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The diet of early birds based on modern and fossil evidence and a new framework for its reconstruction

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ABSTRACT

Birds are some of the most diverse organisms on Earth, with species inhabiting a wide variety of niches across every major biome. As such, birds are vital to our understanding of modern ecosystems. Unfortunately, our understanding of the evolutionary history of modern ecosystems is hampered by knowledge gaps in the origin of modern bird diversity and ecosystem ecology. A crucial part of addressing these shortcomings is improving our understanding of the earliest birds, the non-avian avialans (i.e. non-crown birds), particularly of their diet. The diet of non-avian avialans has been a matter of debate, in large part because of the ambiguous qualitative approaches that have been used to reconstruct it. Here we review methods for determining diet in modern and fossil avians (i.e. crown birds) as well as non-avian theropods, and comment on their usefulness when applied to non-avian avialans. We use this to propose a set of comparable, quantitative approaches to ascertain fossil bird diet and on this basis provide a consensus of what we currently know about fossil bird diet. While no single approach can precisely predict diet in birds, each can exclude some diets and narrow the dietary possibilities. We recommend combining (*i*) dental microwear, (*ii*) landmark-based muscular reconstruction, (*iii*) stable isotope geochemistry, (*iv*) body mass estimations, (*v*) traditional and/or geometric morphometric analysis, (*vi*) lever modelling, and (*vii*) finite element analysis to reconstruct fossil bird diet accurately. Our review provides specific methodologies to implement each approach and discusses complications future researchers should keep in mind. We note that current forms of assessment of dental mesowear, skull traditional morphometrics, geometric morphometrics, and certain stable isotope systems have yet to be proven effective at discerning fossil bird diet. On this basis we report the current state of knowledge of non-avian avialan diet which remains very incomplete. The ancestral dietary condition in non-avian avialans remains unclear due to scarce data and contradictory evidence in *Archaeopteryx*. Among early non-avian pygostylians, *Confuciusornis* has finite element analysis and mechanical advantage evidence pointing to herbivory, whilst *Sapeornis* only has mechanical advantage evidence indicating granivory, agreeing with fossilised ingested material known for this taxon. The enantiornithine ornithothoracine *Shenqiornis* has mechanical advantage and pedal morphometric evidence pointing to carnivory. In the hongshanornithid ornithuromorph *Hongshanornis* only mechanical advantage evidence indicates granivory, but this agrees with evidence of gastrolith ingestion in this taxon. Mechanical advantage and ingested fish support carnivory in the songlingornithid ornithuromorph *Yanornis*. Due to the sparsity of robust dietary assignments, no clear trends in non-avian avialan dietary evolution have yet emerged. Dietary diversity seems to increase through time, but this is a preservational bias associated with a predominance of data from the Early Cretaceous Jehol Lagerstätte. With this new framework and our synthesis of the current knowledge of non-avian avialan diet, we expect dietary knowledge and evolutionary trends to become much clearer in the coming years, especially as fossils from other locations and climates are found. This will allow for a deeper and more robust understanding of the role birds played in Mesozoic ecosystems and how this developed into their pivotal role in modern ecosystems.

Key words: Avialae, birds, dental microwear, diet, theropods, dinosaurs, finite element analysis, fossil, mechanical advantage, morphometrics, stable isotopes

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I. INTRODUCTION

(1) Modern and ancient bird diet

Living birds [Aves: used herein to refer to crown birds (see Pittman *et al*., 2020*a*)] have been studied more than almost any other organisms, and are at the forefront of human efforts to understand global ecology (Tietze, 2018). In large part this is because birds display some of the most varied diets in the animal kingdom. Many people are familiar with their neighbourhood songbirds which feed on worms and seeds. However, birds are able to thrive in aquatic, terrestrial, and aerial environments around the world (Rico-Guevara *et al*., 2019) and consume nearly every source of nutrition imaginable therein. Rodents, fruit, fish, leaves, plankton, blood, beeswax, and organic mud are just a few of the food sources living birds may utilise (Lopes *et al*., 2016). This rich diversity has also evolved in incredible ways. The ancestral avian has been proposed as an aquatic predator (Brusatte, O'Connor & Jarvis, 2015), granivore (Larson, Brown & Evans, 2016), or omnivore (Felice & Goswami, 2018) with myriad dietary radiations occurring during avian evolution including at least three origins of nectarivory, seven origins of aquatic predation, and 18 origins of frugivory (Felice *et al*., 2019*a*).

Dietary diversification outside of Aves among the non-avian avialan birds [Avialae: used herein to refer to crown birds plus relatives as distant as *Archaeopteryx* (Gauthier, 1986; and see Pittman *et al*., 2020*a*)] is much less well understood. Two species of early-diverging avialans preserve evidence of granivory, a single enantiornithine preserves an ingested invertebrate, and 10 ornithuromorph species preserve evidence of granivory or piscivory (O'Connor, 2019). Beyond these, the diet of non-avian avialans is virtually unknown, and accordingly an ancestral avialan diet has not been proposed. It remains unclear if the vast dietary breath of living birds is unique or has deeper roots in the avialan tree, and if birds played the same unique ecological roles during the Late Jurassic and Cretaceous periods as they do in extant ecosystems.

(2) Diet and morphology in Aves

While avian diet itself has been well reported, few correlations between diet and morphology are known in living birds, and fewer still from more than a single quantitative study. We provide a convenient glossary for the various descriptors of diet used herein in Table 1. Invertivorous birds possess skulls with a low mechanical advantage (Corbin, Lowenberger & Gray, 2015; Olsen, 2017), while probing feeders [e.g. sandpipers (Pettigrew & Frost, 1985), ibises (Frederick & Bildstein, 1992), kiwis (Cunningham *et al.*, 2013), and some songbirds (Lockie, 1956; Adamík & Kornan, 2004)] have particularly elongate rostra (Barbosa & Moreno, 1999; Kulemeyer *et al.*, 2009). Granivorous birds tend to have ventrodorsally tall beaks (van der Meij, 2004; Soons *et al.*, 2010) exhibiting high mechanical advantage (Corbin *et al.*, 2015; Navalón *et al.*, 2018*a*) and a high strength (Soons *et al.*, 2010, 2015) [i.e. low peak Von Mises stresses when loaded (Dumont, Grosse & Slater, 2009)]. Raptorial birds possess talons that, on average, are hypertrophied at digit I (Fowler, Freedman & Scannella, 2009; Csermely, Rossi & Nasi, 2012) and are more recurved (Csermely & Rossi, 2006; Tsang *et al.*, 2019) than in non-raptorial birds. Among raptors, specialists in hunting other birds have longer toes (Csermely & Rossi, 2006; Tsang *et al.*, 2019) and a wider skull (Hertel, 1995; Sun *et al.*, 2018) [presumably for housing a larger cerebellum, the part of the brain that processes spatial orientation (Sun *et al.*, 2018)] while those that specialise in hunting fish tend to have all four talons enlarged (Einoder & Richardson, 2007; Fowler *et al.*, 2009). Scavenging raptors appear to be the most morphologically diagnostic group, characterised by large body size (Einoder & Richardson, 2007; Fowler *et al.*, 2009) and a narrow, shallow (Bright *et al.*, 2016; Navalón *et al.*, 2018*a*; Sun *et al.*, 2018) and long (Hertel, 1995; Kulemeyer *et al.*, 2009; Si *et al.*, 2015; Sun *et al.*, 2018; Pecsics *et al.*, 2019) skull with a highly recurved rostrum (Hertel, 1995; Kulemeyer *et al.*, 2009).

Beyond these, diet/morphology correlations are at best known from a single study [e.g. small body size as indicative of nectarivory (Pigot *et al.*, 2020)] and at worst contradicted among studies [e.g. bill curvature has been positively (Kulemeyer *et al.*, 2009), negatively (Navalón *et al.*, 2018*a*), or not (Barbosa & Moreno, 1999) correlated with probing behaviour]. Characters known from a single study may be awaiting corroboration by future studies, but contradictions among studies suggest that we do not yet understand some aspects of avian diet/morphology relations fully. If living birds are to be used as proxies for fossil birds (i.e. bird taxa known only from fossils), then further work on understanding what they eat and why is imperative.

(3) Techniques for determining diet

When an ornithologist wants to know what a bird eats, the most straightforward technique is to directly observe them feeding and record what they ate [reviewed in Rosenberg & Cooper (1990) alongside most of the following methods]. Proxies for direct dietary observation include remote observation (detailed in Sullivan *et al.*, 2009; Zhang *et al.*, 2019) and examination of faeces [critiqued in Carlisle & Holberton (2006); augmented in Jarman *et al.* (2013); detailed in Ralph, Nagata & Ralph (1985)], pellets (critiqued in Votier *et al.*, 2001), uneaten prey remains near the nest (critiqued in Tornberg & Reif, 2007), or stomach contents [from dead birds (reviewed in Duffy & Jackson, 1986), those

Table 1. Glossary of dietary categories used in this review. Note that these are general classifications that may or may not be mutually exclusive and may be employed differently by different studies. A reference providing additional detail for each classification is provided. The prefix 'hyper-' is occasionally applied to diet categories, indicating a particularly high percentage of the animal's diet consists of that food source

Term	Definition	Source
Carnivorous	Energy acquired primarily by consuming animal tissue.	Ullrey (2018)
Durophagous	Consuming hard parts of organisms, or otherwise breaking their hard parts before consumption.	Crofts & Summers (2014)
Frugivorous	Consuming the nutritive tissue ('flesh') of fruits.	Jordano (2000)
Granivorous	Consuming plant seeds, before or after dispersal.	Hulme & Benkman (2002)
Herbivorous	Energy acquired primarily by consuming plant tissue.	Karban & Agrawal (2002)
Invertivorous	Consuming invertebrate animal tissue.	Thomas (2014)
Molliphagous	Consuming food that is soft, i.e. requiring relatively little energy to fracture.	Present study
Nectarivorous	Consuming nectar, a sugary liquid exuded by flowers.	Nicolson & Fleming (2014)
Omnivorous	Consuming a variety of foods, with no one source providing the majority of energy.	Thompson *et al.* (2007)
Osteophagous	Consuming bone or bone marrow.	Wroe *et al.* (2005)
Piscivorous	Consuming 'fish' (non-tetrapod gnathostome) tissue.	Eklöv & Diehl (1994)
Predatory	Consuming tissue of animals killed by the consumer.	Taylor (2013)
Raptorial	Predation in which the pes plays a major role in killing and/or restraining the prey.	Fowler *et al.* (2009)
Scavenging	Consuming tissue of animals not killed by the consumer.	Turner *et al.* (2017)
Vertivorous	Consuming vertebrate animal tissue.	Garrard *et al.* (2012)

captured and forced to regurgitate (critiqued in Gales, 1987; Carlisle & Holberton, 2006), or collected natural non-pellet regurgitations (detailed in Oro *et al.*, 1997)]. These 'direct evidence' data provide an unambiguous association between an organism and a certain diet. Unfortunately, these techniques require an animal to be alive or recently deceased, and the closest fossil equivalents to these forms of direct evidence, preserved meals, rarely fossilise and are prone to a variety of preservational biases. This makes them insufficient to reconstruct the diet of non-avian avialans without other lines of evidence. Chemical analysis of stable isotopes in the soft tissues of living birds is commonly used to reconstruct trophic webs (detailed in Kloskowski, Trembaczowski & Filipiuk, 2019), with similar methods applied to bioapatite and amino acids preserved in bird fossils (see Section III.2). However, the wide variety of factors affecting stable isotope ratios make them more ambiguous lines of evidence.

While not used to determine diet *per se*, several physical approaches have been used to study extant birds to explain observed dietary trends. These approaches, in turn, have been applied to extinct organisms with unknown diets. Body mass has recently been found to predict large amounts of dietary variance in extant birds (Navalón *et al.*, 2018*a*; Pigot *et al.*, 2020). Body mass estimation, then, may represent a key metric that has been relatively unexplored in fossil birds. With that said, most past studies have adopted 'physical approaches', those grounded in morphology and/or mechanics, to the study of avian diet. Dietary studies tend to focus on the skull, the most important tool for feeding in living birds (Rico-Guevara *et al.*, 2019), and the pes, their most important tool for manipulation of food prior to feeding (Clark, 1973; Sustaita *et al.*, 2013) and the primary tool for killing prey in raptorial birds (Fowler *et al.*, 2009). Traditional (detailed in Hertel, 1994) and geometric (detailed in Bright *et al.*, 2016) morphometrics both seek to quantify the shape of body parts, under the assumption that form will reflect function. Other studies investigate functional capacity directly. Lever model simplifications of skulls (detailed in Corbin *et al.*, 2015) describe the efficiency of force production and speed of the jaw, while finite element analysis (detailed in Soons *et al.*, 2010) models the response of body parts to loading in order to compare their relative strength among organisms. Each of these techniques have been applied to living birds and non-avialan theropods, but only the two forms of morphometrics have included non-avian avialan taxa. While physical approaches have some of the broadest applications to fossil organisms, they also introduce a variety of complications (see Section VI.4).

There are also a select few lines of direct evidence that have been applied to fossil taxa but never to living or fossil birds. Dental wear analysis is commonly applied to living and fossil mammals (Green & Croft, 2018) with a recent application in theropods (Bestwick *et al.*, 2018; Torices *et al.*, 2018). While inapplicable to avians in its current form because they are all toothless, it is of potential value in the study of toothed non-avian avialans. Neck musculature has been proposed to inform food disassembly behaviours in non-avialan theropods (Snively & Russell, 2007*b*), although the study of food disassembly in living birds has focused on the head and pes exclusively (Sustaita, 2008; Fowler *et al.*, 2009; Sustaita *et al.*, 2019). Additionally, ultrastructure of dentine (Brink *et al.*, 2016) and enamel (Li *et al.*, 2020) have been put forth as dietary proxies applicable across Dinosauria. Each of these techniques is also addressed in this review due to their potential application in fossil birds.

(4) Fossil birds and the focus of this review

Avialans appear in the fossil record as early as the Late Jurassic, and by the Middle Cretaceous inhabited tropical to polar latitudes and were present on every continent (Pittman *et al.*, 2020*b*). While most Mesozoic birds are considered to fall somewhere along a continuum of arboreal and terrestrial lifestyles (Mayr, 2017; Serrano *et al.*, 2017; Cobb & Sellers, 2020), *Ichthyornis* and Hesperornithiformes are undisputedly aquatic (Rees & Lindgren, 2005; Hinić-Frlog & Motani, 2010). Enantiornithes are the most widespread and speciose Mesozoic birds. They comprise roughly 60% of all non-avian avialan genera followed by non-avian ornithuromorph avialans (~25%) with the remainder made up by *Archaeopteryx*, Jeholornithiformes, Confuciusornithidae, Jinguofortisidae, and *incertae sedis* taxa [see Table 5 in Pittman *et al.* (2020*b*); uncertainty based on their notes of taxa possibly referable to non-avialan clades]. Anchiornithinae and Scansoriopterygidae have been placed in Avialae previously, but their inclusion is controversial (Pittman *et al.*, 2020*a*). This review will err on the side of inclusivity and discuss these two clades as 'avialans' in addition to well-established Avialae [although personally we only see anchiornithines as avialans (see Pittman *et al.*, 2020*a*)].

A variety of dietary habits have been proposed for non-avian avialans. The vast majority are based on qualitative methodologies vulnerable to individual interpretation (Thulborn & Hamley, 1985; Zinoviev, 2009; Martyniuk, 2012; O'Connor *et al.*, 2013*b*; Dumont *et al.*, 2016) or a few preserved meals which provide a definite but limited glimpse of diet (O'Connor, 2019; O'Connor & Zhou, 2019). More comparable, quantitative approaches to fossil avialan diet have been made (Navalón, 2014; Wang *et al.*, 2014*b*; Attard *et al.*, 2016) but these are few and far between. We seek in this review to establish techniques that have proved effective at discriminating diet in living birds as well as fossil dinosaurs and to construct a framework for studying non-avian avialan diet. Parts of this framework not relying on teeth can also be applied to fossil avians, which have a narrower and better-constrained extant phylogenetic bracket (Witmer, 1995). On this basis, we then present a consensus of what we currently know about non-avian avialan diet and how this can be improved moving forward. With this, future studies could make strides both in understanding Mesozoic ecosystems and in tracing the evolution of one of the most important groups of living organisms.

II. DIRECT EVIDENCE

(1) Preserved meals

(*a*) Introduction

Preserved meals may take the form of food preserved in the digestive system (consumulites) or as closely associated excretions (coprolites) or egestions (regurgitilites) (all *sensu* Hunt *et al.*, 2012). Identification of consumulites may be problematic as accessing them often requires destroying the overlying remains, and misdiagnosis of ingested material may lead to erroneous dietary inferences (e.g. Nesbitt *et al.*, 2006). Coprolites, while ostensibly simpler to analyse, are often taxonomically indeterminate (e.g. Chin *et al.*, 1998; Hollocher *et al.*, 2001; Hunt *et al.*, 2012; Qvarnström *et al.*, 2019) and of questionable association with surrounding body fossils (e.g. James & Burney, 1997; Wood *et al.*, 2008; Hunt *et al.*, 2012; Wang, Zhou & Sullivan, 2016*a*). Regurgitilites are sparse in the fossil record, possibly due to collection biases and/or misdiagnosis as coprolites (Myhrvold, 2012), but otherwise provide similar information to coprolites with similar referral issues. Hunt *et al.* (2012) provide a detailed review of the study of coprolites, and Myhrvold (2012) provides one for regurgitilites (which he refers to as emetolites). There appears to be no comprehensive review of consumulites across fossil taxa other than the two discussed in the following section. Reports are typically centred on individual specimens. Smith & Scanferla (2016) provide an example of a single specimen with both strong and weak candidates for being true consumulites (lizard and insect, respectively).

A preserved meal sheds light on only a single meal in an organism's life. Extant organisms are known to consume a wide variety of food (Cortés, 1997; Vitt & Pianka, 2005; Wilman *et al.*, 2014), so any preserved meal should be viewed as a single data point in reconstructing diet. Taphonomic effects should also be taken into account, as meals with elements that fossilise easier are more likely to be preserved inside of their consumer (O'Connor, 2019). As the remains of deceased individuals, the meals associated with a fossil may be the thing that killed them rather than a normal food source. This is more likely in the context of consumulites or minimally processed regurgitilites than coprolites, given that coprolites require time and digestion to produce. In short, the possibility of a preserved meal being atypical cannot be ruled out by a single specimen.

(*b*) Avialan consumulites

O'Connor (2019) reviews the consumulites known from traditional Cretaceous avialans which consist of seeds, fish, and invertebrate exoskeletons. O'Connor & Zhou (2019) expand this review to cover all paravians, attributing lizard and fish consumulites to anchiornithines. A coprolite containing fish bones has been associated with a specimen of *Baptornis* (Martin & Tate, 1976), and an indistinct coprolite is known from a *Sapeornis* specimen (Zheng *et al.*, 2011). Four specimens record evidence of avialans themselves as prey of other organisms [ichthyosaurs (Kear, Boles & Smith, 2003), non-avialan theropods (O'Connor, Zhou & Xu, 2011; Xing *et al.*, 2012), and an indeterminate pellet-producing animal (Sanz *et al.*, 2001)].

There is particular controversy around enantiornithine consumulites, which merits discussion. Only a single uncontroversial consumulite is known from an enantiornithine: small (<5 mm) sections of crustacean exoskeleton in the abdomen of the holotype of *Eoalulavis hoyasi* (Sanz *et al.*, 1996). The fish bones associated with the holotype of *Piscivorenantiornis inusitatus* (Wang *et al.*, 2016*a*; Wang & Zhou, 2017) and the amber in the abdomen of the holotype of *Enantiophoenix electrophyla* (Dalla Vecchia & Chiappe, 2002; Cau & Arduini, 2008) were both rejected as consumulites by O'Connor (2019). The former is interpreted as a fish coprolite (but see Xu *et al.*, 2020) and the latter as elements reworked from surrounding soil (O'Connor, 2019). Spherical inclusions in two *incertae sedis* enantiornithines (and specimens of *Jeholornis* and *Eoconfuciusornis*) have been proposed as consumed plant matter (Mayr & Manegold, 2013; Mayr, 2016; O'Connor & Zhou, 2019; Mayr *et al.*, 2020*b*), although other studies have suggested that these inclusions are fossilised ovarian follicles (Zheng *et al.*, 2013; O'Connor *et al.*, 2014*b*; Wang *et al.*, 2016*b*; Bailleul *et al.*, 2019, 2020; O'Connor, 2019; O'Connor & Zhou, 2019).

Consumulite preservation is known from at least four specimens of *Jeholornis*, eight specimens of *Sapeornis*, and 14 specimens of ornithuromorph birds (*Eogranivora edentulata*, *Piscivoravis lii*, and 12 specimens of *Yanornis martini*) (see Table 1 in O'Connor, 2019). The absence or scarcity of consumulites in confuciusornithid and enantiornithine specimens (none in the former, one in the latter) has been used to suggest that they were generally molliphagous (feeding on soft things; opposite of durophagous) (O'Connor, 2019, p. 191). However, several other factors may be at play. Preservation of a consumulite is dependent on the meal being inside the animal's body (i.e. retained in the gut) and for parts hard enough to fossilise not to be dissolved at time of death. Thus, a longer gut retention time and a lower gut acidity favour the preservation of consumulites. Gut retention times vary among extant birds due both to long-term lifestyle differences and short-term events. Lifestyle differences include locomotor habits (Barton & Houston, 1992; Jackson, 1992; Hilton *et al.*, 1999; Caviedes-Vidal *et al.*, 2007; Frei *et al.*, 2014) and nutrient density of diets (Hilton, Houston & Furness, 1998; Hilton, Furness & Houston, 2000*a*; McWhorter & Martínez del Rio, 2000; Levey & Del Rio, 2001). Events include coincidental dietary switching (Hilton, Furness & Houston, 2000*b*), migration (McWilliams, Caviedes-Vidal & Karasov, 1999), and rearing young (Thouzeau *et al.*, 2004). Stomach acidities are also known to vary among extant raptors, with less bone remaining in the pellets of raptors with lower stomach pH (Duke, 1997). To our knowledge explanations of differing stomach pH have not been explored. Of these complicating factors, locomotor habits are of particular note as enantiornithines have been viewed as more arboreally inclined than contemporary ornithuromorphs (Field *et al.*, 2018*a*). In living birds, fully terrestrial species tend to have much longer gut retention times than flighted species (Frei *et al.*, 2014). Among flighted species, those that are more active in flight tend to have shorter gut retention times (Jackson, 1992; Hilton *et al.*, 1999; Caviedes-Vidal *et al.*, 2007). If enantiornithines were more active fliers than contemporary ornithuromorphs they likely also had shorter gut retention times. This would contribute to a lower incidence of consumulite preservation. Other possibilities, such as diets with higher nutrient density or a generally higher stomach pH than contemporary ornithuromorphs, can only be tested by future discoveries of consumulites or potentially corroborated by the other methods explored below.

(2) **Dental wear**

(*a*) Introduction

Teeth are dynamic systems worn continuously both by contact with ingested material and other occluding teeth (Green & Croft, 2018). As such, the way teeth are worn provides direct evidence of the diet of an animal. Dental wear analysis traditionally occurs at two distinct scales: mesowear, visible to the naked eye and reflecting periods of months to years (Green & Croft, 2018); and microwear, visible only under magnification and reflecting the animal's final days before death (Ungar, 2019). Green & Croft (2018) provide a review of both scales while Ungar (2015, 2018, 2019) provides more in-depth reviews of microwear in particular. Studies of larger-scale wear (e.g. fracture and erasure of denticles) have been used to examine patterns of occlusion (Lambe, 1917; Farlow & Brinkman, 1994; Sankey *et al.*, 2002), penetration angle (Farlow & Brinkman, 1994; D'Amore, 2009), and potentially grooming (Currie & Evans, 2019) in dinosaurs. All of these studies have remained purely qualitative and do not address diet.

(*b*) Mesowear

Dental mesowear has only been analysed in herbivorous mammals in order to distinguish between browsers and grazers (Green & Croft, 2018). Its underlying principle is worth unpacking for potential broader use. Teeth experience two distinct types of mesowear: attrition, from contact with occluding teeth; and abrasion, from contact with ingested materials (Fortelius & Solounias, 2000). In mammalian herbivores, these sharpen and dull the teeth respectively (Fortelius & Solounias, 2000; Green & Croft, 2018). Dental mesowear can be seen as the interaction between these two forces: in softer food diets attrition dominates and cusps are sharper, in tougher food diets abrasion dominates and cusps are rounder and are eventually completely flattened (Fortelius & Solounias, 2000; Green & Croft, 2018; see supporting online material of Mihlbachler *et al.*, 2011).

This approach is likely applicable to hadrosaurian dinosaurs whose dentition is reminiscent of equid mammals (Carrano, Janis & Sepkoski, 1999) and possibly to ceratopsian dinosaurs where attrition is believed to play a more complicated role (Erickson *et al.*, 2015). Both possess teeth with tight occlusion upon which interactions between attrition and abrasion similar to those of extant herbivorous mammals may have occurred. The teeth of known theropods occlude only slightly, although to a greater extent than the unoccluding teeth of extant saurians (Schubert & Ungar, 2005). Because of this, the interpretation of mesowear in theropods is obscure. Schubert & Ungar (2005) propose "wear facets" on tyrannosaurid teeth to be the product of attrition while "enamel spalling" is the product of abrasion; the former completely obliterates the latter over time. Candeiro *et al.* (2017) identify two additional attritional features (vertical and perpendicular attritional surfaces) and one additional abrasional feature (apical grooves). They also broaden the phylogenetic bracket of these features to Theropoda. All attritional/abrasional features may or may not overwrite one another based on chance, and so cannot be quantified as simply as the antagonistic mesowear seen in herbivorous mammals. Mesowear analysis as it currently exists, then, is inapplicable to the currently known fossil birds. Instead, a new system would need to be constructed. Because theropod teeth occlude on only one surface (the lingual surface of upper teeth and labial surface of lower teeth), the difference in wear between the two surfaces may provide similar information to mesowear analysis. The mesowear paradigms of attrition and abrasion balance can, instead of being quantified from cusp shape, be quantified as a ratio between the number and depth of marks on occluding and non-occluding surfaces. Assuming Schubert & Ungar (2005) are correct and that attritional wear would overwrite abrasional wear, the non-occluding surface would provide a baseline for abrasion while the occluding surface would provide information on attrition. However, a lack of extant analogues with theropod-like occlusion renders the validity of such an approach dubious; digital or practical modelling of theropod tooth occlusion may provide a baseline for study.

