Cranial functional morphology of the pseudosuchian *Effigia* and implications for its ecological role in the Triassic

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ABSTRACT

Pseudosuchians, archosaurian reptiles more closely related to crocodylians than to birds, exhibited high morphological diversity during the Triassic and included numerous occurrences of morphological convergence with post-Triassic dinosaurs. A prominent example is the shuvosaurid *Effigia okeeffeae*, which possesses an "ostrich-like" bauplan combining a gracile, bipedal postcranial skeleton with edentulous jaws and large orbits, similar to those of ornithomimid dinosaurs and extant palaeognaths. This bauplan is regarded as an adaptation for herbivory, but this hypothesis assumes that morphological convergence confers functional convergence and has received little explicit testing. Here, we restore the skull morphology of *Effigia*, perform myological reconstructions, and apply finite element analysis to quantitatively investigate skull function. We also perform finite element analyses on the crania of the ornithomimid dinosaur *Ornithomimus edmonticus*, the extant palaeognath *Struthio camelus* and the extant pseudosuchian *Alligator mississippiensis* in order to assess the degree of functional convergence in extinct taxa with "ostrich-like" bauplans and their closest extant relatives. We find that *Effigia* possesses a mosaic of mechanically strong and weak features, including a weak mandible that likely restricted feeding to the anterior portion of the jaws. We find limited functional convergence between *Ornithomimus* and *Struthio* and limited evidence of phylogenetic constraints with extant pseudosuchians. We infer that *Effigia* was a specialist herbivore that likely fed on softer plant material, a unique niche among the study taxa and, potentially, among contemporaneous Triassic herbivores. This study increases the known functional diversity of pseudosuchians and highlights that morphological convergence between unrelated taxa does not always imply functional and ecological convergence.

Key words: pseudosuchian, *Effigia*, Triassic, convergence, herbivory, functional morphology, *Ornithomimus*, *Struthio*

INTRODUCTION

The Triassic Period was a key time in evolutionary history that witnessed the emergence and radiation of Archosauria – the group of reptiles that includes crocodylians and birds (Nesbitt, 2003, 2011, Nesbitt et al., 2010, Butler et al., 2011). The Late Triassic is considered to have been particularly important for the Pseudosuchia – archosaurs more closely related to crocodylians than to birds – as this clade exhibited high levels of morphological diversity at this time (Brusatte et al., 2008, 2010). Numerous instances of morphological convergence have been noted between Late Triassic pseudosuchians and other more distantly related archosaurs, many of which post-date the Triassic (Stocker et al., 2016). Examples of these include: the large, broad crania of ornithosuchids and rauisuchids, which are reminiscent of those in large theropod dinosaurs (Walker, 1964, Brusatte et al., 2009, Weinbaum, 2011, 2013); the quadrupedal, armoured bodies of aetosaurs, which converged on the body plans of ankylosaurian dinosaurs (Desojo et al., 2013, Stocker et al., 2016); and the elongate rostra and aquatically-adapted postcrania of phytosaurs, which are similar to those of extant crocodylians (Chatterjee, 1978, Stocker, 2012, Witzmann et al., 2014). Pseudosuchians were some of the dominant tetrapods in many Late Triassic food webs and filled a diverse array of ecological roles within terrestrial and freshwater ecosystems (Brusatte et al., 2008).

A well-known case of morphological convergence concerns the shuvosaurid poposauroid *Effigia okeeffeae* from the Late Triassic of the southwestern USA (Nesbitt and Norell, 2006, Nesbitt, 2007). *Effigia has been* described as having a theropod-like body plan due to its gracile morphology, bipedal posture and the way in which its femora articulate with the pelvis (Nesbitt, 2007). More specifically, although all known cranial material of *Effigia* is partially crushed, reconstructions suggest a remarkable level of cranial convergence with Late Cretaceous ornithomimid dinosaurs, including large cranial fenestrae, enlarged orbits and edentulous jaws that were likely covered with rhamphotheca (Nesbitt, 2007, Stocker et al., 2016). Similar cranial morphology is also present in extant palaeognath birds, most notably the ostrich (*Struthio camelus*) (Zusi, 1993), and, to a lesser

extent, the abelisauroid dinosaur *Limusaurus* from the Late Jurassic (Xu et al., 2009, Stocker et al., 2016). This independent, repeated evolution of an edentulous, bipedal and gracile bauplan (informally referred to as "ostrich-like") not only further highlights the morphological disparity of Late Triassic pseudosuchians but also acts as an example of the extent to which archosaurs repeatedly occupied the same areas of morphospace (Brusatte et al., 2008, 2010, Nesbitt, 2011, Stocker et al., 2016).

An ostrich-like bauplan has been cited as a possible adaptation for herbivory (Osmólska, 1997, Makovicky et al., 2004, Barrett, 2005, Nesbitt, 2007, Stocker et al., 2016) because extant birds with these features are known to be herbivorous and have been studied in detail (e.g. in *Struthio*; (Williams et al., 1993, Milton et al., 1994). Observational studies are not possible for extinct taxa but inferences can be made in various ways. Most dietary interpretations of *Effigia* and ornithomimids come from: (i) comparative morphology of anatomical characters with extant birds such as palaeognaths and Anseriformes (waterfowl) (Norell et al., 2001, Barrett, 2005, Nesbitt, 2007); (ii) assessing the evolutionary pathways of cranial eco-functional characters that likely facilitated herbivory (Zanno and Makovicky, 2011, Button and Zanno, 2020); (iii) preserved gut contents; and iv) other evidence such as the presence of a gastric mill (Kobayashi et al., 1999, Makovicky et al., 2004). These types of evidence, however, are limited either by the quality of the fossil record or by assumptions on the strength of relationships between morphology and inferred function (Bestwick et al., 2018 and references therein). Quantitative investigations into the degree of functional convergence between *Effigia* and morphologically similar, but distantly related, archosaurs are thus needed for inferring the likelihood that these taxa performed similar ecological roles.

Few studies have investigated the functional morphology of Triassic pseudosuchians, particularly with regard to potential feeding behaviours. Nevertheless, some valuable insights have been gained into pseudosuchian diets, how these taxa partitioned or competed for resources, and on their broader evolution by using various biomechanical modelling methods (Desojo and Vizcaíno, 2009, Baczko et

al., 2014, Baczko, 2018). Two-dimensional muscle reconstructions and lever mechanical modelling of aetosaur jaws, for example, found that some aetosaurs had slow and powerful bites, interpreted as an adaptation for processing tough vegetation, whereas others exhibited faster, weaker bites interpreted as evidence of facultative insectivory (Desojo and Vizcaíno, 2009). Similar techniques found that ornithosuchids were capable of intermediately powerful, slower bites and were thus likely to have occupied a mesopredator and/or scavenger roles in Late Triassic food webs (Baczko, 2018). Two-dimensional models are, however, a simplified version of complex three-dimensional anatomy and are only capable of modelling jaw function via simple lever mechanics (Kammerer et al., 2006, Davis et al., 2010, Anderson et al., 2011, Porro et al., 2011, Santana, 2016). This is particularly problematic for many archosaur groups, such as extant crocodylians, which can generate high mediolateral forces from their jaw muscles (Porro et al., 2011). By contrast, three-dimensional techniques, such as finite element analysis (FEA), can more accurately predict the performance of organic structures because they can: i) predict biomechanical stresses and strains across the whole 3D skull; ii) allow incorporation of soft tissue elements such as rhamphothecae to improve biological realism (Lautenschlager et al., 2013, Cuff and Rayfield, 2015) and; iii) can enable modelling of a wider range of feeding-related behaviours, such as twisting, shaking and pecking (Porro et al., 2011, Rayfield, 2011, Walmsley et al., 2013, McCurry et al., 2015). Representative investigations into the functional morphology of *Effigia* can thus help to elucidate the true level of functional convergence between this pseudosuchian and other morphologically-similar members of Avemetatarsalia (thos archosaurs more closely related to birds than crocodiles).

Here, we restore the original morphology of the crushed and deformed skull of *Effigia*, perform myological reconstructions, and apply 3D FEA to investigate the functional morphology of this Late Triassic pseudosuchian, in order to assess its degree of functional convergence with other taxa that exhibit an ostrich-like bauplan. To achieve the latter aim we used previously published 3D cranial models from the ornithomimid dinosaur *Ornithomimus edmontonicus* and the palaeognath bird

Struthio camelus (Cuff et al., 2015, Cuff and Rayfield, 2015). We also included a cranial dataset from *Alligator mississippiensis* in order to include an extant pseudosuchian and a morphological outgroup (Montefeltro et al., 2020). Finally, we modelled the impacts of different-sized rhamphothecae for our extinct study species and simulated pecking-like behaviours for all taxa in order to provide more stringent tests on the degrees of functional convergence and to better assess whether unrelated ostrich-like taxa performed the same ecological roles.

Institutional Abbreviations

AMNH, American Museum of Natural History, New York, NY, USA; ROM, Royal Ontario Museum, Toronto, Ontario, Canada; RTMP, Royal Tyrrell Museum of Paleontology, Drumheller, Alberta, Canada; OUVC, Ohio University Vertebrate Collections, Athens, OH, USA.

