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Functional niche partitioning in therizinosauria provides new insights into the evolution of theropod herbivory

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1 **FUNCTIONAL NICHE PARTITIONING IN THERIZINOSAURIA PROVIDES NEW**
2 **INSIGHTS INTO THE EVOLUTION OF THEROPOD HERBIVORY**

3

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9

10 **Abstract:** Dietary specialisation is generally considered to be a crucial factor in driving
11 morphological evolution across extant and extinct vertebrates. The ability to adapt to a
12 specific diet and to exploit ecological niches is thereby influenced by functional morphology
13 and biomechanical properties. Differences in functional behaviour and efficiency can
14 therefore allow dietary diversification and the coexistence of similarly adapted taxa.
15 Therizinosauria, a group of secondarily herbivorous theropod dinosaurs, is characterised by a
16 suite of morphological traits thought to be indicative of adaptations to an herbivorous diet.
17 Digital reconstruction, theoretical modelling and computer simulations of the mandibles of
18 therizinosaur dinosaurs provides evidence for functional niche partitioning in adaptation to
19 herbivory. Different mandibular morphologies present in therizinosaurians were found to
20 correspond to different dietary strategies permitting coexistence of taxa. Morphological traits
21 indicative of an herbivorous diet, such as a downturned tip of the lower jaw and an expanded
22 post-dentary region, were identified as having stress mitigating effects. **The more widely**
23 **distributed occurrence of these purported herbivorous traits across different dinosaur clades**
24 **suggests that these features also could have played an important role in the evolution and**
25 **acquisition of herbivory in other groups.**

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Key words: functional niche partitioning, finite element analysis, Dinosauria, herbivory, functional morphology

Niche partitioning is a viable mechanism among sympatric species to allow the coexistence of similarly adapted taxa and to minimise competition for resources (MacArthur 1972; Chase & Leibold 2003; Finke & Snyder 2008). With regard to diet, niche partitioning can act upon food type, habitat, foraging time and foraging behaviour (Schoener 1974; Patterson *et al.* 2003; Adams & Thibault 2006). These differentiations are directly influenced by how and how efficiently taxa can exploit available resources, and dictated by physiological, anatomical, and functional properties. Differences in functional morphology and the ability to adapt to a different diet, such as herbivory, can therefore allow the occupation of new or further subdivision of existing ecological niches. Consequently, the acquisition of herbivory has often been considered an important key innovation and has been acquired numerous times in vertebrate evolutionary history (Sues 2000). Within Dinosauria, herbivory has evolved convergently in Ornithischia, Sauropodomorpha and Theropoda (Barrett *et al.* 2011; Barrett 2014). In the latter, the adaptation to an herbivorous diet represents a departure from the carnivorous condition of most basal theropods, which occurred presumably independently in Oviraptorosauria, Ornithomimosauria and Therizinosauria (Barrett 2000, 2005; Zanno & Makovicky 2011), and appears to have been a major driver for morphological diversity and speciation in theropods.

Therizinosauria, a group of herbivorous theropods predominantly found in Cretaceous sediments of Asia and North America, has a complicated taxonomic history and their unusual skeletal morphology has long obfuscated their phylogenetic position (Clark *et al.* 2004). Derived members of this group are characterised by small skulls with an edentulous

51 premaxilla and a rostral rhamphotheca, an elongate neck, hypertrophied manual unguals and
52 a broad, opisthopic pelvis (Zanno 2010a; Lautenschlager *et al.* 2014). This mosaic of
53 morphological features resulted in a variety of phylogenetic hypotheses (Barsbold & Perle
54 1984; Paul 1984; Gauthier 1986) and it was not until the discovery of new fossils that
55 Therizinosauria was firmly established as a derived clade within Theropoda (Russel & Dong
56 1993).

57 Within the last two decades a number of new fossil findings have further substantiated
58 the phylogenetic position of therizinosaurians (Zanno 2010a; Averianov 2015). These new
59 discoveries revealed that therizinosaurians were more widely distributed across North
60 America and Asia than originally thought. Furthermore, the coeval occurrence of different
61 taxa and morphotypes within the same locality (Sues & Averianov 2016; Zanno *et al.* 2016)
62 indicates that different species might have occupied different ecological niches. While the
63 skeletal morphology of Therizinosauria is strongly divergent from that of other theropods, it
64 is also very diverse across different therizinosaurian species. In particular, tooth morphology,
65 claw shape and body size were found to be highly variable, presumably reflecting different
66 palaeoecological specialisations and herbivorous dietary strategies among Therizinosauria
67 (Zanno 2010a; Zanno & Makovicky 2013; Lautenschlager 2014).