(*c*) Microwear

(i) Introduction. Dental microwear has been studied across vertebrates (Purnell, 1995; Purnell *et al.*, 2006; Nevatte *et al.*, 2017; Bestwick, Unwin & Purnell, 2019; Ungar, 2019; Winkler *et al.*, 2019). Dental microwear describes the surface scarring of tooth enamel at a microscopic level, which can provide insight into the hardness (resistance to fracture) and toughness (resistance to tearing) of an animal's last meals, typically within the last few days of its life (Ungar, 2019).

Traditionally, microwear analysis involves directly counting surface features under light microscopy or from electron micrographs, where greater numbers of pits are considered indicative of consuming harder foods while greater numbers of scratches are indicative of consuming tougher foods (Ungar, 2019). This technique is inconsistent, with counting errors regularly reaching 10% among trained professionals (Grine, Ungar & Teaford, 2002; Mihlbachler *et al.*, 2012).

In order to remove measurement noise, wear surfaces have more recently been imported as point clouds and analysed as fractal surfaces (Ungar, 2019) using techniques and software common in micro-scale manufacturing (e.g. Ţălu *et al.*, 2014). An increased area-scale fractal complexity is associated with harder foods in the diet, while an increased surface texture anisotropy is associated with tougher foods (Ungar, 2015). The only known source of error exclusive to fractal surface quantification is inter-microscope variability, which can be minimised by incorporating consistent automated treatments (Arman *et al.*, 2016). Purnell, Seehausen & Galis (2012) propose an alternative surface quantification method involving multivariate analysis of International Organization for Standardization (ISO) standard measures. While this alternative method captures more objective data about the surface and aspects of this can be correlated with diet (Purnell *et al.*, 2012; Bestwick *et al.*, 2019), we do not recommend this method at present. This is because the dietary significance of any given measurement is not well understood.

While microwear has been viewed as phylogenetically independent, this may be because it was studied among closely related taxa. A recent study comparing disparate clades of herbivorous mammals found microwear to describe phylogeny better than diet, but to distinguish diet successfully within each phylogenetic group (Mihlbachler *et al.*, 2016). It seems, then, that dental microwear comparisons should be restricted in taxonomic scope out of caution in order to avoid potential biases. This restriction may be less important outside of Mammalia though as dental microwear trends have proved consistent within percomorph fishes (Purnell & Darras, 2015) and across Lepidosauria (Winkler *et al.*, 2019). Because the temporal coverage of dental microwear is so short, analyses also require a large sample size properly to encompass the full breadth of an animal's diet (Ungar, 2019). Green & Croft (2018) imply that a minimum of 10 individuals should be sampled. Individual tooth sets can still act as individual examples of diet similar to preserved meals, and differently worn teeth within a single jaw have been proposed to give insight into non-dietary behaviours such as grooming (see Section VI.4*f.i*).

(ii) Rhamphotheca microwear. The possibility of applying techniques like those used in dental microwear to bird rhamphothecae (the horny covering of the beak) is interesting, but remains uncertain in viability. Sload (2014) is the only researcher to apply microwear techniques to biological structures other than teeth: claws of Florida stone crabs, *Menippe mercenaria*. He notes that the lower hardness of the carapace [average microhardness of 1.33 GPa in melanised Florida stone crab carapace (Melnick, Chen & Mecholsky, 1996) *versus* 3.56 GPa in human enamel (Eimar *et al.*, 2012)] leads to atypical patterns of microwear, with many surfaces worn completely away (Sload, 2014, p. 11). Reported averages for rhamphotheca hardness range from 1/4 [woodpecker *Melanerpes carolinus* (Lee *et al.*, 2014)] to 1/11 [starling *Sturnus vulgaris* (Bonser & Witter, 1993)] that of Florida stone crab carapace, and so may experience even more extreme destruction of surface features. Rhamphotheca microwear is expected to reflect only very short periods of dietary input, requiring accordingly large sample sizes in order to acquire meaningful data about diet. However, hardness alone cannot predict wear resistance or patterns. Material behaviour and contact angle with abrading particles also play major roles (Zum Gahr, 1998). Enamel and crab carapace are both brittle ceramics for whom wear resistance increases near-linearly with hardness, but more flexible materials like metals and, potentially, keratin can display neutral or even negative correlations between hardness and wear resistance (see Fig. 4 in Zum Gahr, 1998). The combined differences in material type and contact angles of food particles (with a rhamphotheca likely straighter and smoother than any dental battery) means rhamphothecal microwear patterns will not resemble any known dental microwear patterns. A ground-up approach will be necessary to make this application feasible: just as early mammal researchers identified scratches and pits to reflect tough and hard foods, diagnostic features of rhamphotheca wear have to be identified. The most straightforward method for identifying features would be laboratory experiments feeding birds known diets with differing mechanical properties. Such features could provide additional insight into living birds with obscure dietary habits as well as potentially being applicable to fossilised rhamphothecae (see Section II.3).

(iii) Microwear in fossil theropods. Owing to their lack of teeth, dental microwear studies have not been performed on any extant avians (see above). There are two studies of dental microwear in fossil theropods, both of which address diet. Candeiro *et al.* (2017) provide little detail of their methodology but stated that analysis was "undertaken with the support of a scanning electron microscope" (p. 230). They observed the presence of an elongated groove worn into select teeth and proposed it as evidence of osteophagy (Candeiro *et al.*, 2017). Torices *et al.* (2018) combine qualitative analysis of dental microwear with finite element analysis (see Section VI.3*c.iii*). They found all theropod teeth from the area of study to be worn with only scratches and no pits (Torices *et al.*, 2018), indicating a diet of tough but soft material (Ungar, 2019). Torices *et al.* (2018) interpret this as a lack of bone-crushing behaviour, where either flesh was removed selectively or prey was swallowed whole. They also cite the bimodal distribution of scratch directions as evidence of a puncture-and-pull feeding style. They propose scratches parallel to the tooth margin are formed while biting down while those oblique to the margin form when pulling back to disassemble prey (Torices *et al.*, 2018). Finally, they comment on possible omnivory in the troodontid *Troodon* based on finite element analysis. In their example micrographs though, the scratches on the *Troodon* teeth appear longer, more numerous, and less parallel to the tooth margin than those in *cf. Pyroraptor* or *Gorgosaurus* (Fig. 2 in Torices *et al.*, 2018). This may reflect *Troodon* incorporating more abrasive foods into its diet than the contemporary theropods studied. If not an artefact of the small number of examples provided, quantification of microwear may provide additional insight into dietary

differences among toothed theropods. Also of note is a conference abstract finding the dental microwear of *Archaeopteryx* to resemble most closely that of invertivorous saurians (Bestwick *et al.*, 2018). These results are planned for full publication, but dietary conclusions for *Archaeopteryx* are tentative due to a small sample size (Jordan Bestwick, personal communication 2020).

(iv) Application to fossil avialans. Fractal quantification of microwear (Ungar, 2015) has not been applied to any theropod taxon, and may be of particular interest in testing the proposed durophagy of certain enantiornithines including *Shenqiornis* (Wang *et al.*, 2010*a*; O'Connor & Chiappe, 2011) and *Sulcavis* (O'Connor *et al.*, 2013*b*). Successful application of the technique to fossil lepidosaurians of a similar size (Bestwick *et al.*, 2019) shows promise for success in toothed avialans. Should dental microwear of toothed avialans prove exclusively scratch-dominated as in non-avialan theropods (Torices *et al.*, 2018), only durophagy can be effectively ruled out. Other techniques are necessary to refine a dietary niche further. It is worth noting that, while complications from swallowing prey whole have been raised (Torices *et al.*, 2018; O'Connor & Zhou, 2019), microwear in particular has been observed to reflect diet in extant lepidosaurs and archosaurs despite their limited use of the teeth in prey processing (Bestwick *et al.*, 2019; Winkler *et al.*, 2019). Purely tooth-based approaches avoid many of the issues of reconstructing skull material. However, the possibility of anterior or posterior rhamphothecae in toothed avialans (Wang *et al.*, 2020*a*) acting as an additional feeding surface may complicate conclusions drawn from dental analysis only.

Application of microwear to beaked fossil avialans is contingent on the preservation of the rhamphotheca and on validation studies in extant birds. Microwear represents only a short window of time in tooth enamel usage (Green & Croft, 2018), and appears to turn over even faster in crab carapace (Sload, 2014). Thus rhamphothecae, which are even softer, will likely require large sample sizes for meaningful data. With less than a dozen rhamphothecae reported in the entire vertebrate fossil record (see Section II.3) this avenue requires the discovery of more specimens before it can be attempted. Procedures may also need to be devised to account for alterations to the microstructure of the keratin during burial, as in feathers (Fig. 3 in Saitta, Kaye & Vinther, 2019).

(3) Soft tissue

While not direct evidence of diet, the preservation of muscular tissue can aid in determining the inputs for functional models of extinct animal feeding. Unfortunately, fossilised jaw musculature has only been reported in placoderm fish (Trinajstic *et al.*, 2007) and fossilised gular musculature in an ornithomimosaurian theropod (Briggs *et al.*, 1997). The more commonly preserved postcranial musculature (e.g. Schultze, 1989; Kellner, 1996; Dal Sasso & Signore, 1998) may become useful in reconstructing dietary habits as the alliance between cranial and postcranial systems in feeding becomes better understood (Montuelle & Kane, 2019). Similar can be said for body outlines (Wang *et al.*, 2017*a*) for corroborating landmark-based muscular reconstructions (see Section II.3*a*).

Fossilised rhamphothecae are invaluable when studying the diet of edentulous fossil taxa. Fossilised rhamphotheca impressions are known from a pterosaur (Frey, Martill & Buchy, 2003), hadrosaurid (Sternberg, 1935; Morris, 1970; Farke *et al.*, 2013) and ceratopsian (Lingham-Soliar, 2008) ornithischians, and ornithomimosaurid (Norell, Makovicky & Currie, 2001; Barrett, 2005) and confuciusornithid (Hou *et al.*, 1999*b*; Zhang, Zhou & Benton, 2008*a*; Chiappe & Meng, 2016, p. 156; Falk *et al.*, 2019; Miller *et al.*, 2020; Zheng *et al.*, 2020) theropods. While preservation of rhamphothecae appears to be rare from this small sample size, the fact that half of known confuciusornithid rhamphothecae are only visible with the use of UV or laser-stimulated fluorescence (LSF) imaging (Chiappe & Meng, 2016, p. 156; Falk *et al.*, 2019; Miller *et al.*, 2020) shows promise for modern imaging techniques revealing previously unknown rhamphothecae. These fossils allow construction of more accurate models of beaked organisms in the fossil record. They also narrow the phylogenetic bracket for studying taxa with rhamphothecae that were not preserved.

(*a*) Landmark-based cervical reconstructions in fossil theropods

While the skull is often the first point of contact and/or the primary tool used in feeding, it functions only with the aid of postcranial systems (Montuelle & Kane, 2019). Once the jaws have bitten down, the neck powers further disassembly of food by using the teeth and/or beak to tear material into a swallowable size [except in cases of chewing, which is not known in theropods (Zanno & Makovicky, 2011)]. In an animal that uses its neck for disassembly, selection is expected to favour an increase in size of those muscles that power disassembly. While not studied at length in living birds, comparisons of radiographs of *Gallus* and *Anas* appear to show greater muscle volume spanning the areas of most intense flexion during feeding (Figs 3 and 4 in van der Leeuw, Bout & Zweers, 2001) and one study (Marek *et al.*, 2021) found the cervical vertebrae of insectivorous and tetrapod-eating birds to have distinct overall shapes. Thus, reconstruction of neck musculature can elucidate what way, if any, non-avian avialans disassembled their food before swallowing.

Among theropods, neck muscles have been reconstructed in therizinosaurians (Smith, 2015), ceratosaurids (Snively & Russell, 2007*b*), allosaurids (Bakker, 1998; Snively & Russell, 2007*b*; Snively *et al.*, 2013), and tyrannosaurids (Bakker & Williams, 1988; Snively & Russell, 2007*a*,*b*; Tsuihiji, 2010) based primarily on the occipital region of the skull. The general consensus of these studies is that ceratosaurids and allosaurids could exhibit greater force in dorsiflexion while therizinosaurians and tyrannosaurids could exhibit greater lateroflexive force. This leads to reconstruction of ceratosaurids and allosaurids pulling their heads back to disassemble prey and tyrannosaurids shaking their heads side-to-side (Snively & Russell, 2007*b*). Such reconstructions have yet to be attempted in paravian theropods.

(i) Application to fossil avialans. Tsuihiji (2005, 2007) compiled homologies of cervical muscles across extant diapsids, including crocodilians and birds. This provides an extant phylogenetic bracket for reconstruction of non-avian avialan cervical muscles, although typically two-dimensional fossil preservation may prove to be an obstacle to the reconstruction process. Aside from the possibility of digital reconstruction (see Section VI.1), only *Archaeopteryx* (Alonso *et al.*, 2004; Rauhut, 2014), *Neuquenornis* (Chiappe & Calvo, 1994), *Piscivorenantiornis* (Wang & Zhou, 2017), *Enaliornis* (Elzanowski & Galton, 1991), *Hesperornis* (Elzanowski, 1991), and *Ichthyornis* (Field *et al.*, 2018*b*) preserve the occipital region well enough to potentially identify muscular insertions. Of these, only *Neuquenornis*, *Hesperornis*, and *Ichthyornis* preserve any other regions of the skull. However, cervical muscles can be mapped onto cervical vertebrae in lateral view (Snively & Russell, 2007*b*; Tsuihiji, 2010), and the relative size of muscle insertions on the skull are consistent with those on the vertebrae (Snively & Russell, 2007*b*). Muscles that in both crocodilians and birds contribute to dorsoventral flexion (e.g. *m. spinalis capitis*) and lateral flexion (e.g. *m. obliquus capitis*) can be identified from the cervical columns of avialan compression fossils preserved in lateral view [e.g. IVPP V13313 (Dalsätt *et al.*, 2006), IVPP V13558 (Zheng *et al.*, 2014), STM 2–15 (O'Connor *et al.*, 2018), STM 29–11 (O'Connor *et al.*, 2016*c*)]. Once identified, their relative areas can be compared following the methodology of Snively & Russell (2007*b*) to determine predispositions in cervical flexion and, in turn, methods of prey disassembly. We propose that prey disassembly method, in turn, can be extrapolated to inform the typical loading of the jaw. Their work implies that dorsiflexion shifts the muscular load vector cranially, ventroflexion shifts it rostrally, and lateroflexion shifts it laterally although they did not explicitly state this.

(4) Discussion

Lines of direct evidence are the most powerful and unequivocal data that we can obtain about avialan diet but have a small scope for application. The study of dental mesowear is not recommended to investigate toothed avialan diet due to the lack of occlusion in the clade. While the information they provide is vital, the paucity of avialan consumulites in the fossil record prevents reliance on them for understanding diet in most specimens. The lack of fossilised avialan musculature means that reconstructions must currently rely on landmarks for their attachment. Landmarks on the cervical vertebrae in particular can inform habits of prey disassembly by presenting adaptations for cervical flexion (see also Section VI.3*b.iv*) in both toothed and beaked avialans. The most promising line of direct evidence of avialan diet is dental microwear due to its broad applicability. In particular, its utility in detecting the input of hard foods into animals' diets makes it ideal for investigations of possible durophagy in enantiornithines. The main drawback of this technique is the requirement for a large sample size, and so referral of unidentified specimens to known taxa may be necessary before such studies can be undertaken at phylogenetically meaningful levels. Rhamphotheca microwear requires a foundation in extant taxa before any application to beaked avialans can be attempted.

III. STABLE ISOTOPES

(1) Introduction

Natural abundances of stable isotopes (i.e. those not known to show radioactive decay) vary both geographically and in the way they are preferentially incorporated into biomolecules. With knowledge of these variations observed in living communities, the abundance of stable isotopes in the tissues of extinct animals can be used to reconstruct various aspects of palaeobiology (Clementz, 2012). The preservation window of stable isotope systems cited in all publications post-2010 can be traced to those listed in Table 5.2 of Koch's (2007) review of the stable isotope chemistry in fossil vertebrates. Koch, however, does little to justify the ranges of these windows. He justifies the preservation window of bone, enamel, and soft tissues, but the provided temporal limits of individual isotope systems in these tissues are not justified. As such, the exclusion of an isotope system from analysis because the specimen is 'too old' is unfounded. Therefore, in addition to the traditional systems of carbon, oxygen and calcium isotopes commonly analysed in Mesozoic enamel and bone (bioapatite), we will also address hydrogen, nitrogen, and sulphur systems found in collagen [convincing evidence of preservation dating to the Early Jurassic (Lee *et al.*, 2017)] as well as heavy metal (strontium, neodymium, lead, iron, copper, magnesium, and zinc) systems found in bioapatite. Keratin can theoretically preserve all isotope systems collagen does (Koch, 2007), although preservation of keratin chemistry in deep time is currently debated (Moyer, Zheng & Schweitzer, 2016; Schweitzer *et al.*, 2018; Saitta *et al.*, 2019).

(*a*) Carbon isotopes

^{13}C is enriched relative to ^{12}C in plants utilising a C4 photosynthetic pathway relative to those using the C3 pathway (Park & Epstein, 1960). The isotopic ratio of the carbon contained in the CO_3 components of bioapatite and within the amino acids of collagen can be used to determine what photosynthetic source(s) the nutrition in question ultimately came from. DNA and palynological evidence agree on an Oligocene origin of the C4 pathway (Sage, Sage & Kocacinar, 2012), and so this aspect of the isotope system is uninformative of diet in specimens older than roughly 30 million years.

Marine ecosystems are known to be enriched in ^{13}C relative to terrestrial ecosystems, although upper extremes of terrestrial species tend to overlap with those of marine species (Schoeninger & DeNiro, 1984) likely due to terrestrial input from C4 plants. Thus, prior to the emergence of C4 plants, we may expect a more bimodal distribution of ^{13}C enrichment, with high enrichment of ^{13}C indicating marine input into an organism's diet.

(*b*) Oxygen isotopes

^{18}O is enriched relative to ^{16}O in the leaves of plants relative to their other tissues, with increasing enrichment for leaves higher in the canopy (Koch, 2007). So, an enrichment in ^{18}O in the CO_3 and PO_4 of bioapatite or the amino acids of collagen may indicate a higher proportion of leaves in the diet or feeding on leaves higher in the canopy. While not directly indicative of foraging height, ^{18}O could potentially be used as a proxy. However, this enrichment must be evaluated based on comparisons with specimens from the same locality, as atmospheric temperature and water temperature are stronger controls on the enrichment of ^{18}O.

More frequently, ^{18}O enrichment is used to discern metabolic activity, which can confound the use of this isotope system in dietary studies. Body fluids are known to fractionate ^{18}O with temperature (Koch, 2007). Specifically homeothermy can be identified by comparisons of ^{18}O enrichment among different bones within an organism (Barrick & Showers, 1994; Barrick, Showers & Fischer, 1996; but see Kolodny *et al.*, 1996) and comparing global trends of ^{18}O enrichment to that of known ectotherms (Fricke & Rogers, 2000; Amiot *et al.*, 2006). So, if used in dietary reconstruction, metabolic rate must be kept constant when making comparisons.

(*c*) Calcium isotopes

^{44}Ca is known to deplete relative to all other calcium isotopes with increasing trophic level (Clementz, 2012), and so ratios of ^{44}Ca/Ca in bioapatite across a locality may allow for rough approximation of the trophic pyramid. However, carnivorous taxa that do not consume the mineralised tissues of prey (e.g. early hominids) appear to be at a lower trophic level from these ratios (Reynard, Henderson & Hedges, 2010). Osteophagous herbivorous taxa (Esque & Peters, 1994; Hutson, Burke & Haynes, 2013) will presumably appear to be at a higher trophic level.

(*d*) Hydrogen isotopes

^{2}H is enriched relative to ^{1}H with similar trends in plant tissues to ^{18}O/^{16}O, but with less contribution from evaporative conditions and greater contribution from differences in plant tissues (Koch, 2007). If collagen can be recovered, then this system appears more appropriate than oxygen for comparing between different localities and between organisms with differing metabolic rates.

(*e*) Nitrogen isotopes

^{15}N is enriched relative to ^{14}N with increasing trophic level, and is used widely in analyses of extant food webs (e.g. Rau *et al.*, 1992; Gu, Schelske & Hoyer, 1996; Davenport & Bax, 2002). The baseline enrichment of ^{15}N varies based on locality, and so comparisons must be made within a given locality (Koch, 2007). Nitrogen is sourced in the amino acids of an organism which are more difficult to avoid consuming than bone, and so if collagen can be recovered nitrogen isotopes may provide a superior reflection of trophic level to calcium isotopes.

^{15}N is also known to be enriched in marine ecosystems relative to terrestrial ecosystems, and with significant separation in levels between the two except in reef fish (Schoeninger & DeNiro, 1984). As such, an ecosystem with organisms feeding on exclusively marine or terrestrial organisms should display a bimodal distribution and not affect the signal for trophic level, but organisms taking from both sources may muddy the waters.

(*f*) Sulphur isotopes

Sulphur isotopes are known to vary among plants in extant ecosystems, but not in any predictable manner (Connolly *et al.*, 2004; Koch, 2007). Sulphur extracted from collagen may provide evidence of consumers with different producers contributing to their diet. Without fossilised plant proteins, which taphonomic studies rule unlikely (Fogel & Tuross, 1999), greater precision appears impossible.

(*g*) Heavy metal isotopes

^{87}Sr/^{86}Sr (Koch, 2007), ^{144}Nd/^{143}Nd (van de Flierdt *et al.*, 2006), and ^{207}Pb/^{206}Pb (Scheuhammer & Templeton, 1998) are not known to fractionate in biological systems, and so are typically used as indicators of location. In fossil terms, differences in these systems in the bioapatite of organisms from a given locality would represent different migratory patterns of those organisms in life. These could be used to identify distinct populations, potentially drawing on different food sources.

In extant mammals, ^{56}Fe/^{54}Fe is higher in females than males while the reverse is true for ^{65}Cu/^{63}Cu (Jaouen *et al.*, 2012; Martin, Tacail & Balter, 2017). This is potentially useful for identifying sexual dimorphism from bioapatite, and in turn identifying sexually dimorphic diets (Shine, 1989). However, the isotopic trend is hypothesised to be linked to menstrual cycles (Martin *et al.*, 2017) and thus may not be applicable outside of Eutheria.

Enrichment of both ^{26}Mg and ^{66}Zn in bioapatite with increasing trophic level have also been reported, but these isotopes appear more vulnerable to small regional variations than calcium or nitrogen (Martin *et al.*, 2017). They may prove to be effective as secondary systems to confirm predictions based on calcium and/or nitrogen.

(2) Stable isotopes in extant birds

The first record of stable isotopes analysed in extant birds comes from a study across vertebrates by Schoeninger & DeNiro (1984), followed by Hobson (1987) as the first to focus specifically on birds. Both studies focused on determining marine or terrestrial input to the diet *via* ^{13}C and/or ^{15}N. Hobson (1990) was the first to apply ^{13}C towards determining trophic level, and proposed ^{15}N as a superior alternative. His following paper (Hobson, 1993) codified the role of ^{15}N in determining trophic level and served as a basis for all subsequent avian studies. ^{18}O (Farmer *et al.*, 2003; Hobson *et al.*, 2004), ^{2}H (Chamberlain *et al.*, 1996; Farmer *et al.*, 2003; Lott, Meehan & Heath, 2003; Hobson *et al.*, 2004; Norris *et al.*, 2006), ^{34}S (Farmer *et al.*, 2003; Lott *et al.*, 2003; Sanpera *et al.*, 2007), ^{87}Sr (Chamberlain *et al.*, 1996; Blum, Taliaferro & Holmes, 2001), and ^{207}Pb (Scheuhammer & Templeton, 1998; Scheuhammer *et al.*, 2003; Svanberg *et al.*, 2006) have all only been used as indicators of locality in extant birds, typically by comparing sets of feathers from known localities to determine an isotopic signature without regard to the ecological drivers described above. To our knowledge no studies of calcium, neodymium, iron, copper, magnesium, or zinc stable isotopes in birds have been performed.

(3) Stable isotopes in fossil theropods

Among fossil avians, stable isotopes have been used in dietary reconstructions in recent (Hobson & Montevecchi, 1991; Miller *et al.*, 2005) and Palaeocene–Eocene (Angst *et al.*, 2014, 2015) taxa. Dietary studies older than this are restricted to non-avialan dinosaurs, primarily analyses of ^{13}C determining that ecosystems were based on C3 plants (Ghosh *et al.*, 2003; Amiot *et al.*, 2010, 2015; Montanari & Norell, 2011; van Baal *et al.*, 2013). Two studies (Frederickson, Engel & Cifelli, 2018, 2020) do incorporate paravian teeth, and also show evidence for niche partitioning through differences in carbon isotopes. The latter proposes a direct predator–prey relationship between two taxa based on carbon isotope signatures (Frederickson *et al.*, 2020), although we are dubious of this being broadly useful as many herbivores in extant ecosystems have similar carbon isotope ratios to one another (Ambrose & DeNiro, 1986). There are two studies that have investigated diet in fossil theropods specifically using stable isotopes. The first is Ostrom *et al.* (1993) who tabulated ^{15}N enrichment in bulk bones and teeth of vertebrates from the Judith River Formation, and recovered expected trends of greater enrichment in proposed hypercarnivorous taxa (e.g. tyrannosaurs, plesiosaurs) than proposed herbivorous/omnivorous taxa (e.g. hadrosaurs, sturgeon). The second is Hassler *et al.* (2018), who manage to separate carnivores and herbivores as well as terrestrial and aquatic predators in the Late Cretaceous of Northern Africa by measuring ^{44}Ca depletion in tooth enamel and fish scale ganoine. To our knowledge no stable isotopes of any non-avian avialan tissue have been analysed.