MATERIALS AND METHODS

Specimen Information

The holotype of *Effigia okeeffeae* (AMNH FR 30587) was computed tomography (CT) scanned at Stony Brook University Hospital on a GE Systems Lightspeed 16 scanner with an interslice thickness of 0.625 mm. For full image specifications and post-processing procedures, see Nesbitt (2007). The unretrodeformed dataset can be requested through the AMNH.

For comparisons, we modelled the crania of *Struthio*, *Ornithomimus* and *Alligator*. The *Struthio* specimen was micro-computed tomography (µCT) scanned at the University of Hull, UK, using a X-Tek HMX 160 scanner. Due to specimen size, it was scanned in two parts (anterior and posterior; 758 slices and 846 slices, with voxel sizes of 0.1594 mm and 0.1425 mm respectively). Both scan sets were rotated and resampled to the same voxel size (0.1594 mm resolution; see also Cuff et al. 2015). The *Ornithomimus* specimen (RTMP 1995.110.0001) was scanned along the coronal axis for

a total of 420 slices (0.63 mm thickness) with a General Electric (GE) LightSpeed Plus CT scanner (see also Tahara and Larsson (2011) and Cuff and Rayfield (2015)). The *Alligator* specimen (OUVC 9761) was scanned at O'Bleness Memorial Hospital, Athens, Ohio, using a GE Lightspeed Ultra Multislice CT scanner equipped with the Extended Hounsfield option and a "bow-tie" filter. The specimen was scanned helically at a slice thickness of 625 µm, 120–140 kV and 200–300 mA (see also Witmer and Ridgely (2008)).

Struthio was chosen for comparison as it is the taxon most often used by palaeontologists as a reference for inferring palaeognath-like behaviours in extinct taxa (Barsbold and Osmólska, 1990, Osmólska, 1997, Ji et al., 2003, Zanno and Makovicky, 2011), and it has also been the subject of several biomechanical studies (Rayfield, 2011, Cuff et al., 2015). For this study, sutures were not separately modelled from the rest of the cranium, producing a model that does not exhibit functional kinesis. We acknowledge that this results in asimplified cranium as sutures are known to alter and modulate stress and strain distributions in many taxa, both at the sutural junction and, in some cases, across the entire cranium (Herring and Teng, 2000, Rafferty et al., 2003, Kupczik et al., 2007, Moazen et al., 2009, Curtis et al., 2013, Jones et al., 2017, Dutel et al., 2021). However, we simplified our model reflected the fact that sutures substantial time and anatomical expertise to model, particularly in *Struthio* where some cranial sutures may become partially fused as individuals mature (Cuff et al., 2015). Consequently, the degree of sutural fusion is not always clear from CT scans and isdifficult to model representatively. However, some general inferences are still possible from our results without modelling sutures and we can make some post hoc inferences as to how the sutures might alter our results based on other more detailed analyses. Furthermore, our *Struthio* muscle model is already somewhat hypothetical We did, however, produce a second *Struthio* model with simulated palatobasal (parasphenoid-pterygoid) and otic (quadrate-squamosal) joints (Bailleul et al., 2017). The inclusion of these joints allows some insight to be gained into their functional role during feeding behaviors. Results from the 'jointed' *Struthio* model can be found in the

Ornithomimus was chosen due to its frequently noted high degree of morphological convergence with *Struthio* and the availability of complete and three-dimensionally preserved cranial material (Cuff and Rayfield, 2015). *Alligator* was included as an extant representative of the pseudosuchian lineage and as an outgroup with markedly different cranial morphology from the other study taxa due to the presence of teeth and a dorsoventrally flattened and mediolaterally broader skull (Busbey, 1989). This sample enables a more thorough investigation into whether morphological convergence leads to functional convergence among unrelated taxa with ostrich-like bauplans.

Retrodeformation and Digital Reconstruction

The CT image files of *Effigia* were imported into Avizo (version 7.0 & 8.0, Visualisation Science Group) for segmentation from the surrounding matrix. The individual skull elements were highlighted and separately labelled using the segmentation editor in Avizo to produce surface models and volumes. In some cases, individual skull bones had broken into multiple pieces during fossilization and post-fossilization processes (compaction, uplift, etc.; Fig. S1). All elements were subsequently retrodeformed to their hypothesised original morphology and realigned to restore the skull to an approximate non-deformed condition (Fig. S1). Retrodeformation was carried out in Avizo. Only two *Effigia* skulls are known, one largely complete and one partially preserved, and both exhibit some deformation in the form of breakage, displacement, plastic deformation, or a combination of some or all three (Nesbitt and Norell, 2006, Nesbitt, 2007). The restoration process followed the steps outlined by Lautenschlager (2016) and was informed by: the topographic relationships of individual elements in the 3D CT scan data; identification and subsequent repair of cracks and holes; and osteological comparisons with closely related taxa, such as extant crocodylians. Osteological features that were badly damaged, or missing entirely, on one side of the

skull were substituted by mirroring the corresponding feature from the opposite side of the skull, assuming bilateral symmetry. Palatal features were assembled first, followed by the remainder of the cranium, and lastly the mandibles, in order to better identify the original dimensions of the skull, in particular, reconstruction of the cranial and mandibular widths through the quadrate-squamosal and quadrate-articular articulations and through the contact point of the ectopterygoid-mandible, lacrimal and jugal (Fig. S1). It should be noted that the palate morphology of *Effigia* is unique, so the reconstruction was based on the constraints of other skull bones and with broad comparisons with other archosaurs such as crocodylians. Annotated diagrams of the complete retrodeformed cranium and mandible are shown in Fig. 1.

The full *Ornithomimus* retrodeformation protocol can be found in Cuff and Rayfield (2015) but the main steps are noted here for completeness. Retrodeformation took place in Avizo 7.0. All *Ornithomimus* cranial material exhibits some form of deformation, thus specimens ROM 841 and ROM 851 were observed first-hand to inform the process. Where relevant, the cranial morphology of other ornithomimids such as *Sinornithomimus dongi* (Kobayashi and Lü, 2003) and *Gallimimus bullatus* (Osmólska et al., 1972) were used to aid the process. The palatines and pterygoids exhibited quite large degrees of mediolateral displacement and overlap. The palatal bones were therefore individually segmented and aligned and then used as a marker for estimating the mediolateral dimensions for the rest of the cranium. Subsequent filling of cracks, holes and missing material were performed as per Lautenschlager (2013).

To increase the degree of model realism, keratinous rhamphothecae were added to the crania and mandibles of the three edentulous study taxa using Avizo. All rhamphothecae were modelled around 3 mm thick, informed by tentative soft tissue preservation in ornithomimids (Norell et al., 2001, Cuff and Rayfield, 2015), and modelled as a homogenous and isotropic layer that attached directly to the bone. Although this does not capture the full biological complexity of rhamphothecae, it does enable

more representative comparisons between the study taxa. The modelled *Struthio* rhamphotheca covers much of the premaxilla and maxilla on the cranium, partially surrounding the nares, and extends to the jugal bar along the upper jaw. Accurately inferring the presence and shape of rhamphothecae in extinct taxa is difficult as these non-mineralised tissues are rarely preserved (Norell et al., 2001), and there are no conclusive osteological correlates for these structures (see Lautenschlager et al. (2014) and Cuff and Rayfield (2015) for a discussion). Two different rhamphotheca morphologies, dubbed 'small beak' and 'large beak', were therefore created for both *Effigia* and *Ornithomimus* to encompass the lower and higher ranges of possible shapes based on the shapes of the cranial bones (Fig. 2). The small beak cranial rhamphotheca of *Effigia* covers the anterior half of the premaxilla (Fig. 2A; 2B) and the small beak rhamphotheca of *Ornithomimus* covers the ventrolateral and ventral margins of the premaxilla and anterior half of the maxilla (Fig. 2I; 2J). The large beak cranial rhamphotheca of *Effigia* extends to the anterior edges of the nasal and maxilla bones (Fig. 2C; 2D), and the large beak rhamphotheca of *Ornithomimus* extends to the anterior margins of the antorbital fenestrae without covering the nares (Fig. 2K; 2L). The small beak mandibular rhamphotheca of *Effigia* covers the anterior half of the dentary (Fig. 2E; 2F) and the large beak mandibular rhamphotheca extends to the posterior margin of the dentary (Fig. 2G; 2H).

Muscle Reconstructions

Muscle origination and insertion sites for *Effigia* (Fig. 3) were identified for each jaw adductor muscle independently based on osteological correlates such as muscle scars, ridges and depressions. Where such features were badly preserved, obscured or altogether absent, extant phylogenetic bracketing was used to infer the positions and extents of muscle attachment sites. Following Holliday and Witmer (2007), *Effigia* myoanatomy was bracketed between that of extant crocodylians (Busbey, 1989, Holliday et al., 2013) and birds (Webb, 1957, Lautenschlager et al., 2014), with the extant

lepidosaur *Sphenodon punctatus* (Holliday and Witmer, 2007) used as an outgroup. Reconstructions of the myoanatomy of non-avian theropod dinosaurs (Holliday, 2009, Lautenschlager, 2013) were also consulted as independent reference points.

The origin and insertion sites for each muscle were connected by thin cylinders connecting the centre of each site. Where necessary, cylinder pathways were adjusted to avoid cross-cutting each other and osteological structures (Curtis et al., 2009). Additional cylinders were then plotted from the edges of each muscle attachment site to produce simplistic frames that were 'fleshed out' to create full 3D muscle reconstructions. The final size and shape of each muscle was determined by the geometry of the surrounding bone surfaces and by preventing any cross-cutting between muscles.

