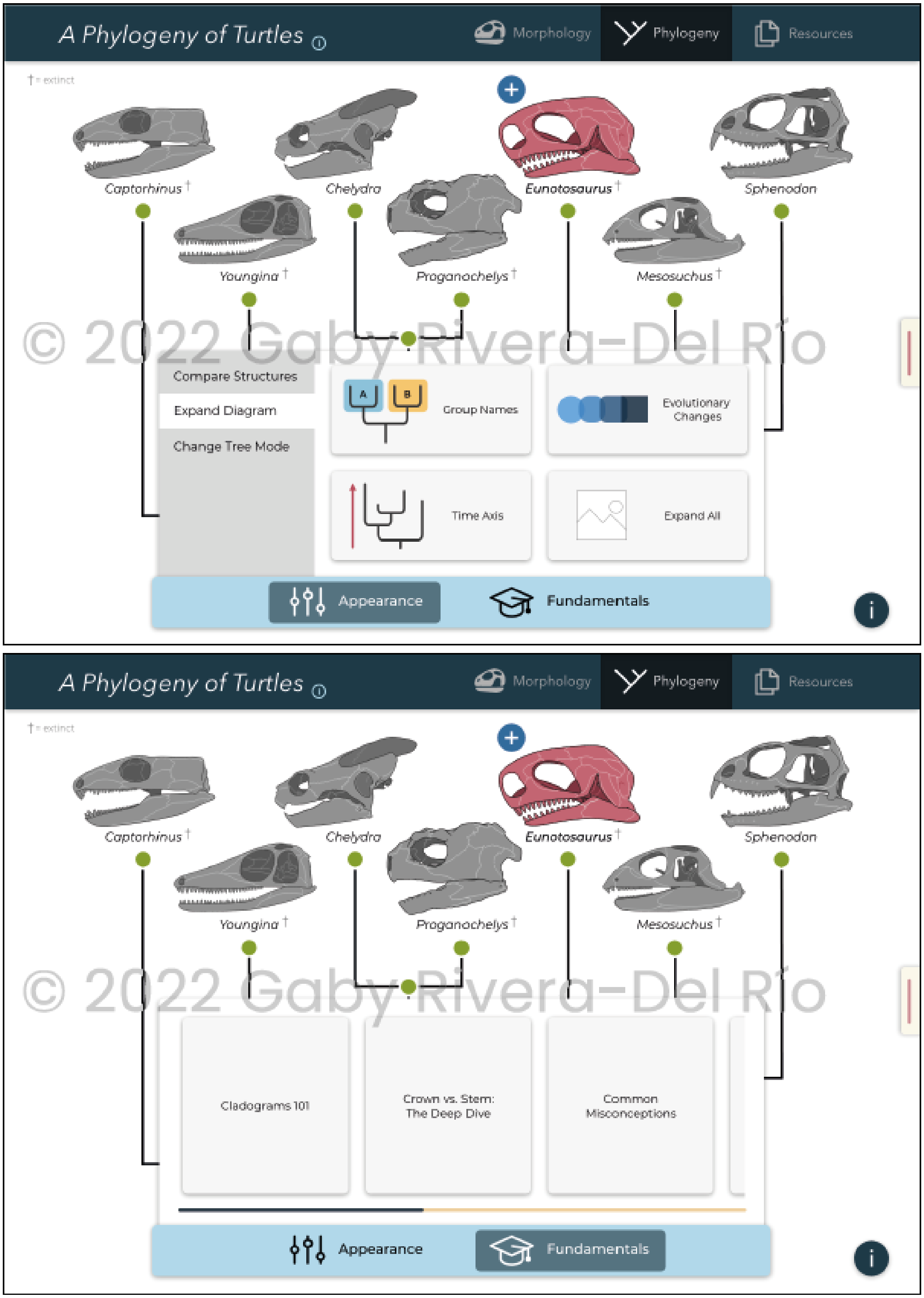


Figure 46a-b. Application Interfaces. (Top) Option change showcasing icon design for Appearance panel. **(B)** Fundamentals panel design. Text not intended to be read.

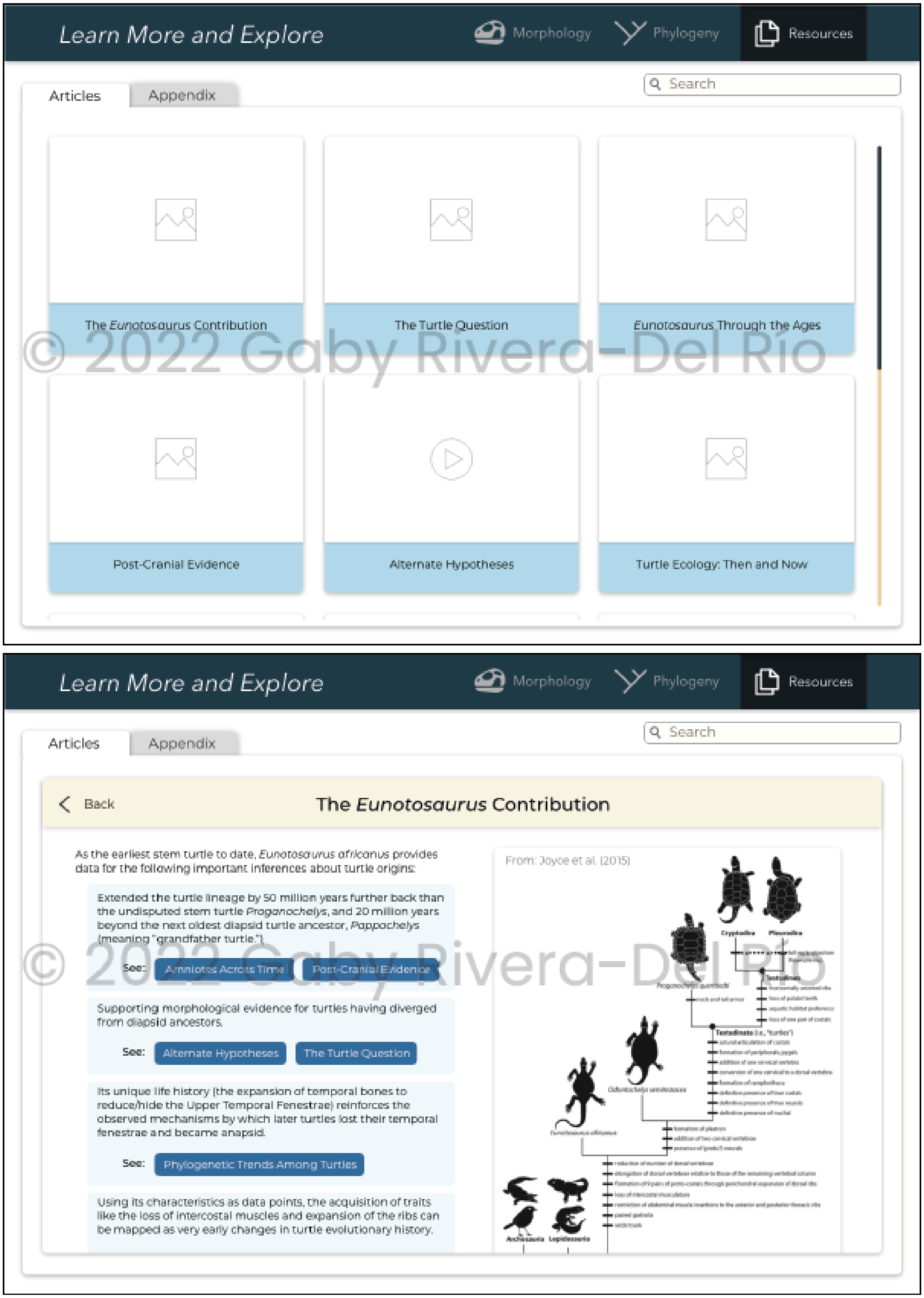


Figure 47a-b. Application Interfaces. (Top) Resources section landing page in Articles tab, with placeholder images. **(B)** Module open dialog box and design. Text not intended to be read.

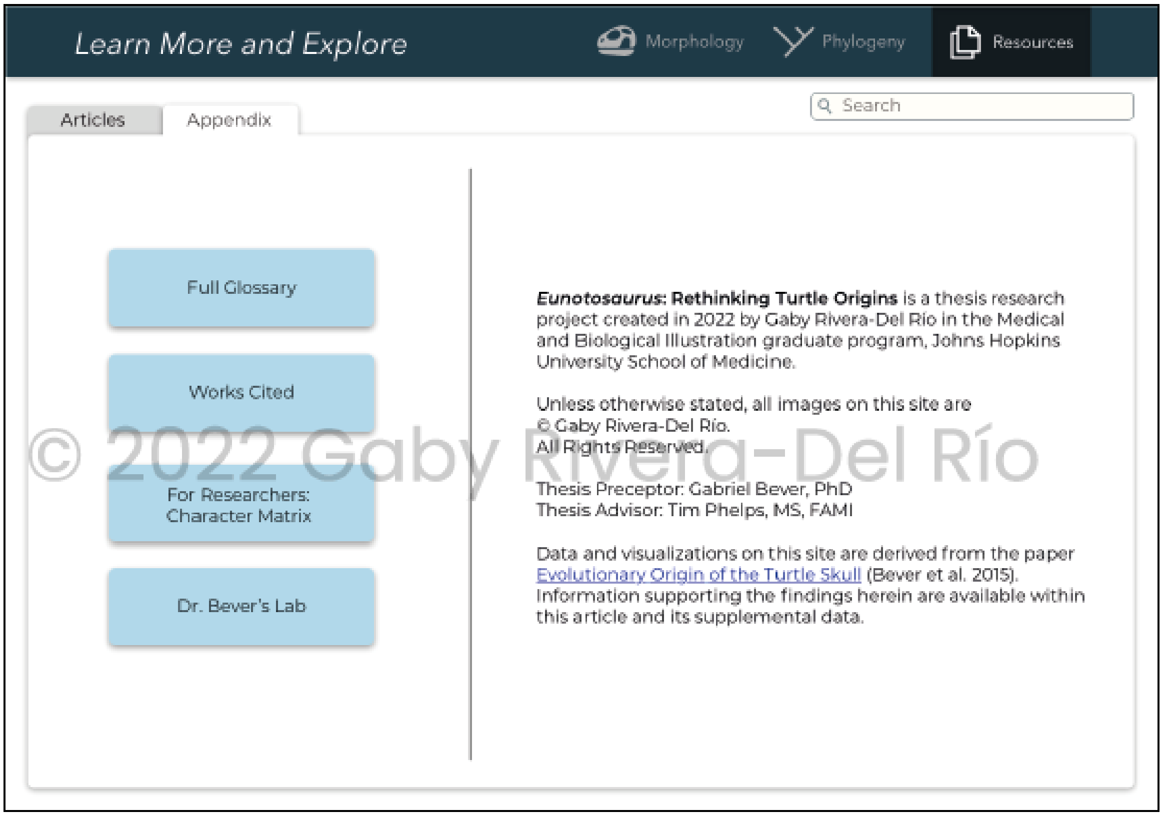


Figure 48. Application Interface. Appendix tab. Text not intended to be read.