68 However, while the increasing number of newly discovered taxa have significantly
69 improved knowledge of therizinosaurians, the often fragmentary nature of many specimens
70 have not only confounded phylogenetic analyses, but also comprehensive understanding of
71 their anatomy, palaeobiology and palaeoecology. In particular cranial remains are rare and
72 only few skeletal elements are equally represented in all taxa. Amongst them, the dentary is
73 the most consistently preserved element known from at least six therizinosaurian taxa (Fig.
74 1). It shows a high degree of morphological variation and characteristic features, such as a
75 downturned symphyseal region, rostral edentulism, and a lateral shelf, all of which are

76 thought to be indicative of dietary specialisation patterns (Zanno & Makovicky 2011).
77 Furthermore, lower jaw elements are ideally suited for biomechanical studies, as the
78 mandible is primarily adapted for foraging and biting, whereas the cranial skeleton represents
79 a compromise of multiple functions (e.g., bony housing of brain and sensory systems). Still,
80 the problem remains that fragmentary preservation, taphonomic artefacts and the availability
81 of specimens preclude comprehensive biomechanical studies (Zanno 2010a).

82 The use of theoretical, virtual models can provide a versatile solution. While
83 kinematic abstractions have been used to model theoretical and actually realised jaw
84 morphologies in dinosaurs in the past (e.g. Weishampel 1984, 1998), high computational
85 demands considerably limited the necessary complexity of such models. Recent advances in
86 hard- and software technology now allow the simulation of complex and thus more realistic
87 models. Consequently, the use of biomechanical analysis techniques in palaeontological
88 research using approaches, such as finite element analysis (FEA), has increased in recent
89 years, but theoretical modelling of anatomical features has been used only in a handful of
90 studies (Rayfield & Milner 2008; Anderson *et al.* 2011; Xing *et al.* 2015). Although it
91 involves the use of idealised models, which do not reflect the fossil morphology completely,
92 recent studies have attested this approach to be very informative (Bright 2014; Rahman &
93 Lautenschlager *in press*) as it allows studying morphofunctional properties unimpeded by
94 preservation and taphonomic artefacts.

95 Using actually preserved specimens as well as theoretical models, the functional
96 morphology of the dentary (and as far possible also the complete mandibles) of six
97 therizinosaurian species were investigated with biomechanical analysis techniques. The
98 complete and well-preserved mandibles of the derived therizinosaurid *Erlikosaurus andrewsi*
99 was employed as a template to create theoretical models incorporating morphological
100 information provided by fossil specimens of other taxa, spanning the full phylogenetic and

101 morphological range across Therizinosauria (Fig. 1). The biomechanical behaviour and
102 performance of different dentary morphologies was studied using FEA to test for possible
103 dietary and functional specialisations of Therizinosauria within the herbivorous regime. The
104 combined use and integration of actually preserved specimens and theoretical models helped
105 overcome limitations posed by the incomplete fossil record and to evaluate the functional
106 morphology of mandibular characters associated with herbivory. This approach further
107 allowed testing the hypothesis that functional niche partitioning permitted the coeval
108 diversification of taxa and the refinement of dietary strategies, thereby elucidating the
109 evolutionary dynamics of ecological partitioning and the evolution of herbivory in theropod
110 dinosaurs.

111

112 **MATERIAL AND METHODS**

113 *Institutional abbreviations*

114 HGM, Henan Geological Museum, China; IGM, Geological Institute of the Mongolian
115 Academy of Sciences, Ulaanbataar, Mongolia; IVPP, Institute of Vertebrate Paleontology
116 and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; UMNH, Utah
117 Museum of Natural History, Salt Lake City, Utah, USA.

118

119 *Specimens and model creation*

120 The complete mandible of the therizinosaurid *Erlikosaurus andrewsi* (IGM 100/111)
121 was used as a template for the creation of the digital models. The specimen was digitised at
122 X-Tek Systems (now Nikon Metrology) using a XT-H-225ST CT scanner with parameters
123 set at 180kV and 145 μ A. Slice data consisting of 1998 slices with a slice thickness of 145 μ m
124 were imported into Avizo (versions 6.3.1 and 7.0.0; VSG, Visualization Science Group) for

125 image segmentation and further processing. Moderate digital restoration was necessary to
126 remove preservational artefacts, such as small breaks and cracks (Lautenschlager *et al.* 2014).

127 The digitally restored model of the mandible of *Erlikosaurus andrewsi* was
128 subsequently modified to create mandible models of five further therizinosaurian taxa for
129 which the dentary is known: *Falcarius utahensis* (UMNH VP 14527, 14528 and 14529)
130 (Zanno 2010b), *Beipiaosaurus inexpectus* (IVPP V11559) (Xu *et al.* 1999), *Jianchangosaurus*
131 *yixianensis* (HGM 41HIII-0308A) (Pu *et al.* 2013), *Alxasaurus elesitaiensis* (IVPP 88402)
132 (Russel & Dong 1993), and *Segnosaurus galbinensis* (IGM 100/80) (Zanno *et al.* 2016). For
133 that purpose all mandibular elements of *Erlikosaurus andrewsi* were imported into the 3D
134 modelling and visualisation software Blender (www.blender.org) as .obj files. Photographs in
135 different orientations derived from personal observations (*Falcarius utahensis*, *Beipiaosaurus*
136 *inexpectus*) and from published figures of the dentary and (where preserved) other
137 mandibular elements of the above listed taxa were imported as reference images in Blender.
138 Using the mesh manipulation tools in Blender, the models of *Erlikosaurus andrewsi* were
139 each modified: The outlines of the digital models were fitted to the morphology of the
140 reference images in different views. Individual elements were scaled, rotated and translated
141 to correspond to the shape of the specific modelled taxa (Rahman & Lautenschlager *in press*).
142 Where necessary, different components, such as teeth, were duplicated and placed as
143 indicated by the reference images. In taxa for which the postdentary morphology is unknown
144 (*Falcarius utahensis*, *Alxasaurus elesitaiensis*), only the dentary was modelled in the way
145 described above. Postdentary elements were supplemented unchanged (except for uniformly
146 scaling to match the size of the dentary) from the *Erlikosaurus* models. This step assumes
147 that the respective taxa shared a similar postdentary morphology, which might not correspond
148 to the actual condition. However, the supplemented postdentary elements provide attachment
149 for the dentary and thereby allow analysing the preserved morphology. Results for the