Based on phylogenetic bracketing, we infer that *Effigia* had a fibrocartilaginous sesamoid, similar (though not necessarily homologous) to the cartilago transiliens of extant crocodylians, within its adductor chamber (Tsai and Holliday, 2011). In extant crocodylians, this structure develops as a fibrous nodule within the medial portion of the m. pseudotemporalis superficilias tendon, becoming continuous with the m. intramandibularis and eventually forming connections with immediately surrounding muscles and a fibrous connection to the coronoid eminence (Tsai and Holliday, 2011). The sesamoid serves to prevent damage and tendon flattening as associated muscles wrap around a trochlear surface; in the case of crocodylians this relates to the m. pseudotemporalis and m. intramandibularis complex passing over the pterygoid wing, although analogous structures are found in turtles within the adductor mandibulae externus group where it passes over the trochlear process of the quadrate (Bramble, 1974), in a range of squamates where it is associated with the quadrate (Montero et al., 2017), and in birds where sesamoids are commonly found within the jugomandibular ligament (Burton, 1973).

A fibrocartilaginous linkage between the m. pseudotemporalis superficialis and the m. intramandibularis was noted in birds and turtles by Holliday and Witmer (2007), leading Tsai and

Holliday (2011) to suggest the possibility of homology between these structures; if this were the case a fibrocartilaginous link between these muscles would be plesiomorphic for archosaurs.

In *Effigia* the path of the m. pseudotemporalis superficialis and m. intramandibularis wraps around the pterygoid wing and at the same point is laterally constricted by the surangular. The pterygoid wing itself is dorsolaterally broad and rounded rather than thin and flat, therefore providing a smooth trochlear-like surface for a hypothetical intertendon to articulate around. Due to the similarity in position to the fibrocartilaginous linkage in turtles and birds (Holliday and Witmer, 2007), the presence of cranial sesamoids at tendinous pressure-points in a range of phylogenetically-bracketing taxa and the likely application of regular pressure at this point, we reconstructed a small sesamoid at this point in *Effigia.* The sesamoid was considered in our muscle reconstructions and in placing the muscle forces for the FEA models. Due to the difficulty in modelling fibrocartilaginous structures suspended between muscle bodies, the sesamoid was not incorporated as a separate component in the FEA models. However, the effect of this sesamoid on muscle vectors was retained during analyses as the mandible and cranium are modelled separately.

Bite Force

Muscle force estimates (F_{mus}) were calculated using a modified version of the dry skull method of Thomason (1991). Average cross-sectional areas (CSA) of each muscle were obtained using the Avizo material statistics module, which lists the respective CSA values for each individual material (in this instance the muscles). Muscle force was calculated for each muscle individually (i.e. for one side of the skull), using Eq. 1, assuming an isometric muscle stress value (σ) of 0.3 N mm^{-2}, following Thomason (1991) and Lautenschlager (2013):

$$F_{\text{mus}} = \text{CSA} \times \sigma$$

This method is rather simplistic as it does not account for the pennation angle of the individual muscle fibres, likely resulting in underestimations of muscle and bite forces. Muscle forces acting in

dorsoventral directions were used for bite force lever mechanics as anteroposterior and mediolateral muscle forces have a very limited influence on jaw closure (Cuff and Rayfield, 2015). Muscle insertion angles from the vertical axis were measured directly in the three-dimensional model in both the sagittal (α) and the coronal planes (β) using the Avizo measurement tool. The resulting muscle force that accounts for insertion angle (F_{res}) was calculated using Eq. 2:

$F_{res} = F_{mus}$ x cosα x cosβ

Final bite force estimates (F_{bite}) were calculated independently for each muscle using Eq. 3:

$F_{bite} = (F_{res}$ x $L_{inlever})/L_{outlever}$

$L_{outlever}$ denotes the distance between the bite point to the jaw joint and $L_{inlever}$ denotes the distance between the insertion point of the respective muscle and the jaw joint. All distances were measured in horizontal view in Avizo. The calculated values for these parameters can be found in Supplementary Table S1.

Muscle forces for *Alligator* and *Ornithomimus* were derived from Montefeltro et al. (2020) and Cuff and Rayfield (2015) respectively. It should be noted that the *Ornithomimus* muscle forces are rather conservative estimates and the actual forces in life might have been slightly greater (Cuff and Rayfield, 2015). Estimated jaw muscle forces for *Struthio* have never been published, so these forces were estimated by identifying origin and insertion sites based on osteological correlates (Webb, 1957). Where correlates were not clear, the myoanatomy of the extant common buzzard, *Buteo buteo* (Lautenschlager et al., 2014), and rock dove, *Columba livia* (Jones et al., 2019), were consulted. Despite the long independent evolutionary histories of *Struthio* and neognath birds, avian adductor muscle morphology is relatively conserved (Holliday and Witmer, 2007), allowing neognath muscles to be used as proxies where necessary. The CSA of each muscle was measured in ImageJ (National Institutes of Health), multiplied by the isometric stress value to attain the muscle force.

Finite Element Analysis

The 3D models of all specimens were imported into Hypermesh 11 (Altair Engineering) for the generation of solid tetrahedral meshes (consisting of approximately 300,000 elements per model). All cranial models were scaled to the same surface area as the *Effigia* cranium to enable more representative comparisons between archosaurs (Dumont et al., 2009). The muscle forces of the other archosaurs were also scaled accordingly. Scaling information can be found in Table 1. All models were loaded with maximum adductor muscle forces as calculated in Table 2. Loads were applied across multiple nodes at the inferred muscle origination and insertion sites of the crania and mandibles, respectively. This was performed using a custom-built macro (Altair UK) which simultaneously loads multiple nodes projected towards a node(s), resulting in a vector equivalent to the line of action of each muscle.

To further enable realistic comparisons between these archosaur taxa, specimens were assigned the same material properties for bone based on values for *Alligator* mandibular bone (E = 15.0 GPa, v = 0.29; (Zapata et al., 2010)). Material properties for teeth were also based on values for *Alligator* (E = 60.4 GPa, v = 0.31; (Zapata et al., 2010)). Material properties for the keratinous rhamphothecae (E = 1.04 GPa, v = 0.4) were based on extant bird beaks and taken from Chen et al. (2008). Material properties for the areas of bone that immediately surround the palatobasal and otic joints in the jointed *Struthio* model were based on *Alligator* connective tissue (E = 0.09 GPa, v = 0.3; (Porro et al., 2013)). All material properties within the models were treated as isotropic and homogeneous. The skull models were constrained from rigid body motion in all degrees of freedom at the parietals and the condyles of the mandibular capitulum of the quadrates. For all models and feeding simulations four nodes were constrained at the parietals and four nodes were constrained on each of the quadrates (12 in total). Usually, the occipital condyle and paroccipital process are used as the positions for these constraints (e.g. Lautenschlager et al. (2013)), but the posterior braincase of *Effigia* was not scanned and is therefore unavailable. For the *Effigia* mandible, four nodes were

constrained in all degrees of freedom at the articulation point on the dorsal surface of the articular (eight in total).

All models were imported into Abaqus (Version 6.10; Simulia) for analysis and postprocessing. The following feeding-related simulations were performed for each model:

i) Anterior bite. Bilateral biting at the tip of the snout in the premaxilla. One node was constrained on each of the left and right side of the jaws (two in total) in all degrees of freedom. For all cranial models except *Alligator*, the constraints were placed on the rhamphotheca covering the anteroventral tip of the premaxillae. For both *Effigia* mandible models, the constraints were placed on the rhamphotheca covering the dorsoanterior tip of the dentaries. For *Alligator*, the constraints were placed on the anterior-most tooth on each side of the premaxilla.

ii) Middle bite. Bilateral biting at the middle of the snout. One node was constrained on each of the left and right side of the jaws (two in total) in all degrees of freedom. For the small-beaked *Effigia* models, the constraints were placed on the posterior-most edge of the premaxilla and dentary in the cranium and mandible, respectively. For the small-beaked *Ornithomimus*, the constraints were placed on the maxilla. For the large-beaked cranial models of *Effigia* and *Ornithomimus* and for *Struthio*, the constraints were placed on the rhamphothecae that covers the maxillae. For the large-beaked *Effigia* mandible model, the constraints were placed on the rhamphotheca that covers the posterior edge of the dentary. For *Alligator*, the constraints were placed on the 4th tooth in the maxillary tooth row as these are the main teeth used for seizing prey (Erickson et al., 2012).

iii) Posterior bite. Bilateral biting at the inferred posterior functional end of the snout. One node was constrained on each of the left and right side of the jaws (two in total) in all degrees of freedom. For both beak models of *Effigia*, the constraints were placed on the maxilla and surangular of the crania and mandibles, respectively. For *Struthio*, the constraints were placed on the rhamphotheca that covers the posterior region of the maxillae. For both beak models of *Ornithomimus* the constraints

were placed on the jugals. For *Alligator*, the constraints were placed on the posterior-most tooth in the maxilla and dentary.

iv) Pecking. An external force moving dorsoposteriorly towards the cranium was used to simulate a feeding-related pecking action at the inferred functional tip of the snout. We applied a force of 340 N to one node at the snout tip. The adductor muscles generate this magnitude (Table 2) after accounting for both halves of the cranium. As the cranium can withstand this force, we applied it to the rostrum. For both beak morphologies of *Effigia* and *Ornithomimus,* and for *Struthio*, the external force contacts the anterior tip of the rhamphotheca. For *Alligator*, the external force contacts the anterior tip of the premaxilla.