Access to Assets. The products created from this thesis can be viewed at www.riverabiovisuals.com, or by contacting the author at agrivera.delrio@gmail.com. The author may also be contacted through the Department of Art as Applied to Medicine at Johns Hopkins University School of Medicine, https://medicalart.johnshopkins.edu/.

Discussion

On the Final Product

The *Eunotosaurus* story concerns an ancient relative that supports justified inferences about the origins of the turtle body plan. For one, a life history that is in line with the trend towards reduction of the temporal fenestrae, established from the fossorial behavior of early turtles. Second, its place as the earliest known stem turtle relative provides insights into the order of transformations that resulted in the weird and wonderful creatures we know today. To appreciate the former, a novel digital skull reconstruction was generated for this application. To implement this model and communicate the importance of the former to how turtle evolution is understood, the didactic application "*Eunotosaurus*: Rethinking Turtle Origins" was mocked up.

Interactive media was chosen to deliver the information for this project because it is ideal for communicating biological concepts. It provides an engaging medium to leverage best practices for information design, visual storytelling, and managing cognitive load. Furthermore, the structural possibilities with web application design allow for the material to be updated, expanded, and iterated with ease. Overall, the didactic challenge of this project was to accurately and accessibly convey the macro-evolutionary concepts that underpin the contribution *Eunotosaurus* brings to science.

Importance of Evolution Pedagogy. Evolutionary biology is crucial for helping us understand and appreciate the interrelated past, present, and future of life on Earth. Moreover, it has wide-reaching consequences for humankind in areas such as health, biotechnology, and agriculture (Turcotte *et al.* 2017; Thrall, 2010; Zimmer, 2010). For example, evolutionary medicine examines the evolutionary roots of health and sickness. Reconstructing the phylogeny of pathogens is crucial to the development of new medicines, with coevolutionary pressures contributing to our understanding of public health, infectious disease, and chronic illness (Zimmer, 2010). Additionally, any model-based studies done on mice, for example, exploit the recent common ancestry we share with them to try and extrapolate what physiological processes are conserved between us. In all, a basic understanding of how to interpret evolutionary relationships and to use those relationships as an analytical framework is needed to prepare a scientifically literate citizenry to tackle the world's problems.

Part of that preparation involves the teaching of tree-thinking, or the ability to evaluate and make inferences about the relationships mapped on an evolutionary tree diagram (O'Hara, 1992; Gregory, 2008; McLennan, 2010). A related skill is the ability to appreciate how morphological characters inform these relationships (Scotland *et al.* 2003). These skills have significant value in modern science, and yet individuals with even extensive post-secondary education can hold lingering misconceptions about how to read and interpret these diagrams. Hence the goal is to not only communicate the *Eunotosaurus* story but do so in a manner that bridges these gaps.

Didactic Content and App Development. The development of the didactic content for this project follows best practices for visualizing and teaching phylogenetics. Focus on the design of the cladogram, specifically, is validated by the universal importance of diagrammatic literacy in the sciences (Novick & Catley, 2012). Schematic diagrams translate the structural underpinnings of abstract concepts, making them vital tools for theory development, communication, and problem-solving. Think of how many biological concepts are taught through diagrams: food webs, gene maps, family trees, flow charts, and – of course – cladograms. Interpreting any diagram, however, relies on learned conventions, as their meaning is not always transparent. Pedagogic practice, therefore, strives to intuitively map diagrammatic elements with their conceptual meaning (Novick, 2006, June; McCullough, 2020).

This was achieved in a couple of ways. One was through signaling, which draws user attention to areas of interest. The cladogram uses color-coding and shape language to associate nodes with the groupings they encompass when a user interacts with them. This is reinforced using legend icons that tie in these groupings to their descriptions. As a user investigates specific characters, their relevance to the cladogram is made visually apparent. The skull reconstructions at the terminal nodes recreate the evolutionary transformations while keeping their relational context intact.

The curation of terminal taxa also adds to the didactic messaging by creating a visual flow supporting the story of secondary anapsidy in turtles. That is, the change from anapsid, to diapsid, and then back to anapsid that characterizes the evolutionary trajectory of turtles. *Eunotosaurus* sits at the center, highlighted as an 'intermediate' form between the more derived turtles and their diapsid cousins. The format of the tree is a vertical and horizontal line grid, which visually reinforces the concept of speciation via divergence, where populations of an ancestral species diversify into descendant lineages. This is all achieved while avoiding a "ladderized" (or sequential) appearance in the diagram, which not only disrupts erroneous mental models about the progression of evolution but makes it easier for viewers to interpret relationships correctly (Novick & Catley, 2012).

This careful attention to the importance of visual hierarchy and design is per Mayer's Cognitive Theory of Multimedia Learning and Sweller's Cognitive Load Theory. As important as the structure of the diagram and related graphics are to the story being told, the accompanying text is also vital to this project's didactic goals. As such, the text was iterated several times for accuracy and clarity by Dr. Bever and other stakeholders. Take, for example, the avoidance of characterizing taxa as "basal" and "primitive," which carry intuitive value judgments that can muddle the important takeaways in evolutionary analysis (Bronzati, 2015). Instead, the goal of the accompanying text is to drive home the distinction between "crown" and "stem" groups, which are the crux of all work on evolutionary origins. Any text presented in the application is related directly to the visual content, with extraneous information available only through links that redirect the user. With added information revealed as a user explores, new visuals are generated to accompany them. Doing this offloads the cognitive strain of having too much information presented at once.

As for the novel 3D reconstruction, its inclusion in the application is intended to leverage the innate human skills for relating spatially to our environment and handling physical objects. While 2D reconstructions are useful for quick and accessible visualizations of fossil data, they are limited in how much spatial information they can convey. This can be used to favorable effect in diagrams like the cladogram in the Phylogeny section. The 2D reconstructions attempt, through shading, to convey information about the midline cranial structures (which are often left out of reconstructions in the primary literature, and so had to be generated from extensive research.) This is intentional, as many internal features of the skull in *Eunotosaurus* (prootic-quadrate contact and ossification of orbital cartilage) are expressions of its relationship to turtles (Bever *et al*. 2015, Evers *et al.* 2020). Instead of creating more complexity in the cladogram to demonstrate these cranial features, the 3D model was made a core part of the information architecture.

Novel Digital Reconstruction. Computer-aided 3D reconstruction of fossils, also called virtual paleontology, is well suited for use in public outreach and biocommunication. While the display of original fossils in institutions is a cornerstone of scientific outreach, digital technologies can reach a wider audience (Ziegler *et al.* 2020). Furthermore, digital scans and reconstructions can reveal previously unknown details of a specimen's internal and external morphology (Conroy & Vannier, 1984; Bever *et al.* 2015, 2016). Better still, they allow for continued research to be done on fossil data without risking damage to fragile materials.

In this project, the antemortem state of *Eunotosaurus* specimen M777 was restored, representing the most significant scientific undertaking in this project. It involved intense observation of the segmented CT data, reference to a sparse set of primary literature, and extrapolation wherever necessary. Given that this was the first reconstruction of its kind, it was heavily reliant on existing morphological descriptions of available specimens, 2D reconstructions, and feedback from Dr. Bever. The literature in question spanned the works of H.G. Seeley (1892), D.M.G. Watson (1914), C.B. Cox (1969), A.W. Keyser (1981), C.E. Gow (1981, 1997), Gabriel Bever, and his colleague, Tyler Lyson, (2016, 2016, 2020). Additionally, the extrapolation of features that were ill-preserved or extremely deformed came from examining the works of E.S. Gaffney (1979, 1990).

Future Directions

Reconstruction. Once the second stage of the reconstruction (cleaning the mesh and restoring smooth contours) is done, the model can be uploaded to the application, used in articles and animations for outreach, and - most importantly – biomechanical research. The last point refers to Finite Element Analysis (FEA) which is a rich avenue to test evolutionary hypotheses derived from biomechanical principles and details of skeletal architecture.

Finite Element Analysis (FEA) is a technique that reconstructs how load-induced stresses and strains are distributed within structures. It has been applied in engineering and orthopedic medicine, but in recent years has gained major traction in the field of functional morphology (Prado *et al*. 2014). The potential for FEA to engage with questions of organismal diversity and form comes from our understanding that changes to the geometry and composition of bones can be load-driven (Rayfield, 2001, 2007). The skeleton is a living tissue capable of modifying its shape and properties in response to environmental stimuli; this is known as bone modeling and remodeling. During the process, bone cells participate in the breakdown and formation of bone matrix at sites of low and high loading, respectively. The parameters of this load-adaptive regulation (e.g., the threshold at which adaptation occurs, the changes to microstructure or mineral content in the bone) are determined by genetics, making the bone remodeling process susceptible to evolutionary selection (Krane, 2005; Christen *et al.* 2014; Oton-Gonzalez *et al.* 2022).

As such, techniques like FEA allow us to explore how and why organisms developed their form. In the case of *Eunotosaurus*, studying load-adaptive remodeling of its skull could explain why the supratemporal bone expands to cover the UTF in adulthood. Evidence suggests that it was a fossorial, or burrowing, animal (Joyce, 2004; Lyson *et* al. 2016). As such, it would have used its head and neck to brace its body against the earth while digging with its forelimbs. Could the consistent loading of the top of the skull have contributed to the expansion of the temporal region and subsequent 'loss' of the UTF in its lifetime? Knowing that genetically codified life-history changes can have evolutionary implications, could the anapsid condition in crown-ward turtles be related to the fossorial ecology of the turtle stem? This reconstruction can be used to answer these and other questions.

For these analyses to work, however, the reconstructions must be as accurate as possible. It bears keeping in mind that any reconstruction is subject to an acceptable margin for error. Preserved bones and fragments can align in more than one way as a natural consequence of their deformations, missing anatomy, or functional plasticity. As such, *any* reconstruction is a hypothesis that reflects interpretations of morphological or functional constraints, symmetry, and level of deformation. Still, it is paramount that the work undertaken to restore the living shape of a fossil is grounded in as much data as possible. Secondarily distorted skulls will provide misleading results and create more problems than they solve. This work is the critical first step in the FEA process and thus of great scientific importance.

Application. Future directions for the application include adding the full functionality that could not be addressed in this development cycle. Among the tasks remaining are mapping out all the potential didactic content, interactions, modules, and animations that were alluded to in the current design. Inserting more 3D reconstructions of related taxa are also envisioned for this project.