150 postdentary morphology of *Falcarius utahensis* and *Alxasaurus elesitaiensis* might therefore
151 reflect these assumptions and are treated accordingly. The final models were remeshed using
152 Blender's remeshing modifier and exported as .stl files for FEA.

153

154 *Finite element analysis*

155 For FEA, all models were scaled to the same surface area (based on the mandible of
156 *Erlikosaurus andrewsi*) to remove size-related effects during analyses (Dumont *et al.* 2009)
157 and imported into Hypermesh (version 11, Altair Engineering) for the creation of solid mesh
158 FE models. All models consisted of approximately 1,500,000-2,000,000 four-noded
159 tetrahedral elements (see supplementary table 1). Material properties for crocodylian bone and
160 teeth were assigned in Hypermesh (bone: $E = 20.49$ GPa, $\nu = 0.40$; teeth: $E = 60.40$ GPa, $\nu =$
161 0.31) and treated as homogenous and isotropic following (Creech 2004; Chen *et al.* 2008). A
162 keratinous rhamphotheca covering the premaxilla and the rostral part of the dentary had been
163 reconstructed in *Erlikosaurus andrewsi* (Lautenschlager *et al.* 2013, 2014) and is thought to
164 be present in some derived therizinosaurid. However, such a rhamphotheca was not
165 incorporated in the current FE models, as basal therizinosaurians most likely lacked this
166 structure (Zanno 2010b). While the presence of a keratinous sheath has been shown to
167 mitigate stress and strain in the underlying bone (Lautenschlager *et al.* 2013), further
168 sensitivity tests demonstrated that a keratin cover only changed the magnitude but not the
169 distribution of stress and strain (Lautenschlager 2014; Lautenschlager *et al.* 2016). Similarly,
170 sutures between the individual mandibular elements were not included. The inclusion of
171 cranial sutures in FE models can have an effect on stress and strain magnitudes (e.g. Bright &
172 Gröning 2011, Porro *et al.* 2011; Reed *et al.* 2001; Bright 2012), but material properties of
173 cranial sutures in archosaurs are often poorly known (Porro *et al.* 2013, Cuff *et al.* 2015),

174 However, in a comparative context as employed here, these factors can be assumed to affect
175 all models equally so that it is possible to extract shape as the crucial parameter only.

176 All FE models were restrained from rigid body movement in all directions at the
177 articular (15 constraints). Further constraints were applied according to the tested functional
178 scenarios (see below). Muscle loads were applied at the mandibular insertions according to
179 the reconstructed jaw adductor arrangement for *Erlikosaurus andrewsi* (Lautenschlager
180 2013), with a total of 569 N applied to each hemi-mandible (supplementary table 2). *Each*
181 *muscle group was modelled as a series of loads to represent and cover the extent of the*
182 *attachment area*. Muscle forces and locations were kept constant for all models to allow
183 analysis of shape in a comparative context. Although it is likely that some variation in muscle
184 arrangement and mass existed in the different taxa, a conservative approach was taken here.
185 This approach avoids the introduction of functional variance due to different loading
186 properties, which would mask mechanical differences due to mandibular shape. All models
187 were subsequently imported into Abaqus (version 6.10, Simulia) for analysis and
188 postprocessing. Biomechanical performance was assessed by comparison of von Mises stress
189 and strain distribution. In addition, reaction forces were obtained from the solved FE models
190 at the bite points. Ratios between input forces and output forces and average von Mises stress
191 values were calculate to quantify biomechanical efficiency. Variation in deformation for each
192 model and loading scenario was quantified using a landmark-based approach (for the
193 undeformed and deformed models). Twenty-six landmarks were placed at morphologically
194 homologous points (supplementary fig. 11) using Avizo and subjected to Procrustes
195 superimposition and a principal component analysis (PCA) performed in PAST (Hammer *et*
196 *al.* 2001).