(4) Discussion

Stable isotopes promise information with validity akin to that of direct evidence, but the variety of influences on their ratios complicates the signals they provide. As such, the range of tissues and elements used in dietary inference is inherently small. Any attempts at bioapatite stable isotope analysis should be performed on teeth rather than bone if possible to ensure the highest level of accuracy (Hollund *et al.*, 2015). The only locality with a large number of published avialan teeth is the Jehol Group (O'Connor & Chiappe, 2011; Chiappe & Meng, 2016). All evidence points to the Jehol Group being entirely terrestrial (Zhou, Barrett & Hilton, 2003) so distinction of marine and terrestrial producer input *via* carbon isotopes is irrelevant. Use of oxygen isotopes to determine foraging height may be effective in the earliest-diverging avialans. However the variability of histological character in enantiornithines (Cambra-Moo *et al.*, 2006; O'Connor *et al.*, 2014*a*) and early-diverging ornithuromorphs (Wang *et al.*, 2019) would predict variation in metabolic rates acting as a confounding factor. The only isotope systems of interest in all avialan bioapatite, then, would be calcium isotopes with potential secondary confirmation with magnesium and zinc. While calcium isotopes could reliably be recovered (Hassler *et al.*, 2018), the aforementioned exceptions to their trends make them less desirable than nitrogen [although paravian theropods are known to swallow prey whole (O'Connor & Zhou, 2019) which requires consumption of mineralised tissues and negates this issue in at least some taxa]. Reconstructing trophic levels *via* nitrogen isotopes after Ostrom *et al.* (1993) seems ideal, but collagen in bone is easily contaminated and enamel preserves only small amounts of protein (Hollund *et al.*, 2015). Leichliter *et al.* (2020*a*) display a promising preliminary replication of Ostrom *et al.* (1993)'s results using oxidation-denitrification methods (Leichliter *et al.*, 2020*b*) to extract nitrogen from enamel more efficiently. Because these results are still preliminary, we recommend that nitrogen isotope studies of bird fossils use specimens that are incomplete or otherwise of low scientific value so that priceless fossils are not damaged unnecessarily. Exploratory studies should compare calcium and nitrogen isotope ratios across a given fossil site to ensure that trends agree between the two.

IV. BODY MASS

(1) Introduction

While not traditionally used to determine diet in fossil organisms, recent studies of extant birds (Bright *et al.*, 2016; Navalón *et al.*, 2018*a*; Pigot *et al.*, 2020) have found body mass to explain more of the variance in diet than physical approaches. Invertebrate feeders tend to be smaller than those that scavenge or hunt vertebrates (separation near 300 g) (Navalón *et al.*, 2018*a*), and among raptorial birds scavengers are distinctly larger than active hunters or omnivores (Bright *et al.*, 2016). It is worth noting that this trend appears to apply only to feeding on animals, as herbivorous diet types are spread across the range of measured body masses (Fig. 6 in Navalón *et al.*, 2018*a*). However, body mass alone can only consistently predict nectarivory in extant birds (Pigot *et al.*, 2020). Body mass has a major influence on feeding strategy in extant birds, but can be used only as a component in analysis [e.g. coupled with traditional morphometrics as in Pigot *et al.* (2020)] or as a secondary determinant. For instance, if other methods within the framework provide evidence of general carnivory, mass may help specify prey to vertebrates or invertebrates.

(2) Discussion

Body mass is a universal metric among animals, but the reasons behind its observed effects on bird diet remain unclear. Thus, its application to fossil avialans is questionable. The previously proposed reason for size having such influence in raptorial birds is the tight integration of the rostrum and cranium, disallowing significant change of one without the other (Bright *et al.*, 2016). If this is true, then this means that the control of size on diet is developmental, not mechanical. Bird skulls have undergone extreme changes from the early-diverging avialan condition, thought to be brought about by radical shifts in developmental controls (Bhullar *et al.*, 2016). Certain features of non-ornithuromorph skulls [small premaxilla (except in confuciusornithids), large maxilla (except in confuciusornithids), robust nasal and lacrimal, prominent postorbital (O'Connor & Chiappe, 2011; Rauhut, 2014; Hu *et al.*, 2020*a*)] more strongly resemble that of early-diverging theropods than extant birds. As such, developmental constraints on extant bird skulls are unlikely to be acting upon groups diverging earlier than Ornithuromorpha.

However, size explaining the largest portion of dietary variance persists across extant birds (Navalón *et al.*, 2018*a*; Pigot *et al.*, 2020) despite differences in modularity between avian clades and a general decoupling of the rostrum and braincase shape across living birds as a whole (Felice & Goswami, 2018). The relationship between diet and body mass, we propose, may be more under mechanical control rather than developmental control. For instance, invertebrate taxa tend to be smaller than vertebrate taxa, so larger birds are less likely to feed on them. With that assumption, it is recommended that mass calculations be factored into dietary reconstructions of fossil birds if possible.

Serrano, Palmqvist & Sanz (2015) provide mass estimates of 43 Mesozoic birds based on extant bird skeletons (see their Table 8). Table 2 expands on their work, using their equations to provide mass estimates for 71 additional specimens of non-avian avialans representing 61 species and based on scaled photographs in the literature. Combined with the estimates of Serrano *et al.* (2015), ~65% of non-avian avialan species likely fell below the 300 g dietary transition observed by Navalón *et al.* (2018*a*). However, this is largely driven by ornithothoracine species. Among non-ornithothoracine taxa only three specimens of *Archaeopteryx* have an estimated mass range below 300 g (Table 8 in Serrano *et al.*, 2015). There may be some taphonomic bias against preservation of large ornithothoracines, as the largest enantiornithine (Atterholt, Hutchison & O'Connor, 2018) and non-avian ornithuromorph (Buffetaut & Angst, 2016) taxa are only known from highly fragmentary material. Of taxa known from more-complete material, it appears that predatory ornithothoracines would be more likely to prey on invertebrates. Conversely, non-ornithothoracine avialans lacking distinct evidence of herbivory (*Archaeopteryx* and Confuciusornithidae) are more likely to have taken vertebrate prey. Some ornithothoracine groups [Bohaiornithidae (e.g. *Bohaiornis*), Pengornithidae (e.g. *Pengornis*), Songlingornithidae (e.g. *Yanornis*)] also tend to have body masses above 300 g (Table 2) and may represent a secondary adaptation to take vertebrate prey. Thirteen specimens of *Yanornis* (a songlingornithid) preserving ingested fish (O'Connor, 2019) support this premise.

V. DENTAL ULTRASTRUCTURE

(1) Dentine ultrastructure

Brink *et al.* (2016) report that the tubule density of dentine in archosaur teeth (imaged *via* multiple harmonic generation microscopy) is able to discriminate between taxa proposed as hypercarnivorous and hyperherbivorous. Hypercarnivorous taxa, according to their study, possess a higher density of tubules within the dentine. While potentially promising in the future, the authors provide an incomplete explanation for the functional significance of this difference. The taxonomic breadth of the study leaves room for the differences observed at least partially to reflect phylogeny (as proposed by Wang *et al.*, 2015*a*) rather than function.

(2) Enamel ultrastructure

Li *et al.* (2020) performed similar investigations into theropod enamel. They found loss of interglobular porous spaces and thinning of enamel at the avialan transition. These are proposed as reductions in tooth strength coincident with a dietary shift away from hard foods. However, while the authors propose interglobular porous spaces as restricting crack propagation, the mechanical differences between enamel and dentine are sufficient for this purpose in extant species (Bechtle *et al.*, 2010). Enamel thinning has alternatively been proposed as a by-product of selection for rapid incubation (Yang & Sander, 2018). This does not preclude enamel thinning from coincidentally causing a dietary transition as another by-product. The thickening of enamel in enantiornithines proposed as durophagous (Li *et al.*, 2020, p. 6) would seem to imply an ecological effect. This hypothesis will be worth examining against the overall jaw strength

Table 2. Mass estimates of avialan individuals. Input measurements are taken from scaled images in the literature. When scales of specimen photographs were in conflict (i.e. when scaled elements were larger or smaller than in the whole body photograph) we scaled all measurements so that humeral length was equal to measurements provided in the publication. Estimates are made using the equations of Serrano *et al.* (2015). The ORNnl equation is less precise and used in cases where a key component in the ENAN or ORPH equations is not preserved. The source text has a typographical error in four of the equations (Serrano, 2020). The corrected equations are:

$\mathrm{JEHO}: -1.933 + 1.486\,\mathrm{HL} + 0.416\,\mathrm{bcL} + 0.965\,\mathrm{dHW} - 0.36\,\mathrm{deHW} - 1.536\,\mathrm{UL} + 0.635\,\mathrm{peUW} - 0.397\,\mathrm{FL} + 0.834\,\mathrm{dFWml} + 0.302\,\mathrm{TL}$

$\mathrm{SAPE}: -2.876 + 0.952\,\mathrm{HL} + 0.352\,\mathrm{bcL} + 0.424\,\mathrm{dHW} + 0.967\,\mathrm{UL} + 0.615\,\mathrm{deUW} + 0.340\,\mathrm{dUW} - 1.891\,\mathrm{RL} - 0.343\,\mathrm{DCmW} + 0.589\,\mathrm{dFWcc} + 0.878\,\mathrm{TL} - 0.446\,\mathrm{TmL}$

$\mathrm{ENAN}: -2.626 + 1.528\,\mathrm{HL} + 0.34\,\mathrm{bcL} + 0.828\,\mathrm{dHW} - 1.451\,\mathrm{UL} + 0.811\,\mathrm{dUW} + 0.378\,\mathrm{TL}$

$\mathrm{ORNnl}: -2.392 + 1.799\,\mathrm{HL} + 0.355\,\mathrm{bcL} + 1.014\,\mathrm{dHW} + 1.003\,\mathrm{dUW} - 1.475\,\mathrm{RL} - 0.363\,\mathrm{DCmW}$

See Serrano *et al.* (2015) for measurement details. Body mass correction factors were not included in the original paper and so were back-calculated from the reported values; all were very close to 1. Equation abbreviations are as follows: bcL, length of bicipital crest; DCmW, midshaft width from the cranial edge of major metacarpal to the caudal edge of minor metacarpal; dFWcc, craniocaudal width at femoral midshaft; dFWml, mediolateral width at femoral midshaft; deHW, dorsoventral width of distal humerus; deUW, dorsoventral width of distal ulna; dHW, dorsoventral width at midshaft of humerus; dUW, craniocaudal width at midshaft of ulna; FL, length of femur; HL, length of humerus; peUW, dorsoventral width of proximal ulna; RL, length of radius; TL, length of tibiotarsus; TmL, length of tarsometatarsus from the crista medial to the trochlea of metatarsus III; UL, length of ulna

Taxon	Specimen	Mean mass estimate (kg)	Lower mass estimate (kg)	Upper mass estimate (kg)	Equation used
Jeholornithiformes					
Jeholornithiformes indet.	DLNM D2139	1.418	1.173	1.664	JEHO
Jeholornis curvipes	YFGP-yb2	1.504	1.244	1.764	JEHO
Jeholornis prima	STM 2-15	1.442	1.193	1.692	JEHO
Kompsornis longicaudus	AGB-6997	0.952	0.787	1.117	JEHO
Shenzhouraptor sinensis	LPM 00193	0.883	0.730	1.036	JEHO
Confuciusornithidae					
Confuciusornis sanctus	IVPP V13313	0.598	0.497	0.700	CONF
Yangavis confucii	IVPP V18929	0.564	0.468	0.659	CONF
Sapeornithiformes					
Omnivoropteryx sinousaorum	CAGS 02-IG-gausa-3	1.429	1.193	1.665	SAPE
Enantiornithes					
Alethoalaornis agitornis	LPM 00038	0.158	0.127	0.189	ENAN
Bohaiornis guoi	IVPP V17963	0.300	0.242	0.358	ENAN
B. guoi	LPM B00167	0.249	0.201	0.298	ENAN
Cathayornis yandica	IVPP V9769a/b	0.062	0.050	0.074	ENAN
Chiappeavis magnapremaxillo	STM 29-11	0.465	0.375	0.556	ENAN
Dalingheornis liweii	CNU VB2005001	0.008	0.007	0.010	ENAN
Dapingfangornis sentisorhinus	LPM 00039	0.204	0.164	0.243	ENAN
Dunhuangia cuii	GSGM-05-CM-030	0.124	0.099	0.149	ORNnl
Elsornis keni	MPD-b 100/201	1.512	1.206	1.817	ORNnl
Eopengornis martini	STM 24-1	0.193	0.155	0.230	ENAN
Fortunguavis xiaotaizicus	IVPP V18631	0.296	0.236	0.356	ORNnl
Grabauornis lingyuanensis	IVPP V14595	0.127	0.102	0.151	ENAN
Gracilornis jiufotangensis	PMOL-AB00170	0.027	0.021	0.032	ENAN
Gretcheniao sinensis	BMNHC Ph-829	0.455	0.367	0.543	ENAN
Houornis caudatus	IVPP V10917/1, IVPP V10917/2	0.107	0.086	0.129	ORNnl
Huoshanornis huji	DNM D2126	0.071	0.057	0.085	ENAN
Jibeinia luanhera	Drawing in Hou (1997), holotype lost	0.065	0.053	0.078	ENAN

(Continues)

Table 2. *(Cont.)*

Taxon	Specimen	Mean mass estimate (kg)	Lower mass estimate (kg)	Upper mass estimate (kg)	Equation used
Junornis houi	BMNHC-PH 919a/b	0.074	0.059	0.088	ENAN
Liaoningornis longidigitris	IVPP V11303	0.180	0.145	0.215	ENAN
Linyiornis amoena	STM 11-80	0.215	0.173	0.256	ENAN
Longipteryx chaoyangensis	DNHM D2889	0.154	0.124	0.184	ENAN
Longusunguis kurochkini	IVPP V17964	0.171	0.137	0.204	ENAN
L. kurochkini	IVPP V18693	0.237	0.191	0.283	ENAN
Microenantiornis vulgaris	PMOL AB00171	0.067	0.054	0.080	ENAN
Monoenantiornis sihedangia	IVPP V20289	0.355	0.286	0.424	ENAN
Noguerornis gonzalezi	LP.1702.P	0.020	0.016	0.024	ORNnl
Orienantius ritteri	BMNHC Ph-1154a/b	0.071	0.057	0.085	ENAN
O. ritteri	BMNHC Ph-1156a/b	0.083	0.067	0.100	ENAN
Parabohaiornis martini	IVPP V18691	0.221	0.178	0.263	ENAN
Parapengornis eurycaudatus	IVPP V18687	0.429	0.345	0.512	ENAN
Paraprotopteryx gracilis	STM V001	0.046	0.037	0.055	ENAN
Parvavis chuxiongensis	IVPP V18586/1, IVPP V18586/2	0.024	0.020	0.029	ENAN
Piscivorenantiornis inusitatus	IVPP V22582	0.281	0.227	0.336	ENAN
Protopteryx fengningensis	BMNHC Ph-1060a/b	0.109	0.088	0.130	ENAN
P. fengningensis	BMNHC Ph-1158a/b	0.088	0.071	0.105	ENAN
Pterygornis dapingfangensis	IVPP V20729	0.080	0.064	0.095	ENAN
Shangyang graciles	IVPP V25033	0.108	0.087	0.129	ENAN
Shanweiniao cooperorum	DNHM D1878/1, DNHM D1878/2	0.057	0.046	0.068	ENAN
Shengjingornis yangi	PMOL AB00179	0.340	0.274	0.406	ENAN
Shenqiornis mengi	DNHM D2950/1	0.340	0.274	0.406	ENAN
Sulcavis geeorum	BMNH Ph-000805	0.333	0.268	0.397	ENAN
Yuanjiawaornis viriosus	PMOL AB00032	0.418	0.337	0.499	ENAN
Zhouornis hani (subadult)	BMNHCPh 756	0.253	0.204	0.303	ENAN
Z. hani	CNUVB-0903	0.758	0.611	0.905	ENAN
Non-avian Ornithuromorpha					
Abitusavis lii	IVPP V14606	0.326	0.263	0.389	ORPH
Archaeorhynchus spathula	IVPP V17075	0.282	0.227	0.336	ORPH
A. spathula	IVPP V17091	0.153	0.123	0.183	ORPH
Archaeornithura meemannae	STM 7-145	0.136	0.109	0.162	ORPH
Bellulia rectusunguis	IVPP V17970	0.778	0.627	0.928	ORPH
Changzuiornis ahgm	AGB5840	0.240	0.193	0.286	ORPH
Dingavis longimaxilla	IVPP V20284	0.526	0.424	0.629	ORPH
Eogranivora edentulata	STM 35-3	0.291	0.235	0.348	ORPH
Gansus yumenensis	GSGM-05-CM-014	0.142	0.114	0.169	ORPH
Hongshanornis longicresta	DNHM D2945	0.075	0.061	0.090	ORPH
Mengciusornis dentatus	IVPP V26275	0.452	0.364	0.540	ORPH
Patagopteryx deferrariisi	MACN-N-11	1.130	0.911	1.349	ORPH

Table 2. *(Cont.)*

Taxon	Specimen	Mean mass estimate (kg)	Lower mass estimate (kg)	Upper mass estimate (kg)	Equation used
Piscivoravis lii	IVPP V17078	0.849	0.684	1.013	ORPH
Schizooura lii	IVPP V16861	0.377	0.304	0.450	ORPH
Similiyanornis brevipectus	IVPP V13278	0.634	0.511	0.757	ORPH
Tianyuornis cheni	STM 7-53	0.112	0.090	0.133	ORPH
Xinghaiornis lini	XHPM 1121	0.539	0.434	0.643	ORPH
Yanornis martini (juvenile?)	IVPP V13358	0.117	0.094	0.140	ORPH
Yanornis sp.	STM 9-15	0.577	0.465	0.689	ORPH
Yanornis sp.	STM 9-46	0.984	0.793	1.175	ORPH
Yumenornis huangi	GSGM-06-CM-013	0.321	0.256	0.386	ORNnl

using finite element models of non-avian avialans (see Section VI.3*c*).

(3) Discussion

As stated above, future studies of dentine ultrastructure require better sampling to support it reflecting diet rather than other factors like phylogeny. One clear way to test for phylogenetic influence would be to study dentine ultrastructure of herbivorous theropods like therizinosaurians or *Sapeornis*. Enamel ultrastructure has shown promising preliminary results (Li *et al.*, 2020), but the researchers' proposals of mechanical significance are yet to be supported. Physical approaches (Section VI) and phylogenetic controls are necessary to corroborate their findings. Should future studies validate the dietary signal of these techniques they would be applicable to any specimens in which dental wear analysis can be used.

VI. PHYSICAL APPROACHES

(1) Skull reconstruction

(*a*) Existing reconstructions

All of the physical approaches described below, when applied to skulls, require reconstruction of the skull. A listing of all reported avialan skulls is provided in Table S1. No complete non-avian avialan skull is preserved in three dimensions. A composite reconstruction of the skull of the non-avian ornithuran *Ichthyornis dispar* has been created in 3D (Field *et al.*, 2018*b*). The available elements of *Falcatakely forsterae* have been reconstructed in 3D (O'Connor *et al.*, 2020), but this only represents roughly three-quarters of the upper jaw. A team has also assembled a full 3D model of *Archaeopteryx*, but it is unreleased and intended for public education so its accuracy is unclear (Carney *et al.*, 2018). All other non-avian avialan skull reconstructions to date are 2D, owing to the flattened preservation of most avialans.

Over a dozen 2D skull reconstructions of *Archaeopteryx* exist (Elzanowski, 2001*b*; Rauhut, 2014). These tend to agree with one another, differing mostly in how bones contact at the antorbital fenestra and in the dorsocranial region. The same is true of *Hesperornis*, with some variation in the structure of the orbit (compare Gingerich, 1973; Bühler, Martin & Witmer, 1988) and the addition of the predentary to later restorations (Martin & Naples, 2008). Reconstructions of *Sapeornis* are less consistent, with the skull generally seen as more robust with a more downturned rostrum and mandible over time (compare Zhou & Zhang, 2003; Hu *et al.*, 2020*a*). Skull reconstructions of *Confuciusornis* (Chiappe *et al.*, 1999; Zhou & Hou, 2002; Navalón, 2014; Elzanowski, Peters & Mayr, 2018) have no clear trend in their variation. Most differences between reconstructions are in the length of the rostrum and height of the frontal, possibly representing intraspecific variation. *Anchiornis* sees the most variability in skull reconstruction, with noticeable differences in the size of fenestrae, shape of the mandible, and placement of sutures in all reconstructions (Xu *et al.*, 2011; Xu *et al.*, 2014; Wang *et al.*, 2017*a*). In each case the skull was merely illustrative with no record of reconstruction methods, and so a more intentional reconstruction of the skull of *Anchiornis* is necessary. For quite a few avialans there is only a single skull reconstruction. These include *Yi* (Xu *et al.*, 2015) [probably a non-avialan pennaraptoran (Pittman *et al.*, 2020*a*)], *Xiaotingia* (Xu *et al.*, 2011), *Jeholornis* (O'Connor *et al.*, 2013*a*), *Gobipteryx* (Elzanowski, 1977), *Cathayornis* (Martin & Zhou, 1997), *Eoenantiornis* (Hou *et al.*, 1999*a*), *Shenqiornis*, *Rapaxavis*, *Pengornis* (O'Connor & Chiappe, 2011), *Piscivorenantiornis* (Wang *et al.*, 2016*a*), *Falcatakely forsterae* (O'Connor *et al.*, 2020), an indeterminate enantiornithine hatchling (Sanz *et al.*, 1997), *Patagopteryx* (Chiappe, 2002), *Yanornis* (Huang *et al.*, 2016), and *Yixianornis* (Clarke, Zhou & Zhang, 2006).

(*b*) Avenues for improvement

Due to most avialan specimens being compression fossils, relatively little material lends itself to construction of 3D models. A 3D reconstruction of *Parahesperornis*, or at least a general hesperornithiform, should be possible with reported material. A nearly complete 3D skull of *Parahesperornis* is known, alongside well-preserved 3D pieces of the skull of *Hesperornis* (Bell & Chiappe, 2020) and *Pasquiaornis* (Sanchez, 2010). Excellent skulls of *Gobipteryx minuta* (Elzanowski, 1974, 1977; Chiappe, Norell & Clark, 2001) are nearly complete and preserved in three dimensions, and represent the most complete picture of the enantiornithine skull. The skulls of *Gobipipus reshetovi* (Kurochkin, Chatterjee & Mikhailov, 2013) and an unnamed gobipterygid (Lu *et al.*, 2011) are more fragmentary, but are similar enough to *Gobipteryx* that complete reconstruction is possible. Unfortunately, the skulls of these taxa are highly derived (Hu *et al.*, 2019) and are of dubious use in reconstructing the skulls of other enantiornithines (O'Connor & Chiappe, 2011). One complete enantiornithine skull is preserved in amber (Xing *et al.*, 2017), but is of an extremely early ontogenetic stage, damaged from preparation, and extremely difficult to image (Xing *et al.*, 2017, p. 266). The remainder of three-dimensionally preserved non-avian avialan skull material (Table S1) is too fragmentary for reconstruction. While an avian, the holotype of the Mesozoic bird *Asteriornis* includes a well-preserved and nearly complete skull (Field *et al.*, 2020) which can also offer insight into avialan roles in ecosystems of the Late Cretaceous.

As the vast majority of avialan skulls are preserved two-dimensionally (Table S1), 2D reconstructions will likely remain standard in the coming years. As such, valid approaches to 2D reconstruction are imperative for applying physical approaches to avialans. In an ideal scenario of a near-perfect skull (Sanz *et al.*, 1997) reconstruction is often just a matter of retrodeformation. When no one skull can supply all the information needed, multiple skulls must be combined into a chimera. O'Connor & Chiappe (2011) set the standard for enantiornithines by restricting the phylogenetic bracket to only other members of the clade. Within Enantiornithes, however, there is still ample variation in skull morphology (Zhang, Ericson & Zhou, 2004; Morschhauser *et al.*, 2009; O'Connor *et al.*, 2013*b*). We therefore recommend a refinement of current 2D avialan reconstructions by narrowing the phylogenetic bracket of reference taxa further. Four distinct families are generally recognised within Enantiornithes [Avisauridae (Brett-Surman & Paul, 1985; Atterholt *et al.*, 2018), Bohaiornithidae (Wang *et al.*, 2014*b*; O'Connor, 2019; Shi & Li, 2019; *contra* Chiappe *et al.*, 2019*b*), Longipterygidae (O'Connor *et al.*, 2009; O'Connor, 2019; Shi & Li, 2019; Pittman *et al.*, 2020*a*), and Pengornithidae (Wang *et al.*, 2014*b*; O'Connor, 2019; Pittman *et al.*, 2020*a*)], and so missing information can be preferentially filled by family members. A similar situation is true for the three widely recognised families of non-avian ornithuromorphs [Hesperornithiformes (Clarke, 2004; Bell & Chiappe, 2016), Hongshanornithidae (O'Connor, Gao & Chiappe, 2010*a*; Wang *et al.*, 2015*b*; Pittman *et al.*, 2020*a*), and Songlingornithidae (Hou, 1997; Clarke *et al.*, 2006; Pittman *et al.*, 2020*a*)]. In addition, the level of error introduced by chimerisation can be estimated by creating similar chimeras of extant bird skulls and comparing results of individuals to that of the composite. Skulls or individual teeth of lizards can help estimate the effects of chimeric dentition for toothed avialans. This will provide information on the accuracy of any analyses performed on inevitably chimeric avialan skull reconstructions.

Alternatively, technological advances may allow for 3D reconstruction from 2D sources. 3D images of specimens can be taken using computed tomography (CT) (Abel, Laurini & Richter, 2012) or augmented laminography (AL) (Zuber *et al.*, 2017). Subsequently, broken parts can be segmented and reconstructed according to techniques described by Lautenschlager (2016). Unfortunately, in addition to the man hours necessary to segment and manipulate the numerous shards of a shattered skull, there are significant obstacles to collecting these data. Typically, avialan skulls are part of slab specimens. These slabs do not yield good results when imaged with standard scanners on site and are often too large for higher-resolution scanners (Michael Pittman, personal observations). Preparation can resolve the size issue, but most museums are hesitant to approve preparation work, especially as slab specimens are generally beautifully articulated (Michael Pittman, personal observations). This means that to obtain CT data, whole slabs must be sent to distant specialist scanners (large-chamber μCT scanner and synchrotron scanner) which involves time-consuming permit- and logistics-related paperwork, high transport costs (usually personal courier *via* air travel) and an elevated risk of damage to the specimen during its transport. Thus, 3D data have been difficult to collect from avialan skulls and will continue to be a challenge whilst these obstacles remain. The 2D approach described above is recommended to circumvent these issues and preserve fossils for future study, although fossils whose skulls are already disarticulated [e.g. *Longusunguis* (Wang *et al.*, 2014*b*; Hu *et al.*, 2020*b*) or *Eogranivora* (Zheng *et al.*, 2018*a*)] (see also Table S1) would be ideal for pilot studies of 3D reconstruction of avialan skulls.