Appendices

Appendix A: Didactic Content

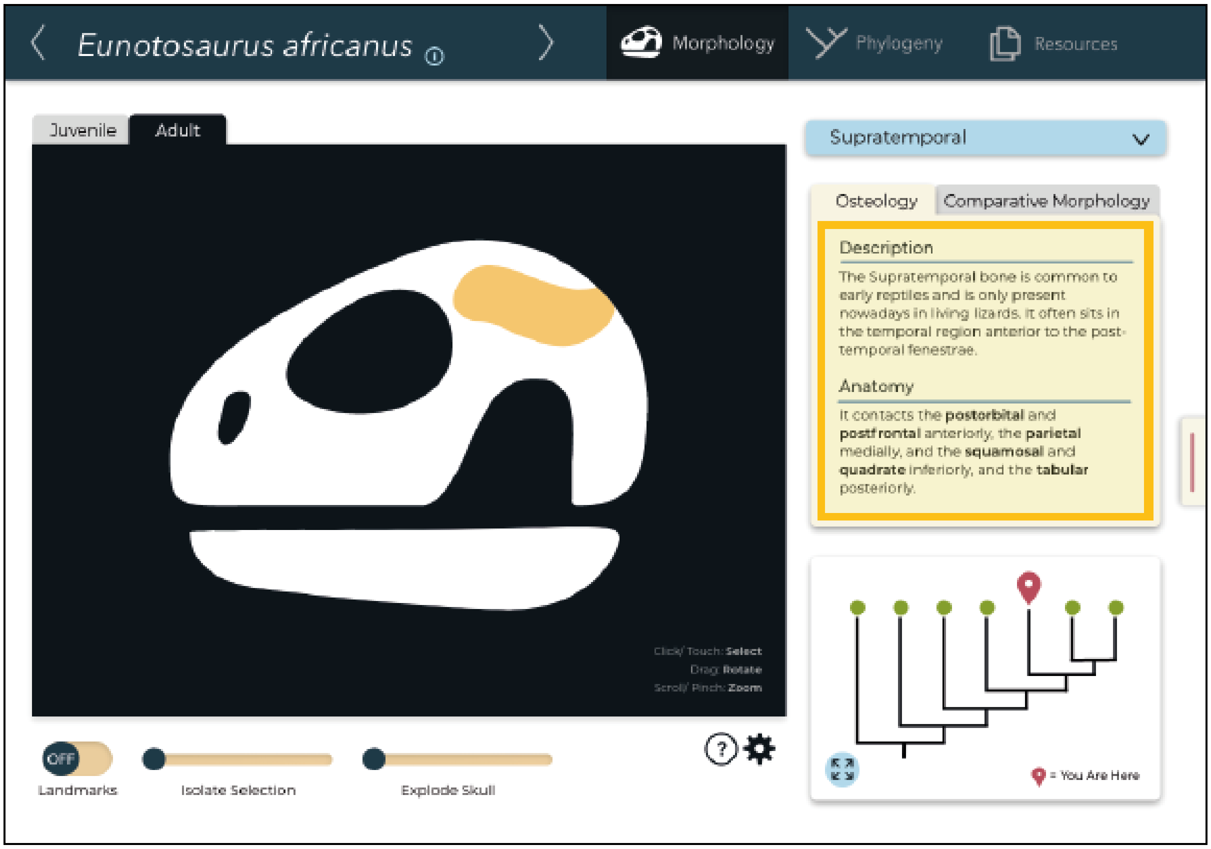


Figure 49. Wireframe #7. Morphology tab. The text below corresponds to the area highlighted in the yellow box.

Description

The Supratemporal bone is common to early reptiles and is only present nowadays in living lizards. It often sits in the temporal region anterior to the post-temporal fenestrae.

Anatomy

It contacts the **postorbital** and **postfrontal** anteriorly, the **parietal** medially, and the **squamosal** and **quadrate** inferiorly, and the **tabular** posteriorly.

Adult *Eunotosaurus* has a graceful, elongate supratemporal bone that covers a hole that matches the upper temporal fenestrae in other reptiles.

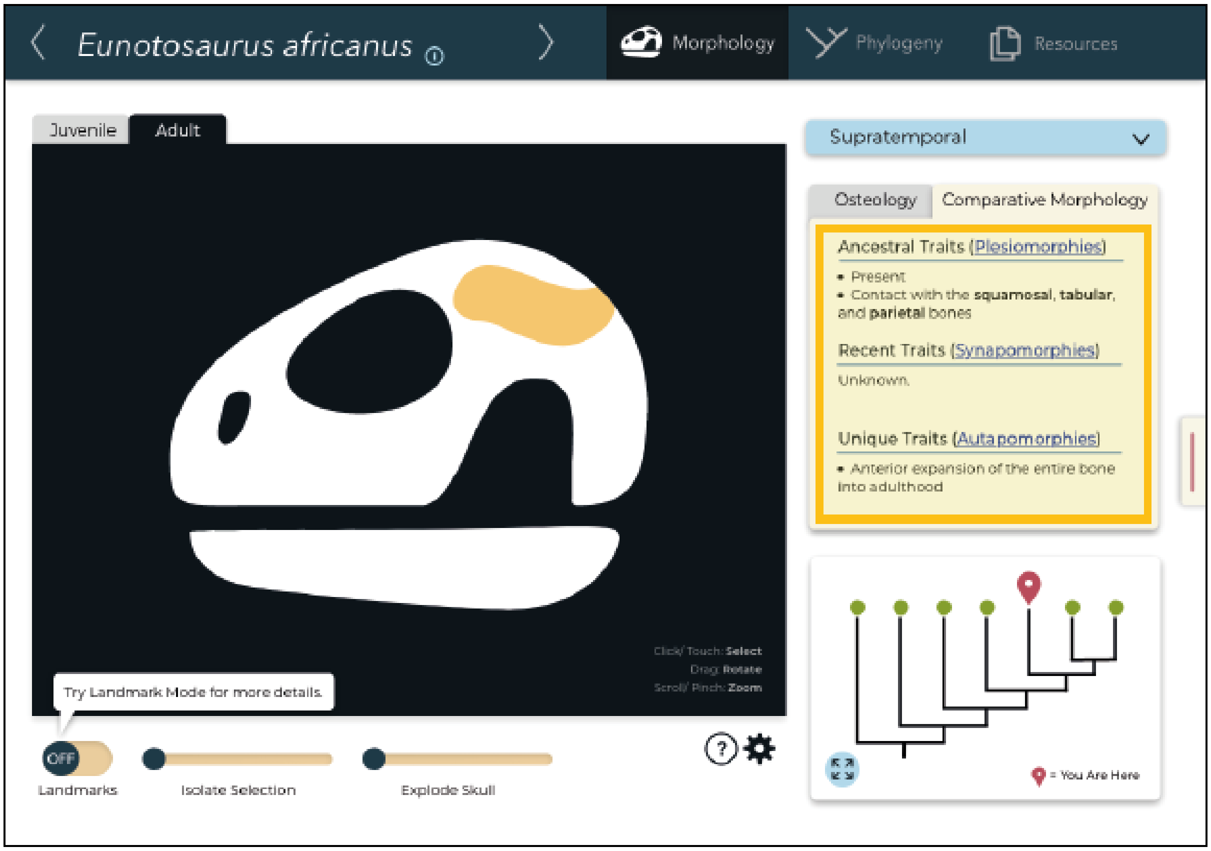


Figure 50. Wireframe #8. Morphology tab. The text below corresponds to the area highlighted in the yellow box.

Ancestral Traits (Plesiomorphies)

- Present
- Contact with the **squamosal**, **tabular**, and **parietal** bones

Recent Traits (Synapomorphies)

Unknown.

Unique Traits (Autapomorphies)

- Anterior expansion of the entire bone into adulthood

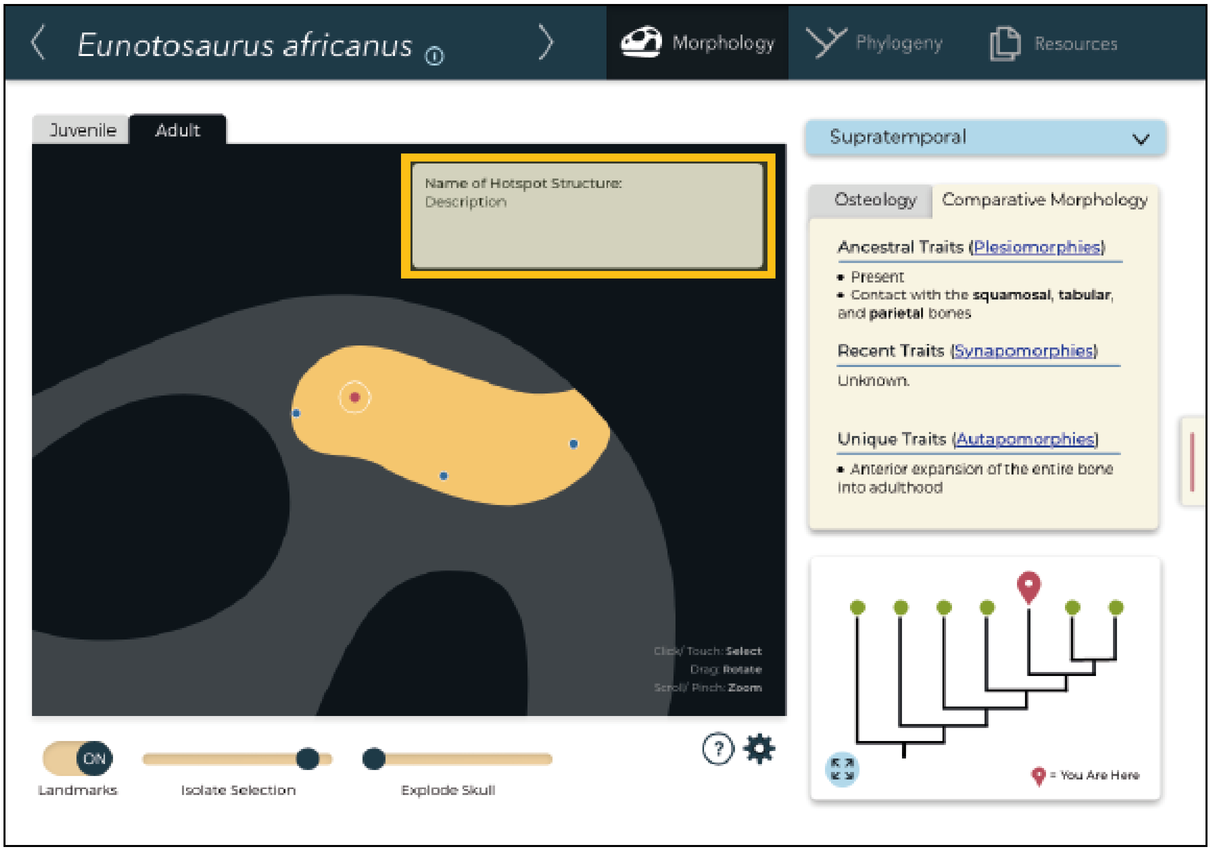


Figure 51. Wireframe #9. Morphology tab. The text below corresponds to the area highlighted in the yellow box.