Von Mises stress (a measure of overall structure strength under loading conditions) were displayed as contour plots for all simulations to enable visual assessments of the relative performance of the crania and mandibles. Stresses were also measured at 10 equally spaced locations along the dorsal and palatal surfaces of each cranium to provide more detailed assessments on model performance. The highly derived condition of the bones in the *Struthio* cranium (Cuff et al., 2015) hinders identification of homologous landmarks between pseudosuchian and avemetatarsalian skulls. Therefore, the dorsal and palatal surfaces of each cranium was divided into 10 sections of equal length along a longitudinal axis with von Mises stresses measured in the approximate centre of each section. For *Alligator*, many of the sampling locations along the palatal surface are from the secondary, or closed, palate; a bony plate comprising the maxillae, palatines and pterygoids that separates the nasal and oral passages (Busbey, 1995, Rayfield and Milner, 2008). This structure is unique to *Alligator* among our study taxa. Measurement locations across the dorsal and palatal surfaces of all crania are shown in Fig. S2. Measurement locations are the same in the jointed and non-jointed *Struthio* models.

RESULTS

Retrodeformation re-descriptions

Retrodeformation enabled new anatomical information to be gained on the overall morphology of the skull as well as on specific cranial elements. Some of the main results are highlighted here and further detailed descriptions can be found in the Supplementary Information. As a disclaimer, accurate anatomical interpretations of *Coelophysis* Quarry material can be problematic due to the difficulty in identifying whether material has been subjected to taphonomic processes and the extent to which these processes have occurred. Notably, plastic deformation has been observed in *Coelophysis* Quarry material, such as specimens of the theropod dinosaur *Coelophysis bauri* (Colbert, 1989, Schwartz and Gilette, 1994). Our interpretations and re-descriptions of the retrodeformed *Effigia* material are therefore cautious and based on the available osteological evidence as preserved.

With respect to general skull morphology, the skull table is reconstructed as generally flat in lateral view, in contrast to the dorsally bowed outline shown in Nesbitt and Norell (2006) and in *Shuvosaurus,* due to the lack of dorsal curvature of the frontals in the new reconstruction (Fig. 1). The ventral border of the cranium, comprising the premaxillae, maxillae and jugals, is inferred here to be anteroposteriorly concave in lateral view (Fig. 1) rather than straight as described previously (Nesbitt and Norell, 2006, Nesbitt, 2007). Consequently, the craniomandibular joint is now deflected ventrally with respect to the rest of the skull (Fig. 1). Our new reconstruction results in mandibles that are reconstructed as dorsoventrally taller in lateral view than those presented by Nesbitt (2007) due to the greater curvature of the angular (Fig. 1). The dorsal surface of the dentaries exhibited strong anteroventral curvature towards their anterior extremities following segmentation, contrasting with the flat dorsal surface that was recognised previously (Nesbitt and Norell, 2006). As a result, the

dentaries now have a more precise contact and greater overlap with the ventral shelves of the premaxillae during full jaw closure (Fig. 1).

With regard to specific elements, a posterolaterally projecting prong from the main body of the nasal bone fits within, and partially overlies, a complementary groove on the dorsal margin of the lacrimal. The articulation of the lacrimal with the jugal differs from the reconstruction of Nesbitt and Norell (2006); the distal end of the lacrimal ventral process does not appear to expand anteroposteriorly along the dorsal surface of the jugal. Instead, the lacrimal tapers towards its ventral extremity, ending in a rounded tip that inserts into a sulcus on the dorsal surface of the jugal. The ventral process of the prefrontal, which was not described by Nesbitt (2007), abuts the lacrimal obliquely and tapers ventrally. Lastly, upon segmentation of the pterygoids, a pair of deep sockets were identified medially to the quadrate ala, which form recesses for the reception of the basipterygoid processes.

Effigia Musculature

m. Pterygoideus dorsalis (m. PTd)

The m. pterygoideus dorsalis most likely originates from a deep fossa on the dorsal surface of the palatines, directly posterior to the pila postchoanalis (Fig. 3A). The dorsal extent of the m. PTd is bounded by a secondary palatine plate, dorsal to the main element, extending laterally from the palatine's medial expansion. This is inferred largely from the generally plesiomorphic muscle position in extant crocodylians, birds and lepidosaurs (Busbey, 1989, Holliday and Witmer, 2007, Holliday et al., 2013, Lautenschlager et al., 2014) and from reconstructions in dinosaurs (Holliday, 2009, Lautenschlager, 2013). Medially, the m. PTd is bordered by the dorsal vaulting at the sagittal contact of the pterygoids and laterally by their dorsally expanded wing. As in extant archosaurs, the m. PTd passes over the posterior edge of the lateral process of the pterygoid and plunges posteroventrally towards its mandibular insertion (Fig. 3A).

The mandibular insertion is clearly defined as a flat ventromedial surface of the surangular and articular, ventral to the quadrate articulation (Fig. 3A). The dorsal extent of the attachment is defined by a medially-projecting crest at the junction of the surangular and prearticular, and posteriorly it extends to the posterior limit of the short retroarticular process. The anterior extent of the attachment is poorly defined.

m. Pterygoideus ventralis (m. PTv)

The origin of the m. pterygoideus ventralis is poorly defined. The condition in *Effigia* is therefore inferred from the condition in crocodylians and birds; attachment along the posteroventral edge of the pterygoid flange. As with the m. PTd, the m. PTv is directed ventrally and posteriorly before wrapping ventrally around the mandible, directly ventral to the quadrate-articular articulation (Fig. 3B).

The insertion of the m. PTv is marked by a fossa on the ventrolateral surface of the mandible (Fig. 3B). This inference is supported by extant phylogenetic bracketing as the muscle attaches to this area in crocodylians and palaeognaths (Holliday, 2009). The reconstructed size of the m. PTv is based on that from a juvenile *Alligator* (Holliday et al., 2013) due to a lack of constraining osteological evidence.

m. Adductor Mandibulae Posterior (m. AMP)

The m. AMP is one of the most phylogenetically conserved muscles within the adductor chamber, maintaining generally consistent origination and insertion points throughout Sauropsida (Holliday and Witmer, 2007). The m. AMP originates from the lateral surface of the quadrate in *Sphenodon* and *Struthio* (Holliday and Witmer, 2007); and has been reconstructed in a similar position in the therizinosaurian dinosaur *Erlikosaurus andrewsi* (Lautenschlager, 2013), a range of

ornithomimosaurian dinosaurs (Cuff and Rayfield, 2015) and sauropod dinosaurs (Young et al., 2012, Button et al., 2016). Extant crocodylians display a derived condition, with the m. AMP originating from the ventral surface of the quadrate; as the quadrate of *Effigia* is far more similar to those of birds, dinosaurs and *Sphenodon* an origination for the m. AMP based on extant crocodylians is excluded. The insertion of the m. AMP is within the internal mandibular fossa (Holliday, 2009), a condition shared in all taxa noted above. *Effigia* displays a clear fossa on the lateral surface of the quadrate, constraining the muscle posteriorly and laterally (Fig. 3C). This muscle is inferred to extend anteriorly into a groove that excavates the dorsomedial surfaces of the angular and prearticular, at the anterior end of which the muscle terminates (Fig. 3C).

m. Adductor Mandibulae Externus Superficialis (m. AMES)

The origin of the m. AMES is based on a combination of the muscle and bone morphology in crocodylians and ancestral lepidosaurs, and the large dorsal temporal fenestra of *Effigia*. In crocodylians, the origin is on the ventrolateral surface of the quadrate whereas the origination in ancestral lepidosaurs is the medial surface of the supratemporal bar (Holliday and Witmer, 2007, Holliday et al., 2013). The origin of the m. AMES in crocodylians is defined by a groove created by a flange of the quadrate following its curve posterodorsally until it nears the mandibular articulation (Holliday et al., 2013). In *Effigia*, the quadrate, by contrast, curves posterodorsally but displays a similar flange and groove to that seen in crocodylians (Fig. 3D) (Nesbitt, 2007). This flange forms a dorsally/anterodorsally orientated channel that is directed posterodorsally towards the lateral border of the supratemporal fenestra. The m. AMES of *Effigia* is therefore suggested to have originated from the lateral border of the supratemporal fenestra and formed additional attachments to the lateral quadrate as it followed this channel towards its mandibular insertion (Fig. 3D).

The insertion includes the flattened dorsal surface of the posterior surangular, immediately anterior to the quadrate articulation (Fig. 3D). This is consistent in the majority of phylogenetic bracketing taxa. The primary medial constraint of the m. AMES is the quadrate, although it is also bordered medially by the m. adductor mandibulae externus medialis. Laterally, the m. AMES is bordered by the squamosal, postorbital, quadratojugal and jugal (Fig. 3D). Between these bones the muscle is able to bulge into the lateral temporal fenestra.

m. Adductor Mandibulae Externus Medialis (m. AMEM)

The m. AMEM likely attached to the posterior margin of the supratemporal fenestra (Fig. 3E). Although no distinct demarcations of where this muscle attached are preserved in *Effigia*, its fenestral morphology closely resembles those of non-avian dinosaurs and lepidosaurs, whose m. AMEM originate from a similar area (Holliday and Witmer, 2007, Holliday, 2009, Lautenschlager, 2013), in contrast to the condition in crocodylians, where the m. AMEM originates from the trapezoidal region of the quadrate (Busbey, 1989).

