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Extreme and rapid bursts of functional adaptations shape bite force in amniotes

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1 **RUNNING HEAD: Bite force evolution in amniotes**

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3 **Extreme and rapid bursts of functional adaptations shape bite force**

4 **in amniotes**

5

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21 ABSTRACT

22 Adaptation is the fundamental driver of functional and biomechanical evolution.
23 Accordingly, the states of biomechanical traits (absolute or relative trait values) have long
24 been used as proxies of adaptations in response to direct selection. However, ignoring
25 evolutionary history, in particular ancestry, passage of time and the rate of evolution, can
26 be misleading. Here, we apply a recently developed phylogenetic statistical approach using
27 significant rate shifts to detect instances of exceptional rates of adaptive changes in bite
28 force, in a large group of terrestrial vertebrates, the amniotes. Our results show that bite
29 force in amniotes evolved through multiple bursts of exceptional rates of adaptive changes,
30 whereby whole groups – including Darwin’s finches, maniraptoran dinosaurs (group of non-
31 avian dinosaurs including birds), anthropoids and hominins (the group of species including
32 modern humans) – experienced significant rate increases compared to the background rate.
33 However, in most parts of the amniote tree of life we find no exceptional rate increases,
34 indicating that coevolution with body size was primarily responsible for the patterns
35 observed in bite force. Our approach represents a template for future studies in functional
36 morphology and biomechanics, where exceptional rates of adaptive changes can be
37 quantified and potentially linked to specific ecological factors underpinning major
38 evolutionary radiations.

39

40 KEYWORDS

41 Bite force, evolution, phylogenetic comparative methods, adaptations, amniotes, rate-shifts

42 **BACKGROUND**

43 Adaptation is the fundamental driver of functional and biomechanical evolution. Measures
44 of biomechanical performance – e.g. bite force – characterize and quantify specific
45 functional performances to fulfil ecological demand – e.g., diet [1, 2]. Functions are
46 therefore typically assumed to be under direct selection – i.e. a change in biomechanical
47 performance indicates selection for changes in function. For instance, taxa with higher bite
48 force are often interpreted as having diets requiring powerful bites, driving selection on
49 associated morphological features [3-5]. However, observable trait states can be the result
50 of multiple confounding factors independent of direct selection for a specific function,
51 including scaling effects [6] and evolutionary history (ancestry and the passage of time).
52 That is, species can often achieve relatively high bite forces owing to the accumulation of
53 evolutionary changes that is within expectation given the passage of time, without invoking
54 exceptionally strong selection pressures towards increased bite forces. Assuming that the
55 states of biomechanical traits can be used as proxies for strong selection/functional demand
56 while ignoring such confounding factors (in particular evolutionary history) can be and often
57 are misleading [7, 8]. Thus, it is important to identify cases in which trait values exceed the
58 amount of evolutionary change expected given confounding factors – i.e., objectively
59 detecting instances of *exceptional rates of adaptive changes* [9].

60 It has long been interpreted that the intensity of natural selection acting on a
61 phenotype is linked to rates of evolution [9, 10], and significant shifts in rates can be
62 interpreted as instances of adaptive responses to strong selective pressures – e.g., positive
63 phenotypic selection [9] akin to positive genetic selection [11, 12]. Positive selection is
64 invoked as an explanation for trait evolution along a branch on a phylogenetic tree if the
65 amount of evolutionary change exceeds the amount of change expected from the passage

66 of time given the background rate of evolution. In the context of biomechanical evolution,
67 evidence for exceptional rates of adaptive changes in biomechanical traits can be detected
68 as significant rate shifts using this phylogenetic comparative framework. However, in spite
69 of the ever-increasing numbers of comparative biomechanical studies employing a
70 phylogenetic framework [13-27], studies attempting to detect episodes of exceptional rates
71 of adaptive changes in biomechanical traits that can be interpreted as evolutionary
72 responses to strong levels of natural selection using a statistically rigorous comparative
73 framework are still comparatively rare [but see, e.g., 23].