Name of Hotspot Structure

Description

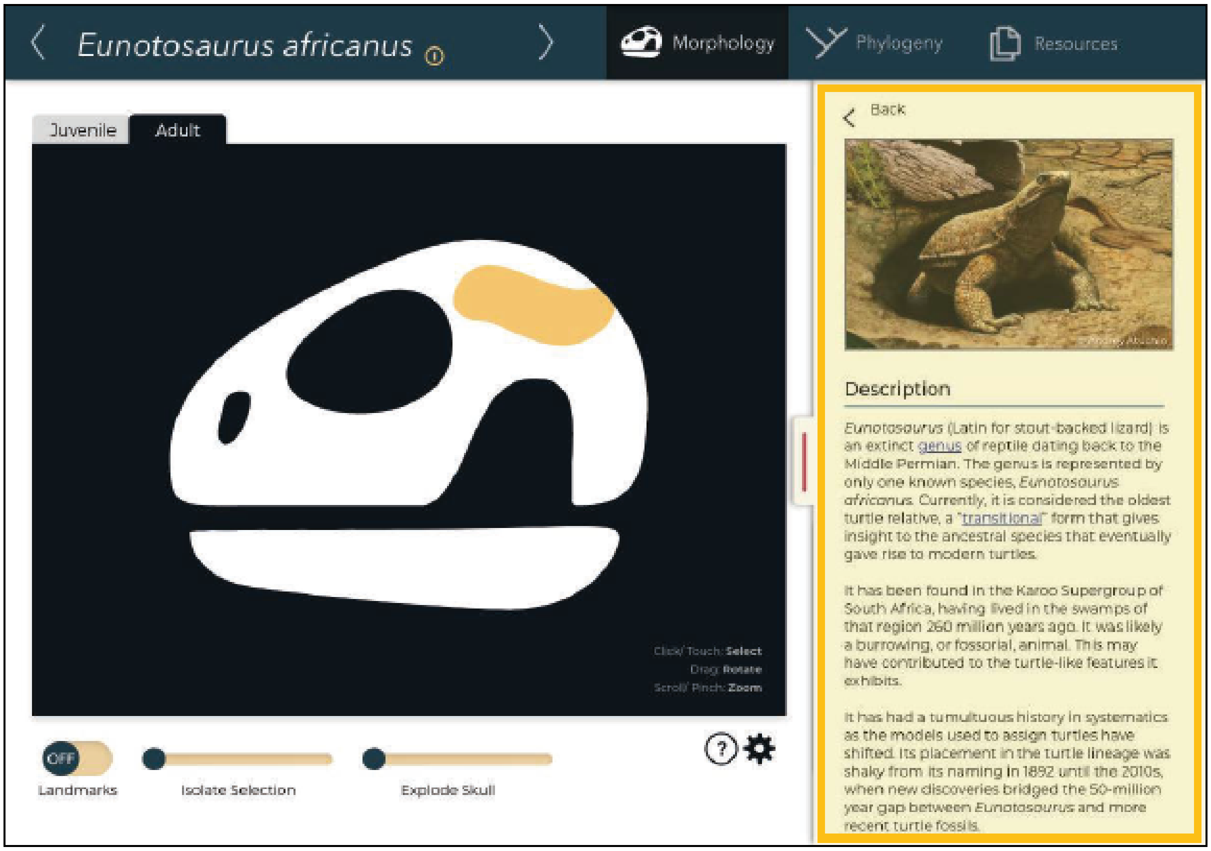


Figure 52. Wireframe #10. Morphology tab. The text below corresponds to the area highlighted in the yellow box.

Description

Eunotosaurus (Latin for stout-backed lizard) is an extinct genus of reptiles dating back to the Middle Permian. The genus is represented by only one known species, *Eunotosaurus africanus*. Currently, it is considered the oldest turtle relative, a "transitional" form that gives insight to the ancestral species that eventually gave rise to modern turtles.

It has been found in the Karoo Supergroup of South Africa, having lived in the swamps of that region 260 million years ago. It was likely a burrowing, or fossorial, animal. This may have contributed to the turtle-like features it exhibits.

It has had a tumultuous history in systematics as the models used to assign turtles have shifted. Its placement in the turtle lineage was shaky from its naming in 1892 until the 2010s, when new discoveries bridged the 50-million year gap between *Eunotosaurus* and more recent turtle fossils.

See Also

(Link) *Eunotosaurus* Through the Ages
(Link) Turtle Ecology: Then and Now

References

1) Seeley, H. G. (1892). On a new reptile from Welte Vreden (Beaufort West), Eunotosaurus africanus (Seeley). Quarterly Journal of the Geological Society, 48(1-4), 583-585.

2) Cox, C.B. (1969). "The problematic Permian reptile Eunotosaurus". Bulletin of the British Museum of Natural History. 18: 167–196.

3) Keyser, A.W., & Gow, C. (1981). First complete skull of the Permian reptile Eunotosaurus africanus Seeley. South African Journal of Science, 77(9), 417-420.

4) Joyce, W. G., & Gauthier, J. A. (2004). Palaeoecology of Triassic Stem Turtles Sheds New Light on Turtle Origins. Proceedings: Biological Sciences, 271(1534), 1–5.
http://www.jstor.org/stable/4142753

5) Joyce, WG. (2015). The origin of turtles: A paleontological perspective. Journal of Experimental Zoology (Molecular and Developmental Evolution) 324B: 181– 193.

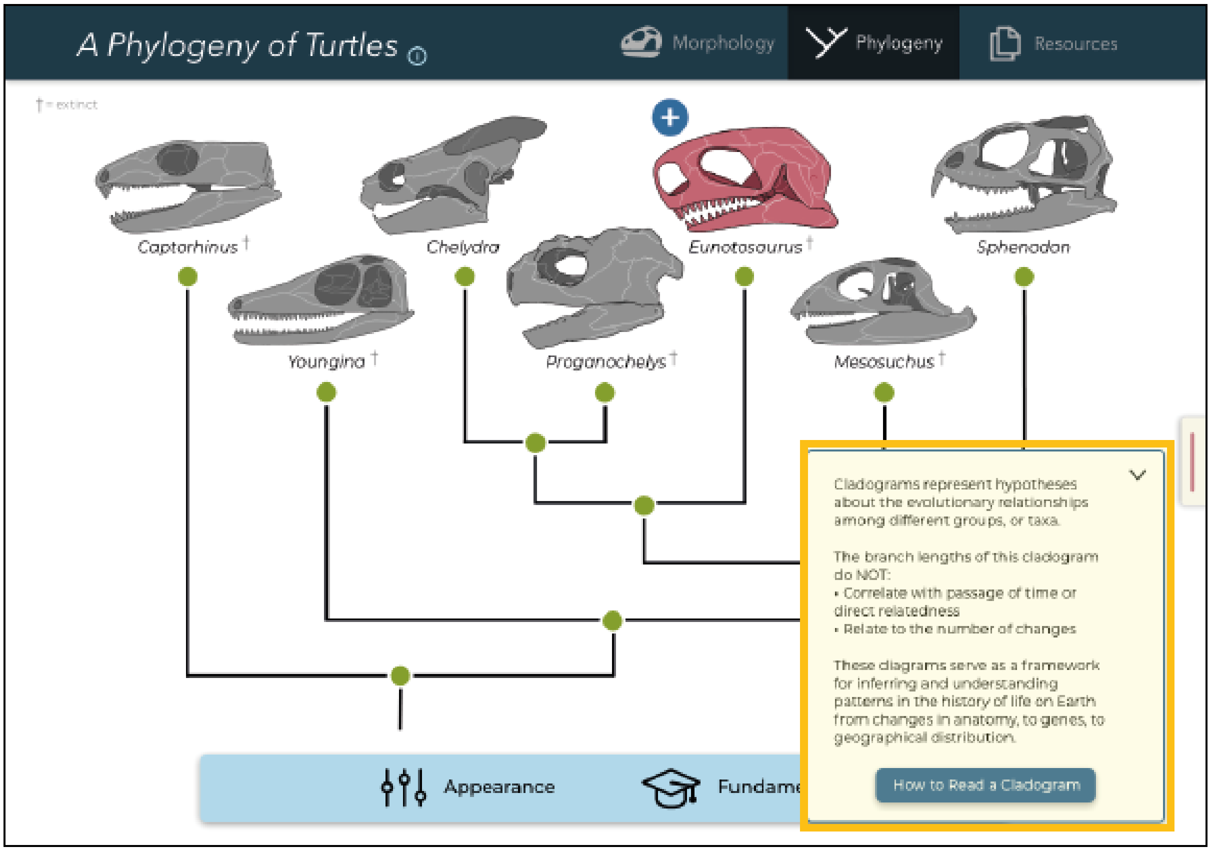


Figure 53. Wireframe #12. Phylogeny tab. The text below corresponds to the area highlighted in the yellow box.

Cladograms represent hypotheses about the evolutionary relationships among different groups, or taxa.

The branch lengths of this cladogram do NOT:
- Correlate with the passage of time or direct relatedness
- Relate to the number of changes

These diagrams serve as a framework for inferring and understanding patterns in the history of life on Earth from changes in anatomy, to genes, to geographical distribution.

