

## RESEARCH ARTICLE

# 2D and 3D visualizations of archosaur jaw muscle mechanics, ontogeny and phylogeny using ternary diagrams and 3D modeling

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## ABSTRACT

Comparing patterns of performance and kinematics across behavior, development and phylogeny is crucial to understand the evolution of complex musculoskeletal systems such as the feeding apparatus. However, conveying 3D spatial data of muscle orientation throughout a feeding cycle, ontogenetic pathway or phylogenetic lineage is essential to understanding the function and evolution of the skull in vertebrates. Here, we detail the use of ternary plots for displaying and comparing the 3D orientation of muscle data. First, we illustrate changes in 3D jaw muscle resultants during jaw closing taxa (the American alligator (*Alligator mississippiensis*)). Second, we show changes in 3D muscle resultants of jaw muscles across an ontogenetic series of alligators. Third, we compare 3D resultants of jaw muscles of avian-line dinosaurs, including extant (*Struthio camelus*, *Gallus gallus*, *Psittacus erithacus*) and extinct (*Tyrannosaurus rex*) species to outline the reorganization of jaw muscles that occurred along the line to modern birds. Finally, we compare 3D resultants of jaw muscles of the hard-biting species in our sample (*A. mississippiensis*, *T. rex*, *P. erithacus*) to illustrate how disparate jaw muscle resultants are employed in convergent behaviors in archosaurs. Our findings show that these visualizations of 3D components of jaw muscles are immensely helpful towards identifying patterns of cranial performance, growth and diversity. These tools will prove useful for testing other hypotheses in functional morphology, comparative biomechanics, ecomorphology and organismal evolution.

**KEY WORDS:** Archosaur, Ternary diagram, Biomechanics, 3D visualization, Orientation

## INTRODUCTION

Recent advances in imaging and computational methods are enabling researchers to capture three-dimensional (3D) morphology at high resolutions. Researchers are ushering in a renaissance of imaging approaches in areas such as astronomy (Cohen et al., 2003; Prosser et al., 2015; Korsun et al., 2016), biochemistry (Lüthy et al., 1992; Zemla, 2003; Arnold et al., 2006), and archaeology and anthropology (Hughes et al., 2005; Lee et al.,

2007; Carlson et al., 2011; Du Plessis et al., 2015). Similarly, biological sciences are greatly enhanced by morphological studies incorporating large amounts of high-resolution 3D data. Morphologists frequently model diverse morphological systems in entomology (Klaus et al., 2003; Friedrich and Beutel, 2008), physiology (Witmer et al., 1999; Schachner et al., 2013; Tsai and Holliday, 2015; Stephenson et al., 2017), neuroanatomy (Evans et al., 2009; Lautenschlager et al., 2012; Kawabe et al., 2013) and skeletal tissue biomechanics (Grosse et al., 2007; Cuff et al., 2015) using high-resolution data. Modeling musculoskeletal systems in 3D is now enabling researchers to investigate the underlying biomechanics of behaviors, such as feeding (Gans et al., 1985; Zusi, 1987; Witmer and Rose, 1991; Hoese and Westman, 1996; Herrel et al., 1999; Dumont et al., 2005; Dawson et al., 2011; Srinively et al., 2013; Sellers et al., 2017; Bates and Falkingham, 2018; Cost et al., 2020) and locomotion (Hutchinson, 2004; Charles et al., 2016; Manafraedch and Padian, 2018), using computational and imaging methods such as finite element analysis (e.g. Keyak et al., 1993; Rayfield, 2007; Santana et al., 2010), XROMM (e.g. Brainerd et al., 2010; Baier et al., 2013) and multibody dynamics (e.g. Moazen et al., 2009; Curtis et al., 2010; Srinively et al., 2015).

Shared among many biomechanical studies is the measurement and visualization of the magnitudes (e.g. Newtons) and orientations of forces (e.g.  $x$ ,  $y$ ,  $z$ ), often across time ( $t$ ). Biologists often report the most biomechanically and ecologically important portions of forces, such as the vertical (orthal) component of bite force or vertical component of ground-reaction force. Additionally, we also often disregard component forces in the transverse or axial planes, in part as a product of the historical focus on mammalian feeding and locomotor systems where muscles largely act in parasagittal planes (e.g. Maynard Smith and Savage, 1959; Dullermeijer, 1956; Carmill, 1974, 1985) relative to the systems in other vertebrates. But also, pragmatically, it is simply challenging to visualize all force components simultaneously or in a fashion understandable by readers in traditional publishing. Thus, the complicated 3D nature of musculoskeletal anatomy remains difficult to convey in two-dimensional (2D) publications and other media (e.g. Greaves, 1982; Sinclair and Alexander, 1987; Bimber et al., 2002; Lockwood et al., 2002; Holliday and Witmer, 2007; Vincent et al., 2007; Huber et al., 2008; Sastita, 2008; Holliday, 2009; Kolmann and Huber, 2009; Pfaffler et al., 2011; Figueirido et al., 2013; Holliday et al., 2013; Cost et al., 2020). The solution has been to decompose multidimensional measurements into more simplified plots that are designed specifically for 2D publishing including iterative columns, box plots and line graphs. This, in turn, causes higher-order questions of behavior, ontogeny and phylogeny to be even more challenging to analyze and disseminate. One solution is to project 3D force components in a ternary diagram. Ternary diagrams have a long history of

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