(2) Morphometrics

(*a*) Introduction

Morphometrics is the study of shape and the quantification of shape change, typically in a biological context (Rohlf, 1990). Shapes are quantified by defining landmarks, "(*i*) homologous anatomical loci that (*ii*) do not alter their topological positions relative to other landmarks, (*iii*) provide adequate coverage of the morphology, [and] (*iv*) can be found repeatedly and reliably…" (Zelditch *et al.*, 2004, p. 24). In studies that that are concerned with only two dimensions of geometry, all landmarks must also lie in the same plane (Zelditch *et al.*, 2004, p. 24). Once landmarks are placed on the structure in question, the methods with which they are analysed differentiate traditional morphometrics (TM), based on pre-selected distances and angles between landmarks (Marcus, 1990), and geometric morphometrics (GM), where the differences between landmark positions in all models are quantified and significant variables are identified *a posteriori* (Zelditch *et al.*, 2004, p. 24). Guillerme *et al.* (2020) review the collection, analysis, and interpretation of all morphometric data.

(*b*) Traditional morphometrics

(i) Introduction. Comparing linear measurements of animals likely predates the formalisation of science itself. TM are differentiated by rigorous statistical considerations of measurements taken, and selection of measurements believed to be relevant to the topic of study. The full range of statistical techniques used in TM are detailed by Marcus (1990).

The traditional appeal of TM has been the low computing power required. Measurements can be taken by hand and compiled into a spreadsheet for analysis of relatively low complexity. Now that computing power is no longer a limiting factor, the main appeals of TM are the lower investment of time and money into the project. TM does not necessitate creating two- or three-dimensional models nor placement of landmarks and semi-landmarks onto models (Rohlf, 1990). TM also allows for *a priori* selection of measures believed to have functional significance [although this may lead to arguments of cherry picking or p-hacking (e.g. Warton & Hui, 2011)]. TM has been recently applied in studies of diet with positive results (Hertel, 1994, 1995; McBrayer & Corbin, 2007; Surkov & Benton, 2008; Fraser & Theodor, 2011).

(ii) Traditional morphometrics in extant bird skulls. Hertel (1994, 1995) defines 21 linear and four angular measurements to describe the avian skull, with all skull measurements in subsequent studies representing some subset of these. However, subsequent studies of the skull tend to focus exclusively on linear (Ladyguin, 2000; Li & Clarke, 2016) or angular (Button, 2018) morphometrics. These studies, as well as those incorporating postcranial morphometrics (Barbosa & Moreno, 1999; Corbin, 2008; Herrel *et al.*, 2010*b*; Pigot *et al.*, 2020) and mechanical properties of the skull (Herrel *et al.*, 2010*b*; Corbin *et al.*, 2015), have all been successful in predicting diet in extant birds. However, as is always true with TM, the *a priori* selection of measurements may limit their broader applicability. Beak curvature, for instance, is a major axis of the morphospace in vultures (Hertel, 1994) but considered irrelevant in shorebirds (Barbosa & Moreno, 1999) and flycatchers (Corbin, 2008). Pigot *et al.* (2020) successfully applied their morphometrics to 99.7% of extant bird species, but their reliance on soft tissue landmarks means they are inapplicable to most fossil taxa.

(iii) Traditional morphometrics in fossil theropod skulls. While TM has been applied to non-avialan theropods across a broad range of taxa, the diets of all extinct theropods are necessarily speculative. So TM use has mostly been restricted to detecting inter-population differences (Smith, 1998) or niche partitioning (Henderson, 1998; Van Valkenburgh & Molnar, 2002; Holtz, 2008) in fossil theropods. Holtz (2008) frames his study of tyrannosaurids in terms of hunting style, but the section therein focusing on skull morphometrics only shows a lack of separation of tyrannosaurid and non-tyrannosaurid morphospaces with no comments on diet. Button & Zanno (2020) incorporate many skull measurements typical of TM in a study of theropod diet, such as skull length or premaxillary angle. However, because they investigate them in context of function rather than shape the study is covered in Section VI.3*b.iii*.

While most rigorously defined for phylogenetic use (Hendrickx & Mateus, 2014), TM has been applied twice to non-avialan theropod teeth as an exploration of diet. Holtz, Brinkman & Chandler (1998) found a trend of generally coarser denticles in herbivorous vertebrates than carnivorous ones, with therizinosauroids and some troodontids plotting near the former. This technique is inapplicable to currently known avialans as all reported avialan teeth are unserrated [O'Connor (2019); but see Dumont *et al.* (2016) and Wang *et al.* (2015*a*)]. Holtz (2008) examined the height, length, and width of theropod tooth crowns, which can be applied to unserrated teeth. While tyrannosaurid teeth weakly separated in the morphospace from non-tyrannosaurids, they were only effectively distinguished when examining functional indices (with an implication of increased strength indicating osteophagy). No comparisons to taxa with known diets were made.

(iv) Traditional morphometrics in extant and extinct theropod feet. Every TM study of the fossil theropod pes has included extant taxa for comparison, and few studies of extant avians exclude fossil taxa. It is, therefore, unhelpful to divide these studies by their subject, and so instead they are divided by their focus on angular or linear measurements. In addition to studies concerned directly with dietary cues (Csermely & Rossi, 2006; Einoder & Richardson, 2007; Fowler *et al.*, 2009, 2011; Csermely *et al.*, 2012; Mosto & Tambussi, 2014; M. Wang *et al.*, 2014*b*) and grasping ability (Kambic, 2008), we also include studies concerned purely with locomotion (Peters & Görgner, 1992; Feduccia, 1993; Clark *et al.*, 1998; Zhou, 1999; Hopson, 2001; Pike & Maitland, 2004; Glen & Bennett, 2007; Morschhauser *et al.*, 2009; Dececchi & Larsson, 2011; Tinius & Russell, 2017; Cobb & Sellers, 2020). Locomotion can provide insight into what resources would be available to individuals to feed on and how free the hind limbs were to manipulate food while feeding.

(A) Angular measures. Feduccia (1993) and Pike & Maitland (2004) define the major forms of angular TM in theropod claws. Both model the arc of the claw as a circle, with Feduccia (1993) concerned with the ventral arc (Fig. 1A) and Pike & Maitland (2004) measuring the dorsal arc (Fig. 1C). Both proposed that a greater degree of curvature (i.e. larger central angle measure) of said arc indicated a greater degree of arboreal behaviour within avians. Csermely & Rossi (2006) utilised the latter to investigate feeding behaviour. They investigated if it could distinguish between raptorial and non-raptorial birds, as the former are known to utilise their feet extensively in prey restraint and manipulation (e.g. Goslow, 1972; Csermely & Gaibani, 1998; Ward, Weigl & Conroy, 2002; Sustaita *et al.*, 2013). Subsequent studies measuring curvature either measured the dorsal arc exclusively (Glen & Bennett, 2007;

Csermely *et al.*, 2012; Mosto & Tambussi, 2014) or both the dorsal and ventral arcs (Fowler *et al.*, 2009, 2011; Birn-Jeffery *et al.*, 2012; Tinius & Russell, 2017; Cobb & Sellers, 2020) [although note that Fowler *et al.* (2009, 2011) and Tinius & Russell (2017) use an alternative ventral arc proximal landmark (Fig. 1B)]. Dececchi & Larsson (2011) code claws as either "straight", "recurved", or "highly recurved" without clarification of how these codings are determined. Of these methods, the angle from the dorsal arc as defined by Pike & Maitland (2004) or the ventral arc as defined by Fowler *et al.* (2009) appear to be the most informative as both utilise unambiguous landmarks that represent the proximal and distal extents of the keratinous covering of the talon (Hedrick *et al.*, 2019*a*). Because the majority of studies incorporate other measurements in addition to curvature it is impossible to pinpoint which measure most effectively discriminates between groups.

(B) Linear measures. Zhou (1999) included a chapter which systematised linear pedal TM in birds, although the paradigm was popularised by and is commonly attributed to Hopson (2001). Both studies followed similar methodologies to determine locomotor behaviour in extinct birds. Csermely & Rossi (2006) used these to investigate dietary signal (specifically predatory behaviour), while Kambic (2008) searched for signals specific to grasping ability. Unlike angular measurements, linear measurements of the avian pes are far from standardised. Non-ungual phalanges may have measurements of length [whole toe (Clark *et al.*, 1998; Zhou, 1999; Hopson, 2001; Kambic, 2008; Morschhauser *et al.*, 2009; Dececchi & Larsson, 2011; Wang *et al.*, 2014*b*; Abourachid *et al.*, 2017; Falk, Lamsdell & Gong, 2020) and individual phalanges (Clark *et al.*, 1998; Zhou, 1999; Hopson, 2001; Kambic, 2008; Morschhauser *et al.*, 2009; Dececchi & Larsson, 2011; Wang *et al.*, 2014*b*; Abourachid *et al.*, 2017)], width [whole toe (Csermely & Rossi, 2006; Csermely *et al.*, 2012) and individual phalanges (Kambic, 2008; Abourachid *et al.*, 2017)], and height [whole toe (Csermely & Rossi, 2006; Csermely *et al.*, 2012) and individual phalanges (Kambic, 2008; Abourachid *et al.*, 2017)] on record (Fig. 2A–C). Ungual phalanges may have measures of length [chord (Csermely & Rossi, 2006; Fowler *et al.*, 2009, 2011; Csermely *et al.*, 2012; Hedrick *et al.*, 2019*a*), arc length (Mosto & Tambussi, 2014; Abourachid *et al.*, 2017), and flexor tubercle chord (Mosto & Tambussi, 2014; Abourachid *et al.*, 2017)], width [at the base of the claw (Csermely & Rossi, 2006; Csermely *et al.*, 2012) and of the flexor tubercle

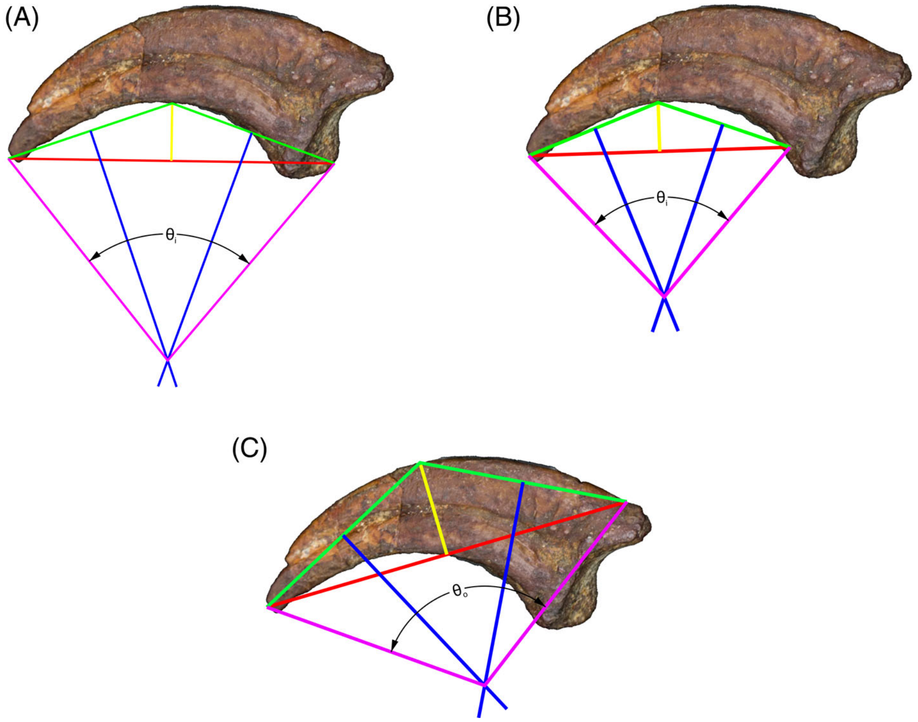


Fig 1. Methods employed in measuring the angle of bird claw curvature. Methods are diagrammed onto the digit I ungual of the enantiornithine *Mirarce eatoni*, as depicted by Atterholt *et al.* (2018). (A, B) Inner arc angle (A) as codified by Feduccia (1993) and (B) Fowler *et al.* (2009). (C) Outer arc angle as codified by Pike & Maitland (2004). In all cases, an initial chord (red) is drawn between the tip of the claw and the (A) proximal walking surface of the ungual, or the (B) ventroproximal or (C) dorsoproximal extent of the horny sheath of the claw (visible as inflection points in bony cores). A perpendicular line (yellow) is drawn from the midpoint of this chord to the ventral (A and B) or dorsal (C) arc of the ungual. Lines connecting the endpoints (green) are drawn, as well as lines perpendicular to the midpoint of these green lines (blue). The intersection of the blue lines defines the centre of a circle approximated by the arc. From this centre, lines (magenta) are drawn to the endpoints of the initial chord, and the angle between the magenta lines is the angle of curvature of the claw arc.

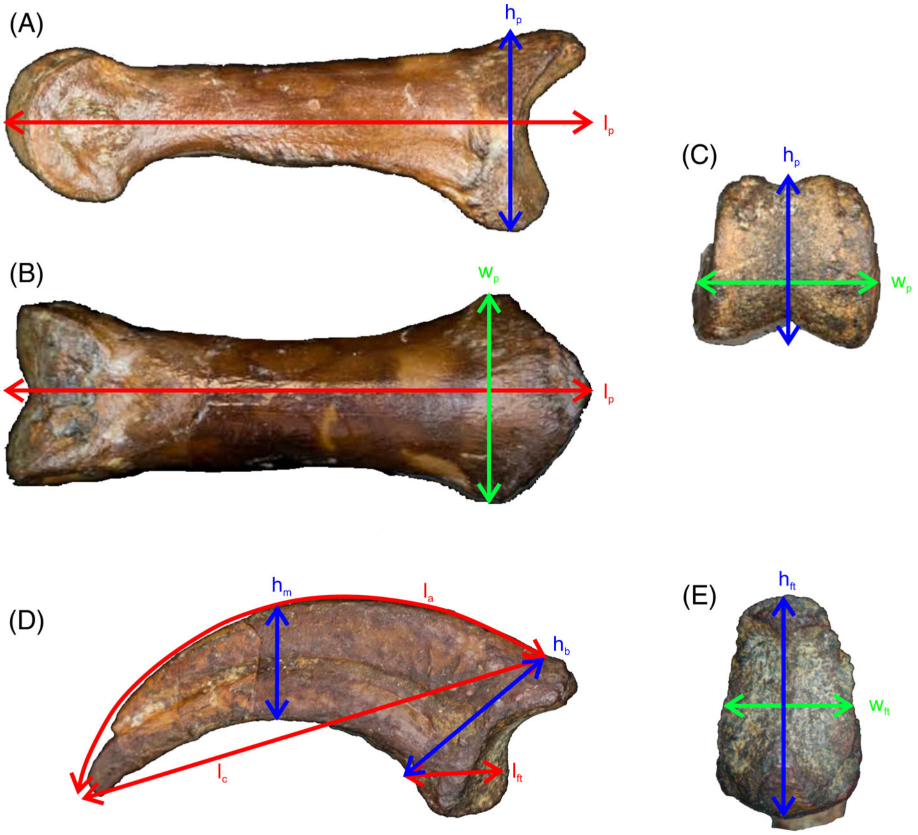


Fig 2. Length, width, and height measurements of the avian pes. Length (red), width (green) and height (blue), diagrammed onto the digit I phalanx I and digit I ungual of *Mirarce eatoni* as depicted by Atterholt *et al.* (2018). (A–C) Measurements of the non-ungual phalanges in (A) lateral, (B) dorsal, and (C) distal views. (D–E) Measures of the ungual phalanx in (D) lateral and (E) proximal views. Note that most measures refer to the greatest distance measurable in a given dimension, but some such as w_{ft} are shown as being less than the greatest measurable distance without explanation in the works in which they are used. Abbreviations: l_a, arc length of ungual; l_c, chord length of ungual; l_{ft}, proximodistal length of flexor tubercle; l_p, proximodistal length of phalanx; h_b, height at the base of the ungual; h_{ft}, dorsoventral height of the flexor tubercle; h_m, height at the mid-arc of the ungual; h_p, dorsoventral height of phalanx; w_{ft}, mediolateral width of flexor tubercle; w_p, mediolateral width of phalanx.

(Mosto & Tambussi, 2014)], and height [at the base of the claw (Fowler *et al.*, 2009; Fowler *et al.*, 2011), at the midpoint of the arc (Fowler *et al.*, 2009, 2011), and of the flexor tubercle (Mosto & Tambussi, 2014)] on record (Fig. 2D, E). The only linear measurements comparable among the majority of studies of linear phalangeal measurements are ungual chord length and individual phalanx length [which closely approximates total toe length (Falk, 2014)]. Arguments have been made for the inclusion of certain measurements, e.g. the ungual chord length, as a proxy for body size (Pike & Maitland, 2004) or phalangeal lengths indicating flexibility of the toes [Zhou (1999) citing Fisher (1946)]. However, the inconsistency of measures attests to how little justification there is for any given set of linear measurements to quantify properly the shape of avian feet.

This category includes two of the three quantitative studies focused on avialan diet, although both were directly examining locomotion and only refer to diet as a secondary result. Hou *et al.* (2004) hypothesised that *Longirostravis* was a probing feeder, and Morschhauser *et al.* (2009) tested this hypothesis through the closely related *Rapaxavis*. Morschhauser *et al.* (2009) incorporated digit III phalanx measurements of *Rapaxavis* into the data set of Hopson (2001) and found it to fall into the arboreal morphospace. From this they propose that, instead of being ground probers comparable to charadriiforms, they may have instead been bark probers (Morschhauser *et al.*, 2009, p. 553). Wang *et al.* (2014*b*) took a similar approach to Bohaiornithidae, adding their phalangeal measurements to the data set of Hopson (2001) and adding claw curvature measurements of Pike & Maitland (2004); it appears comparisons to the latter are merely qualitative, referring only to "high" and "low" curvature. Narrowing the data set to raptorial birds due to high claw curvature and lack of specialised limb proportions associated with climbing, they found the closest phalangeal proportions to be those of *Pandion*. While the researchers propose a piscivorous diet in bohaiornithids because of this similarity, they attenuate the diagnosis with qualitative assertions of their teeth seeming to be more adapted for durophagy (Wang *et al.*, 2014*b*, p. 68).

(v) Discussion. Pilot studies are necessary to examine the application of TM to non-avian avialan skulls to predict diet. All TM frameworks that rely on the curvature of the

premaxilla (Hertel, 1994, 1995; Barbosa & Moreno, 1999; Button, 2018) cannot be applied to toothed avialans as nearly all possess straight premaxillae. The exceptions are for *Sapeornis*, *Ichthyornis* and the Hesperornithiformes which are interpreted as possessing rhamphothecae which replaced the rostralmost teeth (Wang *et al*., 2020*b*); premaxillary curvature is likely a product of edentulism with teeth no longer serving as a gripping surface for food. Whether the straight beaks of all known fully edentulous avialans (Chiappe *et al*., 2001; Zhou & Li, 2010; Zhou, Zhou & O'Connor, 2012, 2013; Elzanowski *et al*., 2018; O'Connor, 2019) represents a dietary or developmental signal is unclear. Frameworks reliant on the width of the skull (Corbin, 2008; Corbin *et al*., 2015; Li & Clarke, 2016; Pigot *et al*., 2020) would require referral of more specimens with skulls preserved in dorsal or ventral views. Skull width is unknown in all described non-avian avialan genera except *Anchiornis*, *Confuciusornis*, *Sapeornis*, *Dalingheornis*, *Eopengornis*, *Fortunguavis*, *Longusunguis*, *Monoenantiornis*, *Archaeorhynchus*, *Yixianornis*, *Ichthyornis*, *Hesperornis*, and *Parahesperornis* (Table S1). Of these all but *Ichthyornis*, *Hesperornis*, and *Parahesperornis* are crushed skulls whose widths we consider dubious. TM seems more likely to prove useful when applied to dentition. Dental TM is already known to determine effectively the phylogenetic placement of most theropods (Hendrickx & Mateus, 2014; Hendrickx, Tschopp & d'Ezcurra, 2020), with universal characters already defined in the literature (Hendrickx, Mateus & Araújo, 2015). While preliminary studies of lizard teeth have shown only a tenuous link with diet (Estes & Williams, 1984; Melstrom, 2017), they remain the best extant group to compare with due to the much more narrow range of tooth form in crocodilians (Erickson *et al*., 2012). We therefore recommend a study of extant lizard teeth using the existing TM framework (Hendrickx *et al*., 2015) as a baseline dietary morphospace. Otherwise, the lack of effective application of skull TM to non-avialan theropod diet does not bode well for applying this technique to non-avian avialans.

TM studies of the theropod pes have both a more consistent focus on dietary analogues and a more consistently applied set of measurements, and so a more thorough evaluation of methods is possible. Most TM studies of the pes concerned themselves only with digit III (DIII) (Peters & Görgner, 1992; Feduccia, 1993; Clark *et al*., 1998; Pike & Maitland, 2004; Glen & Bennett, 2007; Kambic, 2008; Morschhauser *et al*., 2009; Dececchi & Larsson, 2011; Wang *et al*., 2014*b*; Tinius & Russell, 2017; Cobb & Sellers, 2020), two studies with digit I (DI) and DIII (Csermely & Rossi, 2006; Csermely *et al*., 2012), two studies with digit II (DII)–digit IV (DIV) (Zhou, 1999; Hopson, 2001), and the remainder with all four digits (Einoder & Richardson, 2007; Fowler *et al*., 2009, 2011; Mosto & Tambussi, 2014; Falk *et al*., 2020). Studies that rely solely on DIII justify this choice by DIII being the weight-bearing toe (Glen & Bennett, 2007; Hedrick *et al*., 2019*a*), and all but (Kambic, 2008) are concerned with locomotion. Studies on DII–DIV (Zhou, 1999; Hopson, 2001) are similar in concept, disregarding DI as it rarely bears weight during forward motion. Zhou (1999) compared the phalangeal proportions of DII–IV individually and found that each digit discriminated between locomotor categories equally well (his Figs 38–42). Backus *et al*. (2015) provide a strong argument for the efficacy of the two-dimensional simplification of avian grasping (i.e. the action of DI and DIII) as such simplification is adequate to create functioning artificial 'hands' for robots (Dollar & Howe, 2011; Backus, Odhner & Dollar, 2014). Abourachid *et al*. (2017), however, note that in non-anisodactyl pedal arrangements DII and DIV supplement or supplant the role of DI and DIII in grasping. The subdivisions of anisodactyl arrangements recently proposed by Falk *et al*. (2020) may prove to have similar influence on the grasping role of digits. Measuring all digits of the pes acquires the most data possible about its structure but imposes additional complexity in the analysis and time for data collection. Significant interdigital variation is often cited as a reason to avoid measurements of the whole pes (Hedrick *et al*., 2019*a*; Cobb & Sellers, 2020), but Fowler *et al*. (2009, 2011) argue that interdigital variation itself is a diagnostic that separates ecological niches. Given that all studies of all four digits were able to discriminate ecological groups it seems unlikely that measuring four digits is detrimental to TM analysis, but any benefit from analysing all digits over the analysis of a single digit is equivocal.

It is recommended in TM (and GM) studies of ungual phalanges to compare the bony cores of claws rather than the keratin sheaths. Studies measuring both sheath and core found both to give similar information (Hedrick *et al*., 2019*a*; Cobb & Sellers, 2020), and many fossils do not preserve the keratin sheath. In those that do, the keratin stain is likely more deformed than the bone (Saitta *et al*., 2019). Therefore empirical conversion factors (e.g. Glen & Bennett, 2007; Hedrick *et al*., 2019*a*) or direct measurements of the stain give less valid data than measuring the core. Extant avian ungual bones can be found in many museum skeletal collections, and remaining keratin can easily be removed from the claws of macerated skeletons by soaking the claws in dilute ammonia (Stephen Rogers, Carnegie Museum of Natural History, personal communication 2019). Among styles of applying TM, Fowler *et al*. (2009, 2011) produced the finest scale of discrimination. Their framework delineated not only arboreal/ground and raptor/non-raptor groups, but also the individual hunting guilds among raptors. However, these studies did not employ phylogenetic correction. Thus, some authors have proposed that they simply group talons based on familial relations (Hedrick *et al*., 2019*a*), which happen to correlate with predatory style in extant raptors (Goslow, 1972; Csermely & Gaibani, 1998; Sustaita, 2008; Fowler *et al*., 2009). More fundamentally, the Fowler *et al*. (2009, 2011) studies appear to utilise improper statistical analysis. They apply correspondence analysis, designed to utilise categorical data. Numerical data can be binned and analysed as categorical data (Kim, 2011), but Fowler *et al*. (2009, 2011) do not indicate doing so in either study. When the more appropriate principal component analysis is applied to these data (see Fig. S1) groups inhabit less distinct regions of the morphospace. With that said, they still show more distinction than that of the next most discriminating study, Csermely *et al.* (2012). It is recommended that any pes-based TM investigation of non-avian avialan diet be based on the analytical procedures of Fowler *et al.* (2009) with an appropriate phylogenetic correction (see Section VI.4*a*).

One study of avialan ecology which should be mentioned here is that of Mitchell & Makovicky (2014). This study translates traditional morphometric indices into discrete characters rather than using the measurements themselves. This brought considerable success both in discriminating ecology among extant birds and in matching preserved meals and depositional environments of fossil birds [although we are sceptical of their prediction of *Bohaiornis* as herbivorous and insectivorous, as the "gastroliths" in its stomach are believed to be preservational artefacts (O'Connor, 2019) and its body mass is greater than expected for an invertivore (Section IV; Table 2)]. This approach necessarily removes data without an intuitive explanation. For instance, there is no reason given why birds with skulls whose length/width ratio is below, near, or above one should be expected to be ecologically distinct. This approach is appealing, though, in its ability to combine form with qualitative traits (e.g. known preserved meals) as in Zanno & Makovicky (2011). So for taxa with dietary evidence not easily converted into morphometrics, this combination approach may yield superior results. When this approach is used we suggest taking the extant morphometric data and performing some form of cluster analysis (Jain, 2010) to determine where the appropriate points are to discretise characters. For most non-avian avialans, however, we expect TM approaches to be superior at determining diet than conversion into discrete characters.