197

198 *Simulated feeding scenarios*

199 To analyse ecomorphological differences between taxa, a variety of feeding scenarios
200 was simulated: (i) unilateral biting at the first, fifteenth and last tooth with single constraints
201 applied at the respective positions. The fifteenth tooth position was chosen as it represents the
202 average midpoint of the tooth row; (ii) bilateral biting at the first, fifteenth and last tooth
203 position, with single constraints applied accordingly; (iii) clipping of an object at the tip of
204 the dentary with a single constraint at the centre of the dorsal margin of the symphysis; (iv)
205 upwards-pull movement, which simulates grasping of an object at the tip of the dentary and
206 pulling dorsally. An additional load (150 N) was applied at the symphyseal region in dorsal
207 direction; (v) a downwards-pull movement, which simulates the grasping of an object at the
208 tip of the dentary and pulling ventrally. An additional load with a magnitude within the range
209 of the bite force (150 N) was applied at the symphyseal region in ventral direction; (vi) lateral
210 pull, simulating sideways movement while holding an object at the rostral teeth. An
211 additional load (150 N) was applied at the symphyseal region in lateral direction.

212

213 RESULTS

214 *Stress distribution*

215 As postdentary elements are unknown in some taxa and were extrapolated on the
216 basis of the preserved material of *Erlikosaurus andrewsi*, results largely focus on the dentary.
217 The comparison of the stress and strain distributions obtained from FEA demonstrates
218 distinct differences between the analysed mandibular models. *Beipiaosaurus inexpectus* and
219 *Erlikosaurus andrewsi* show the lowest stress and strain levels in the dentary but also the
220 complete mandible during unilateral and bilateral bite scenarios (Fig. 2, supplementary figs.
221 1-7) simulating biting at the first, middle and last tooth positions. In comparison, the models
222 of *Jianchangosaurus yixianensis* and *Alxasaurus elesitaiensis* experience the highest stress
223 and strain levels (Fig. 2, supplementary figs. 2, 3). If only the dentaries are considered,

224 *Falcarius utahensis*, *Jianchangosaurus yixianensis* and *Alxasaurus elesitaiensis* show the
225 highest stress magnitudes. In all models the dentary shows the relatively lowest stress
226 magnitudes during unilateral and bilateral biting, with stress hotspots centred on the angular
227 and articular region. Stress in the dentaries is mostly focused on the ventral surface for biting
228 at the first and middle tooth position, but shifts posteriorly to the postdentary elements when
229 simulating a bite at the last tooth. Stress magnitudes are moderately higher on the balancing
230 side, whereas stresses are reduced and more uniformly distributed on both sides in the
231 bilateral biting scenarios (supplementary fig. 4). The same patterns are observed for strain
232 and deformation distributions (supplementary figs. 5-7) throughout all models.

233 In addition to different bite positions, further functional scenarios were analysed
234 simulating clipping at the tip of the dentary, and the mandible pulling an object in dorsal,
235 ventral and lateral direction as would be experienced during foraging. Among these, clipping
236 models experience the lowest stress levels throughout the mandible, but considerably higher
237 levels than biting at the first, middle and last tooth (Fig. 3, supplementary fig. 8). Increased
238 stress levels are induced in the symphyseal region for simulated clipping. As with the
239 different biting scenarios, *Beipiaosaurus inexpectus* and *Erlikosaurus andrewsi* show the
240 lowest stress magnitudes in the mandibles during clipping (Fig. 3). The same patterns,
241 however, are also observed, if only the dentaries are considered.

242 Among the extrinsic scenarios with additional forces applied to the mandible to
243 simulate pulling of an object in different directions, the upwards-pull scenario produces the
244 highest stress and strain magnitudes for all models (Fig. 3, supplementary figs. 8-10), with
245 stress and strain hotspots found around the articular region. In comparison, the lateral-pull
246 scenario produces slightly lower, but still high levels of stress and strain. In this scenario,
247 stress hotspots are centred on the lateral surface of the dentary in addition to the postdentary
248 elements (Fig. 3). A downwards pull movement shows the relatively lowest stress and strain

249 levels (supplementary figs. 8-10). Stresses are mostly concentrated on the ventral surface of
250 the dentary, the angular and the articular regions. For all extrinsic feeding scenarios, the
251 mandibles of *Beipiaosaurus inexpectus* and *Erlikosaurus andrewsi* show the lowest stress and
252 strain levels, whereas the highest magnitudes were generally observed in *Jianchangosaurus*
253 *yixianensis* and *Alxasaurus elesitaiensis*. If only the dentaries are considered, *Erlikosaurus*
254 *andrewsi*, *Segnosaurus galbinensis* and to a lesser degree *Beipiaosaurus inexpectus*
255 experience the lowest stress magnitudes during the extrinsic feeding scenarios. The
256 calculation of average von Mises stress for all models is consistent with these results obtained
257 from the contour plots (Fig. 4A): *Beipiaosaurus inexpectus* and *Erlikosaurus andrewsi* have
258 the lowest per-element average stress values for both the intrinsic and extrinsic scenarios. In
259 contrast, average von Mises stress is highest in *Falcarius utahensis* and *Alxasaurus*
260 *elesitaiensis*, confirming the aforementioned observations of the contour plots quantitatively.