(Link) How to Read a Cladogram

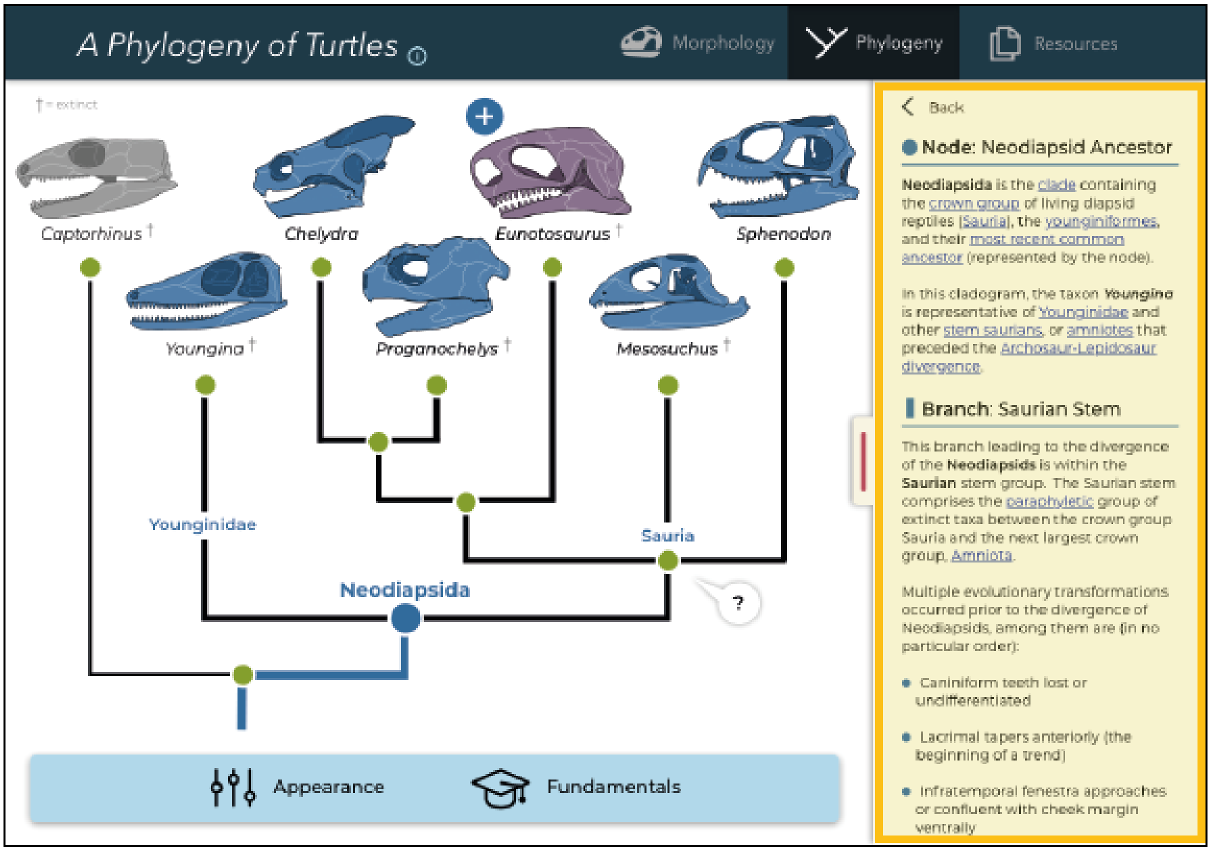


Figure 54. Wireframe #16. Phylogeny tab. The text below corresponds to the area highlighted in the yellow box.

Node: Neodiapsid Ancestor

Neodiapsida is the clade containing the crown group of living diapsid reptiles (Sauria), the younginiformes, and their most recent common ancestor (represented by the node).

In this cladogram, the taxon ***Youngina*** is representative of Younginidae and other stem saurians, or amniotes that preceded the Archosaur-Lepidosaur divergence.

Branch: Saurian Stem

This branch leading to the divergence of the **Neodiapsids** is within the **Saurian** stem group. The Saurian stem comprises the paraphyletic group of extinct taxa between the crown group Sauria and the next largest crown group, Amniota.

Multiple evolutionary transformations occurred before the divergence of Neodiapsids, among them are (in no particular order):

- Caniniform teeth lost or undifferentiated
- Lacrimal tapers anteriorly (the beginning of a trend)
- Infratemporal fenestra approaches or confluent with cheek margin ventrally
- Posterior coracoid lost

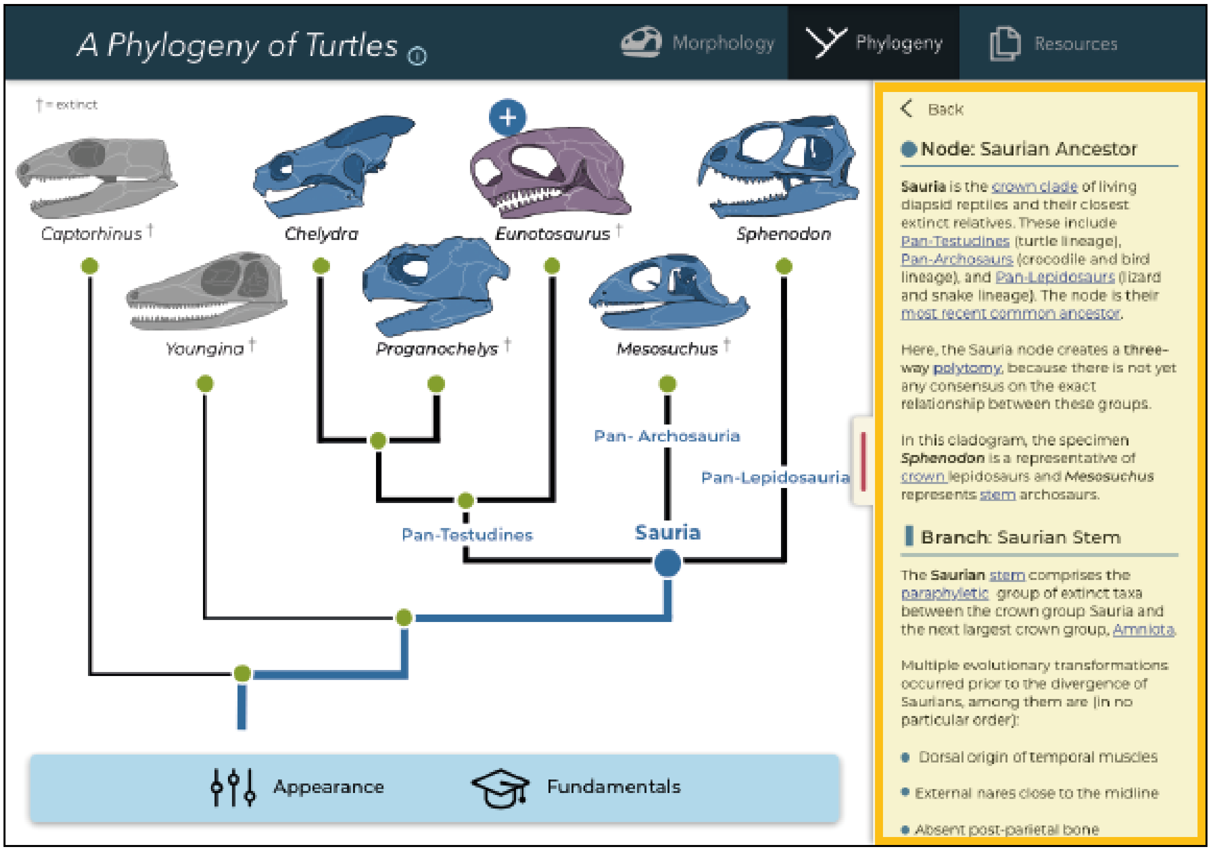


Figure 55. Wireframe #17. Phylogeny tab. The text below corresponds to the area highlighted in the yellow box.

Node: Saurian Ancestor

Sauria is the crown clade of living diapsid reptiles and their closest extinct relatives. These include Pan-Testudines (turtle lineage),
Pan-Archosaurs (crocodile and bird lineage), and Pan-Lepidosaurs (lizard and snake lineage). The node is their most recent common ancestor.

Here, the Sauria node creates a three-way polytomy, because there is not yet any consensus on the exact relationship between these groups.

In this cladogram, the specimen ***Sphenodon*** is a representative of crown lepidosaurs and *Mesosuchus* represents stem archosaurs.

Branch: Saurian Stem

The **Saurian** stem comprises the paraphyletic group of extinct taxa between the crown group Sauria and the next largest crown group, Amniota.

Multiple evolutionary transformations occurred prior to the divergence of Saurians, among them are (in no particular order):

- Dorsal origin of temporal muscles
- External nares close to the midline
- Absent post-parietal bone
- Squamosal bone narrow anteriorly, and restricted to the top of the skull
- Stapes is slender and has an unossified dorsal process

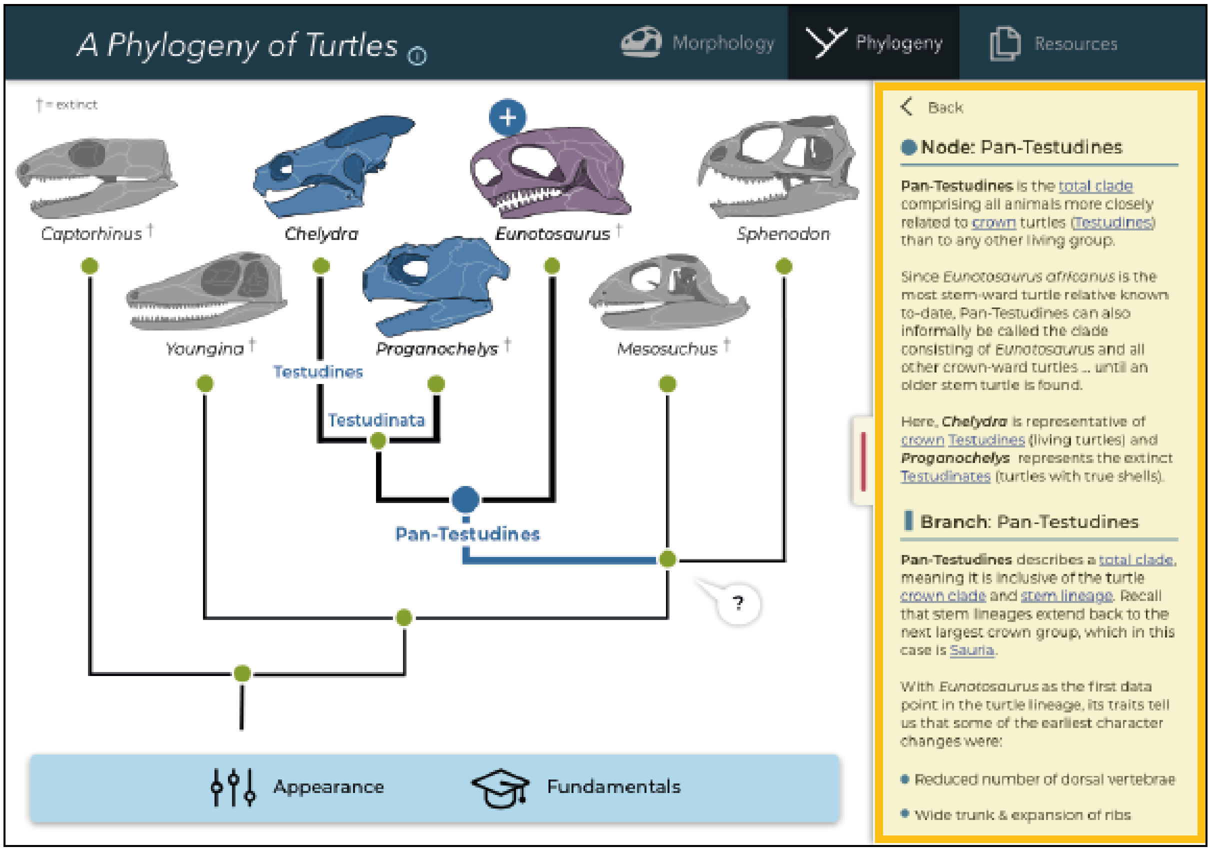


Figure 56. Wireframe #18. Phylogeny tab. The text below corresponds to the area highlighted in the yellow box.

Node: Pan-Testudines

Pan-Testudines is the total clade comprising all animals more closely related to crown turtles (Testudines) than to any other living group.