(*c*) Geometric morphometrics

(i) Introduction. Geometric morphometrics (GM) uses digital models, either full 3D models or 2D dorsal/lateral silhouettes, with landmarks placed just as one would with TM (Zelditch *et al.*, 2004). Landmarks are typically supplemented by sliding semi-landmarks, a digitisation of the curve(s) between landmarks (Perez, Bernal & Gonzalez, 2006). The shifts in the relative position of landmarks and semi-landmarks between models can be quantified and analysed digitally (Adams & Otarola-Castillo, 2013).

While GM can be significantly more time-consuming than TM (Rohlf, 1990), GM provides at least as much information about the shape of the element in question as every possible measurement taken between every pair of landmarks (Zelditch *et al.*, 2004, p. 2–7). With the introduction of semi-landmarks the information increases beyond that possible in TM (Zelditch *et al.*, 2004, p. 396). Perez *et al.* (2006) detail different methods of creating semi-landmarks. Note that at an inter-species or higher level, such as that typically employed in palaeontology, the differences between methods should be negligible. Because GM creates an unbiased representation of form it has proved effective in tracing evolutionary trends (Figueirido *et al.*, 2011; Miyashita, 2013; Openshaw *et al.*, 2016; Polly *et al.*, 2016; Fernandez Blanco, Cassini & Bona, 2018) but has returned only mixed results in feeding studies (Samuels, 2009; Meloro, Hudson & Rook, 2015; Gailer *et al.*, 2016; Klaczko, Sherratt & Setz, 2016; Tarquini *et al.*, 2019).

Another form of GM, outline-based GM, has been introduced as an alternative method of quantifying 2D shape. This method interprets and compares the outlines of bodies as composites of trigonometric curves (Fourier analysis). The primary advantage over landmark-based methods is applicability to bodies with few homologous landmarks (Bonhomme *et al.*, 2014). While the concept dates back several decades (Kaesler & Waters, 1972) this method has been used very little in vertebrate palaeontology to date (Navarro, Martin-Silverstone & Stubbs, 2018; Schaeffer *et al.*, 2019) and so by default 'GM' will be used herein to refer to landmark-based GM. In phylogenetically broad studies in which homology is unclear this method may prove useful in the future.

(ii) Geometric morphometrics in extant bird skulls. GM studies of extant avian diet can be divided into those that include only the bill (van der Meij, 2004; Sustaita & Rubega, 2014; Matsui *et al.*, 2016; Cooney *et al.*, 2017; Olsen, 2017; Button, 2018; Navalón *et al.*, 2018*a*), those that treat the beak and cranium as a single unit (Navalón, 2014; Si *et al.*, 2015; Bright *et al.*, 2016, 2019; Tokita *et al.*, 2017; Sun *et al.*, 2018; Felice *et al.*, 2019*a*; Pecsics *et al.*, 2019; Chávez-Hoffmeister, 2020), and those that examine each individually (Kulemeyer *et al.*, 2009; Bright *et al.*, 2016; Felice *et al.*, 2019*a*). Landmarks for the bill tend to be consistent. The bill tip and the base of the frontal are used in nearly every study (van der Meij, 2004; Kulemeyer *et al.*, 2009; Navalón, 2014; Si *et al.*, 2015; Bright *et al.*, 2016, 2019; Matsui *et al.*, 2016; Tokita *et al.*, 2017; Button, 2018; Navalón *et al.*, 2018*a*; Sun *et al.*, 2018; Chávez-Hoffmeister, 2020) alongside either the rostral extreme of the jugal (van der Meij, 2004; Navalón, 2014; Matsui *et al.*, 2016; Tokita *et al.*, 2017; Button, 2018; Navalón *et al.*, 2018*a*; Bright *et al.*, 2019; Chávez-Hoffmeister, 2020) or the ventrocranial extreme of the palatine (Kulemeyer *et al.*, 2009; Si *et al.*, 2015; Tokita *et al.*, 2017; Sun *et al.*, 2018; Pecsics *et al.*, 2019). Landmarks of the cranium are less consistent, with only the border of the orbit commonly mapped (Kulemeyer *et al.*, 2009; Si *et al.*, 2015; Tokita *et al.*, 2017; Sun *et al.*, 2018; Felice *et al.*, 2019*a*). Discrimination of diet is inconsistent. GM can often discriminate diet in restricted phylogenetic groups (family to superfamily level) (van der Meij, 2004; Kulemeyer *et al.*, 2009; Sustaita & Rubega, 2014; Si *et al.*, 2015; Olsen, 2017; Sun *et al.*, 2018; Pecsics *et al.*, 2019; Chávez-Hoffmeister, 2020), but dietary morphospace tends to overlap heavily between groups (Bright *et al.*, 2016, 2019; Tokita *et al.*, 2017) and across birds overall (Navalón, 2014; Button, 2018; Navalón *et al.*, 2018*a*; Felice *et al.*, 2019*a*). It seems likely that more distantly related clades of birds face developmental constraints that either prevent them from attaining converging morphotypes or predisposes them towards differing solutions under similar

environmental pressures (Gould, 2002). Similar levels of craniofacial integration within most families of land birds (Telluraves) (Navalón *et al.*, 2020) implies similar developmental patterns among them. Constraints preventing shape/diet correlation, then, are less expected within Telluraves.

(iii) Geometric morphometrics in fossil theropod skulls. Marugán-Lobón & Buscalioni (2004) laid the groundwork for non-avialan theropod GM, focusing purely on disparity (quantified difference in shape). Shychoski & Snively (2008*a*) published an abstract that reported juvenile tyrannosaur mandibles to be closer in shape to non-tyrannosaurid morphotypes than their adult forms, but full publication of the data is not planned (Eric Snively, personal communication 2020). Brusatte *et al.* (2012) found oviraptorids and, to a lesser extent, ornithomimosaurians and alvarezsaurians [all proposed as herbivorous (Zanno & Makovicky, 2011)] to cluster outside the 'carnivorous' morphospace. The lack of any confirmed diets in the data set limits confidence in these results. Foth & Rauhut (2013) reported similar results with a significant correlation between purported diet and shape. They saw more overlap in dietary morphospace and also did not include taxa with known diets. Recoding taxa based on more explicit evidence of diet (Fig. S2; see Table S2 for recoding rationale) provides a division between herbivorous and carnivorous morphospace if *Anchiornis* and *Bambiraptor* are excluded (which inhabit a unique region of the morphospace overlapping with herbivores). This study was the first to include early-diverging avialan taxa in GM analysis (Table S1 in Foth & Rauhut, 2013). Schaeffer *et al.* (2019) were the first to incorporate outline-based GM to study theropod diet, and compare it to both landmark-based GM and discrete characters. The authors found all three approaches to be of similar effectiveness, although it is noteworthy that separation of morphospace *via* discrete characters appears more vulnerable to changes in sample size (compare their Figs 3C and 7C). When diets are more conservatively assigned (Fig. S3; see Table S3 for recoding rationale) resolution between herbivores/omnivores and small carnivores increases. Their graphs show landmark-based GM as less effective at discriminating between large and small carnivores than outline-based GM (their Figs 3 and 7), although this appears to be due to principal components defining different shapes between the two (their Fig. 4). When plotted as PC1 *versus* PC3 a similar trend is seen in landmark-based GM to that shown for outline-based (their Fig. S7 and supplemental files; our Fig. S3E). Button (2018) and Navalón (2014) are the only researchers to combine GM analysis of extant avian taxa with known diets and early-diverging theropods. The dietary morphospace of most extant avians in these studies overlap and are often completely enveloped in another morphospace [Fig. 33 in Button (2018); Fig. 8 in Navalón (2014)]. In both studies almost all fossil taxa either plot in regions of heavy overlap or fall completely outside the dietary morphospace. The exception is two unidentified taxa in Button (2018), which plot in a region inhabited only by terrestrial herbivores.

All GM studies of early-diverging theropod diet are performed in two dimensions, all are concerned with the upper jaw except for Schaeffer *et al.* (2019) and Shychoski & Snively (2008*a*) (who investigated the lower jaw), and all landmarks are placed in only lateral view except for in Button (2018) where they are placed in lateral and dorsal view. Landmarks of theropod skulls are variable. The only landmarks shared between the four studies of the upper jaw are the rostroventral extreme of the premaxilla and the contact between the jugal and maxilla (Brusatte *et al.*, 2012; Foth & Rauhut, 2013; Navalón, 2014; Button, 2018). Landmarks used in both studies of the lower jaw (Shychoski & Snively, 2008*b*; Schaeffer *et al.*, 2019) are the anterodorsal and anteroventral corners of the dentary, the dentary–surangular suture, the dentary–angular suture, and the articular glenoid. None of the studies include any landmarks on teeth, allowing toothed organisms to be examined using the same landmarks as those with varying extents of edentulism (Button, 2018; Wang *et al.*, 2020*a*). The importance of tooth morphology in lepidosaur (Smith, 1993) and mammal (Bergqvist, 2003; Pineda-Munoz *et al.*, 2017) diet raises questions of error introduced in this practice. A single study (D'Amore, 2009) studied theropod teeth in isolation using GM, but focused on penetration angle independent of diet.

(iv) Geometric morphometrics in extant bird feet. Tinius & Russell (2017) introduced the concept of using GM on bird claws, finding GM to be the only one of six claw angle measures capable of discriminating locomotor groups in the taxa studied [GM, the aforementioned methods of Feduccia (1993) and Peters & Görgner (1992) – although note their execution of Feduccia (1993) more closely resembles that of Fowler *et al.* (2009) –, one method applied to insects (Petie & Muller, 2007), one to lizards (Zani, 2000), and one theorised in but never applied to amniotes (Thompson, 1942)]. Hedrick *et al.* (2019*a*) were the first group to investigate dietary signal with geometric morphometrics. They found neither TM nor GM could discriminate between ecological groups. Abourachid *et al.* (2017) and Tsang *et al.* (2019) incorporate 3D models and landmarks into their studies, but Abourachid *et al.* (2017) uses them primarily to automate the collection of linear measurements for TM. Tsang *et al.* (2019) were able to discriminate both between predatory and non-predatory taxa and between sizes of prey that predators fed on. This level of precision presents a promising outlook for the future. While theoretically 3D GM provides the most accurate representation of claw shape, the merits of this technique have not yet been proved consistent in discrimination of avian ecology.

(v) Discussion. GM studies of theropod taxa both extant and extinct have been highly variable in both methodology and results. 3D GM studies of skulls, presumably capturing the largest amount of data about shape, tend to find strong relationships between form and diet at the family to superfamily level (Kulemeyer *et al.*, 2009; Olsen, 2017) that disappear when comparing larger-scale trends (Bright *et al.*, 2016;

Navalón *et al.*, 2018*a*; Felice *et al.*, 2019*a*). GM analysis of non-avian theropods is inhibited by the lack of known diets in the group. Certain groups, in particular oviraptorids, tend to cluster distinctly from other theropods (Brusatte *et al.*, 2012; Foth & Rauhut, 2013). A study incorporating both oviraptorids and caenagnathids [both beaked but respectively hypothesised to be herbivorous and carnivorous (Ma *et al.*, 2020)] may clarify if the segregation in these studies stems from edentulism or a dietary shift. Schaeffer *et al.* (2019) found considerable overlap of dentary morphospace in herbivorous and small carnivorous taxa. However, they coded all oviraptorosaurians as herbivorous (including caenagnathids) and all troodontids as small carnivorous [including those proposed as omnivorous (Holtz *et al.*, 1998; Torices *et al.*, 2018)] (Table S5 in Schaeffer *et al.*, 2019). This study highlights the necessity for calibrating dietary morphospaces with organisms whose diet is not controversial. When assumptions of herbivory in oviraptorosaurians and carnivory in avialans are discarded, the morphospaces become more distinct (Fig. S3C–E). The study also shows that landmark- and outline-based GM can provide similar information about skull shape, although comparisons between the two should be preceded by comparing thin spline plates to ensure the same shape changes are being modelled on each axis (Fig. S3E). While Button (2018) successfully combined extant and extinct theropods in skull GM analysis, he reported that only landmarks placed in dorsal/ventral view are effective at discriminating diet categories. Even then, his model appears to separate terrestrial feeders from other groups rather than any particular diet categories (his Fig. 33). Regardless, dorsal/ventral placement of skull landmarks excludes most published non-avian avialan specimens (Table S1). Navalón (2014) managed to assign non-avian avialans to a diet category using GM, but only in conjunction with mechanical advantage (see Section VI.3*b.iii*). In sum, skull shape tends to be a poor predictor of diet in extant avians. Studies of non-avian theropod morphospaces are limited by a lack of knowledge about the diet of taxa included, and still provide only mixed results. An attempt to combine avian and non-avian theropods shows poor resolution in the dietary morphospace and has limited application to fossil avialans. Therefore, GM of the non-avian avialan skull is recommended as at most a complement to a functional study (e.g. Navalón *et al.*, 2018*a*) if it is utilised at all.

Tsang *et al.* (2019) were able to distinguish non-predatory taxa (both non-raptors and scavenging raptors) from predatory taxa, and to partially distinguish between predators hunting large prey and small prey. Unfortunately, there are few fossil bird claws preserved in three dimensions. Large-scale 2D geometric morphometric analysis of bird claws has only been undertaken by Hedrick *et al.* (2019*a*) who failed to discriminate between any ecological groups. By their own admission, their ecological categories may have been too broad to allow for delineation (Hedrick *et al.*, 2019*a*, p. 9), and the ratio between the lengths of keratin sheaths and bone cores was a major element of the first principal component in their analysis (Hedrick *et al.*, 2019*a*, p. 6). It is possible that a similar study landmarking solely bone cores and with a more diverse set of ecological groupings [e.g. the ecological groups of Fowler *et al.* (2009), Glen & Bennett (2007) and Pigot *et al.* (2020)] may produce more useful results. Therefore, we recommend utilising the techniques of Tsang *et al.* (2019) where possible and an improved 2D GM framework where not possible.

(3) Functional studies

(*a*) Introduction

Of the two styles of functional study described herein, finite element analysis (FEA) is typically preferred for fossil dietary inference. Lever models, which provide measures of mechanical advantage (MA), are more commonly used as broad approximations that can be calculated easily and quickly. However, recent questions of the validity of FEA results in small animals (see Section VI.3*c.ii*) may apply to non-avian avialans [in which the largest taxa other than *Hesperornis* (Martin & Naples, 2008) and possibly *Gargantuavis* (Mayr *et al.*, 2020*a*) have a skull length less than 9 cm (Field *et al.*, 2018*b*)]. Both techniques, then, should be taken into consideration.

Relevant to both techniques are concerns of dimensionality and comparison taxa. In both cases, researchers will likely be restricted to 2D analysis due to reconstruction issues related to incomplete skull preservation (detailed in Section VI.1). But, if possible, validation studies with smaller sample sizes using both 2D and 3D techniques should be performed. A 3D model of the skull of *Ichthyornis dispar* is already published (Field *et al.*, 2018*b*), and the phalanges of *Mirarce eatoni* are three-dimensionally preserved (Atterholt *et al.*, 2018). Both are prime candidates for such studies.

Both FEA and lever models of fossil taxa are only interpretable in comparison with other models. The choice of comparative taxa then is of vital importance. To create a phylogenetic bracket, beyond the obvious extant avians, it is recommended that early-diverging non-avialan paravians with preserved meals (O'Connor & Zhou, 2019) are included. Certain lepidosaurian taxa that share similarities in dentition (Smith, 1993) with toothed avialans may be necessary to include as well.

(*b*) Lever modelling

(i) Introduction. The jaw of most animals acts as a third class lever: the joint acts as a fulcrum about which a load – the distal bone – is rotated by the effort – a muscle – attached in between (Fig. 3). Because jaws act as levers we can use mathematical principles to predict their behaviour. Examples include models utilising known muscle vectors to calculate bite vectors (Santana, Dumont & Davis, 2010) or to compare torque generation (Kiltie, 1982). However, when studying fossils, muscle size can often only be very roughly approximated. Instead, they tend to rely on the concept of MA.

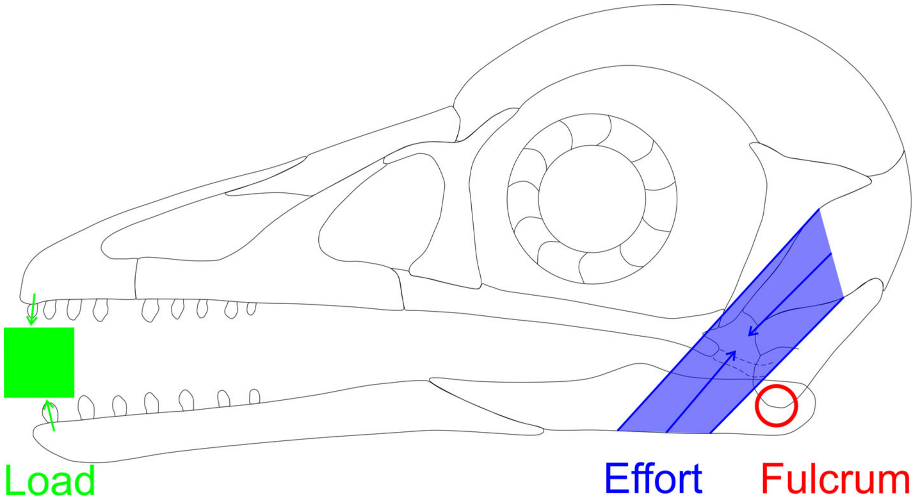


Fig 3. Third-class lever nature of animal jaws. Here a reconstruction of *Shenqiornis* after O'Connor & Chiappe (2011) is used as an example. The load (green) is represented as a square of theoretical foodstuff between the teeth. The effort (blue) is represented as a simplification of the *m. adductor mandibulae* complex (see Fig. 4A for full reconstruction of attachments). The fulcrum (red) is represented as the circled articulation between the upper and lower jaws.

The basic principle of MA was outlined in antiquity by Archimedes of Syracuse (1897, p. 192–194): the force exerted on a lever will be multiplied by the distance from it to the fulcrum (the inlever) and divided by the distance from the fulcrum to the load (the outlever). MA, then, is the useful ratio defined as the inlever divided by the outlever. In practical terms, it can be viewed as the ratio of the output force to the input force of a system, or as the factor by which the input force is multiplied to determine the output force. When mechanical advantage is lowered, the load is moved across a greater distance in the same amount of time and thus at a higher speed. As a trade-off, the output force is reduced.

In animal jaws the inlever is the distance from the site of adductor muscle attachment to the joint between the cranium and mandible. The outlever is the distance from that joint to the point at which the animal is biting down. The bite point is typically operationalised as the rostralmost or cranialmost point of the occlusal surface (either of the rhamphotheca or apices of teeth) (Ma *et al.*, 2020; Navalón *et al.*, 2018*a*). More rarely MA will be calculated for each tooth in the row (Sakamoto, 2010; Therrien *et al.*, 2016; Cox, 2017). Functionally, MA is seen as the trade-off between speed and power in skull architecture (Stayton, 2006; Dumont *et al.*, 2014; Corbin *et al.*, 2015; Adams *et al.*, 2019), although this trade-off is a simplification and can be circumvented (McHenry & Summers, 2011; Corbin *et al.*, 2015). Organisms feeding on immobile sources, such as plant matter, experience selective pressure for high jaw forces (high MA) that can efficiently process food. By contrast, those hunting mobile prey, such as insects or small vertebrates, experience selective pressure for jaws able to open and close quickly (low MA) in order to capture prey (Stayton, 2006; Corbin *et al.*, 2015; Adams *et al.*, 2019). Some trophic specialisations involving elongation of the snout such as nectarivory (Dumont *et al.*, 2014) or probe-feeding (Navalón *et al.*, 2018*a*) necessarily also reduce MA.

(ii) Lever models of extant birds. Small-scope studies of avian MA include those on cormorant (*Phalacrocorax*) species (Burger, 1978) and suliform birds (Carlos, Alvarenga & Mazzochi, 2017). Both found higher MA to correlate with capturing large prey and lower MA to correlate with hunting small, fast-moving prey. Corbin *et al.* (2015) examined trends in bite force across extant avians (especially among passerines) and in the process laid the groundwork for modern avian MA measurements. Corbin *et al.* (2015) found that bite force and velocity correlate positively and negatively with MA, respectively. They briefly and qualitatively comment on diet by predicting low MA in insectivorous birds and high MA in granivorous birds (Corbin *et al.*, 2015, p. 813). When analysed quantitatively the data they provide show only a weak correlation ($r^2 \approx 0.05$) between MA and diet. The correlation increases to moderate strength ($r^2 \approx 0.40$) when restricted to passerine taxa (Fig. S4). Olsen (2017) was the first to examine the relationship between MA and diet quantitatively, finding that increased MA correlates with increased consumption of leaves in Anseriformes. Navalón *et al.* (2018*a*) broadened the scope of this technique by applying it across extant avians, but found MA to explain dietary components only weakly. Their data show that MA better predicts the use of the beak during feeding (UBF), particularly when combined with beak curvature (Navalón *et al.*, 2018*a*). Further research may translate UBF into a set of possible dietary categories: taxa with tearing UBFs are often raptorial, cracking UBFs at least partly granivorous, etc. It is of note that all quantitative dietary analyses of avian skull MA have focused on the upper jaw, with those regarding the lower jaw (Burger, 1978; Carlos *et al.*, 2017) being purely qualitative (but see Fig. S4).

(iii) Lever models of fossil theropods. Sakamoto (2010) and Brusatte *et al.* (2012) calculated MA across the tooth row for a variety of non-ornithothoracine tetanurans and found lower values of MA in smaller taxa. This was tentatively interpreted as smaller taxa being adapted for hunting more agile prey. Sakamoto (2010, p. 3330), however, proposes the potential for saw-motion biting in dromaeosaurids feeding on large prey. Noticeable in their figures [Fig. S6 in Brusatte *et al.* (2012); Fig. 2b in Sakamoto (2010)] but not commented on in the text is the high MA of oviraptorosaurians, studied in depth by Ma *et al.* (2017, 2019, 2020). Oviraptorosaurians consist of two distinct groups, Oviraptoridae and Caenagnathidae (Funston *et al.*, 2018). Only the Oviraptoridae was included in previous studies (Sakamoto, 2010; Brusatte *et al.*, 2012). Ma *et al.* (2017) in passing, and later with statistical rigour (Ma *et al.*, 2019), noted that caenagnathids tend to have a lower MA than oviraptorids. This was proposed to reflect herbivory in oviraptorids and carnivory in caenagnathids. Caenagnathid MA indeed falls within ranges of other theropods, while oviraptorid MA is significantly higher (Ma *et al.*, 2020). Ma *et al.* (2020) introduce MA measurements of *Jeholornis* as well as anchiornithines and scansoriopterygids. Button & Zanno (2020) include six measures of MA, five additional mechanical indices, and 22 traditional morphometric ratios believed to have functional implications in diet. While the study is incredibly effective at delineating herbivory and carnivory as well as distinct herbivorous strategies, the lack of variance explained by the principal components used is problematic for use in diagnosing diet (discussed further in the next section). Navalón (2014) is the only MA study to focus chiefly on non-avian avialans. Combining MA with GM, it recovers *Confuciusornis* and *Sapeornis* as herbivorous and *Eoconfuciusornis* as omnivorous. While it presents initial promise, additional MA measurements of the fossil taxa should be taken before broader comparisons are made (Guillermo Navalón, personal communication 2020), and a subsequent study discussed above that expanded the avian taxa included (Navalón *et al.*, 2018*a*) resolved diets much less effectively. This highlights the importance of including not only extant taxa but a *wide range* of extant taxa for ecological comparisons.

(iv) Discussion. While MA has proved an effective predictor of diet in lepidosaurs (Stayton, 2006) and small mammals (Dumont *et al.*, 2014; Adams *et al.*, 2019), Navalón *et al.* (2018*a*) report minimal association between diet and MA across extant birds. This is likely due to the fact that, as they point out, similar diets can often be associated with radically different foraging strategies (Navalón *et al.*, 2018*a*, p. 423). In particular, only some granivorous birds crack open the hard outer coating of seeds (Prosser & Hart, 2005). Those that do not de-husk in this way instead crush them in the muscular gizzard (Janzen, 1981). Confuciusornithids and enantiornithines are not believed to possess a gizzard (O'Connor & Zhou, 2019) meaning they would not be susceptible to this source of signal interference. With this trend accounted for, mechanical advantages above 0.15 in Navalón *et al.* (2018*a*)'s data set appear to correspond to herbivory while those below 0.15 correspond to carnivory, nectarivory, and frugivory, although the latter is complicated by the inclusion of nuts as fruits rather than with seeds. For instance, *Anodorhynchus* has an MA near 0.35 (Fig. 6 in Navalón *et al.*, 2018*a*) and is coded as 70–100% frugivorous depending on species (Wilman *et al.*, 2014). However these 'fruits' are palm nuts (Faria *et al.*, 2008) which are hard enough that a close relative has been used as a model for construction materials (Staufenberg, Graupner & Müssig, 2015). Together, these factors make MA promisingly informative of diet in confuciusornithids and enantiornithines. MA may still provide insight into other non-avian avialans, but low MA cannot definitely rule out herbivory in these other groups.