261

262 *Relative bite forces*

263 Relative bite forces obtained from the FE models reveal considerable differences in how
264 muscle forces are translated into bite forces among the studied taxa. As expected, relative bite
265 forces increase with a posterior shift of the bite position, due to the skull acting as a third-
266 class lever. *Alxasaurus elesitaiensis* records the highest relative bite forces for biting at the
267 first (23-32% of muscle force), middle (27-35%) and last tooth position (56-66%) (Fig. 4B).
268 Relative bite forces for *Falcarius utahensis* fall within the same, although somewhat lower
269 range (first tooth: 19-24%, middle tooth: 23-27%, last tooth: 43-59%). By comparison,
270 *Beipiaosaurus inexpectus* and *Erlikosaurus andrewsi* possess the lowest relative bite forces
271 ranging from 14-18% (first tooth), to 20-27% (middle tooth) and maximally 28-38% (last
272 tooth) (Fig. 4b).

273

274 *Functional morphospace*

275 Principal component analysis (PCA) plots obtained from the morphometric analysis of the
276 undeformed and deformed mandible models illustrate the biomechanical behaviour of the
277 different morphologies in response to functional scenarios (Fig. 5, supplementary fig. 12). PC
278 axes 1 and 2 account for over 70% variation in deformation of the mandibular models. PC 1
279 correlates with the dorsal displacement of the posterior dentary and postdentary region,
280 whereas PC 2 represents the displacement in mediolateral width (i.e. mandibles draw closer
281 together moving along positive axis). Although a large overlap exists between the individual
282 models and functional scenarios (Fig. 5), differences in the degree of deformation are visible.
283 *Alxasaurus elesitaiensis* (8%) and *Beipiaosaurus inexpectus* (12%) occupy relatively smaller
284 regions of the morphospace, whereas *Jianchangosaurus yixianensis* (32%) and *Erlikosaurus*
285 *andrewsi* (33%) show the highest degree of morphospace occupation.

286

287 **DISCUSSION**

288 The combination of digital reconstruction, theoretical modelling and biomechanical analysis
289 demonstrates the functional diversity of therizinosaurian mandibles. As attested by the results
290 obtained from FEA, differences in mandibular morphology correlate with different functional
291 behaviours and likely reflect dietary specialisation patterns within this group of herbivorous
292 theropods.

293 Considerable differences in mechanical performance (stress and strain magnitudes,
294 relative bite forces, deformational variation) between the modelled taxa suggest distinctive
295 morphofunctional trends. For all tested loading scenarios, the dentary and complete
296 mandibular morphologies of *Beipiaosaurus inexpectus* and *Erlikosaurus andrewsi* were
297 found to experience the lowest stress and strain magnitudes (but also the lowest relative bite
298 forces). Both taxa differ from other therizinosaurians in the dorsoventrally expanded

299 postdentary and coronoid region. An elevated coronoid eminence is frequently found in
300 herbivorous dinosaurs and is a unifying feature of Ornithischia, culminating in prominently
301 heightened coronoid processes in derived groups, such as ceratopsids and hadrosaurids
302 (Ostrom 1961; Upchurch *et al.* 2004; Weishampel 2004; Bell *et al.* 2009; Tanoue *et al.*
303 2009). While it has been demonstrated that the elevation and expansion of the coronoid
304 region is mechanically beneficial by increasing moment arms and mechanical advantage
305 (Nabavizadeh 2016), further stress reducing effects have been hypothesised by providing an
306 enlarged surface for ligamentous tissues (Bell *et al.* 2009). As observed here, the dorsolateral
307 expansion of the postdentary and coronoid region appears to provide additional stress
308 mitigating benefits. However, it should be noted that the postdentary elements of *Falcarius*
309 *utahensis* and *Alxasaurus elesitaiensis* are unknown. It is therefore possible that these taxa
310 might have possessed similar morphological adaptations to mitigate stresses. Comparing the
311 results for the dentaries of the analysed taxa only suggests a similar pattern. The ventrally
312 curved and downturned symphyseal region in *Erlikosaurus andrewsi* and *Segnosaurus*
313 *galbinensis* experience lower stress and strain magnitudes, in particular for the extrinsic
314 feeding scenarios. Additionally, the symphyseal region of the dentary in *Erlikosaurus*
315 *andrewsi* (and possibly also in *Segnosaurus galbinensis*) was likely covered by a keratinous
316 sheath (Lautenschlager *et al.* 2014), which has been shown to further mitigate stress and
317 strain magnitudes (Lautenschlager *et al.* 2013). Among Therizinosauria (and other
318 herbivorous coelurosaurs), a downturned and convex symphyseal region of the dentary has
319 been assumed to be a primary adaptation to herbivory (Zanno & Makovicky 2011). By
320 comparison, the elongate and straight dentary morphologies of *Falcarius utahensis*,
321 *Jianchangosaurus yixianensis*, and *Alxasaurus elesitaiensis* record the highest stress and
322 strain magnitudes. This indicates that the relatively unmodified jaw morphology
323 reassembling the plesiomorphic coelurosaurian and dinosaurian condition (Langer 2004;

324 Choiniere *et al.* 2010) offers less stress resistance. This may seem surprising, considering
325 basal coelurosaurs were adapted to carnivory. However, within hypercarnivorous clades,
326 including Tyrannosauroidae, a trend towards the dorsoventral expansion of the postdentary
327 and coronoid region in derived members is observable, which might likely have served the
328 same stress mitigating purpose (Holtz 2004; Holtz *et al.* 2004; Eddy & Clarke 2011).