74 Here, we test the hypothesis that instances of exceptional rates of adaptive changes
75 have shaped the observed diversity in biomechanical traits focusing on bite force evolution.
76 Our hypothesis specifically relates to detecting exceptional rates of adaptive changes and
77 not in detecting rate heterogeneity – exceptional rates of adaptation is defined as instances
78 of exceptionally large rate increases (at least twice the background rate, see Methods and
79 [9] for details). Bite force relates to species' niche and feeding ecology, is correlated with
80 several ecological and behavioural traits [28-31], and is widely available from the literature
81 across several fields of study (e.g., biomechanics, ecology, palaeobiology) for a broad
82 sample of the tree of life, making it an ideal biomechanical trait to test our hypothesis using
83 a phylogenetic framework. To this end, we assembled the largest dataset of bite forces
84 collected to date for amniotes, both extinct (including non-avian dinosaurs, sabre-toothed
85 cats, and hominins) and extant.

86

87 **METHODS**

88 **Data.** Bite force and body mass data were collected primarily through the literature,
89 augmented with novel estimates (ESM), spanning 434 extant and extinct amniote species

90 (Table S1). We used the Time Tree of Life (TTOL) [32] as the backbone phylogeny, with fossil
91 tips/clades inserted at the appropriate phylogenetic and temporal positions (ESM) using
92 fossil dates from the Paleobiology Database (accessed 9 Feb 2017).

93

94 ***Variable-Rates Phylogenetic Regression Models.*** We fitted a variable-rates (VR) regression
95 model [9] using BayesTraits [33] on \log_{10} bite force against \log_{10} body mass (*Single-slope VR*
96 *model*). The VR regression model as implemented in BayesTraits works to modify the branch
97 lengths to “detect heterogeneity in rates of phylogenetically structured residual errors” [9].
98 That is, once the appropriate level of variance in the response variable – e.g., bite force – is
99 explained by some predictor variable(s) – e.g., body mass – outlying deviations from the
100 regression line will be explained as rate shifts (Fig. S1). Under Brownian motion, bite force –
101 after accounting for body mass and other confounding variables – evolves at a rate
102 proportional to time (and an estimated background variance) across the phylogeny, and for
103 any evolutionary change along a given branch that is greater/less than the expected amount
104 of change for the duration of time to occur (given body mass), that branch must be
105 stretched/compressed in length in proportion to the observed amount of phenotypic
106 change – corresponding to a rate increase/decrease. The magnitude of branch
107 stretching/compressing is the rate scalar (r).

108 As previous research indicated that scaling of bite force is group-specific [34-36] we
109 tested an additional model in which separate slopes were estimated for five different
110 groups (*5-Group VR model*). Each taxon was assigned to one of five groups: mammals
111 excluding bats (hereafter “Mammals”), bats, finches (Fringillidae, Estrildidae, and Darwin’s
112 finches); non-finch dinosaurs (including other birds, hereafter “Dinosaurs”); and non-
113 dinosaurian diapsid reptiles (hereafter “Reptiles”) (Fig. 1; Table S1). We chose these five

114 groups because they act as good descriptors of the distribution of data (Fig. S3) as well as
115 conforming to widely recognized taxonomic groups (see ESM for details). Birds and
116 dinosaurs were grouped together, as fossil evidence points to a blurred distinction in their
117 physiology and biology [37-40], while dinosaurs are very different from other reptiles [41].
118 Intercept differences were not modelled – group-wise offsets will trade off with rate scalars
119 on branches leading to the last common ancestors of the respective groups (Fig. S1). In
120 order to account for potential differences owing to bite force acquisition type and biting
121 positions (ESM), two additional models were fitted with the confounding variables Bite Type
122 and Bite Point individually added to the regression model as covariates (ESM).

123 We tested for instances of exceptional bursts of evolutionary change in bite force
124 based on rate shifts along branches on the phylogeny [9], based on the premise that
125 phenotypic changes owing to adaptations (potentially as a response to strong selective
126 pressure) would be proportional to r . Thus, we define exceptional change following the
127 criteria of [9]: 1) certainty of rate shifts, the branch in question must be scaled in >95% of
128 the posterior sample of scaled trees; and 2) magnitude of rate shifts, the r in question must
129 be greater than two. Rate heterogeneity that do not fulfil these two criteria were not
130 considered as instances of exceptional rates of adaptive changes. There are two types of
131 rate shifts: branch-wise rate shifts (branch shifts), are cases in which significant increases in
132 rates with respect to background rate are detected along individual branches; and clade-
133 wise rate shifts (clade shifts), occur across all branches within a clade and represent cases in
134 which rapid divergences in trait values have occurred (Fig. S1). We determined whether
135 rate-shifts constituted exceptional rates of adaptive changes if they satisfied the criteria set
136 out above in all of three independent replicate Markov Chain Monte Carlo (MCMC) chains.