The broad scope of the study by Button & Zanno (2020), combining MA with TM and some less commonly used functional indices, is highly effective at delineating diet. Taxa such as ornithopods and sauropods that are well established as herbivorous occupy a region of the morphospace distant from theropods well established as carnivorous (e.g. tyrannosauroids). Their methods, at first, appear promising to diagnose the diet of non-avian avialans. However, this study was intended to track stepwise evolutionary changes, not to determine diet, so several issues arise when adapting it for that purpose. While Button and Zanno cite their resolution as a reason to incorporate large complexes of characters in dietary analyses (Button & Zanno, 2020, p. 163), the small amount of variance explained by their graphs makes this less than ideal. The authors perform statistical operations within the first three principal components of morphospace which only explains 45.7% of the total variance observed; nine principal components are required to pass 70% explanation (their Data S2) as is the common standard (Jolliffe & Cadima, 2016, p. 4). PCA functions to reduce the number of dimensions worked within an analysis by creating axes that explain large amounts of the variance. But once data encompasses a large number of dimensions it is unlikely that principal components will be able to explain adequate amounts of variance in the three dimensions humans can easily work in (Brown, 2009). It is therefore recommended here that the number of variables investigated are reduced to reduce the dimensionality of the data [but see Guillerme *et al.* (2020) for alternatives to dimension reduction]. Of the 34 measurements taken by Button & Zanno (2020), only nine (C2–8, 22, 23) can be applied to compression fossils and have proved effective to our knowledge at discriminating diet among extant groups other than ungulates. We found that when only these measurements are used, the first three principal components explain more than 70% of the variance while maintaining the same general structure of the morphospace (Fig. S5). Data can be further reduced as the MAs for each individual muscle group have a similar influence on the principal components (Fig. S2A in Button & Zanno, 2020) and represent redundant information. They can be merged into anterior and posterior jaw-closing MA. Ma *et al.* (2020) additionally define jaw-opening MA and two other functional indices which have proved discriminative of diet across a wide range extant taxa. We recommend combining these studies to, in total, three forms of MA and five accompanying functional indices (Fig. 4). However, unlike these two studies which measure MA based on the lower jaw, we recommend measurements of the upper jaw after the sensitivity analysis of Brusatte *et al.* (2012). They found the upper jaw, not the lower jaw, has the greatest effect on the overall MA of the jaw system (their Fig. S27). Transition from the lower to upper jaw will necessarily require adaptation of landmarks from which measurements are taken. Landmarks at the anterior and posterior of the occlusal margin, attachment sites of the adductor muscles, and those for *m. depressor mandibulae* will refer to their locations on the upper jaw rather than the lower jaw. The articular glenoid of the surangular will be replaced with the articular condyle of the quadratojugal (Fig. 4B–D). All other landmarks

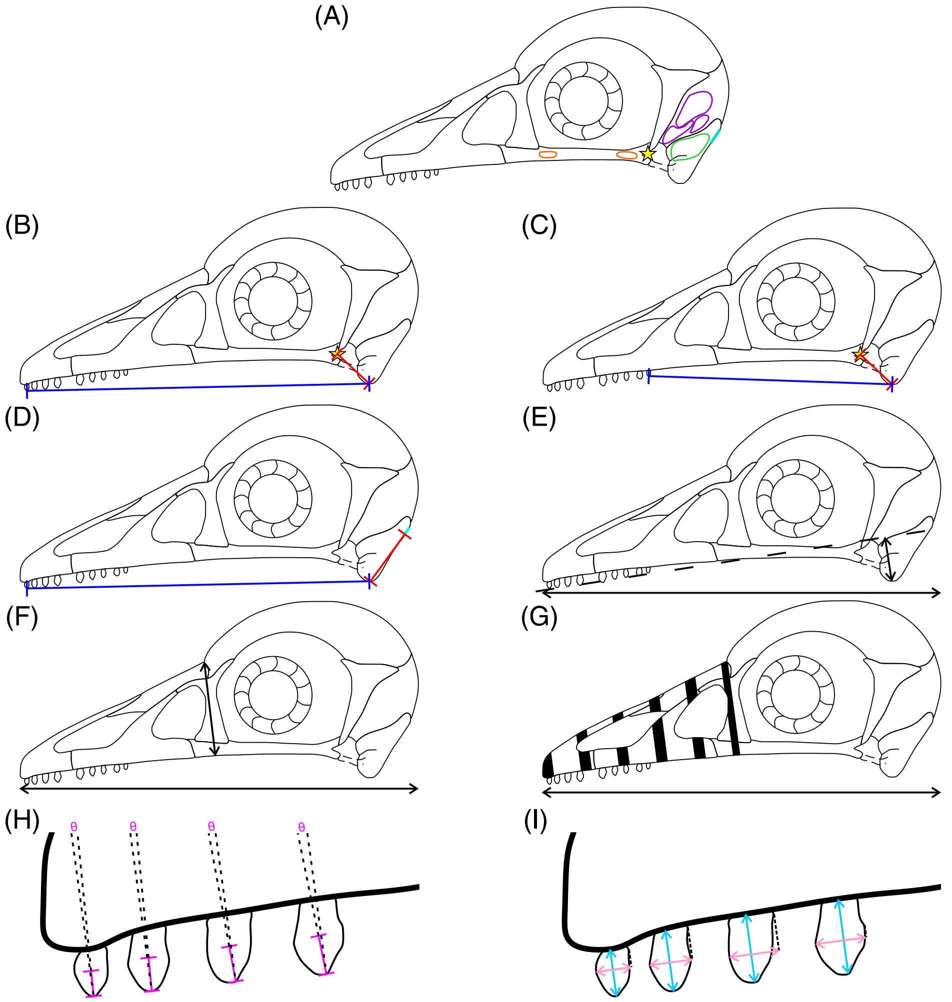


Fig 4. Illustration of the functional measurements used by Ma *et al.* (2020) as well as characters 22 and 23 from Button & Zanno (2020). The example is a reconstruction of *Shenqiornis* after O'Connor & Chiappe (2011). C2–7 of Button & Zanno (2020) are combined into anterior and posterior jaw-closing MA as defined by Ma *et al.* (2020). Articular offset is identical between the two. (A) Reconstruction of skull muscle attachments after Holliday (2009). Reconstructions of *m. adductor mandibulae externus* (purple) and *m. adductor mandibulae posterior* (green) are more certain while reconstruction of *m. pterygoideus* (orange) is tentative due to the uncertain nature of the pterygoid in enantiornithines (Chiappe *et al.*, 2001; O'Connor & Chiappe, 2011). The yellow star is the centroid of the irregular shape bounding all attachments, treated as the centre of force for adduction. Uncertainty of attachment area size precludes more precise weighting of the attachment centroid. The abductor muscle for the jaw, the *m. depressor mandibulae* (cyan), attaches perpendicular to the viewing plane (Lautenschlager *et al.*, 2014*a*) and so is represented as a line along the back of the skull. (B–D) Diagrams illustrating inlevers (red) and outlevers (blue) for calculating (B) anterior jaw-closing mechanical advantage, (C) posterior jaw-closing mechanical advantage, and (D) jaw-opening mechanical advantage. (E–G) Illustrations of measurements to calculate: (E) relative articular offset, (F) relative maximum rostral height, and (G) relative average rostral height. See Ma *et al.* (2020) for an explanation of calculations. (H, I) Close-up of the premaxilla indicating measurements of (H) C22 tooth angle and (I) C23 tooth slenderness index. See Data S4 in Button & Zanno (2020) for an explanation of calculations.

remain unchanged from those in Button & Zanno (2020) and Ma *et al.* (2020).

(*c*) Finite element analysis

(i) Introduction. Finite element analysis (FEA) is a technique originally applied to structural engineering. In it, irregular bodies are partitioned into a mesh of simple shapes, the 'elements', in order to predict the response of the body to a given load (Bathe, 2014). Applications in palaeontology began with structural predictions of depth adaptations in cephalopods (Daniel *et al.*, 1997). Soon after it was used in its most common palaeontological application today: vertebrate jaws (Rayfield *et al.*, 2001). Bright (2014) provides an effective review of techniques up until 2014, but several notable advances have taken place since. The rise of formalised digital reconstruction (Lautenschlager, 2016) augmented by quantification of skeletal asymmetry (Hedrick *et al.*, 2019*c*) has enabled analysis of specimens previously considered hopeless cases. These techniques may allow for a greater number of studies incorporating both the upper and lower jaw. Studies taking both into account (Wroe *et al.*, 2007; Moreno *et al.*, 2008; Wroe, 2008; Lautenschlager *et al.*, 2013; Attard *et al.*, 2014, 2016; Adams *et al.*, 2019) find differing peak Von Mises (VM) stress [a summary statistic of distortion energy in a body (Ugural & Fenster, 2012, p. 189–190)] and differing distribution of VM stresses between the upper and lower jaw. These differences could in theory cause overestimation of jaw strength by only using the upper or lower jaw if the unmeasured element is the limiting factor in jaw strength. To our knowledge no study has been undertaken to explore the potential significance of this error, but no study of the full jaw has reported differing dietary signals between the upper and lower jaws.

Formalisation of applying 2D FEA techniques to organisms (Marcé-Nogué *et al.*, 2013; Neenan *et al.*, 2014) allows FE models to be constructed and analysed much faster with a lower prerequisite of computing power. It also allows for analysis of compression fossils. Simplifying 3D bodies into 2D outlines inherently requires assumptions that will induce error. Most commonly in palaeontology these assumptions are of planar strain, where strain in the excluded dimension is assumed to be negligible, or planar stress, where the stress exerted on the excluded dimension is assumed to be negligible. Planar strain is known to introduce error into sheer strain predictions in bone (Verner *et al.*, 2016). Planar stress requires a known thickness of material (Marcé-Nogué *et al.*, 2013) that will likely vary over models. When thickness is known, creating 3D extrusion models from outlines has proved more valid than 2D assumptions (Morales-García *et al.*, 2019). Plane stress assumptions, then, have little reason for use. For compression fossils, in which thickness is unknown, it is recommended to use planar strain assumptions so that error will be similar across studies. The exception to this recommendation is in groups like ornithopod dinosaurs where significant sheer strain is theorised to be involved in feeding (Rybczynski *et al.*, 2008).

Finally, the comparison of FEA outputs has undergone a major paradigm shift. In the past, FE models have been compared qualitatively (Rayfield, 2005), or their peak (Rayfield *et al.*, 2007) and/or average (Rayfield, 2011*b*) strength criteria compared quantitatively. Both quantitative methods, however, are sensitive to the ways the FE model is constructed and require considerable mathematical correction (Marcé-Nogué *et al.*, 2016). The amount of data required for correction renders comparison across studies nearly impossible. Marcé-Nogué *et al.* (2017) introduced the intervals method as a quantitative comparison robust to model construction. Ultimately, it determines the percentage of the model area/volume which experiences a given interval of stress. These percentages can then be compared directly in a histogram or plotted into principal component space. The intervals method has proved effective in subsequent feeding studies (Zhou *et al.*, 2019; Coatham *et al.*, 2020; Miller *et al.*, 2020), and is recommended here.

(ii) The strength criterion. A strength criterion is the measure of a model by which a researcher judges it. Typically, the lower the value of a strength criterion, the stronger the model. The strength criterion for biological FEA has traditionally been the peak VM stress (Fig. 5A), after the recommendation of Dumont *et al.* (2009). Dumont *et al.* (2009) justify the use of VM stress to predict failure with a textbook on machine component design (Juvinall & Marshek, 2011). By contrast, studies comparing failure criteria in models of human femora found that maximum principal strain, not VM stress, best predicted the location of, and load required for, fracture (Schileo *et al.*, 2008; Yosibash, Tal & Trabelsi, 2010). This criterion remains in use in the medical community as the most effective method of predicting fracture risk in patients (Dahan *et al.*, 2019). This discrepancy likely originates in the use of a failure criterion for machine components, abiotic metallic objects, to describe the behaviour of bones, living composite ceramic (*sensu* Carter & Norton, 2007) objects. The textbook takes into account two forms of failure in machine parts, plastic distortion and fracture (Juvinall & Marshek, 2011, p. 250). Unlike metal, when bones deform plastically they are often capable of rapid repair and light use during rest (Vogel, 2013, p. 342). Therefore, fracture is the more critical component of bone failure. The work of fracture of commercial steel (Tattersall & Tappin, 1966), as one might find in machine components, is nearly 20 times that of bovine femora and still an order of magnitude beyond that of even impact-resistant antler (Currey, 1999). This means that once cracks form in bone they propagate much more readily than in steel. Here it is proposed that principal strain of finite element models best predicts failure in bone because surficial cracks in bone, indicated by extreme principal strain at the surface, propagate readily to the point of failure under normal loading conditions. This allows principal strain-based FEA (Fig. 5B) to predict areas of weakness more precisely (Schileo *et al.*, 2008) and with greater validity (Yosibash *et al.*, 2010)

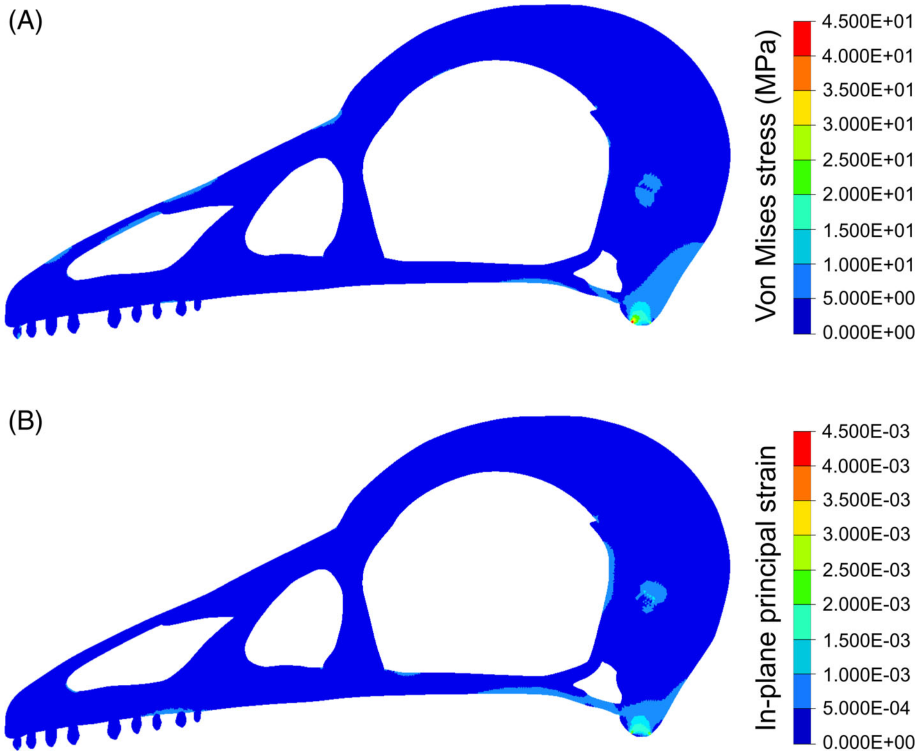


Fig 5. Comparison of finite element analysis (FEA) failure criteria. Comparisons are made using a reconstruction of the upper jaw of *Shenqiornis* after O'Connor & Chiappe (2011). All models use isotropic material properties of ostrich mandible (Rayfield, 2011*a*), make plane strain assumptions, constrain the articular condyle in all directions, constrain the first premaxillary tooth in dorsoventral translation, and load the skull with an equivalent amount of force. Force was applied using the macro in Morales-García *et al.* (2019) which replicates muscle fibres, with attachments based on those pictured in Fig. 4. Legends are scaled to make the models look as similar as possible. (A) Von Mises (VM) stress. (B) Principal strain. Note that while both map very similarly onto the model, the region of high distortion at the occipital condyle is smaller in B than A. In human studies, this smaller region represents a narrower margin of error for the location of failure (Schileo *et al.*, 2008; Yosibash *et al.*, 2010). This implies greater validity for principal strain as a strength criterion.

in bones. For these reasons we suggest that future studies should evaluate the strength of models based on differences in maximum principal strain, not VM stress. The FEA software Abaqus (Dassault Systèmes, France), Ansys (Ansys, Inc., USA), COSMOSWorks (Dassault Systèmes, France), Optistruct (Altair Engineering, Inc., USA), Strand7 (Strand7 Pty. Ltd., Australia), and VOX-FE2 (Banglawala *et al.*, 2015) are already capable of this.

It is worth noting that the maximum principal strain criterion may decrease in validity with decreasing body mass, due to the decreasing importance of fracture in smaller organisms. Work of fracture is a relationship between work (energy) and surface area. The effective work done by an animal and the surface area created by breaks scale differently with size. In an isometric scenario one would expect work output to increase linearly with mass (m^1). It is the product of distance (i.e. length), which scales with $m^{0.33}$, and force, which is known to scale with muscle cross-sectional area at $m^{0.66}$ (Froese, 2006). The surface area of a crack in bone, like any other surface (Froese, 2006), should scale with $m^{0.66}$. As work scales at a higher rate than the surface area it creates in cracks, one would expect cracks in bones to propagate more easily at higher body masses. Conversely at low body masses cracks propagate less readily relative to loading. Thus, in smaller organisms, the formation of cracks *via* principal strain of the surface may impose only a weak selective pressure. McIntosh & Cox (2016, p. 8) point out a similar trend in VM stress. Small animals working far from the yield strength of bone tend to experience selection towards mechanical efficiency of biting over minimising VM stress in the skull. Mechanical advantage analysis of lever models (see Section VI.3*b*) may be more appropriate for dietary inferences in small animals where these pressures hold sway. What size range(s) this shift in selective pressure affects, potential allometric complications [e.g. phylogenetic (Wroe, McHenry & Thomason, 2005) or dietary (van der Meij & Bout, 2004) influences on scaling], and what other measures of feeding efficiency may be applicable [e.g. total strain energy as proposed by Dumont *et al.* (2009)] all warrant further study.

(iii) Finite element analysis in fossil theropod skulls. Rayfield *et al.* (2001) performed FEA on a 3D model of the

upper jaw of *Allosaurus fragilis*. Seeing the skull could withstand stresses greater than predicted bite forces, they proposed the animal fed by slashing its jaws at high velocity into prey. Rayfield *et al.* (2007) combine FEA of extinct and extant taxa, comparing spinosaurid theropods and extant crocodilians. From their analysis, they predict piscivory in *Baryonyx walkeri*. Shychoski & Snively (2008*a*) found the mandibles of adult tyrannosaurids to be more resistant to stress than that of juvenile tyrannosaurids or non-tyrannosaurids, proposing ontogenetic niche partitioning. These results are not currently in preparation for full publication (Eric Snively, personal communication 2020). Torices *et al.* (2018) performed FEA on individual theropod teeth. They found *Troodon* teeth experienced higher stresses than other taxa when loaded non-optimally (i.e. at an angle other than the scratches observed in dental microwear). This is interpreted as its teeth being poorly adapted for struggling prey, and thus *Troodon* more likely fed on plant matter and/or small animals (Torices *et al.*, 2018). Lautenschlager *et al.* (2013) study both the upper and lower jaws of a theropod, finding the lower jaw to display higher VM stress in all loading conditions than the upper jaw. They also apply postcranial forces to the skull, proposing that deconstruction powered by the cervical muscles compensated for low bite forces. This was expanded on in the follow-up study (Lautenschlager, 2017) in which loadings were varied in orientation to compare skulls' adaptation for specific feeding styles. This technique forgoes direct modelling of cervical action and instead simply investigates the resultant forces the jaw would experience in contact with food. Miller *et al.* (2020) incorporate a true fossilised rhamphotheca into an FE model. They found *Confuciusornis sanctus* to be most similar to an extant sally striking predator or general herbivore, the only FEA results from a non-avian avialan so far. Cost *et al.* (2019) present the most complex dinosaur FE models to date, with beams given ligament properties to connect bones. These were used to compare the skull of *T. rex* to that of an extant avian and lepidosaur. This study was concerned with the presence or absence of cranial kinesis, but their increased accuracy of reconstruction used in a manner like Lautenschlager (2017) and Rayfield *et al.* (2007) could show promise for illuminating dietary preferences and feeding strategies.

Two FEA studies on the skulls of fossil avians have been undertaken. Degrange *et al.* (2010) compared the stress distribution in the upper jaw of *Andalgalornis steulleti* to those of *Haliaeetus albicilla* and *Cariama cristata*. They found *Andalgalornis* to experience the lowest stresses in models of pull-back feeding, analogous to extant accipiters. Attard *et al.* (2016) compared five genera of moa (Dinornithiformes) to two extant ratites in a variety of loading conditions to see which they were best suited to. They found that loadings with the lowest stress reflected observed feeding styles of the extant ratites, and that those of the moa match consumulite evidence (Figs S6 and S7 in Attard *et al.*, 2016).

(iv) Finite element analysis in extant bird skulls. Herrel *et al.* (2010*b*) and Soons *et al.* (2010) performed similar FE analyses on the upper jaws of Darwin's finches. Both found that finches that ate harder foods experienced lower peak stresses, and even that taxa known to feed using the tip or base of the beak experienced lower peak stresses when loaded there. Subsequent studies of Darwin's finches (Soons *et al.*, 2015) support these initial results and emphasise the role of keratin in stress dissipation and the necessity of including it in FE models. All other applications of FEA to extant birds have been validation studies performed on a Java finch *Lonchura oryzivora* (Soons *et al.*, 2012*b*), toco toucan *Ramphastos toco* (Seki, Mackey & Meyers, 2012), and ostrich *Struthio camelus* (Rayfield, 2011*a*; Cuff, Bright & Rayfield, 2015). The Java finch study was qualitatively evaluated as showing a "fairly good correspondence" between the model and physical specimen (Soons *et al.*, 2012*b*, p. 190). The same was said of the toucan study despite the *ex vivo* stress/strain curves provided appearing disjointed from those predicted by the model (Fig. 7 in Seki *et al.*, 2012). The ostrich studies (Rayfield, 2011*a*; Cuff *et al.*, 2015) were more thorough in their criticism. They determined that strain patterns (e.g. areas of lower and higher strain and the range of strains experienced) were reflected in FEA but absolute strain and strain angles were not, particularly in the cranial region of the skull. The conclusion these studies support, whether directly or by *post hoc* interpretation of their data, is that FEA is effective at showing stress/strain distributions in bird skulls and thus reflecting dietary habits. However, modelling limitations prevent them from providing any absolute information about *in vivo* strain states. Similar conclusions when testing extant crocodilians (Porro *et al.*, 2011; Reed *et al.*, 2011; Sellers *et al.*, 2017) and mammals (Kupczik *et al.*, 2007; Bright & Rayfield, 2011; Godinho *et al.*, 2017) imply this is true across amniotes.

(v) Finite element analysis in extant bird claws. Birn-Jeffery & Rayfield (2009) were the first to apply FEA to bird claws, and reported preliminary success discriminating between both locomotor and predator/non-predator categories with 2D FEA. A full study has not yet been published. Tsang *et al.* (2019) were the first to analyse 3D FE models of bird claws. FEA revealed differences in strength that, while not easily identified as variables in GM analysis, were diagnostic of the behaviours associated with raptorial predation (Goslow, 1972; Csermely & Gaibani, 1998; Ward *et al.*, 2002). The broad scope and robust results of this study are promising for detection of raptorial behaviour in fossil species. Unfortunately, its application may be limited by the large number of fossil birds known only from compression fossils.

(A) Robotic modelling. While not a form of FEA, the modelling techniques of Backus *et al.* (2015) more strongly resemble FEA than any other techniques commonly applied in palaeontology. Their technique is herein dubbed 'robotic modelling', due to its original application in the construction of robotic hands (Dollar & Howe, 2011; Backus *et al.*, 2014). Their approach models non-ungual phalanges as beams and ungual phalanges as semicircles, with actuators acting as the digital flexor tendons. They evaluate models based on the tensional force exerted in order to maintain a grip with given parameters. Backus *et al.* (2015) were primarily concerned with the differences in actuation between passerine and non-passerine feet: passerine birds have digital flexors inserted distally and proximally while non-passerines have only distal digital flexors. They found both on average to be equally well equipped for grasping but passerine actuation to be uniquely well adapted for minimising forces required to perch. While used to compare perching and grasping behaviours in this study, this technique could easily be expanded for use in more granular studies. Future avenues include comparing adaptations for raptorial behaviour in which prey is completely encircled in the toes (e.g. owls) and held in an open grip (e.g. accipiters) (Fowler *et al.*, 2009), with these results compared to those of fossil taxa.

(vi) Finite element analysis in fossil theropod claws. Birn-Jeffery & Rayfield (2009) incorporated maniraptorans – including the early-diverging avialan *Archaeopteryx* – into their 2D FEA analysis of bird claws. They only report results for *Archaeopteryx*, with stress regimes aligning with those of arboreal perching taxa. Manning *et al.* (2009) were the first full study to apply 3D FEA to a theropod claw. They tested an earlier hypothesis based on a practical model (Manning *et al.*, 2006) that dromaeosaurids utilised their recurved second digit unguals for climbing rather than tearing through flesh. Creating fixed points in a model of a *Velociraptor* claw to replicate use during climbing, the team found the claw to experience levels of stress well below the yield strength of bone under a loading of the estimated body mass of *Velociraptor*. Thus, they proposed the animal could have supported its body weight on the claw during climbing (Manning *et al.*, 2009). Unfortunately, validation studies of FEA in animals find that only patterns of stress/strain distribution, not absolute values, are predicted by FEA (Bright & Rayfield, 2011; Rayfield, 2011*a*; Cuff *et al.*, 2015; Stansfield, Parker & O'Higgins, 2018). As such, this interpretation is called into doubt. Furthermore, it is unclear how their climbing load simulation differs from a theoretical simulation of slashing (both would be loaded at a point slightly proximal to the claw apex and in a direction subparallel to the chord of the claw arc). This work, then, is regarded as inconclusive in its palaeobiological reconstruction. The work of Lautenschlager (2014) on therizinosaurian unguals provides a superior framework for modelling claw use. Manual claws were distinctly loaded as if digging, hooking and pulling, or piercing a substrate. The lowest VM stresses were seen in piercing simulations in all but *Alxasaurus elesitaiensis*. While not linked directly to diet in the study, behavioural optimisation of claws may provide information regarding niche and food available [e.g. fossorial adaptations likely indicate consumption of arthropods (Smith, 1982) or tubers (Andersen, 1987)].