329 Although prone to increased stresses, the mandible models of *Falcarius utahensis* and
330 *Alxasaurus elesitaiensis* produced the highest relative bite forces amongst the analysed
331 therizinosaurian taxa. This suggests that the elongate mandibular morphologies could
332 represent a compromise between high bite forces and increased stress susceptibility.
333 However, in *Falcarius utahensis* and *Alxasaurus elesitaiensis* the tooth row extends
334 relatively closer to the jaw joint, resulting in higher bite forces.

335 The observed differences in mandibular robustness and relative bite forces indicate
336 dietary adaptations and specialisations across the individual therizinosaurian taxa and
337 functional diversification in the course of their evolution. The basal-most therizinosaurian
338 *Falcarius utahensis* is characterised by high relative bite forces, moderate stress and strain
339 magnitudes, in particular during unilateral and bilateral biting scenarios, and moderate
340 deformational variation as indicated by the functional morphospace occupation. Although the
341 exact timing of a shift from carnivory to herbivory in Therizinosauria is difficult to identify,
342 the osteology of *Falcarius utahensis* suggests that this dietary transformation was not yet
343 fully completed at this stage (Zanno 2010b). It is therefore possible that *Falcarius utahensis*
344 retained relatively high bite forces in order to sustain an omnivorous life style. In more
345 derived therizinosaurians, relative bite forces were found to be considerably lower. This
346 pattern indicates that these taxa might have engaged in less oral processing and instead relied
347 on other means to process vegetation, such as gut fermentation or gastric mills (although
348 unambiguous evidence for the latter has not been found) (Zanno & Makovicky 2011; Zanno

349 *et al.* 2009), whereas the low bite forces were compensated for by harnessing the postcranial
350 musculature to crop foliage (Lautenschlager *et al.* 2013). As aforementioned, though, the
351 observed differences in relative bite forces are partially influenced by the length and extent of
352 the tooth row, leading to relatively higher bite forces in *Falcarius utahensis*,
353 *Jianchangosaurus yixianensis* and *Alxasaurus elesitaiensis*.

354 Low stress and strain magnitudes in *Beipiaosaurus inexpectus* and *Erlikosaurus*
355 *andrewsi* show that these taxa would have been more flexible in their foraging behaviour as
356 they were able to engage in different feeding styles without increasing stress levels, which
357 could have been further mitigated by the presence of a keratinous sheath (Lautenschlager *et*
358 *al.* 2013). Although scarce for the majority of therizinosaurian deposits, preserved plant
359 fossils demonstrate the palaeoenvironment of *Beipiaosaurus inexpectus* to be diverse and
360 abundant in conifers, ferns and bennettitaleans (Zhou *et al.* 2003). Results from the extrinsic
361 loading scenarios would further suggest that a downwards pull motion while gripping
362 vegetation is generally more likely for all studied taxa than a lateral or upwards movement.
363 However, taxa with a downturned symphyseal region (*Erlikosaurus andrewsi*, *Segnosaurus*
364 *galbinensis*), which mitigates stresses in the dentary during lateral pulling, could have been
365 more likely to engage in this behaviour. In contrast, the increased stress levels found for a
366 pull-upwards scenarios for all taxa indicate foraging of vegetation at head level, but not
367 below. These findings are consistent with the functional morphology of the postcranial
368 skeleton. The trend towards increased neck length in derived therizinosaurians indicates the
369 importance of extending the browsing range (Zanno 2010b), whereas the manual unguals of
370 most taxa had been adapted for grasping vegetation during foraging (Lautenschlager 2014).
371 In contrast, the claws of *Alxasaurus elesitaiensis* were found to have been used in a more
372 generalist fashion (Lautenschlager 2014), which is reflected also in the results for the

373 mandibular function here, suggesting that this species was ecologically more flexible in
374 comparison to other therizinosaurians.

375 For the sympatric taxa *Erlikosaurus andrewsi* and *Segnosaurus galbinensis* the
376 differences in relative bite force show that *Segnosaurus galbinensis* would have been able to
377 feed on tougher vegetation, whereas overall robustness in *Erlikosaurus andrewsi* suggests a
378 greater flexibility in feeding style as stress levels stay low across different feeding
379 simulations. Adaptation to coarser and tougher food has been shown to be a common, but not
380 exclusive mechanism for niche separation in contemporaneous herbivorous dinosaurs
381 (Fiorillo 1998; Mallon & Anderson 2014). Specialisations in tooth morphology found in
382 *Segnosaurus galbinensis* support the assumption that both taxa were functionally adapted to
383 different foraging behaviour and food selection (Zanno *et al.* 2016). Differentiations of the
384 dentary teeth in *Segnosaurus galbinensis* hint at increased incorporation of the dentition on
385 procuring or processing food, whereas previous findings for *Erlikosaurus andrewsi*
386 demonstrate that this species mostly employed the rhamphotheca as a cropping device, whilst
387 harnessing the neck musculature during foraging (Lautenschlager *et al.* 2013). Actual size
388 differences between the two taxa (estimated mass: *Erlikosaurus* ca. 174-278 kg, *Segnosaurus*
389 ca. 1469 kg; Lautenschlager *et al.* 2012; Zanno & Makovicky 2013) suggest that these
390 effects were likely increased and hint at additional mechanisms of resource partitioning such
391 as height stratification (Bakker 1978; Weishampel & Norman 1989; Zanno & Makovicky
392 2013; Mallon *et al.* 2013). However, considering that many therizinosaurian taxa are more
393 widely separated by time and geography, other factors than intra-clade competition were
394 likely at work in driving biomechanical variability within Therizinosauria. Adaptive
395 responses to different floras and competition with other herbivores might have been a further
396 factor in shaping morphological diversity.