137 In order to determine if rate-heterogeneity was statistically significant, we fitted an
138 *equal-rate (ER) model* (or Brownian motion) as a simpler alternative to each of our VR
139 models. Model selection was performed using the Bayes Factor (BF; see ESM for details): BF
140 is defined as twice the difference in log marginal likelihood (m) between the complex model
141 (model_1) and the simple model (model_0) – i.e., $\text{BF} = 2 \times (m_1 - m_0)$. For instance, we
142 computed BF using m from our 5-Group VR model and the simple alternative 5-Group ER
143 model, and selected the VR model over the ER model when BF value was greater than 2
144 [42].

145 We ran our MCMC chains for 10^9 iterations, with a burn-in period of 10^8 iterations,
146 sampling every 10^5 iterations, resulting in a posterior sample of 900 modified VR trees and
147 model estimates, for each regression model. We used stepping stone sampling (over 1000
148 stones at 10^5 iterations each) to compute marginal likelihoods from which BF were
149 calculated. Post-processing of the BayesTraits outputs were conducted using an online post-
150 processor (www.evolution.reading.ac.uk/VarRatesWebPP), as well as in R [43].

151

152 RESULTS

153 ***Variable-Rates Regression Model.*** We found strong support for the VR model compared to
154 the ER model ($\text{BF}_{\text{VR-ER}} = 474$) for the single-slope regression model. Bite force scales nearly
155 isometrically with body mass, with a slope of 0.674 ($p\text{MCMC}_0 < 0.001$, $R^2_{\text{mean}} = 0.79$; Table
156 S2), which is not significantly different from a theoretical isometric slope of 0.67 ($p\text{MCMC}_{0.67}$
157 = 0.4) [6].

158 There is statistical support for favouring the 5-Group model over the single-slope
159 model (Fig. 1)); significant differences exist among the slopes of different groups (Table S2;
160 Table S3). Finches and bats are not different from each other, but are distinct from

161 mammals, reptiles and dinosaurs (Fig. 1; Table S3); in turn, these three groups are not
162 different from each other (Fig. 1; Table S3). Finches and bats have slopes that deviate from
163 0.67 (Table S4), while the other three groups have slopes that are not significantly different
164 from 0.67 (Table S4). Critically, despite allowing for the variation in slopes among taxonomic
165 groups, our 5-Group VR model ($R^2_{\text{mean}} = 0.809$; Table S2) still outperforms a 5-Group ER
166 model ($\text{BF}_{\text{VR-ER}} = 429$; Table S2).

167 Model selection showed that bite type is not significant ($p\text{MCMC} > 0.05$ in both
168 Single-Slope+BiteType and 5-Group+BiteType models; Table S2) while bite point is ($p\text{MCMC}$
169 < 0.05 in both Single-Slope+BitePoint and 5-Group+BitePoint models; Table S2). Given a
170 similar body size, bite force is comparable in magnitude between *in vivo* measurements and
171 indirect estimates, but it differs in magnitude between posterior and anterior bites
172 (posterior positions have higher forces, as expected). There is no slope difference between
173 bite type categories or between bite point categories (Figs S6, S7). We used the 5-
174 Group+BitePoint model as our final model for detecting exceptional rates of adaptive
175 changes in bite force – this enables us to compare evolutionary rates after accounting for
176 effects owing to body size and bite point.

177
178 **Rate Shifts and Exceptional Rates of Adaptive Changes.** We found substantial amount of
179 rate heterogeneity (elevated rates in >50% of the posterior sample) in the amniote tree of
180 life, along 439 branches out of 866 branches in the phylogeny (51% of branches; Fig. S4).
181 Instances of exceptional rates of adaptive changes are found in a far fewer number of
182 branches: in 182 branches (21% of branches) (Table S5; Figs 1, 2a, S5; Movie S1). Our results
183 show that bite force evolved through multiple bursts of exceptional rates of adaptive
184 changes, whereby whole groups experienced rate increases of bite force evolution

185 compared to the background rate across the entire amniote tree. We find such clade shifts
186 in Darwin's finches (median $r > 55$), the hominin lineage excluding *Australopithecus*
187 *anamensis* ($r > 35$), Anthroidea ($r > 6$), and maniraptoran theropod dinosaurs (the clade
188 including birds and their closest relatives, here *Erlisosaurus* and *Dromaeosaurus*; median $r >$
189 3). Thus, most of the scaled branches are because of a smaller number of node scalars that
190 modify all descendant branches.