Since *Eunotosaurus africanus* is the most stem-ward turtle relative known to date, Pan-Testudines can also informally be called the clade consisting of *Eunotosaurus* and all other crown-ward turtles … until an older stem turtle is found.

Here, ***Chelydra*** is representative of crown Testudines (living turtles) and ***Proganochelys*** represents the extinct Testudinates (turtles with true shells).

Branch: Pan-Testudines

Pan-Testudines describes a total clade, meaning it is inclusive of the turtle crown clade and stem lineage. Recall that stem lineages extend back to the next largest crown group, which in this case is Sauria.

With *Eunotosaurus* as the first data point in the turtle lineage, its traits tell us that some of the earliest character changes were:

- Reduced number of dorsal vertebrae

- Wide trunk & expansion of ribs
- Loss of intercostal musculature
- Paired gastralia
- Restricted abdominal muscle insertions to thoracic ribs

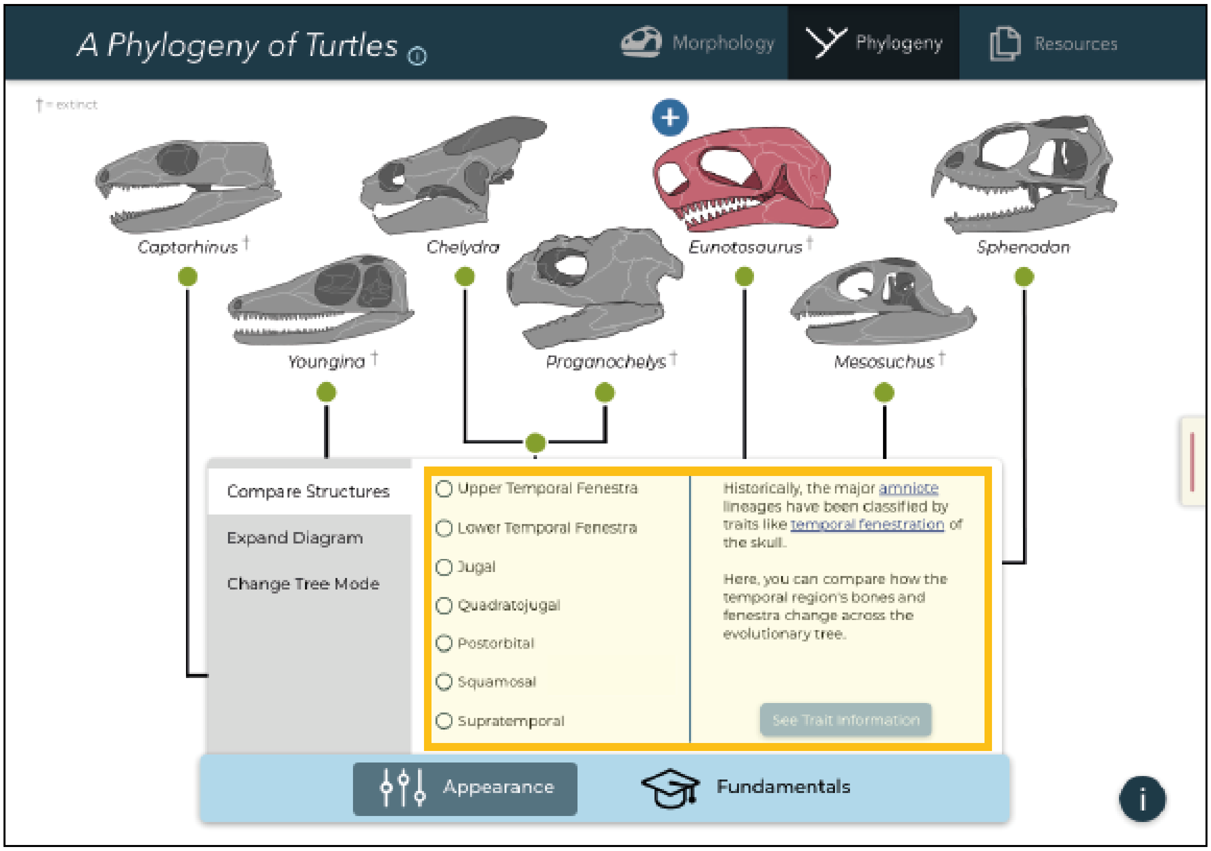


Figure 57. Wireframe #19. Phylogeny tab. The text below corresponds to the area highlighted in the yellow box.

- Upper Temporal Fenestra
- Lower Temporal Fenestra
- Jugal
- Quadratojugal
- Postorbital
- Squamosal
- Supratemporal
-

Historically, the major amniote lineages have been classified by traits like temporal fenestration of the skull.

Here, you can compare how the temporal region's bones and fenestra change across the evolutionary tree.

(Inactive Link) See Trait Information

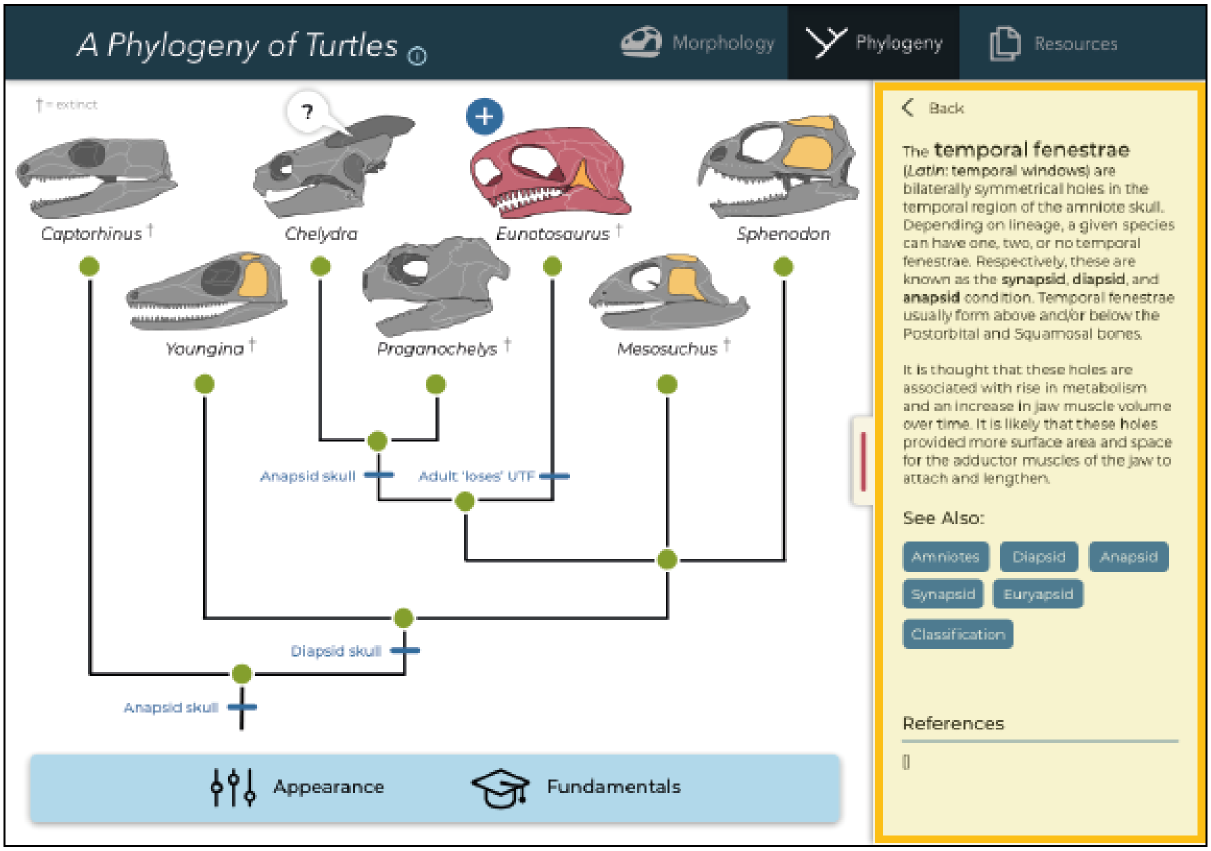


Figure 58. Wireframe #22. Phylogeny tab. The text below corresponds to the area highlighted in the yellow box.

The temporal fenestrae (*Latin*: temporal windows) are bilaterally symmetrical holes in the temporal region of the amniote skull. Depending on lineage, a given species can have one, two, or no temporal fenestrae. Respectively, these are known as the **synapsid**, **diapsid**, and **anapsid** condition. Temporal fenestrae usually form above and/or below the Postorbital and Squamosal bones.

It is thought that these holes are associated with rise in metabolism and an increase in jaw muscle volume over time. It is likely that these holes provided more surface area and space for the adductor muscles of the jaw to attach and lengthen.

See Also:
(Link) Amniotes
(Link) Diapsid
(Link) Anapsid
(Link) Synapsid
(Link) Euryapsid
(Link) Classification

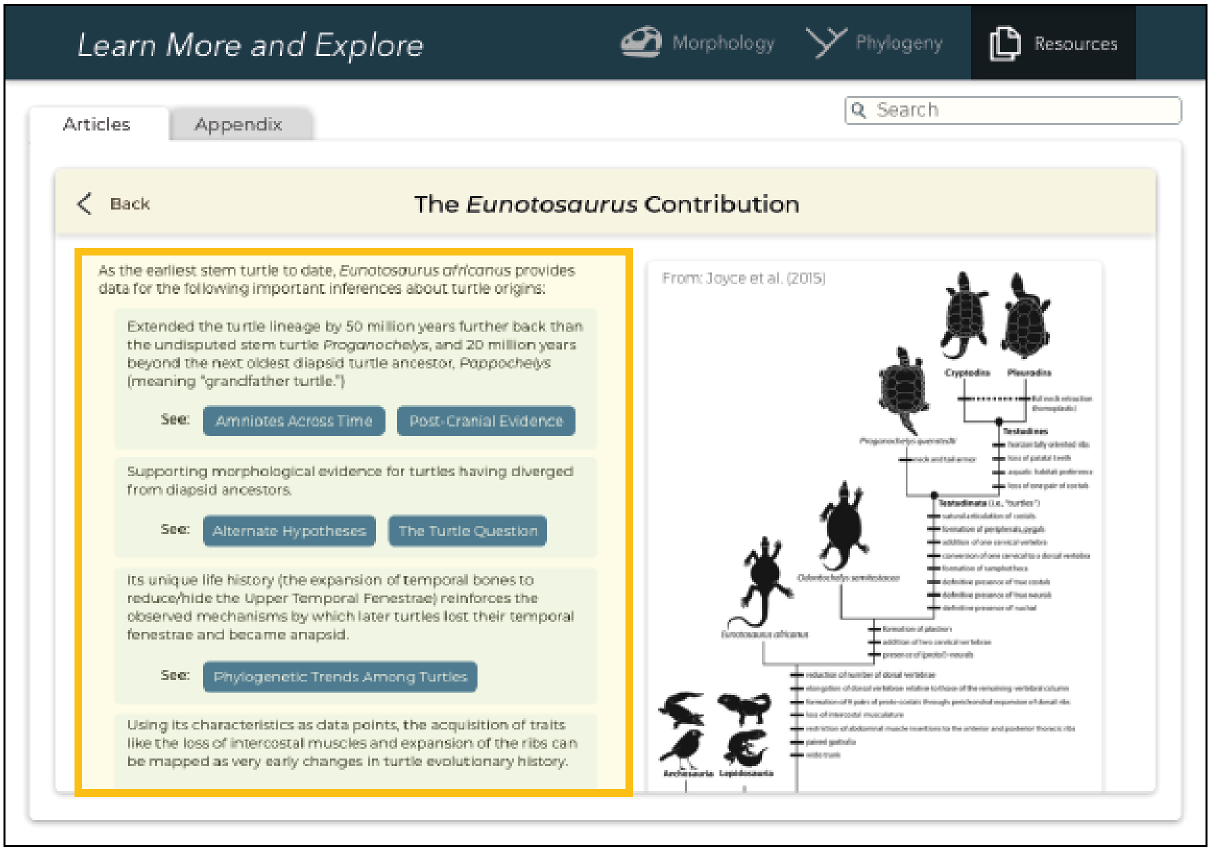


Figure 59. Wireframe #28. Resources tab. The text below corresponds to the area highlighted in the yellow box.