397 A number of morphological traits thought to be indicative of an herbivorous diet have
398 been identified in Therizinosauria, many of which are also more broadly distributed across
399 Coelurosauria (Zanno & Makovicky 2011; Barrett 2014), such as a downturned symphyseal
400 region of the dentary, an elevated coronoid region, rostral edentulism and modifications of
401 tooth shape. Results from the present study thereby offer the chance to evaluate the functional
402 significance of these purported herbivorous characters, allowing general statements to be
403 made regarding the evolution of theropod herbivory in general.

404 As demonstrated by the results, *Falcarius utahensis* differs considerably from other
405 therizinosaurians in possessing relatively high bite forces and moderate stress and strain
406 levels, consistent with its basal position and the retention of some plesiomorphic characters
407 (e.g. elongate, straight mandible, symphyseal teeth). Following this initial stage, a rapid
408 morphological and functional diversification within Therizinosauria took place, manifested in
409 a general decrease of bite forces and the evolution of stress mitigating characters, such as an
410 extended postdentary region and a downturned symphyseal region of the dentary. This trend
411 is paralleled by rostral edentulism and the development of a keratinous rhamphotheca
412 covering the tip of the dentary and skull, which has been shown to provide additional stress
413 reducing effects (Lautenschlager *et al.* 2013). Similar morphological trajectories can be
414 observed in other herbivorous theropod clades (e.g. Ornithomimosauria, Oviraptorosauria)
415 and ornithischians (e.g. Ceratopsia, Ankylosauria, Stegosauria), in which comparable
416 characters have evolved (Ostrom 1966; Barrett *et al.* 2011; Zanno & Makovicky 2011;
417 Mallon & Anderson 2013; Barrett 2014). Features, such as a characteristically downturned
418 dentary, have classically been proposed as primary adaptations to herbivory and are widely
419 distributed across herbivorous dinosaurs (Sues 2000; Zanno & Makovicky 2011; Barrett
420 2014; Novas *et al.* 2015) and some archosauromorphs more generally (Flynn *et al.* 2010).
421 Furthermore, the expression of a downturned dentary has recently been demonstrated to be

422 linked to a dietary shift from omnivory to herbivory with ontogeny in the theropod dinosaur
423 *Limusaurus inextricabilis* (Wang *et al.* 2016). Results obtained here suggest that the presence
424 of this feature provides a viable mechanism for stress mitigation in herbivorous taxa
425 confirming long-held assumption about its functionality (e.g Barrett 2000, 2014 and
426 references therein). The acquisition of additional stress-reducing structures, such as a
427 keratinous sheath covering the symphyseal region of the dentary and the rostrum of the skull,
428 further indicates the importance of bracing the rostral region of the snout. With a shift from a
429 faunivore to a plant-based diet, the functional focus moves from the tooth row to the
430 rostralmost part of the skull and lower jaw as a device for procuring food. As a consequence,
431 this region is being reinforced through the development of a downturned dentary and the
432 acquisition of a keratinous sheath in herbivorous theropods and many ornithischians. A
433 comparable mechanism can be found in sauropods, in which a dorsoventral expansion of the
434 symphyseal region has been shown to achieve the same effect of reducing stresses (Button *et*
435 *al.* 2016). This convergent evolution of morphologically and functionally similar features
436 suggests that these anatomical modifications of the mandible convey an important
437 biomechanical advantage for herbivorous taxa.

438

439 **CONCLUSIONS**

440 As shown in this study, the combined use of digital reconstruction, theoretical modelling and
441 biomechanical analysis techniques provides powerful tools to overcome preservational
442 limitations of the fossil record and to study the functional significance of morphological
443 variation of skeletal structures. **Using this approach, different mandibular morphologies**
444 **present in therizinosaurian dinosaurs were found to correspond to different dietary strategies**
445 **permitting niche-differentiation and coexistence of taxa.** Morphological features indicative of
446 an herbivorous diet, including a downturned tip of the lower jaw and an expanded post-

447 dentary region, were identified as having stress mitigating effects. The more widely
448 distributed occurrence of these purported herbivorous traits in other theropod and dinosaur
449 clades further suggests that these features played an important role in the evolution and
450 acquisition of (dinosaur) herbivory. However, while some morphofunctional trends can be
451 identified using the therizinosaurian dataset, a larger sample size is necessary to further
452 disentangle the functional significance of herbivorous characters and their individual
453 contribution.