The mandibular insertion of the m. AMEM is based largely on that of extant crocodylians. Due to the dorsoventrally flattened morphology of crocodylian skulls, their temporal muscles must project further laterally than in birds and dinosaurs in order to reach their mandibular insertion points. The muscles must therefore wrap around the pterygoid wing. As these muscles wrap around the pterygoid, they link to the m. intramandibularis (m. IRA) via the cartilago transiliens. At this location, these muscles terminate and are secondarily inserted onto the mandible via the m. IRA. The *Effigia* skull is not dorsoventrally flattened, but the anteriorly shifted jaw articulation in *Effigia* forces the temporal muscles to extend further anteriorly to attach to the mandible (Fig. 3E). The temporal muscles must therefore wrap around the pterygoid wing (Fig. 3E).

m. Adductor Mandibulae Externus Profundus (m. AMEP)

The m. AMEP originates from the lateral margin of the supratemporal fenestra (Fig. 3F), similar to lepidosaurs and dinosaurs (Holliday and Witmer, 2007, Holliday et al., 2013, Lautenschlager et al., 2014).

The extent of the m. AMEP mandibular insertions are similar to those of the m. AMEM and it is inferred to have inserted into the cartilago transiliens, as in crocodylians. However, as mentioned above, the sesamoid was not included in our FEA models. The m. AMEP is constrained laterally by the m. AMEM and medially by the m. pseudotemporalis superficialis (m. PSTs) (Fig. 3F). As these constraints would have been made entirely of soft tissue and are hypothesised, the muscle group consisting of the m. AMEM, m. AMEP and m. PSTs was reconstructed with a generally cylindrical cross-section, bulging only to the extent allowed by other better constrained myological and osteological features (Fig. 3F).

m. Pseudotemporalis superficialis (m. PSTs)

The m. PSTs most likely attached to the medial surface of the supratemporal fenestra (Fig. 3G). This is inferred from the high degree of similarity in temporal morphology between *Effigia*, lepidosaurs and dinosaurs (Holliday and Witmer, 2007, Holliday, 2009).

The mandibular attachment is similar to those of the m. AMEM and m. AMEP but, as previously explained, the insertion site is the cartilago transiliens and the m. IRA (Fig. 3G).

m. Pseudotemporalis profundus (m. PSTp)

The m. PSTp has not been reconstructed in *Effigia* for two reasons: (i) an ossified epipterygoid – a clear origin site in lepidosaurs and many dinosaurs (Holliday, 2009) – is not preserved in *Effigia* and appears to have been absent; and (ii) *Effigia* does not display any osteological correlates for the

origin of the m. PSTp. The presence of this muscle is debated in crocodylians and, if present, is

likely to be a vestigial structure consisting of a short, thin muscle originating from the lateral bridge

of the laterosphenoid and merging into the dorsal surface of the m. PTd (Holliday et al., 2013). If the

crocodylian condition was present in *Effigia*, the muscle would contribute very little to bite force.

The m. PSTp is also not reconstructed in the comparative ornithomimid cranial FE models (Cuff et

al., 2015). Without osteological correlates, reconstructing the m. PSTp could compromise the FE

model validity.

m. Intramandibularis (m. IRA)

The m. IRA is interpreted to extend from the anteroventral surface of the hypothesised cartilago

transiliens to the dorsomedial surface of the angular and prearticular (Fig. 3H). The mandibular

insertion is marked by an anteroposterior groove at the contact between these two mandibular

elements. Posteriorly, the m. IRA is constrained by the anterior margin of the m. AMP as the latter

muscle also inserts into this groove. Dorsolaterally, the m. IRA is constrained by the surangular (Fig.

3H).

Finite Element Analysis Results

Muscle force estimates

Our jaw muscle reconstructions demonstrate that *Effigia* has the largest total jaw-closing muscle

force among the scaled archosaur models, and exhibits double the total force of the unscaled

Ornithomimus (Table 2). The reconstruction of the m. IRA in *Effigia* but not in the other study

archosaurs somewhat limits discussion of the relative muscle contributions between archosaur taxa.

Nevertheless, some informative comparisons can be made. For example, in *Effigia* the m. PTv

provides the largest contribution to total muscle force, as in *Struthio* and *Alligator*, and it has the

largest force among the m. PTvs of the scaled archosaurs (Table 2). In contrast, the *Effigia* m. PTd produced the lowest force of those among the scaled archosaurs (Table 2). Overall, the *Effigia* adductor mandibulae forces are most similar to those of *Ornithomimus* (Table 2) among the taxa examined.

Feeding simulations

To facilitate comparisons between the archosaurs considered herein, von Mises stress distributions across crania and mandibles are presented for each feeding simulation (Figs. 4–7) and stress values at specific measurement locations across the dorsal and palatal cranial surfaces (Figs. 8–9 respectively) are presented with reference to taxon and rhamphotheca morphology. Results from the jointed *Struthio* model are broadly similar to those of the un-jointed model, with the exception of lcoalized patterns around the palatobasal and otic joints (see Supporting Information and Fig. S3).

During anterior bite simulations, the *Effigia* small-beaked cranium model displays high stress around the following areas: the anterior surfaces of the squamosals; the ventral and posterior surfaces of the quadrates; the ventral and lateral surfaces of the pterygoids; the contact between the premaxilla and nasal (hereafter referred to as the nasal bridge) and the posterior midline of the parietals (Figs. 4A; 8A; 9A). The *Effigia* large-beaked cranium model displays similar distributions of von Mises stress to the small-beaked model although the former displays slightly lower stress around the quadrates, squamosals, parabasisphenoid and posterior midline of the parietals (Figs. 4B; 8A; 9A). The small-beaked mandible model displays very high von Mises stress distributions across most of the surangular and the ventral surface of the angular (Fig. 4C). The large-beaked mandible model displays very similar stress distributions to the small-beaked mandible model except that the rhamphotheca exhibits much lower stress than the equivalent exposed bone in the small beak model (Figs. 4C; 4D). The *Ornithomimus* small-beaked cranium model displays very low stresses across the cranium with only the ventral and lateral surfaces of the quadrates, the lateral surfaces of the

pterygoids and parietals, and the posterolateral surface of the parabasisphenoid showing small areas of intermediate stress (Figs. 4E; 8A; 9A). The *Ornithomimus* large-beaked cranium model displays very similar stress distributions to the small-beaked model except that the large-beaked model displays more restricted areas of elevated stress around the parietals and ventral surfaces of the quadrates (Figs. 4E; 4F; 8A; 9A). *Struthio* displays very high stresses across: most of the pterygoids and palatines; the anterior surface of the parabasisphenoid; the dorsal surfaces of the jugals and the lateral surfaces of the quadrates (Figs. 4G; 8A; 9A). *Alligator* generally exhibits relatively low stresses across the cranium (Figs. 4H; 8A; 9A). Areas of high stress include: the nasal bridge; the ventral surfaces of the maxilla in between the maxillary teeth; the lateral and ventral surfaces of the pterygoids and the medial surface of the quadrates (Fig. 4H).

During middle bite simulations, the *Effigia* small-beaked cranium model displays similar stress distributions to the anterior bite simulation, with high stresses around the squamosals, quadrates, pterygoids, parabasisphenoid and the ventral surface of the parietals (Figs. 5A; 8B; 9B). However, the middle bite simulation exhibits lower stress around the nasal bridge and higher stress on the medial surfaces of the maxillae (Figs. 5A; 8B; 9B). The *Effigia* large-beaked cranium model displays broadly similar stress distributions to the anterior bite simulation (Figs. 5B; 8B; 9B) but the nasal bridge exhibits much lower stresses (Figs. 5B; 8B; 9B). The *Effigia* small-beaked mandible model displays similar distributions of very high stress to that of the anterior bite simulation, although in the former there are larger areas of very high stress in the ventral and dorsal surfaces of the surangular and angular, respectively (Fig. 5C). The *Effigia* large-beaked mandible model displays larger areas of very high stress across the surangular than the anterior bite simulation (Figs. 5C; 5D). For both the small- and large-beaked *Ornithomimus* model middle bite simulations, the stress distributions during middle biting are very similar to those observed in the anterior bite simulations (Figs. 4E; 4F; 5E; 5F; 8A; 9A). Middle bites in *Struthio* generate very similar stress distributions to the anterior bite simulation with the exceptions that the former displays slightly higher stress around the posterior half

of the jugal and slightly lower stress around the nasal bridge and palatal surface of the vomers (Figs. 5G; 8B; 9B). *Alligator* displays low stresses across the cranium during middle biting (Figs. 5H; 8B; 9B). The ventral surfaces of the pterygoids and of the maxillae between the maxillary teeth exhibit slightly lower stress than the anterior bite simulation (Figs. 5H; 8B; 9B).