(vii) Discussion. Reconstructions of non-avian avialan skulls are recommended to remain in 2D for the time being (see Section VI.1), and so FE models will have to remain 2D as well. However, indications of significant lateroflexion in the neck (see Section II.3*a*) would suggest that 2D models will not fully capture typical loading. Analysis of these models should, for reasons described above, incorporate planar strain assumptions and examine principal strain as a failure criterion using the intervals method (Marcé-Nogué *et al.*, 2017). However, strength may be less strongly selected for than efficiency in smaller animals (Dumont *et al.*, 2014; McIntosh & Cox, 2016). If true, total strain energy may better reflect the efficiency of jaws (Dumont *et al.*, 2009) and thus selection for a given diet. With that said, strength-based FEA of Darwin's finches, smaller than many non-avian avialans, was able to provide a clear dietary signal (Herrel *et al.*, 2010*b*; Soons *et al.*, 2010). Size concerns then may be irrelevant in avialans. It is therefore suggested here that both principal strain and total strain energy be compared to determine which best explains diet among small extant avian taxa. The superior metric can then be applied to fossil avialans. Finally, images of extant avian skulls should ideally be taken as radiographs and modelled with their original keratin thickness so as to model the effects of the rhamphotheca (Soons *et al.*, 2012*a*). However the precise thickness of the rhamphotheca seems to have little effect on stress/strain distributions or magnitudes in bird mandibles in our simulations (Fig. 6). So, in lieu of radiographs, surface photographs may be used for model construction as well (Miller *et al.*, 2020). When possible, fossilised rhamphothecae (see Section II.3) should be modelled directly in FE models of extinct taxa (Miller *et al.*, 2020). Otherwise, hypothetical rhamphothecae can be crafted for extinct taxa as in *Erlikosaurus* (Lautenschlager *et al.*, 2014*b*) with refinement by subsequent studies of beak shape in relation to the underlying bone (Button, 2018; Urano *et al.*, 2018; Miller *et al.*, 2020). Note the sensitivity analyses of Lautenschlager (2017) and Soons *et al.* (2012*a*) find keratin inclusion to affect stress and strain magnitudes but not patterns. Thus, comparisons within a skull, e.g. comparing various theoretical loadings, should not need to incorporate rhamphothecae. They may also then be unnecessary when comparing beaked avialans to one another, and only needed when toothed avialans are examined.

Cranial kinesis plays a major role in feeding in Neognathae (Zusi, 1984; Bout & Zweers, 2001; Bhullar *et al.*, 2016; absent in palaeognaths Gussekloo & Bout, 2005) and thus excluding it will undoubtedly alter the principal strain or total strain energy modelled from the *in vivo* conditions. Conversely, levels of kinesis similar to those in Neognathae are believed never to have been reached in non-neognathous avialans (Bhullar *et al.*, 2016; Hu *et al.*, 2019) with the possible exception of *Gobipteryx* and *Ichthyornis* (Hu *et al.*, 2019, p. 19576). Incorporating connective structures to allow kinesis to present itself as in Cost *et al.* (2019) will in theory increase the validity of models, although our attempts to incorporate them into the skull of an enantiornithine have proved troublesome. Jointing of the skull imposes unreasonable dislocation of the jugal, quadrate, and quadratojugal (Fig. 7A, B). This may be an inherent flaw either with 2D simplification of the skull or the reconstruction itself, although sensitivity analyses showed a considerable influence of the cross section and Young's modulus used for connective tissue in the model (Fig. 7C). This issue can only be addressed with further research of suture and ligament physical properties. Avoiding kinesis by loading models of the upper jaw posterior to the bending zone of extant birds would mean loading at the maxilla/jugal contact in many taxa (Fig. 1 and Table 1 in Zusi, 1984), well cranial to the tooth row in most toothed avialans. The exclusion of kinesis in Darwin's finches seemed to have no major repercussions on FEA reflecting diet (Herrel *et al.*, 2010*b*; Soons *et al.*, 2010) but this likely stems from similar levels of cranial kinesis in all studied groups. To avoid issues in modelling kinesis, comparison between the akinetic lower jaws of taxa is recommended here as a simple solution. While studies including both jaws in FEA (Wroe *et al.*, 2007; Moreno *et al.*, 2008; Wroe, 2008; Lautenschlager *et al.*, 2013; Attard *et al.*, 2014, 2016; Adams *et al.*, 2019) have recovered differing peak VM stresses between the jaws and different stress distributions (thus making models of both jaws ideal) the information has not conflicted in terms of dietary interpretation.

Application of FEA to determining raptorial use of the pes is promising after the results of Tsang *et al.* (2019). However, because their predatory groupings differed markedly on dorsal and lateral curvatures (their Fig. S2), which is not accounted for in 2D FEA and not known in compression fossils, larger 2D FEA studies should be preceded by a comparative analysis of 2D and 3D FE models (see Section VI.3*a*). The reported success of Birn-Jeffery & Rayfield (2009) shows promise for their correspondence, but a lack of published data renders a full proof-of-concept necessary. Refinement of raptorial use type to more precise grips could be achieved by modifying the work of Backus *et al.* (2015). A pilot study will be necessary to determine in extant raptors if their method works using the curvature of ungual bones rather than claw sheaths. If not, reconstructions of keratin sheaths will be necessary [from avialans preserving impressions of the sheath, e.g. AGB-6997 (Wang *et al.*, 2020*b*), DNHM D2945/6 (Chiappe *et al.*, 2014), GMV-2130 (Chiappe *et al.*, 1999), GSGM-05-CM-004 (O'Connor *et al.*, 2016*a*), IVPP V18687 (Hu, O'Connor & Zhou, 2015)]. While Lautenschlager (2014) provides an outline for modelling the effectiveness of varying claw uses, the use of claws directly in acquiring food is rare among extant avians. Piscivorous raptors are known to pierce fish with their talons in order to maintain grip (Fowler *et al.*, 2009, p. 7), so claw FEA may prove useful to test the hypothesis of similar habits in bohaiornithids (Wang *et al.*, 2014*b*). Digging with the claws plays a major role in foraging in Megapodidae (Friedmann, 1931) and a more minor role in shorebirds (Jacobs, 1982). Beyond these cases, claws tend to play a minor role in prey manipulation compared to the whole toes (Clark, 1973; Csermely & Gaibani, 1998; Sustaita *et al.*, 2013), at most increasing traction (Ramos & Walker, 1998; Fowler *et al.*, 2009; Backus *et al.*, 2015) or elongating the toes to increase grasp reach (Csermely, Bertè & Camoni, 1998; Fowler *et al.*, 2009). While general strength trends appear useful in parsing raptorial behaviour, the lack of functional importance of claws outside specialised groups renders more specific loading comparisons a lower priority in lieu of established hypotheses to test.

(4) Complications applicable across physical approaches

While eating is essential to an organism's survival, myriad unrelated factors play into the form and function of body parts. These factors are confounding variables in any

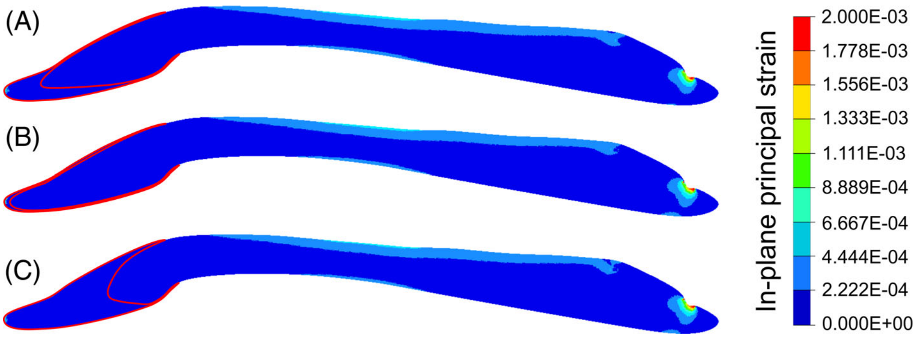


Fig 6. Sensitivity analysis of rhamphotheca thickness in the red-tailed hawk *Buteo jamaicensis*. Comparisons are made using a radiograph of the lower jaw of *Buteo jamaicensis* after Smith & Smith (1990). All models use isotropic material properties of ostrich mandible and rhamphotheca (Rayfield, 2011*a*), make plane strain assumptions, constrain the articular glenoid in all directions, constrain the rostral tip of the rhamphotheca in dorsoventral translation, and load the mandible with an equivalent amount of force. Force was applied using the macro in Morales-García *et al.* (2019) which replicates muscle fibres, with attachments based on Lautenschlager *et al.* (2014*a*). A bite force of 9.0 N was calculated using the regressions of Sustaita & Hertel (2010) assuming a body mass of 1 kg. The rhamphotheca is highlighted with a red outline. Length of the jaw overall is kept constant with the bone underneath modelled (A) realistically (i.e. as in the radiograph), (B) with a greatly thinned rhamphotheca, and (C) with a greatly thickened rhamphotheca. Note that the strain magnitude and distribution in each is nearly identical. Thus, the precise thickness of the rhamphotheca appears unimportant when constructing 2D FE models of avian lower jaws.

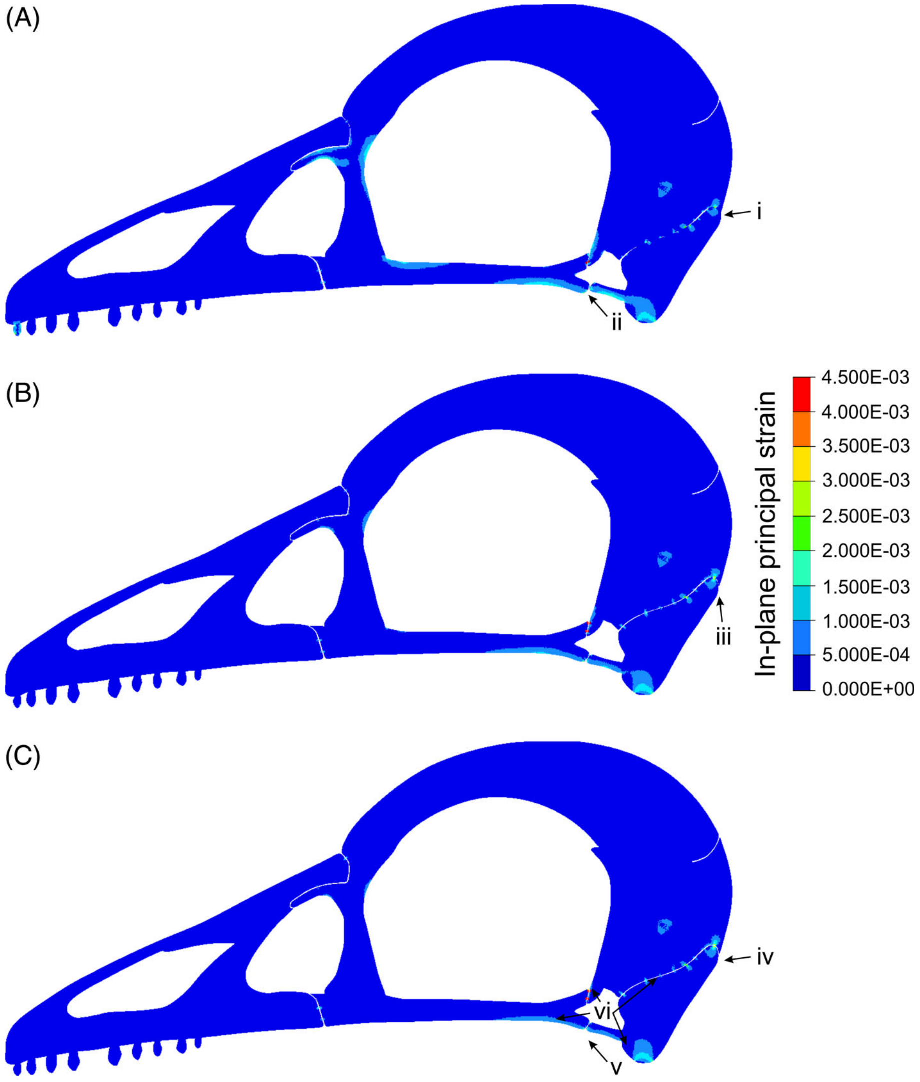


Fig 7. Comparison of construction of finite element models with flexible connective tissue using a reconstruction. Comparisons are made using the upper jaw of *Shenqiornis* after O'Connor & Chiappe (2011). Base models were constructed as in Fig. 5. Breaks were created in the model and filled with beam elements to replicate connective tissue, after the techniques of Cost *et al.* (2019). A bite force of 9.3 N was chosen to be similar to those recorded by Corbin *et al.* (2015). (A) Beams using the cross-sectional area and Young's modulus of rat cranial sutures, as detailed in Chien *et al.* (2008). These properties were used by Cost *et al.* (2019) to model the flexible components of the skull in *Gekko* and *Psittacus*, animals of similar size to *Shenqiornis*. (B) Beams using the cross-sectional area and Young's modulus of canine patellar tendon, as detailed in Haut *et al.* (1992). These properties were used by Cost *et al.* (2019) to model flexible components in the skull of *Tyrannosaurus*. Note that in A the quadrate (i) and jugal (ii) are dislocated to a biologically unreasonable degree and in B the quadrate (iii) is dislocated cranially to a lesser but still unreasonable degree. (C) Beams assigned properties extrapolated from those of a variety of connective tissues reported in the literature and normalized to body mass (Table S4). Note both the lower degree of dislocation of the quadrate (iv) and jugal (v) and the lower principal strains experienced (vi). However, it is unclear how valid this model is. Only three data points are available for calculating cross-section trends. For Young's modulus, even after excluding outliers, r^2 values for a trend line could not be increased above 0.25. Sensitivity analyses show cross section of beams has a stronger control on excursion; rat suture models can only achieve similar excursion to the scaled property model if tendon cross sections are 45 times greater or if their Young's modulus increases 60-fold. In all three models the overall strain experienced is reduced relative to those in Fig. 5B, but artificially inflated at the locations of beam attachment (clearest at the jugal/cranium contact) due to singularities.

palaeodietary reconstruction. Some factors can be corrected for, theoretically negating their influence, but all must be kept in mind when interpreting data from methods described herein. Table 3 provides a convenient reference for when such complications must be accounted for.

Table 3. Quick reference for complications that significantly affect the physical approaches discussed. Rationale is provided within subsections of Section VI.4. Complications with an asterisk (*) are those for which mathematical corrections are available

Physical approaches	Complications						
	Phylogenetic signal*	Allometric signal*	Many-to-one-mapping	Liem's paradox	Integration	Modularity	Behavioural signals
Traditional morphometrics	**X**	**X**	**X**		**X**	**X**	**X**
Geometric morphometrics	**X**	**X**	**X**		**X**	**X**	**X**
Lever modelling		**X**		**X**		**X**	**X**
Finite element analysis		**X**		**X**		**X**	**X**

(*a*) Phylogenetic signal

It is easy to see how phylogeny can affect shape. Genetics is one of the principal factors controlling shape, and thus in the absence of selection one would assume that the more similar the genetics of two organisms the more similar they will appear (Blomberg, Garland & Ives, 2003). At large enough phylogenetic scales, developmental pathways may even completely prohibit an optimised form, or predispose two organisms to find different functionally optimised forms (Gould, 2002). Thus, morphometric comparisons at any timescale over which evolution is a factor should undergo phylogenetic corrections (de Bello *et al.*, 2015). Uyeda *et al.* (2018) review how to craft hypotheses effectively so that phylogenetic corrections can be made. Adams & Collyer (2018) review the mathematical methods and assumptions required for these corrections. Guillerme *et al.* (2020) provide general guidance for the timing of corrections and potential pitfalls of certain evolutionary models.

Over broad enough phylogenetic scales, homologous structures may eventually become functionally incomparable. This is particularly important in the theropod pes due to the evolution of flight. Among coelurosaurian theropods, grasping ability of the manus generally decreases the later a taxon diverges (Hutchinson & Allen, 2008). The proximally fused metacarpals of *Sapeornis* and later-diverging avialans (Fig. 4 in Pittman *et al.*, 2020*a*) likely placed similar constraints on manipulation as in living avians, meaning the two groups would have relied similarly on the pes for grasping. The more refined manual manipulation of some early-diverging paravians (Senter, 2006) means their pes was probably subjected to weaker selective pressures as a device for manipulation. In this example a comparison of pedal proportions of function among Jeholornithiformes and pygostylians should provide meaningful data, but a comparison of all paravians may not.

(*b*) Allometric signal

Different measures of organisms, such as length, surface area, and volume, have different dimensionality. This means they grow at different rates relative to one another. Most organisms would cease to function if they grew isometrically (i.e. with every part scaling the same way as every other part) both through ontogeny and evolution (Schmidt-Nielsen, 1984). Thus, nearly all organisms display some form of allometry, i.e. certain components scaling at different rates than others (Froese, 2006). In other words, body size has an inherent effect on body shape. Klingenberg (2016) reviews methods to quantify and correct for this effect in morphometric studies. Functional effects of allometry have almost exclusively been derived empirically and are known to vary phylogenetically (van der Meij & Bout, 2004; Wroe *et al.*, 2005). Thus, allometry presents a more confounding influence in functional studies. In addition to influencing the strength or efficiency of structures inherently, size may also determine if strength or efficiency is more strongly selected for (see Section VI.3*c.ii*).

(*c*) Many-to-one mapping

Coined by Wainwright *et al.* (2005), many-to-one mapping describes the ability of systems with different forms to perform the same mechanical function. This means that elements that morphometrics classifies as very different may be operating essentially the same in practice. This aligns with the observation above that GM tends to provide mixed results in feeding studies. GM creates a level of abstraction between the data and how the animal interacts with the world. Identifying a case of many-to-one mapping *via* comparison of morphometric and functional studies can be useful. It can formulate hypotheses of evolutionary constraints on form (Ungar & Hlusko, 2016; Button & Zanno, 2020) or illuminate interference of common behavioural signals (e.g. herbivorous and carnivorous taxa engaging in similar bouts of intrasexual competition for mates, or diving predators and foragers facing similar pressures from long-term submersion).

(*d*) Liem's paradox

Occasionally referred to as one-to-many mapping, Liem's paradox was originally coined to describe the peculiarity that a set of cichlid fishes with highly specialised jaws seemed to have no particular dietary speciality (Liem, 1980). The prevailing explanation has been that some specialist morphologies minimally inhibit acquiring 'easy' resources while aiding in obtaining 'difficult' resources (commonly referred to as 'fallback foods') when others are scarce (Robinson & Wilson, 1998). Recent ecological evidence supports this theory (Lambert *et al.*, 2004; Golcher-Benavides & Wagner, 2019; Wiseman *et al.*, 2019). Essentially, this means that organisms that appear morphologically specialised for a certain diet cannot be precluded from being generalists (or specialists feeding on a different easy-to-acquire food source) overall. This is also the reason dental microwear studies emphasise large sample sizes for analysis, to capture signs of rare but important resource use (Ungar, 2018).

(*e*) Integration and modularity

Put simply, integration is when otherwise distinct parts of an organism function and/or evolve as one unit. Modularity is when an organism displays distinct regions (modules) within which integration is high and between which integration is low (Klingenberg, 2014). Farina, Kane & Hernandez (2019) provide more rigorous definitions and a review of the concepts.

Both extreme modularity and extreme integration can encourage diversification (Hedrick *et al.*, 2019*b*). In highly modular systems parts are free to evolve independently from one another. This should, in theory, increase adaptation to environmental changes and thus speciation. Highly integrated systems, on the other hand, restrict parts to evolving as a single unit. While limiting form to a single spectrum, it can allow for rapid diversification and speciation along that spectrum (Hedrick *et al.*, 2019*b*). However, each does not encourage diversification on the same scale. Modularity is associated with diversification overall in high-level clades (class to subclass level) (Marroig *et al.*, 2009; Hu *et al.*, 2016; Felice & Goswami, 2018; Felice *et al.*, 2019*b*) and at smaller scales in several evolutionary circumstances (Tokita, Kiyoshi & Armstrong, 2007; Drake & Klingenberg, 2008; Young, Wagner & Hallgrímsson, 2010; Collar *et al.*, 2014). Integration, by contrast, is known to lead to diversification when lineages invade habitats with a preponderance of unoccupied niches Hu *et al.*, 2016; (Hedrick *et al.*, 2019*b*; Navalón *et al.*, 2020).

Integration and modularity are of most concern in a morphometric context. Integration limits disparity to a single continuum (Hedrick *et al.*, 2019*b*; Navalón *et al.*, 2020). So highly integrated structures are likely to cluster or spread on a single axis of shape. Modularity also can help prioritise functional studies. More modular structures, with more ability to create unique geometries, are more likely to exhibit many-to-one mapping. Thus, they should be checked for functional convergence with higher priority. Adams & Felice (2014) and Adams (2016) provide techniques for quantifying integration and modularity. Because of the complicated relationship they have with evolutionary trajectories no universal correction for their effects has yet been proposed.

(*f*) Behavioural signals

(i) Grooming. The influence of grooming behaviour on morphology has been studied more thoroughly in birds than any other group (Bush & Clayton, 2018). Some anatomical work has been done on specialised dental (Gingerich & Rose, 1979; Rose, Walker & Jacobs, 1981; Asher, 1998) and manual (Bishop, 1962; Koenigswald, Habersetzer & Gingerich, 2011; Maiolino, Boyer & Rosenberger, 2011; Dunkel, 2019) grooming in primates. In birds, destruction of ectoparasites is known to be aided by a short bill (Clayton & Cotgreave, 1994) with a rostral hook (Clayton & Walther, 2001; Clayton *et al.*, 2005; Bush *et al.*, 2012). Intraspecific differences in bill shape are known to reflect ectoparasite load in communities (Bardwell, Benkman & Gould, 2001; Moyer, Peterson & Clayton, 2002). Some birds also have a pectinate ('comb') claw with distinct serrations on the lateral surface thought to play a role in grooming. Studies of its effect, however, have yielded mixed results (Clayton *et al.*, 2010; Bush *et al.*, 2012). It is worth noting that, of these variables, only bill length is always reflected in the animal's skeletal morphology. The same is not true of mammalian toothcombs. Toothcombs convergently evolved in lemurs, flying lemurs, tree shrews, and the arctocyonid *Thryptacodon* (Rose *et al.*, 1981). In toothcombs the mandibular incisors and, variably, canines are deflected rostrally. During grooming they are brushed perpendicular to hair shafts to aid in ectoparasite removal (Schwartz, 1978; Gingerich & Rose, 1979; Rose *et al.*, 1981). This role is augmented or replaced by a specialised, more robust and recurved grooming claw ('toilet claw') in non-simian primates and several polyphyletic simians (Koenigswald *et al.*, 2011; Maiolino *et al.*, 2011). Manual grooming has been reported thoroughly in simian primates, but almost exclusively in social (Schino, 2006; Xia *et al.*, 2019) or spatial (Freeland, 1981; Dunbar, 1991) contexts, rather than its effect on morphology. Opposable thumbs have been proposed as the product of selective pressures related to manual grooming (Bishop, 1962), although this theory remains only one of many (Dunkel, 2019).

From these trends in birds and mammals, oral grooming may be expected to select for perpendicularly oriented structures in the rostrum (beak hook, tooth comb) while manual grooming can be accomplished with more diverse structures (pectinate claw, grooming claw, possibly opposable thumbs). Each of these structures accompanies grooming behaviour with stresses distinct from that of feeding. In turn, structures experience selective pressure to resist those stresses. To our knowledge only circumstantial notes have been made on how significant these stresses may be. There are notes of beak overhangs breaking (Bush *et al.*, 2012) and enamel showing microscopic wear (Rose *et al.*, 1981) from grooming activities. Because wear patterns on tooth combs differ from those of the surrounding teeth, unique wear in teeth has been proposed as indicative of a grooming function in the dromaeosaurid *Saurornitholestes* (Currie & Evans, 2019).

(ii) Thermoregulation. The size of structures is commonly assumed to relate to their strength or speed, but

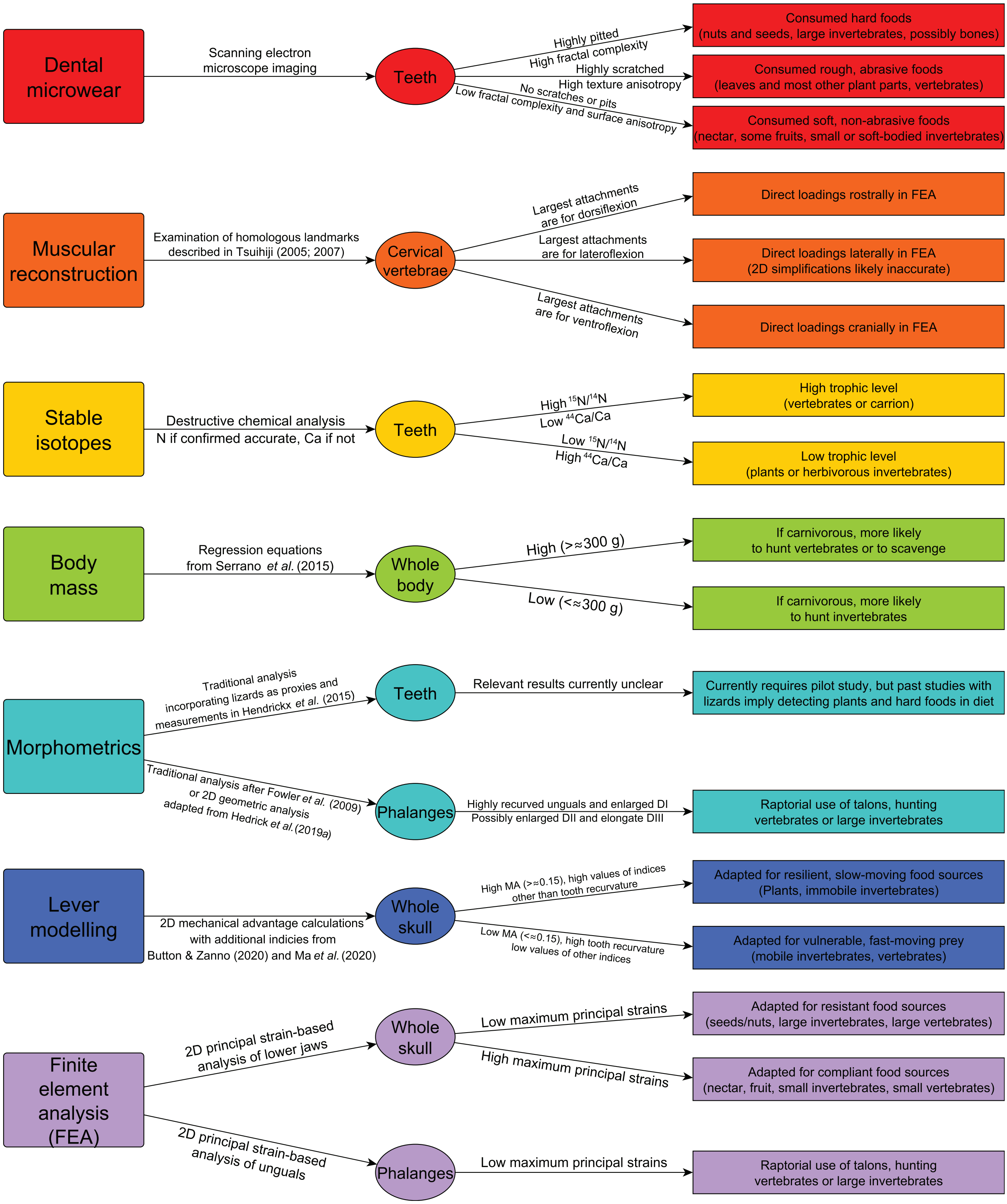


Fig 8. Summary chart of our recommended framework for the study of non-avian avialan diet. Approaches are followed by a brief description of specific prescribed techniques, the body part it would be performed on, relevant results, and recommended dietary and/or modelling interpretations of the results.