454

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464

465 **DATA ARCHIVING STATEMENT**

466 Data for this study are available in the Dryad Digital Repository: doi:10.5061/dryad.vd68s

467 **[FIG S1.** Comparison of displacement distribution for different unilateral biting scenarios in
468 studied therizinosaurian mandibles.

469 **FIG S2.** Comparison of maximum principal strain distribution for different unilateral biting
470 scenarios in studied therizinosaurian mandibles.

471 **FIG S3.** Comparison of minimum principal strain distribution for different unilateral biting
472 scenarios in studied therizinosaurian mandibles.

473 **FIG S4.** Comparison of Von Mises stress distribution for different bilateral biting scenarios
474 in studied therizinosaurian mandibles.

475 **FIG. S5.** Comparison of displacement distribution for different bilateral biting scenarios in
476 studied therizinosaurian mandibles.

477 **FIG. S6.** Comparison of maximum principal strain distribution for different bilateral biting
478 scenarios in studied therizinosaurian mandibles.

479 **FIG. S7.** Comparison of minimum principal strain distribution for different bilateral biting
480 scenarios in studied therizinosaurian mandibles.

481 **FIG. S8.** Comparison of displacement distribution for different feeding scenarios in studied
482 therizinosaurian mandibles.

483 **FIG. S9.** Comparison of maximum principal strain distribution for different feeding scenarios
484 in studied therizinosaurian mandibles.

485 **FIG. S10.** Comparison of minimum principal strain distribution for different feeding
486 scenarios in studied therizinosaurian mandibles.

487 **FIG. S11.** Landmark positions for geometric morphometrics analysis

488 **FIG. S12.** Deformational variation of tested mandibular models and loading scenarios.

489 Principal component plot based on geometric morphometric analysis of undeformed and
490 deformed models.

491 **SUPPLEMENTARY TABLE 1.** Number of tetrahedral elements (rounded to the nearest
492 10,000) for the different FE models

493 **SUPPLEMENTARY TABLE 2.** Muscle forces applied to the different mandible models.

494 **SUPPLEMENTARY MODEL 1.** 3-D model of *Falcarius utahensis* in STL format.

495 **SUPPLEMENTARY MODEL 2.** 3-D model of *Jianchangosaurus yixianensis* in STL
496 format.

497 **SUPPLEMENTARY MODEL 3.** 3-D model of *Beipiaosaurus inexpectus* in STL format.

498 **SUPPLEMENTARY MODEL 4.** 3-D model of *Alxasaurus elesitaiensis* in STL format.

499 **SUPPLEMENTARY MODEL 5.** 3-D model of *Erlikosaurus andrewsi* in STL format.

500 **SUPPLEMENTARY MODEL 6.** 3-D model of *Segnosaurus galbinensis* in STL format.]

501

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701 **FIGURE CAPTIONS**

702

703 **FIG. 1.** Reconstructed therizinosaurian mandibles shown in phylogenetic context. Preserved
704 elements depicted in light grey and missing elements depicted in dark grey in lateral outline
705 images. All models scaled to the same surface area. Phylogeny simplified after Zanno
706 (2010a).

707 [intended for 110 mm two-thirds page width]

708

709 **FIG. 2.** Comparison of von Mises stress distribution for different unilateral biting scenarios
710 in studied therizinosaurian mandibles. (A) *Falcarius utahensis*, (B) *Jianchangosaurus*
711 *yixianensis*, (C) *Beipiaosaurus inexpectus*, (D) *Alxasaurus elesitaiensis*, (E) *Erlikosaurus*
712 *andrewsi*, (F) *Segnosaurus galbinensis*. From left to right, bite point at first, middle and last
713 tooth position indicated by arrows. Scale bar represents 100 mm.

714 [intended for 166 mm full page width]

715

716 **FIG. 3.** Comparison of von Mises stress distribution for different feeding scenarios in studied
717 therizinosaurian mandibles. . (A) *Falcarius utahensis*, (B) *Jianchangosaurus yixianensis*, (C)
718 *Beipiaosaurus inexpectus*, (D) *Alxasaurus elesitaiensis*, (E) *Erlikosaurus andrewsi*, (F)
719 *Segnosaurus galbinensis*. From left to right, clipping at tip of dentary, pulling downwards,
720 upwards and lateral. Direction of pull indicated by arrows. Scale bar represents 100 mm.

721 [intended for 166 mm full page width]

722

723 **FIG. 4.** Quantitative assessment of biomechanical differences for tested mandibular models
724 and loading scenarios. (A) Average von Mises stress. (B) Relative bite forces (calculated as

725 ration between input and output forces). Range of values in each graph derived from
726 unilateral and bilateral bite simulations.

727 [intended for 80 mm column width]

728

729 **FIG. 5.** Deformational variation of tested mandibular models and loading scenarios. Size of
730 individual morphospace correlates with the degree and extent of deformation subjected to
731 loading. Principal component plot based on geometric morphometric analysis of undeformed
732 and deformed models. PC 1 correlates with the dorsal displacement of the posterior dentary
733 and postdentary region, PC 2 represents the displacement in mediolateral width (i.e.
734 mandibles draw closer together moving along positive axis). Filled circles represent
735 undeformed models.

736 [intended for 110 mm two-thirds page width]