During posterior bite simulations, the *Effigia* small-beaked cranium model displays higher stress around the dorsal surface of the palatines, the posterior surfaces of the maxillae, the anterior surfaces of the lacrimals and the parabasisphenoid than in the other bite simulations (Figs. 6A; 8C; 9C). The medial surfaces of the maxillae display lower stress (Figs. 6A; 8C; 9C). The *Effigia* large-beaked cranium model displays larger areas of high stresses than the other bite simulations, including in the maxillae, lacrimals and parabasisphenoid (Figs. 6B; 8C; 9C). The *Effigia* small-beaked mandible model displays large areas of very high stress around the surangular and angular, although stresses in the anterior half of the mandible are lower than in the other bite simulations (Fig. 6C). The *Effigia* large-beaked mandible model displays very high von Mises stresses that are similar to the distributions of the small-beaked mandible model posterior bite simulation (Figs. 6C; 6D). For both the small- and large-beaked *Ornithomimus* models, the stress distributions are very similar to those displayed in the anterior and middle bite simulations (Figs. 4E; 4F; 5E; 5F; 6E; 6F; 8; 9). *Struthio* displays very similar stress distributions to the anterior and middle bite simulation (Figs. 4G; 5G; 6G; 8; 9). *Alligator* displays generally little stress across the cranium; the ventral surface of the pterygoids displays the highest stresses, although the lateral surfaces of these bones display less stress than in other bite simulations (Figs. 4H; 5H; 6H; 8C; 9C).

During pecking simulations, the *Effigia* small-beaked cranium model displays very high stresses in most regions, including: areas of the premaxillae not covered by the rhamphotheca; the anterior-most tip of the premaxillae; the nasal bridge; the anterior and medial surfaces of the maxillae; the lateral and dorsal margins of the parabasisphenoid; the anterior surfaces of the squamosals; and dorsal and palatal midline of the parietals (Figs. 7A; 8D; 9D). The *Effigia* large-beaked cranium model has

comparable stress distributions to the small-beaked model. The main difference is that the larger rhamphotheca displays much lower stress levels in the dorsal and palatal surfaces than the equivalent areas of exposed premaxillae and maxillae in the small-beaked model (Figs. 7A; 7B; 8D; 9D). The *Ornithomimus* small-beaked cranium model displays very high von Mises stresses concentrated in: the nasal bridge; the lateral and palatal surfaces of the maxillae; the palatal surface of the vomers and basisphenoid; and the lacrimals and posterior surfaces of the jugals (Figs. 7C; 8D; 9D). The *Ornithomimus* large-beaked cranium model displays somewhat similar stress distributions to the small-beaked model, the main differences being that the larger rhamphotheca displays much lower stress in the large-beaked simulation than the uncovered premaxillae and maxillae in the small-beaked simulation, while the palatal surface of the vomers and dorsal surface of the parietals exhibit higher stresses in the large-beaked model (Figs. 7C; 7D; 8D; 9D). *Struthio* displays several areas of very high stresses across the cranium during pecking, including: the anterior surface of the rhamphotheca; areas of the nasals that are not covered by the rhamphotheca; the anterior halves of the pterygoid; the parasphenoid; the quadratojugal; and the dorsal surfaces of the quadrates (Figs. 7E; 8D; 9D). *Alligator* generally exhibits high stresses across most of the cranium, including: the dorsal and ventral surfaces of the premaxillae, including the nasal bridge; the dorsal surfaces of the maxillae and the ventral surfaces between the maxillary teeth; the parietals; the postorbitals; and the posterior surfaces of the jugals that border the lateral temporal fenestrae (Figs. 7F; 8D; 9D). By contrast, except for the anterior-most tip of the premaxillae, the palatal surface of the *Alligator* cranium exhibits lower stresses than most of the other models (Fig. 9D).

DISCUSSION

Morphological convergence between Effigia *and 'ostrich-like' avemetatarsalians*

The *Effigia* skull reconstruction presented here reaffirms many of the characters cited as morphological convergences between this pseudosuchian taxon and ornithomimid dinosaurs, including enlarged orbits and edentulous jaws (Nesbitt and Norell, 2006, Nesbitt, 2007), and the ventral deflection of the anterior tip of the dentaries. However, we identify four marked differences between *Effigia* and 'ostrich-like' avemetarsalians. (i) The proportions of the *Effigia* rostrum are anteroposteriorly shorter and mediolaterally broader in relation to overall cranium size, especially in comparison to those of ornithomimids. In addition, the ventrally concave margins of the *Effigia* premaxillae enables contact between the entire length of the dorsomedial and dorsolateral surfaces of the premaxillae and dentaries, a unique condition among the taxa studied herein. (ii) In *Effigia*, the external nares are much larger in lateral view than in either of the avemetatarsalian taxa, are located more posteriorly than in *Ornithomimus,* and differ in having a more triangular outline. (iii) In *Effigia* the nasal bridge is slightly concave whereas in *Struthio* it is strongly concave and in *Ornithomimus* it is convex. (iv) The *Effigia* mandible is dorsoventrally taller than that of the other study taxa and is perforated by a huge external mandibular fenestra. Morphological differences like these are often not considered as strongly as morphological similarities when inferring functional convergence between unrelated taxa (Lauder, 1995), which often results in mismatches between hypothesised function based on comparative anatomy alone versus that inferred from quantitative biomechanical modelling (Bestwick et al., 2018).

Biomechanical modelling comparisons

Overall, the muscle reconstructions and FEA outputs indicate that the skull of *Effigia* possesses a unique mosaic of mechanically strong and weak features for its size (around 2 m long total length and 1 m high total height (Nesbitt, 2007); no mass estimates yet available). For example, the large cross-sectional areas of the jaw-closing muscles and relatively high estimates of muscle force, in particular that for the m. PTv, are perhaps unsurprising given the extremely large diameter of the cranial and mandibular fenestrae, which can potentially provide extensive surfaces for muscle

attachment sites (Holliday, 2009, Pêgas et al., 2021). However, the occurrence of high magnitude stresses in the mandibles and nasal bridge highlight these areas as mechanically weak. This indicates that the jaw muscles may not have exerted forces close to the maximum values calculated in this study during feeding.

The impact of reconstructed rhamphotheca morphology on stress distributions is clearly demonstrated, particularly in the anterior biting and pecking simulations. The large-beaked morphology is more effective at dissipating stresses around the premaxillae and nasal bridges (except for areas not covered by the rhamphotheca), and around the dentary. Similar results have been reported from investigations on rhamphotheca function in extant birds and non-avian dinosaurs (Soons et al., 2012, Lautenschlager et al., 2013, Cuff et al., 2015), highlighting functional convergence between beaked avemetatarsalians and Effigia. We do not draw any conclusions on the actual shape and thickness of the *Effigia* rhamphotheca as that was not a primary aim of this study. We simply infer, based on our results, that larger cranial and mandibular rhamphothecae would have enabled better dissipation of high stresses generated during feeding behaviours.

Model comparisons between *Effigia* and *Ornithomimus* are somewhat limited due to the cautious approach taken with respect to muscle reconstructions of the latter (Cuff and Rayfield, 2015). Although we accept that ornithomimids had disproportionately small jaw muscles and weak bites for their size (Cuff and Rayfield, 2015), these conservative estimates likely resulted in the low stress distributions presented here, artificially indicating a strong cranium. Nevertheless, useful comparisons can be made. For example, extremely high stress magnitudes from the pecking simulations in both taxa are unsurprising since their crania do not exhibit functional kinesis and thus lack a mechanism to facilitate more uniform stress distributions (Rayfield, 2007, Curtis et al., 2013, Moazen et al., 2013, Cuff et al., 2015). However, differences in the distribution of high magnitude stresses are important for inferring the relative likelihoods of this behaviour. In *Effigia*, most of the high magnitude stresses are in the anterior third of the cranium and are partially dissipated by the

rhamphotheca in the large-beaked model. In contrast, most of the high magnitude stresses in *Ornithomimus* are in the posterior two-thirds of the cranium. Less stress is therefore dissipated in the *Ornithomimus* large beak model compared to the *Effigia* large beak model. Whereas 340 N is a high upper estimate of external force, it could be argued that pecking was rarely performed, if at all, by either taxon. This is unexpected given the degree of morphological convergence between ornithomimids and palaeognaths (Makovicky et al., 2004, Barrett, 2005), which further exemplifies the notion that shared form does not necessarily reflect similar function in extinct taxa (Fisher, 1985, Thomason, 1995, Ferry-Graham et al., 2002).

The *Struthio* FEA outputs demonstrate the functional differences between it and the extinct edentulous taxa in this study. The location of the adductor muscle origins in the ventral half of the cranium is a derived condition for Aves, due primarily to expansion of the braincase (Holliday and Witmer, 2007, Lautenschlager et al., 2014, Jones et al., 2019), which results in low magnitude stress distributions around the dorsal half of the cranium. The biting simulations also highlight the palate as the main area of structural weakness, reflecting the fact that *Struthio* does not use orthal biting motions to procure or process food items. The relatively large pterygoideus muscles instead serve to mitigate mandibular retraction from the adductors (Gussekloo and Bout, 2005a). *Struthio* feeds primarily by plucking small grasses, flowers, leaves and fruits from the ground or low-lying plants, and throwing these items to the back of the jaws to be swallowed (Williams et al., 1993, Milton et al., 1994). This is informally termed 'catch-and-throw behaviour' (Zweers et al., 1994). Much of the external force associated with feeding is therefore focused around the anterior-most part of the rostrum as the bill regularly contacts the ground whilst plucking, while the palate is subjected to much lower forces. Our pecking simulations better replicate this behaviour, so it is unsurprising that *Struthio* exhibits generally low magnitude stress distributions in our simulations. It should be noted that stresses in the nasal bridges are artificially high due to the removal of sutural bone from this area, which is known to mitigate stress (Cuff et al., 2015). Nevertheless, adaptations for pecking

behaviours appear to be unique to *Struthio* among our study taxa and casts doubt on distantly related 'ostrich-like' archosaurs exhibiting identical suites of functional behaviours.