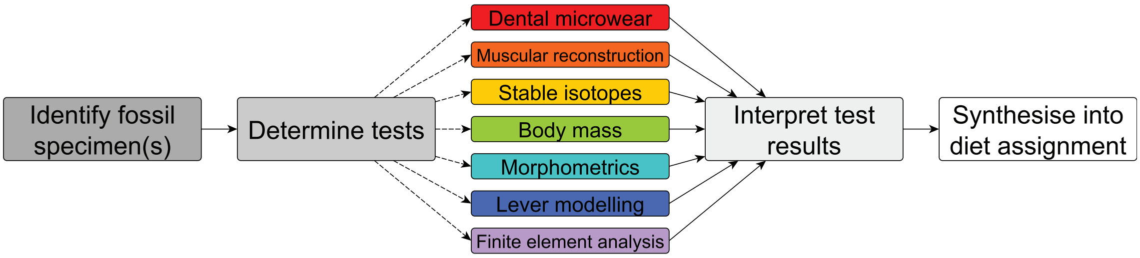


Fig 9. Summary workflow for using the framework described in this paper. (1) Identify fossil specimen(s): Section VII suggests several taxa of particular interest, and Application/Discussion sections throughout this work list published specimens with particular promise. (2) Determine tests: the second column of Fig. 8 lists which preserved body parts are necessary for which tests. Note that while stable isotope analysis can be performed on bones in addition to teeth, this is not recommended as the signatures they give are less reliable. (3) Test: perform one of the seven listed tests on the specimen of interest. The sections in this paper for each technique provide references for methodology. Dashed lines pointing to the test types indicate that not all tests may be possible. The solid lines pointing away from them indicate that any tests which can be performed should have their interpretations contribute to the final synthesis. (4) Interpret test results: the final column of Fig. 8 provides idealised interpretations for test results into a set of potential diets. Section VI.4 may also be pertinent to this workflow stage. (5) Synthesise into diet assignment: combine test results with those of other tests performed. In the simplest terms, this means finding the common elements between each test's interpretations, although the possibility of feeding styles not seen in any extant group may require more creativity at this stage.

thermoregulation is known to influence the scale of elements. Joel Asaph Allen famously noted that animals living in warmer climates tend to have larger extremities and *vice versa* (Allen, 1877, p. 112–119), a trend now referred to as Allen's rule. The rule is supported by several quantitative studies (Nudds & Oswald, 2007; Tilkens *et al.*, 2007; Symonds & Tattersall, 2010; Alho *et al.*, 2011; Greenberg *et al.*, 2012; *contra* Stevenson, 1986). More dramatic structures such as goat horns (Taylor, 1966), elephant ears (Phillips & Heath, 1992), and toucan bills (Tattersall, Andrade & Abe, 2009) have all been proposed as tools for active thermoregulation. The size of body parts should then be interpreted with the climate inhabited by the organism in mind, and hypertrophy of body parts, particularly when not accompanied by significant increases in structural strength, may be a sign of active thermoregulation rather than dietary pressure.

(iii) Sensation. Sensory systems are paramount in both feeding (Montuelle & Kane, 2019) and reproduction (Ptacek, 2000) in living animals. Thus, selective pressure on sensation can be expected to dramatically shape organisms. For instance, enhanced mechanoreception is often associated with elongation and extensive pitting of the skull in amniotes in general (Morhardt, 2009) and birds in particular (Cunningham *et al.*, 2013). In the same vein, an increase in size of amniote eyes often creates a corresponding reduction in bite force (Henderson, 2002; Fortuny *et al.*, 2011). Sensory specialisations that parallel those in extant taxa can be understood and tested for by understanding the biology of those taxa. The possibility of novel forms of sensory augmentation present only in extinct taxa, however, renders sensation a true confounding variable.

(iv) Sexual display. Animals have a variety of tools for communication and competition that improve survival and reproductive success. All of these may alter the body in unpredictable ways. Protuberances may serve as intersexual signals (Mayr, 2018) or as bases for intrasexual combat (Clutton-Brock, 1982; Rico-Guevara & Araya-Salas, 2014). Changes in skull morphology can lead to changes in vocalisation (Huber & Podos, 2006; Herrel *et al.*, 2009; Giraudeau *et al.*, 2014) or altered ability to detect chemical messages (Rouquier & Giorgi, 2007). Sexual dimorphism itself can lead to functional differences on small (Verwaijen, Van Damme & Herrel, 2002) or large (Pietsch, 2005) scales. Sexual dimorphism may be able to be detected in the fossil record given an adequate number of samples (Plavcan, 1994), but other forms of sexual display can drive shape and affect function with little evidence left in the fossil record. Thus, sexual display also remains a true confounding variable.

(5) Discussion

The broad application of physical approaches across fossil taxa makes them ideal for comparative frameworks, but not all frameworks are appropriate approaches to dietary reconstruction. Neither TM nor GM of theropod skulls appears particularly effective at isolating features of diet across phylogenetically diverse groups. In addition, the lack of consistent landmarks in studies highlights how few measurements there are of the theropod skull that would have an intuitive effect on dietary choice. Both forms of morphometrics are more effective at revealing diet when applied to the pes. This is likely because the pes performs a smaller variety of roles in the organism (Montuelle & Kane, 2019) and those other roles are often in service of obtaining food (Fowler *et al.*, 2009; Sustaita *et al.*, 2013). Results have been obtained with both TM and GM analysis of extant avian feet, and so neither is recommended over the other by this review. TM may also prove useful to find dietary signals in teeth due to the large disparity seen across theropods as a whole (Hendrickx & Mateus, 2014; Hendrickx *et al.*, 2020) and Avialae in particular (O'Connor & Chiappe, 2011; Huang *et al.*, 2016; O'Connor, 2019). A lack of prior study in this field leaves this

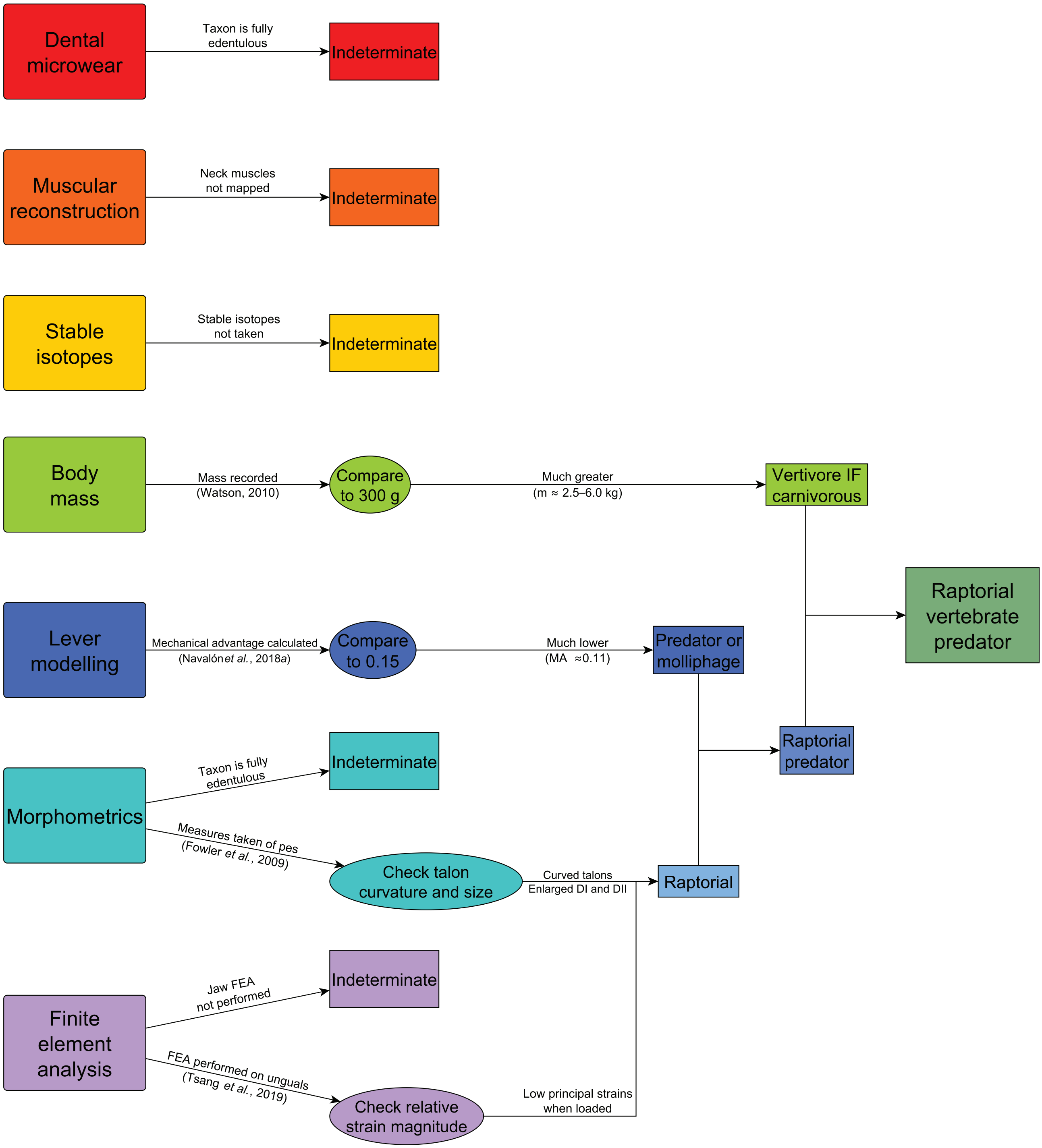
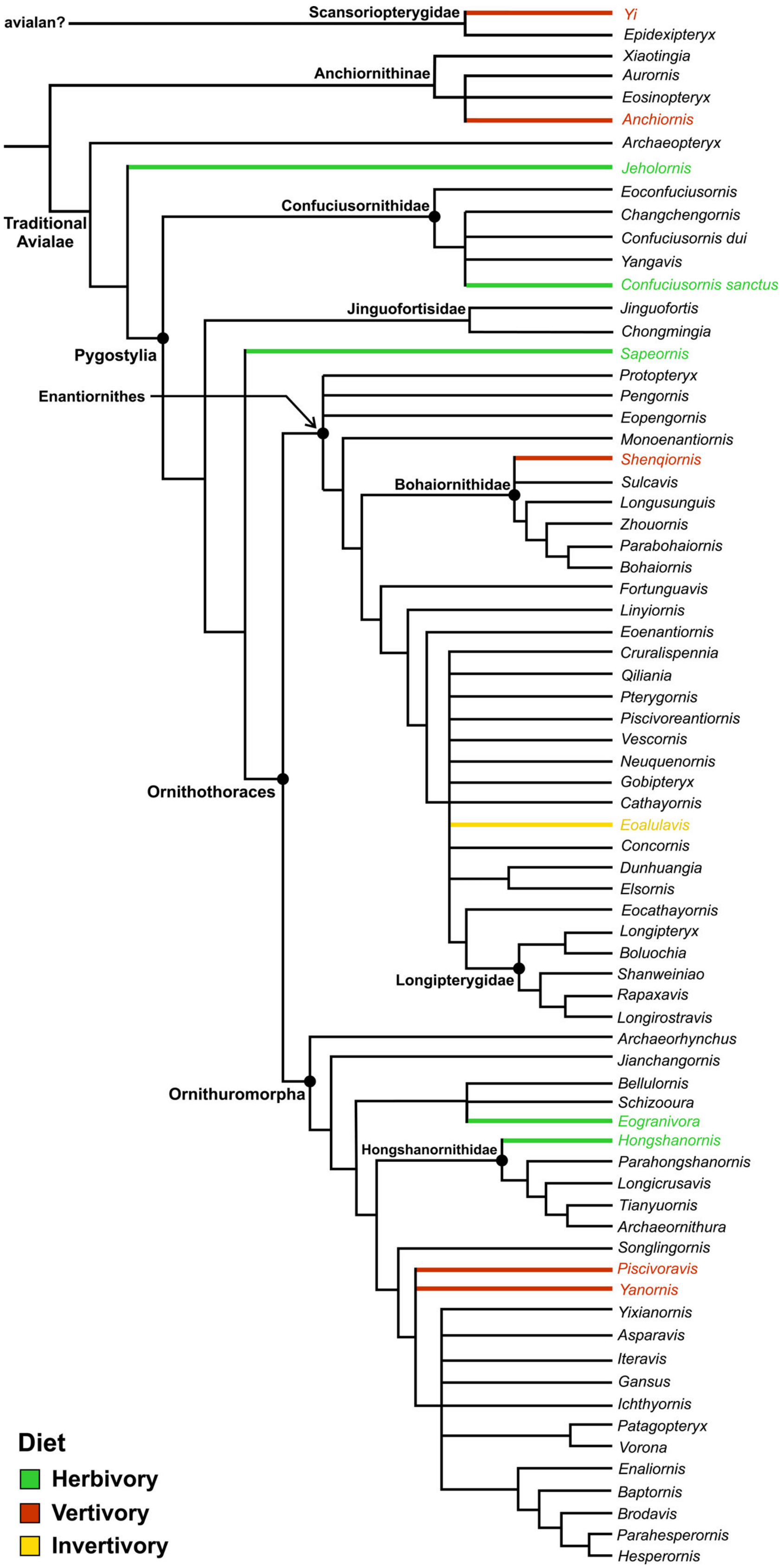


Fig 10. Summary of our recommended study framework, as applied to the extant golden eagle *Aquila chrysaetos*. Morphometrics and lever modelling are transposed from Fig. 8 for clarity. Lever modelling shows adaptation for vulnerable and possibly mobile prey, pointing to either predation or molliphagous herbivory. Morphometrics and FEA of the pes provide evidence of raptorial use, and thus refine the lever modelling findings to predation. Given that the animal is carnivorous, then, body mass makes vertebrate consumption much more likely than invertebrate consumption. Thus. these four lines of evidence point to *Aquila chrysaetos* being a raptorial vertebrate predator, which indeed it is (Watson, 2010).

recommendation only tentative. Lizards are the closest related extant taxon with similarly disparate teeth, and quantitative analyses of lizard teeth have already identified characters indicative of durophagy (Estes & Williams, 1984) and herbivory (Melstrom, 2017) that could be applied to toothed avialans.



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In general, this review recommends functional studies over morphometrics due to the fewer complications that influence them (see Table 3). 2D simplifications of functional models appear necessary for the time being, but if possible, comparisons of 2D and 3D models should be undertaken to confirm the former's validity. Whether more valid dietary signal can be gleaned from lever models of the upper jaw combined with functional indices from Button & Zanno (2020) and Ma *et al.* (2020) (Fig. 4) or principal strain-based FEA of the lower jaw is still unclear. The size at which selection for strength transitions to selection for mechanical efficiency (Adams *et al.*, 2019), if such a transition truly exists, is not yet established. Ideally, a study including both approaches could directly compare the two. Separate studies, each focusing on one functional approach, should have results that can be compared nearly as effectively. Incorporating connective tissue into the skull to create kinetic structures is not recommended pending more precise understanding of the physical properties of those connective tissues. Discovery of fossilised rhamphothecae allows for them to be included in models, as is suggested here.

VII. THE FRAMEWORK AND CURRENT KNOWLEDGE OF NON-AVIAN AVIALAN DIET

As individual techniques described in Sections II–VI provide only limited insight into bird diet, taking the consensus of multiple lines of evidence is essential to gaining useful information. However, from our experience, differences in fossil taxa studied, extant reference taxa, and dietary categories make studies using single techniques difficult or impossible to combine. Thus, we combine the recommended techniques into a framework for narrowing possible fossil avialan diets. Fig. 8 provides a summary of these techniques, the body parts which need to be preserved for their use, expected results from their application, and interpretation of the results. A general workflow for applying the framework is provided in Fig. 9, from determining specimens of interest to synthesising test results into a dietary assignment. All seven of the recommended approaches are not necessary for results to be valid, but agreement of a greater number of techniques should increase the validity of findings.

We provide an example of applying our framework to the extant golden eagle (*Aquila chrysaetos*), a raptorial vertebrate predator. It was chosen as it appears in more studies compatible with our framework than any other bird. Fig. 10 provides a graphical summary of this example. While *Aquila chrysaetos* does not have teeth, if it did, they should have high surface anisotropy from the repeated tearing of tough meat. Its pull-back method of prey disassembly should select for enlarged attachment sites for dorsiflexive muscles, and finite element models of its lower jaw should have muscular loadings deflected cranially. Its bones should be depleted in ^{44}Ca and its proteins enriched in ^{15}N due to its high trophic level. Its body mass should be above 300 g due to vertebrate predation; this is true even in unusually small subspecies (Watson, 2010, p. 33). Its talons should be highly recurved with a hypertrophied DI due to their raptorial use; this has been reported (Fowler *et al.*, 2009). Its jaws should have a low MA, high tooth recurvature if it had teeth, and high values of the other recommended indices as it hunts agile prey; its jaw MA is low among avians (Navalón *et al.*, 2018*a*). Its lower jaw should experience relatively high principal strains when loaded in FEA due to the compliance of animal flesh. Finally, its talons should experience relatively low principal strains when loaded in FEA due to their raptorial use; this has been supported (Tsang *et al.*, 2019). Given the current studies that fit into our framework, there are four lines of evidence which would lead to classifying the golden eagle as a raptorial vertebrate predator if it was extinct (Fig. 10).

While limited by a dearth of quantitative studies, our framework can be used to establish what we currently know of non-avian avialan diet (Fig. 11). The scansoriopterygids [possibly early-diverging avialans or non-avialan pennaraptorans (Pittman *et al.*, 2020*a*)] *Epidexipteryx* and *Yi* appear adapted for carnivory due to low values of mechanical advantage and most of the functional indices recommended herein (Ma *et al.*, 2020). Body mass estimates above 300 g in *Yi* (Dececchi *et al.*, 2020) specifically point to it being a vertivore. To our knowledge, no quantitative study of anchiornithine [possibly early-diverging avialans or troodontids (Pittman *et al.*, 2020*a*)] diet has been performed. Preserved fish and lizard meals are known in *Anchiornis* (Zheng *et al.*, 2018*b*), but it is unclear if this represents a typical part of its diet. Evidence of diet in the earliest-diverging unequivocal avialan *Archaeopteryx* appears contradictory. Studies show dental microwear reminiscent of invertivores (Bestwick *et al.*, 2018), a body mass in the range of vertivores (Serrano *et al.*, 2015), and relatively high jaw MA (Navalón, 2014) expected in herbivores or durophages. The most likely source of this contradiction is the specimens studied. Bestwick *et al.* (2018) studied microwear of the Munich specimen (Jordan Bestwick, personal communication 2020); Serrano *et al.* (2015) measured the London, Berlin, Eichstätt, and Thermopolis specimens; and the work of Navalón (2014)

(Figure legend continued from previous page.)

Fig 11. Currently known diets of non-avian avialans labelled onto an avialan phylogeny. The tree topology is taken from Fig. 3A in Pittman *et al.* (2020*a*), with Scansoriopterygidae and Anchiornithinae grafted on from Fig. 1 in the same chapter. *Eogranivora* is placed in a polytomy with *Bellulornis* and *Schizooura* after O'Connor (2019) grouping it with the former. A taxon is assigned a diet if specimens of it have preserved meals and/or if two lines of evidence agree on a diet. Even with these low bars for assignment, less than 15% of taxa in the tree are assigned a diet, and the tree itself includes less than half of the named non-avian avialan genera.

was based on the reconstruction of Rauhut (2014), which was in turn based primarily on the Eichstätt specimen. Considerable morphological disparity has been noted previously within *Archaeopteryx* (Rauhut, Foth & Tischlinger, 2018) which may yet indicate diverse diets within the genus. Alternatively, the contradictory evidence may be indicative of Liem's paradox at work, with fallback food(s) not captured in the small sample size of dental microwear [see Lambert *et al.* (2004) for an extant equivalent]. Five preserved seed meals are currently known in the early-diverging avialan *Jeholornis* (Zhou & Zhang, 2002; O'Connor & Zhou, 2019), but it is unknown if other major parts of its diet remain unaccounted for. Due to a sparsity of quantitative data, especially the seemingly contradictory evidence in *Archaeopteryx*, the ancestral dietary condition in avialans remains unclear.

The early-diverging pygostylian *Confuciusornis* has jaws with both strength (Miller *et al.*, 2020) and MA (Navalón, 2014) consistent with herbivorous avians (Navalón, 2014; Miller *et al.*, 2020). One study applying pedal morphometrics (Cobb & Sellers, 2020) recovered *Confuciusornis* as raptorial, and its body mass estimates are consistent with vertivory (Serrano *et al.*, 2015; Table 2). However, because the morphometric study measured only curvature of unguals and not their relative sizes, we consider that raptorial behaviour is not ruled out, but is not confirmed. This discrepancy can be directly addressed with stable isotope analysis, for which *Confuciusornis* is a prime candidate due to the large number of specimens known. Its close relative *Eoconfuciusornis* has only had MA measurements taken (Navalón, 2014), which we consider inadequate for dietary assignment. No dietary study has been conducted on any member of Jinguofortisidae to our knowledge. We also consider the single line of quantitative MA evidence (Navalón, 2014) favouring granivory in the early pygostylian *Sapeornis* to be inadequate for diet assignment, although it does agree with previously reported ingested material (Zheng *et al.*, 2011; O'Connor, 2019; O'Connor & Zhou, 2019).

Among the enantiornithine ornithothoracines, *Shenqiornis* is tentatively proposed here as predatory due to low jaw MA (Navalón, 2014) and raptorial pes morphometrics in its close relatives (Wang *et al.*, 2014*b*). Its MA is of particular interest for future studies to attempt to replicate due to qualitative assertions of durophagy in the taxon (Wang *et al.*, 2010*b*). Navalón (2014) additionally reports intermediate values of MA for *Pengornis* and an indeterminate hatchling and low MA for *Rapaxavis*. Again, we consider this single line of evidence inadequate for dietary assignment. One specimen of *Zhouornis* (BMNHC Ph 756) has been reported as having claws as straight as extant ground birds (Cobb & Sellers, 2020), which would rule out raptorial behaviour in the taxon. However the claw measured, DIII, is aberrantly straight in this genus with the other claws highly recurved (Zhang *et al.*, 2013; Zhang *et al.*, 2014) so we do not consider raptorial behaviour ruled out. The holotype of *Eoalulavis* preserves part of a crustacean in its stomach (Sanz *et al.*, 1996), but the lack of a skull or feet in the specimen inhibit investigation of the typical diet of this taxon within our framework.

Finally among non-avian ornithuromorphs, MA values reported in Navalón (2014) are congruent with ingested gastroliths in *Hongshanornis* (Chiappe *et al.*, 2014) indicating herbivory and fish in *Yanornis* (Zhou *et al.*, 2004; Zheng *et al.*, 2014) indicating carnivory. Additionally, *Eogranivora* and *Piscivoravis* have preserved meals that provide evidence of granivory (Zheng *et al.*, 2018*a*) and piscivory (Zhou, Zhou & O'Connor, 2014) respectively, but determining whether these were normal parts of their diet requires further study.

The paucity of dietary assignments renders trends in avialan dietary evolution murky. Our framework supports a mixture of carnivory and herbivory/omnivory among both early-diverging non-avian avialans (*Archaeopteryx*, *Confusciusornis*, *Sapeornis*) and later-diverging ones (*Shenqiornis*, *Hongshanornis*, *Yanornis*) (Fig. 11). Therefore, no particular macroevolutionary trends are currently apparent. Dietary diversity seems to increase through time, but this is a preservational bias associated with the predominance of data from the Early Cretaceous Jehol Lagerstätte (all of these taxa except *Archaeopteryx*). This also means that relatively little geographic and climatic range is accounted for among currently known non-avian avialan diets. Thus, non-avian avialan material from a wider range of localities should also be prioritised for future study.

VIII. CONCLUSIONS

(1) Our aim was to build a framework for studying non-avian avialan diet by reviewing techniques that have proved effective in both avians and non-avian theropods and the use this to summarise our current state of knowledge. With this framework in place, we expect it will generate progress in the reconstruction of Mesozoic ecosystems and in our understanding of the ecological history of birds.

(2) Fig. 8 provides a convenient summary of the techniques discussed in this review and our recommendations for applying them. Expected outcomes and their general interpretations are also provided. We recommend combining direct evidence of diet with dental microwear, stable isotope geochemistry, body mass estimation, pes morphometrics, and functional analysis to obtain multiple lines of evidence relevant to diet.

(3) Due to a dearth of quantitative studies, current knowledge of non-avian avialan diet is sparse. The ancestral avialan diet remains obscure, in large part due to contradictory evidence concerning the diet of *Archaeopteryx*. Both carnivory and herbivory/omnivory are present in early-diverging (*Archaeopteryx*, *Confuciusornis*, *Sapeornis*) and later-diverging (*Shenqiornis*, *Hongshanornis*, *Yanornis*) avialans, but no trends in the dietary evolution of non-avian avialans have presented themselves. We believe that new avialan specimens from a wider range of localities covering different geographies and

climates will be instrumental to elucidating these trends in the future.

(4) Our review demonstrates the need for establishing links between diet and morphology in avians, reconstructing the often-crushed remains of non-avian avialans, and combining the two in robust quantitative frameworks. Combined with a growing understanding of extant ecology, these will provide a new and exciting picture of earth during some of the most groundbreaking evolutionary transitions known.

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XI. Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Listing of published non-avian avialan skulls.

Fig. S1. Principal component analysis (PCA) of avian pedal measurements from Fowler *et al.* (2009, 2011).

Fig. S2. Principal component analysis of theropod skulls from Foth & Rauhut (2013).

Table S2. Table summarising all dietary recoding used in Fig. S2.

Fig. S3. Principal component analysis of theropod skulls from Schaeffer *et al.* (2019).

Fig. S4. Relationship between mechanical advantage and plant consumption in passerines.

Fig. S5. Biomechanical morphospace of Dinosauria from Button & Zanno (2020).

Table S4. Calculation of cranial connective properties of *Shenqiornis*.

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