As the earliest stem turtle to date, *Eunotosaurus africanus* provides data for the following important inferences about turtle origins:

- Extended the turtle lineage by 50 million years further back than the undisputed stem turtle *Proganochelys*, and 20 million years beyond the next oldest diapsid turtle ancestor, *Pappochelys* (meaning "grandfather turtle.")
    - **See**: (Link) Amniotes Across Time; (Link) Post-Cranial Evidence
- Supporting morphological evidence for turtles having diverged from diapsid ancestors.
    - **See:** (Link) Alternate Hypotheses; (Link) The Turtle Question
- Its unique life history (the expansion of temporal bones to reduce/hide the Upper Temporal Fenestrae) reinforces the observed mechanisms by which later turtles lost their temporal fenestrae and became anapsid.
    - **See:** (Link) Phylogenetic Trends Among Turtles
- Using its characteristics as data points, the acquisition of traits like the loss of intercostal muscles and expansion of the ribs can be mapped as very early changes in turtle evolutionary history.
    - **See:** (Link) Post-Cranial Evidence; (Link) Filling Out the Turtle Tree

- While the traits it has tell us much about what occurred early in the turtle lineage, what is lacks says just as much. Eunotosaurus gives evidence to the fact that many turtle traits did not arise in tandem with the shell but came about millions of years prior as a series of unrelated adaptations, also called exaptations.
    - **See:** (Link) Turtle Ecology: Then and Now

In short, *Eunotosaurus africanus* has set a framework for better understanding the origin of the turtle body plan.

Appendix B: Existing Resources

Table 3. Currently available resources for evolutionary biology education.

Type	Name	Description
Web-based interactives and apps	NOVA Labs: Evolution (https://www.pbs.org/wgbh/nova/labs/)	Digital interactive puzzle game aimed at a lay audience that teaches the basics of building phylogenetic trees. It includes video modules and quizzes for use as a teaching aid. Cannot save progress without signing up. A cladogram is based on outdated information.
	Minute Labs Evolution Simulator (https://labs.minutelabs.io/evolution-simulator/#/s/1/viewer?intro=1)	Observation game that runs an algorithm for population dynamics. Users can adjust environmental conditions and see how they can induce change in the population of "blobs" over time. Deals with population dynamics, drift, and microevolution.
	Evolutionary Biology App (http://apple.co/1gUK4f5)	An app made by Brigham Young undergraduate students to teach basic evolution concepts. Has superficial coverage of concepts in population dynamics (natural selection, genetic drift, and other concepts).
Teaching references	Learn Evolution (UBerkeley) (https://evolution.berkeley.edu/)	An NSF-funded comprehensive website on evolution was developed for teachers. Provides content and resources for K-12 science teachers.
	Bioquest.org; **B**ioinformatics **E**ducation **D**issemination: **R**eaching **O**ut, **C**onnecting, and **K**nitting-together (**BEDROCK**)	An NSF-funded bioinformatics teaching website with problem-spaces, or modules, for educators to work into lesson plans on evolution.
Websites	Evolution: Education and Outreach (https://evolution-outreach.biomedcentral.com/)	An online journal that posts articles for K-16 students,

		teachers, and scientists to aid in evolution pedagogy.
	National Center for Science Education (NCSE) Evolution Primers (http://ncse.com/evolution/science/evolution-primers)	A web page linking multiple long-form text articles explaining evolutionary concepts.
	HHMI Biointeractive (http://www.hhmi.org/biointeractive/evolution-collection)	Multimedia library of classroom activities, interactives, and short films for use in tandem with science lesson plans.
	Shape of Life	Short classroom video series introducing multiple evolutionary science topics.
	Misconception Monday (http://ncse.com/users/stephanie-keep)	NCSE blog post series regarding common evolution misconceptions about evolution that appear everywhere from textbooks to science news articles.
Cranial anatomy apps	Head Atlas	A 3D interactive atlas of neuroanatomy, with a fully segmented skull, soft tissues, and 2500+ labels and descriptions. Hotspot labels are available to describe individual features.

Appendix C: User Personas

Experienced Erin

"People will surprise you with their thirst for knowledge. I try to meet them where they are, but most of the time I don't have to try very hard."

Age: 35
Work: Paleobiologist
Family: Partnered
Location: San Francisco, CA
Character: Expert

Critical | Passionate | Smart | Skeptical

Key Traits

Tech Savvy
Open-mindedness
Scientific Background

Goals

- Review new materials for biology communication
- See her herself the summary of arguments for a *Eunotosaurus*- turtle clade
- Find a new tool to encourage greater scientific literacy in her students and followers

Frustrations

- Lack of clear signaling or visually-stimulating graphics to explain abstract information
- Annoyed when new publications overstate their impact on the field
- Incautious or misleading messaging from scientific communications

Bio

Erin has been working as a university paleobiologist for five years, and has been an active member of the online paleo community in that time. Her work is mostly with stem mammals and the origins of amniotes biological systems. She is familiar with the debate about turtle origins and has shared every meme about new turtle papers when they come out. While she has read some articles when *Eunotosaurus* was trending a while back, she is cautious about whether she agrees with the arguments made regarding cranial support for a *Eunotosaurus* - turtle clade. Even so, she is fascinated by reconstructions and is always looking for more resources to share with her followers. Mostly, she enjoys constructively critiquing them, but it's always nice to spread information and enthusiasm with like-minded individuals.

Persona 1/4

Teacher Tom

"I've harped on these concepts for weeks and still my students don't seem to get it. It's...disheartening."

Age:42
Work: Professor
Family: Married, Kids
Location: New Haven, CT
Character: Educator

Tired | Passionate | Adaptable | Friendly

Key Traits

- Tech Savvy
- Open-mindedness
- Scientific Background

Goals

- Help his students understand macro-evolutionary concepts like crown and stem distinctions, clades, and inference
- Give students an appreciation for what the past can contribute to the present
- Incorporate a new, interactive tool into his class

Frustrations

- The concepts are complicated and even he has difficulty explaining them sometimes
- Too much focus on tree building over interpretation of relationships in existing media
- He doesn't get enough time to cover this subject as thoroughly as it requires

Bio

Tom is passionate about his work and his students. He has great respect for the scientific process and tries to encourage a similar enthusiasm in his class. He has been teaching undergraduate-level biology courses for 10 years now, and while the work is rewarding, he does get frustrated with how ill-prepared some students are from their previous schooling. He spends more time reviewing basic concepts and micro-evolutionary processes like natural selection than bigger-picture things like cladistics because of the way the curriculum is set. Once these topics come around towards the end of the course, his students struggle with what to him seems simple. He thinks maybe finding an interactive multimedia resource would hold their attention better than his PowerPoint slides.

Persona 2/4

Curious Catalina

"I'm no expert, but I follow a few paleo scientists and artists on Twitter. You learn a couple things..."

Age: 23
Work: Student
Family: Single
Location:Phoenix, AZ
Character: Enthusiast

Eager | Exploratory | Distractable | Nervous

Goals

- Learn how to interpret fossils and bony structures
- Be able to keep up in conversations about phylogenetic relationships in the community
- See what the fuss is about turtle origins

Frustrations

- Primary academic sources are hard to find for free and are difficult to read through
- She has difficulty sometimes telling between a legitimate resource and misinformation
- Any decent online resources for viewing fossils are low-resolution or behind a paywall

Key Traits

Tech Savvy

Open-mindedness

Scientific Background

Bio

Catalina has always had an interest in paleobiology, and grew up admiring the paleo art in picture books. While she isn't majoring in biology, she has taken several courses and understands enough to get by. Her recent discovery of the paleo community online has reignited her childhood interest and nurtured her curiosity. Since joining it, she has been privy to both scientific and hobbyist discourse on topics ranging from nomenclature to new discoveries to popoular criticisms of media despictions of extinct species, particularly dinosaurs. She tries to bone up on what people are talking about and relies heavily on scientific journalism to explain concepts accessibly. She needs things explained clearly and succinctly a few times before new knowledge sticks with her.

Persona 3/4

Studious Steven

"I didn't think this stuff would be so interesting, but it's kinda crazy how everything is interconnected."