The *Alligator* FEA outputs demonstrate clear morphological and functional differences between it and sEffigia. The dorsoventrally flattened skulls of extant crocodylians are widely regarded as adaptations for semi-aquatic life (Iordansky, 1973, McHenry et al., 2006, Grigg and Kirshner, 2015), and the extended pterygoid flanges provide enlarged attachment sites for the adductor muscles (Holliday et al., 2013, 2015, Sellers et al., 2017). Crocodylians exhibit the largest bite forces among extant tetrapods (Erickson et al., 2003, 2012), and our results are consistent with previous biomechanical studies showing that crocodylian skulls are adapted to resist high feeding-generated forces (McHenry et al., 2006, Walmsley et al., 2013, Montefeltro et al., 2020). This enables extant crocodylians to occupy durophagous and/or apex predator niches (see Somaweera et al. (2020) for a review). The anterior bite simulation highlights the nasal bridge as mechanically weak in *Alligator*, as in *Effigia*, although crocodylians mitigate stresses in this area by using unilateral bites to seize prey (Erickson et al., 2012, Montefeltro et al., 2020), and crushing items in the posterior region of the jaws before swallowing (Cleuren and De Vree, 2000, Labarre et al., 2017). The high magnitude stresses from the pecking simulation are expected since crocodylian skulls are akinetic (Sellers et al., 2017) and so possess no morphological adaptations to dissipate these stresses, suggesting that such a feeding behaviour is not possible. The functional morphology of *Alligator* reflects adaptations for a very different lifestyle from that proposed for *Effigia*.

Possible feeding behaviours of Effigia

The morphological and functional evidence presented here and in previous studies suggests that *Effigia* was most likely adapted for herbivory (Nesbitt and Norell, 2006, Nesbitt, 2007, Zanno and Makovicky, 2011, Lautenschlager et al., 2016, Button and Zanno, 2020). Consequently, *further* questions relating to the ecology and functional morphology of Effigia concern the types of plant

material consumed and the feeding behaviours used to acquire them. As previously mentioned, pecking behaviourwas possible but likely limited. The mechanically weak mandible probably restricted food procurement and processing to the anterior portion of the jaws. It is unlikely that *Effigia* crushed hard food objects with its rostrum due to the weak nasal bridge and the low mechanical advantage when processing foods further away from the jaw musculature and craniomandibular joint (Kammerer et al., 2006, Santana and Dumont, 2009, Santana et al., 2010, Erickson et al., 2012), although the swallowing of small seeds that require no processing cannot be excluded.

An alternative feeding behaviour involves occlusion between the surfaces of the dorsoventrally concave rostrum and ventrally deflected anterior mandible. This would have enabled a shear-like cropping motion as the bite point moves anteriorly along the ventromedial and dorsolateral surfaces of the premaxillae and dentaries during jaw closure. Cropping behaviours generate less stress on the jaws than crushing behaviours (Jasinoski et al., 2009), which may have facilitated consumption of relatively fibrous plant matter. This behaviour would be more likely if the rhamphothecae were large, as their presence would dissipate stresses along more of the occlusal surfaces of the premaxillae and dentaries. However, the overall weakness of the mandible suggests that if cropping was the main feeding behaviour, *Effigia* would likely prioritise soft plants or softer plant parts. Further testing of the speed of *Effigia* jaw closure could reveal more information on the efficiency of cropping behaviours.

Other feeding behaviours associated with herbivory could have been used by *Effigia* but require further investigation. For example, the catch-and-throw behaviour used by extant palaeognaths (Zweers et al., 1994, Gussekloo and Bout, 2005b, Dzemski and Christian, 2007) is theoretically possible as a ventrally deflected anterior portion of the mandible provides a larger, scoop-like surface for procuring items from the ground. However, palaeognaths have highly flexible cervical columns that enable the head to reach down and pluck items from the ground (Dzemski and Christian, 2007),

and extrapolating neck flexibility to extinct taxa requiresa thorough understanding of the soft tissues in the neck (Cobley et al., 2013). The current lack of rigorous cervical muscle reconstructions in *Effigia* therefore limits our understanding of the potential role of the neck in feeding behaviour.

Another possible behaviour involves stripping plant material from branches by recruiting the neck muscles to pull the skull posteriorly while the jaws are closed. This behaviour is used by some extant birds that possess dorsoventrally tall mandibles, such as vultures (Accipitridae) to remove flesh from carcasses (Hertel, 1995). Moreover, pull-back behaviours have been suggested for herbivorous therizinosaurid dinosaurs, as the simultaneous use of the jaw and anterior neck muscles subjects the cranium to lower stresses than the jaw muscles acting alone (Lautenschlager et al., 2013). However, poor preservation of the *Effigia* braincase (Nesbitt, 2007) prevents accurate reconstructions of the craniocervical joint and musculature at present.

Functional and ecological convergence between pseudosuchians and avemetatarsalians

Our biomechanical modelling demonstrates that the functional morphology of *Effigia* is unlike that of either 'ostrich-like' avemetatarsalians or crocodylians. This study thereby emphasises the finding that the repeated evolution of similar bauplans in distantly related taxa does not automatically imply functional and ecological convergence, and that quantitative biomechanical modelling techniques should be used where possible to test such hypotheses (Lauder, 1995, Lautenschlager et al., 2016, Bestwick et al., 2018). Greater consideration of the environmental conditions and evolutionary histories of morphologically convergent taxa are also needed in order to understand the likelihood of ecological and functional convergence. For example, ostriches are opportunistic herbivores that feed almost exclusively on low-lying angiosperms such as grasses and shrubs (Williams et al., 1993), plants that were not present in the Triassic. Furthermore, stress distribution differences between our study pseudosuchians *probably* reflect the ~245 million years of independent evolutionary history between *Effigia* and *Alligator* (Brusatte et al., 2010, Nesbitt, 2011)*,* with crocodylians undergoing

marked morphological changes for adaptation to inhabit aquatic habitats (Iordansky, 1973, Grigg and Kirshner, 2015). However, it is possible that some phylogenetic signal would have been present when considering more closely related pseudosuchian clades. Phylogenetic relationships within Poposauroidea are relatively well resolved, with its constituent lineages exhibiting remarkably high morphological disparity (Butler et al., 2011, Nesbitt, 2011, Schachner et al., 2019). The sister taxon of the gracile, bipedal and edentulous shuvosaurids is *Lotosaurus*, a taxon with edentulous jaws and large external nares, which is a robust quadruped with a distinct dorsal sail (Zhang, 1975, Butler et al., 2011, Nesbitt, 2011). The next most inclusive taxon is *Poposaurus*, a gracile biped that shares many morphological similarities with early diverging theropod dinosaurs, such as recurved teeth (Mehl, 1915, Nesbitt, 2011, Parker and Nesbitt, 2013). The order in which poposauroid bauplans were assembled and/or modified is currently unclear (Nesbitt, 2011). This indicates that the anatomy and functional morphology of shuvosaurids is more likely the result of shared ancestry and rapid experimentation (Stocker et al., 2016), rather than similar selection pressures acting on both shuvosaurids and ostrich-like avemetatarsalians.

Our results, in tandem with morphological data and functional investigations of other contemporaneous archosaurs suggest that *Effigia*, and by extension other shuvosaurids, performed unique functional and ecological roles within Late Triassic terrestrial ecosystems and were likely selective herbivores that fed primarily by browsing on soft plants/softer plant parts (Fig. 10). While there is no direct evidence on the plants that might have formed shuvosaurid diets, new growth from extant plants is structurally weak due to low silica content (Massey et al., 2007). It is therefore possible that shuvosaurids prioritised feeding on new plant growth. In the absence of detailed information on neck function, shuvosaurids are likely to have fed within 1–2 metres of ground level (Fig. 10; upper estimate based on incomplete *Sillosuchus* material (Nesbitt, 2011)). This contrasts with some contemporaneous aetosaurs such as *Stagonolepis* and *Typothorax*, whose robust limbs, shovel-shaped rostra and high bite forces suggest diets of tough vegetation located underground

(Desojo and Vizcaíno, 2009, Heckert et al., 2010, Desojo et al., 2013). In addition, biomechanical studies of sauropodomorphs suggest they were generalised herbivores, perhaps exhibiting facultative faunivory (Button et al., 2016, Lautenschlager et al., 2016), and likely fed on taller plants based on their larger body size (Galton, 1985, Galton and Upchurch, 2004). Overall, our results suggest that Late Triassic food webs were more functionally diverse and complex than previously appreciated.

CONCLUSIONS

Our study shows that despite the high degree of overall similarity between the crania of *Effigia*, ornithomimids and extant palaeognaths, the functional morphology of this pseudosuchian differed substantially from that of 'ostrich-like' archosaurs. *Effigia* possesses an unusual mosaic of mechanical features that most likely restricted habitual feeding functions to the anterior portion of its jaws. A shearing motion between the anterior parts of the mandible and rostrum during orthal closure would have generated the least stress under our modelling conditions. Our analyses indicate that this pseudosuchian was most likely herbivorous and probably a specialist that cropped the softer parts of plants during feeding. Our study indicates that although 'ostrich-like' bauplans evolved independently at least three times in archosaurs over a 230-million-year period, different functional behaviours were employed by each lineage. This study showcases the importance of rigorous, quantitative and repeatable techniques like FEA to deduce whether morphological convergence between unrelated taxa confers functional convergence or not, as well as providing the potential to uncover more detailed information on their specific ecological roles. The inferred functional morphology of *Effigia* indicates that it (and other closely related and morphologically similar shuvosaurids) performed a unique ecological role within Late Triassic food webs. This not only increases our understanding of Late Triassic terrestrial ecosystems, but also emphasises the overall ecological diversity and success of the pseudosuchian archosaurs at this time.

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Fig. 1. Labelled diagrams of the retrodeformed *Effigia okeeffeae* skull. (A) Cranium lateral view. (B) Cranium dorsal view. (C) Cranium palatal view. (D) Mandible lateral view. (E) Mandible dorsal view. Abbreviations: af, antorbital fenestra; an, angular; ar, articular bt, basal tuber; cp; cultiform process; d, dentary; ds, dentary shelf; ect, ectopterygoid; f, frontal; fa, foramen; j, jugal; l, lacrimal; ls, laterosphenoid; m, maxilla; mf, mandibular fenestra; mpr; median pharyngeal recess; na, naris; ns, nasal; o, orbit; p, parietal; pal, palatine; pbs, parabasisphenoid; pf, prefrontal; pm, premaxilla; po, postorbital; pre, prearticular; pt, pterygoid; q, quadrate; qj, quadratojugal; s, splenial; sq, squamosal; sr, surangular; stf, supra-temporal fenestra; v, vomer. All models to scale.

Fig. 2. Different rhamphotheca morphologies for *Effigia okeeffeae* (A–H) and *Ornithomimus edmontonicus* (I–L) used in finite element analysis. (A) Small-beaked *Effigia* cranium, oblique view. (B) Small-beaked *Effigia* cranium, palatal view. (C) Large-beaked *Effigia* cranium, oblique view. (D) Large-beaked *Effigia* cranium, palatal view. (E) Small-beaked *Effigia* mandible, oblique view. (F) Small-beaked *Effigia* mandible, dorsal view. (G) Large-beaked *Effigia* mandible, oblique view. (H) Large-beaked *Effigia* mandible, dorsal view. (I) Small-beaked *Ornithomimus* cranium, oblique view. (J) Small-beaked *Ornithomimus* cranium, palatal view. (K) Large-beaked *Ornithomimus* cranium, oblique view. (L) Large-beaked *Ornithomimus* cranium, palatal view. Models not to scale.

Fig. 3. Reconstructed adductor musculature of *Effigia okeeffeae* shown in right lateral view. (A) m. pterygoideus dorsalis. (B) m. pterygoideus ventralis. (C) m. adductor mandibulae posterior. (D) m. adductor mandibulae externus superficialis. (E) m. adductor mandibulae externus medialis. (**F**) m. adductor mandibulae externus profundus. (G) m. pseudotemporalis superficialis. (H) m. intramandibularis. The mandibular insertions of the muscles in parts (E–H) are reconstructed as attaching to a cartilaginous sesamoid, the cartilago transiliens. The sesamoid was included in the muscle reconstructions but excluded from finite element analyses due to the unknown material properties of cartilaginous structures.

Fig. 4. Comparisons of von Mises stress distribution of study taxa subjected to bilateral anterior bite simulations. (A) Small-beaked *Effigia okeeffeae* cranium. (B) Large-beaked *Effigia* cranium. (C) Small-beaked *Effigia* mandible. (D) Large-beaked *Effigia* mandible. (E) Small-beaked *Ornithomimus edmontonicus* cranium. (F) Large-beaked *Ornithomimus* cranium. (G) *Struthio camelus* cranium. (H) *Alligator mississippiensis* cranium. Bite positions indicated by red arrows (only one side of jaw is indicated for clarity). Models were all scaled to the same surface area, and muscle loads scaled accordingly, for analysis. Scaling information can be found in Table 1. All models are shown in oblique view.

Fig. 5. Comparisons of von Mises stress distribution of study taxa subjected to bilateral middle bite simulations. (A) Small-beaked *Effigia okeeffeae* cranium. (B) Large-beaked *Effigia* cranium. (C) Small-beaked *Effigia* mandible. (D) Large-beaked *Effigia* mandible. (E) Small-beaked *Ornithomimus edmontonicus* cranium. (F) Large-beaked *Ornithomimus* cranium. (G) *Struthio camelus* cranium. (H) *Alligator mississippiensis* cranium. Bite positions indicated by red arrows (only one side of jaw is indicated for clarity). Models were all scaled to the same surface area, and muscle loads scaled accordingly, for analysis. Scaling information can be found in Table 1. All models are shown in oblique view.

Fig. 6. Comparisons of von Mises stress distributions of study taxa subjected to bilateral posterior bite simulations. (A) Small-beaked *Effigia okeeffeae* cranium. (B) Large-beaked *Effigia* cranium. (C) Small-beaked *Effigia* mandible. (D) Large-beaked *Effigia* mandible. (E) Small-beaked *Ornithomimus edmontonicus* cranium. (F) Large-beaked *Ornithomimus* cranium. (G) *Struthio camelus* cranium. (H) *Alligator mississippiensis* cranium. Bite positions indicated by red arrows (only one side of jaw is indicated for clarity). Models were all scaled to the same surface area, and muscle loads scaled accordingly, for analysis. Scaling information can be found in Table 1. All models are shown in oblique view.

Fig. 7. Comparisons of von Mises stress distributions of study taxa subjected to pecking simulations. (A) Small-beaked *Effigia okeeffeae* cranium. (B) Large-beaked *Effigia* cranium. (C) Small-beaked *Ornithomimus*

edmontonicus cranium. (D) Large-beaked *Ornithomimus* cranium. (E) *Struthio camelus* cranium. (F) *Alligator mississippiensis* cranium. The location and direction of the loading force is indicated by the red arrows. Note the different scaling for stress compared to the biting simulations (Figs. 4–6). Models were all scaled to the same surface area for analysis. Scaling information can be found in Table 1. All models are shown in oblique view.

Fig. 8. von Mises stress magnitudes of the of the study archosaur crania at ten measurement locations along their dorsal surfaces for four different feeding simulations. (A) Bilateral anterior bite simulation values. (B) Bilateral middle bite simulation values. (C) Bilateral posterior bite simulation values. (D) Pecking simulation values. Note the different y-axis scales between (A–C) and (D). Measurement point locations along each cranium can be found in Fig. S2.

Fig. 9. von Mises stress magnitudes of the of the study archosaur crania at ten measurement locations along their palatal surfaces for four different feeding simulations. (A) Bilateral anterior bite simulation values. (B) Bilateral middle bite simulation values. (C) Bilateral posterior bite simulation values. (D) Pecking simulation values. Note the different y-axis scales between (A–C) and (D). Measurement point locations along each cranium can be found in Fig. S2.

Fig. 10. Life reconstruction of *Effigia okeeffeae* based on the skull redescription and results of the functional models. *Effigia* is depicted feeding on softer plant material, represented by the fern-like *Cladophlebis* from the Chinle Formation (Parker & Martz 2010). Created by Mark Witton.

Fig. S1. Reconstructed cranial morphology of *Effigia okeeffeae*. (A) Photograph of the CT scanned specimen AMNH FR 30587 in left lateral view adapted from Nesbitt (2007). (B) Digital model of the segmented specimen (lacking mandibles). (C) Cranium with re-aligned elements and post-mortem degradation features,

such as cracks and holes, corrected. (D) Restored cranial morphology used for finite element models in this study.

Fig. S2. Location of measurement points along the dorsal and palatal cranium surfaces of the study archosaurs. (A) Small-beaked *Effigia okeeffeae*, dorsal view. (B) Small-beaked *Effigia*, palatal view. (C) Large-beaked *Effigia*, dorsal view. (D) Large-beaked *Effigia*, palatal view. (E) Small-beaked *Ornithomimus edmontonicus*, dorsal view. (F) Small-beaked *Ornithomimus*, palatal view. (G) Large-beaked *Ornithomimus*, dorsal view. (H) Large-beaked *Ornithomimus*, palatal view. (I) *Struthio camelus*, dorsal view. (J) *Struthio*, palatal view. (K) *Alligator mississippiensis*, dorsal view. (L) *Alligator*, palatal view. Models not to scale.

Fig. S3. von Mises stress distributions (A–D) and point magnitudes (E–F) of *Struthio* with modelled palatobasal and otic joints. (A) Bilateral anterior bite simulation. (B) Bilateral middle bite simulation. (C) Bilateral posterior bite simulation. (D) Pecking simulation. Note the different von Mises scales between (A–C) and (D). (E) Stress magnitudes along the dorsal and palatal cranium surfaces from the anterior, middle and posterior bite simulations. (F) Stress magnitudes along the dorsal and palatal cranium surfaces from the pecking simulation. The location and direction of the loading force is indicated by the red arrows. Note the different y-axis scales between (E) and (F) for consistency with Figs. 8 and 9. Dorsal and palatal measurement locations are the same as the non-jointed *Struthio* model (Fig. S2).