Age: 21
Work: Student
Family: Single
Location: Orlando, FL
Character: Educated

Engaging | Agreeable | Driven | Clever

Goals

- Get a feel for how cladograms are interpreted
- See how fossils are identified and placed into their evolutionary relationships
- Be able to knowledgeably speak about comparative morphology with his peers

Frustrations

- Gets confused about the differences between diagrammatic terms like mono- and paraphyly
- Wishes existing videos and interactive resources actually touched on specific concepts
- Inability to rotate nodes and make equivalent trees

Key Traits

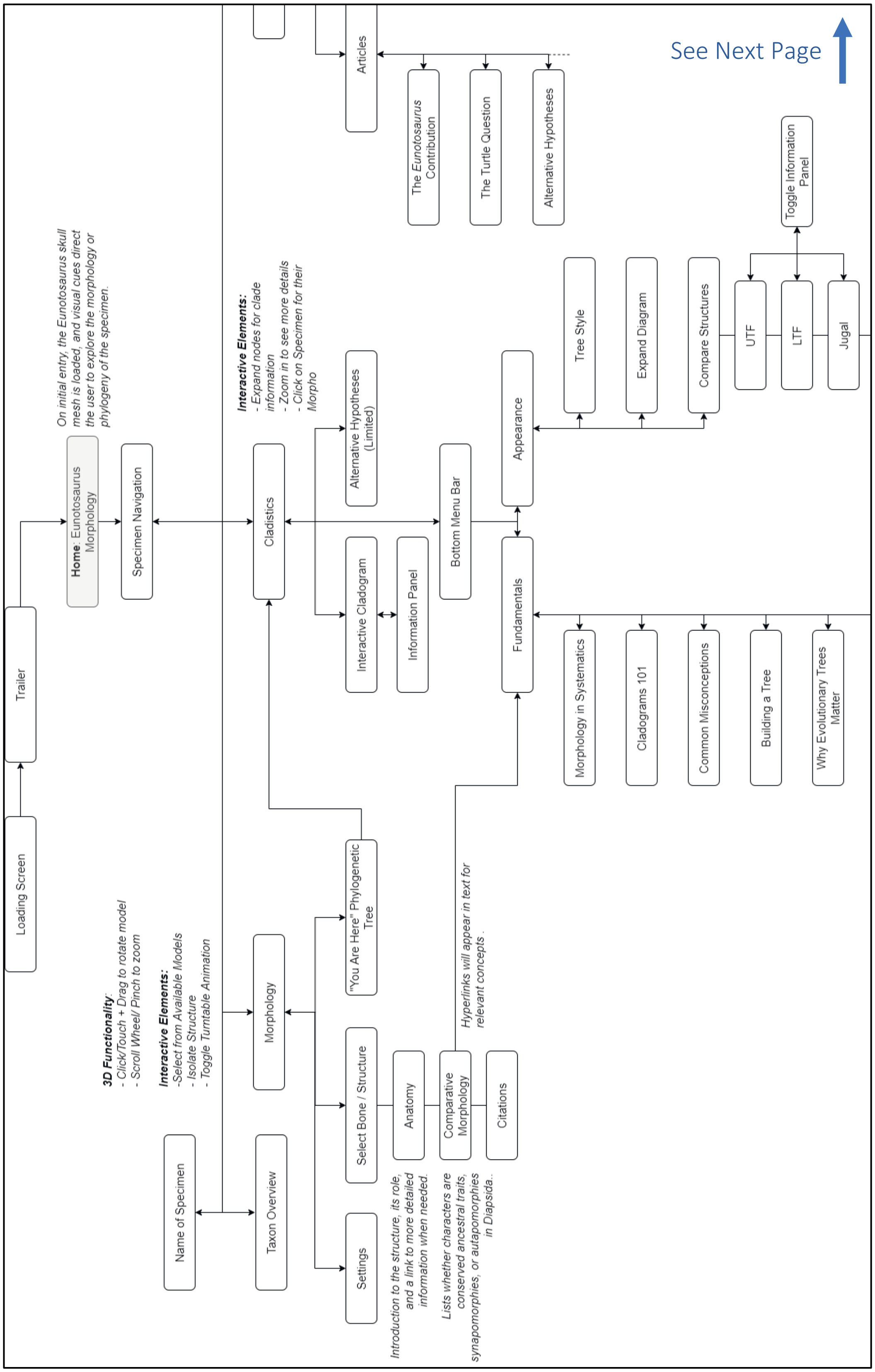
Tech Savvy
Open-mindedness
Scientific Background

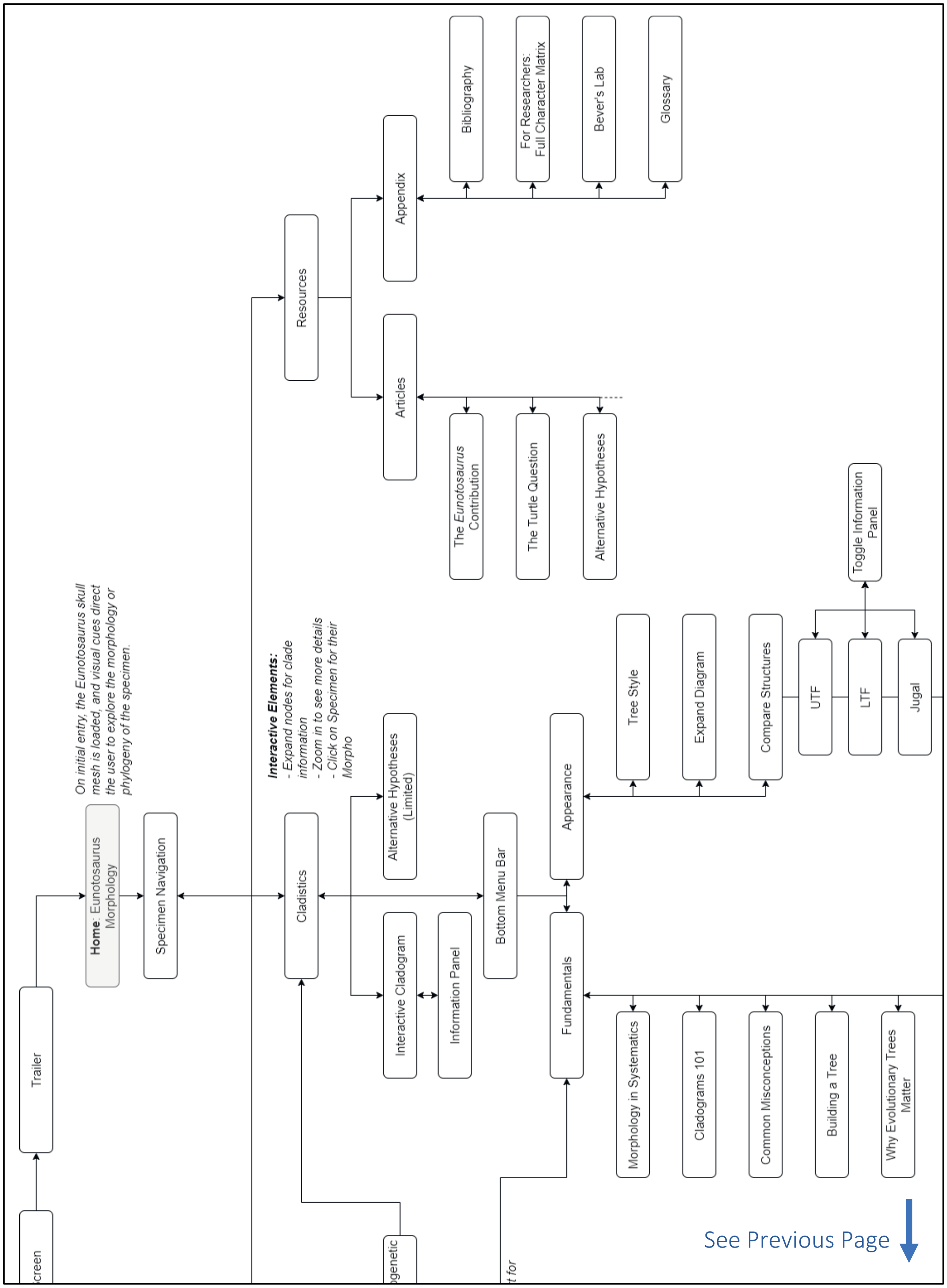
Bio

Steven is well into his Biology degree, and while his introductory courses touched on evolution a bit, he didn't take an interest until this past year when he took Vertebrate Zoology as an elective. Now he is thinking of doing a minor in Geology or Ecology, just to add more context to his growing interest in evolutionary biology. As part of his upcoming end-of-year group project for class, his team are thinking of investigating amniote or reptile evolution. There's just SO much information out there and so many ways to go that they're having a hard time figuring out where to start. Despite his interest, he's also having some trouble with terminology, but is determined to read up as much as he can so he doesn't let his team down.

Persona 4/4

Appendix D: Original Flowchart





Trailer
Home: Eunotosaurus Morphology
On initial entry, the Eunotosaurus skull mesh is loaded, and visual cues direct the user to explore the morphology or phylogeny of the specimen.
Specimen Navigation
Cladistics
Interactive Elements:
- Expand nodes for clade information
- Zoom in to see more details
- Click on Specimen for their Morpho
Resources
Articles
Appendix
Bibliography
For Researchers: Full Character Matrix
Bever's Lab
Glossary
The Eunotosaurus Contribution
The Turtle Question
Alternative Hypotheses
Alternative Hypotheses (Limited)
Interactive Cladogram
Information Panel
Bottom Menu Bar
Appearance
Fundamentals
Tree Style
Expand Diagram
Compare Structures
UTF
LTF
Jugal
Toggle Information Panel
Morphology in Systematics
Cladograms 101
Common Misconceptions
Building a Tree
Why Evolutionary Trees Matter
See Previous Page

Appendix D: Style Guide

Color Palette

Queen Blue	#366a9b
Columbia Blue	#b2d9eb
Max Yellow Red	#f5c56e
Cosmic Latte	#faf4e3
Popstar	#b84b5a
Citron	#849f2d
Charcoal	#1f3a47
Cadet Blue	#547280
Gainsboro	#d9d9d9
Spanish Gray	#919191

Typography

Header 1

Avenir Next Italic | Color: #ffffff | 32pt

SubHeading 1

Avenir Next Regular| Color: #ffffff | 18pt

Heading 2

Monsterrat Medium| Color: #333333 | 18pt

This is body copy. Lorem ipsum dolor et tu brute?

Monsterrat SemiBold| Color: #333333 | 14pt

Emphasis

Monsterrat Medium| Color: #333333 | 14pt

Link

Monsterrat Regular| Color: #0018b4 | 14pt

Interactivity

n/a	n/a	Button	Inactive
	Button	Button	Active
	Button	Button	Hover
	Button	Button	Pressed

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Vita

Gaby Rivera (born Annelis Gabriela Rivera-Del Río) was born in 1995 in Bayamón, Puerto Rico. She emigrated to Miami, Florida at an early age, where she spent long summer days catching critters and drawing on anything she could get her hands on. In high school, her teachers encouraged her love of both the biological sciences and art, and this is where she first learned about medical illustration.

Gaby attended Florida International University (FIU) in Miami, Florida, graduating *cum laude* in 2017 with a Bachelor of Science in Biology and minors in English and Art. While studying at FIU, she was involved in the FIUTeach education certificate program and worked as a Learning Assistant for the Biological Sciences Department. Through this experience, she fostered her love for biology education.

After graduation from FIU, Gaby decided to bet on herself and apply for medical illustration programs. To save money for graduate school and gain new skills, she worked in the University of Miami Office of the Vice Provost for Research & Scholarship. To this day she credits that experience for giving her the professional, interpersonal, and organizational skills to achieve her goals.

In August 2020, at the height of the COVID-19 pandemic, Gaby continued her studies at the Johns Hopkins University School of Medicine's Medical and Biological Illustration graduate program. Her time in the Department of Art as Applied to Medicine was a period of considerable growth. It was also marked by continued engagement with the research community, participation in student mentorship, and appointments representing her program in the Graduate Student Association (GSA) and Council on Graduate Education (COGE). In the future, she hopes to continue working in designing interactive learning experiences. Gaby will be receiving her Master of Arts in May of 2022.