191 Two aspects of the distribution of rate shifts are noteworthy. First, clade-wise rate
192 shifts show a nested pattern (Fig. 1). For example, Darwin's finches exhibit an additional
193 level of rate increase above that of the maniraptoran rate increase (Figs 1, 2a, 2b, S5;
194 Movies S1-S2). The same pattern characterizes hominins (excluding *A. anamensis*) within
195 anthropoid primates (Figs 1, 2a, 2c, S5; Movies S1-S2). In particular, *Homo* species exhibit
196 reductions in bite forces (Fig. 2c), which is in marked contrast to the apparent increase in
197 hominin body size through time (Figs S8) [44]. Thus, humans drastically reduced bite force
198 through time at a rate faster than their anthropoid ancestors and relatives.

199 The second key aspect of the rate shift distribution is that branch-wise rate increases
200 occur in conjunction with clade-wide shifts. We identified an exceptional increase in the rate
201 of bite force evolution along the branch leading to Passeroidea (the clade defined by the last
202 common ancestor of our finches) (median $r > 30$), followed by a reversal to the ancestral
203 maniraptoran rate. We also recovered a scattering of branch-specific shifts on terminal
204 branches (*Proteles cristatus*, *Panthera onca*, *Sus scrofa*, *Stegosaurus*, and *Plateosaurus*),
205 marking sudden changes in the biomechanical performance of some species from their
206 close relatives (Figs 1, 2a, S5; Movie S1).

207

208 **DISCUSSION**

209 **Exceptional Rates of Adaptive Changes in Bite Force.** Working under the premise that the
210 rate of phenotypic trait evolution is proportional to the strength of selection [9, 10], we
211 provide the first evidence for exceptional rates of adaptive changes shaping the diversity of
212 bite force in both extinct and extant amniotes, using a statistically robust evolutionary
213 framework [9]. We find such instances of exceptional rates of adaptive changes in four
214 clades of amniotes and a handful of independent branches. Conversely, in most lineages of
215 amniotes studied here (79% of branches in the phylogeny), bite force does not undergo
216 exceptional rates of adaptive changes (even in lineages with elevated rates; ESM; Fig. S4),
217 indicating that co-evolution with body size is, for the most part, the main factor responsible
218 for bite force variation. A large predator can generate enough bite force to kill its prey just
219 by being large. As an example, *Tyrannosaurus rex* was most likely capable of “pulverizing”
220 bones [45] simply owing to its colossal size (~5-10 tonnes [46-48]). We did not detect
221 instances of exceptional rates of adaptive changes in bite force in this taxon, and therefore
222 there is no evidence of strong selection for a feeding ecology that requires
223 disproportionately high bite force – e.g. “extreme osteophagy (bone consumption)” [45].
224 Similarly, we do not detect signatures of exceptional rates of adaptive changes in classically
225 recognised power-biters such as osteophagous hyenids [49], short-faced hyper-carnivorous
226 felids [50, 51], and small-brained carnivorous marsupials [3, 5, 52] indicating that bite force
227 in these clades were not subjected to strong selection as is often presumed.

228 Interestingly, contrary to our prior expectations, we do not detect exceptional rates
229 of adaptive changes in sabre-toothed cats (Machairodontinae). Although rates are on
230 average higher in Felidae as a whole (including both sabre- and conical-toothed cats along
231 with the basal cats *Proailurus* and *Hyperailurictis*) compared to the background rate in the
232 majority of the posterior sample (i.e., >50%; ESM; Fig. S4), they do not fulfil the criteria for

233 exceptional rates of adaptive changes. Further, there is no difference between rates in
234 machairodontine lineages and other felid lineages. The time elapsed in the lineage leading
235 to sabre-toothed cats since their divergence with conical-toothed cats sufficiently explains
236 the reduction in bite force in sabre-toothed cats.

237 It is possible that for the majority of taxa in our bite force sample, individuals
238 preferentially seek out and consume food items that can be processed within the naturally
239 generated range of bite forces, and rarely actively seek food items that require maximum
240 biting capacity. This equates to a behavioural adaptation, in which species evolve bite force
241 through correlated evolution with body mass, and preferentially consume food items that fit
242 within their natural range of bite force. If this is true, then selection for improved biting
243 performance with respect to higher bite force may not frequently occur. Additionally,
244 functional-morphological adaptations – e.g. tooth morphology – may facilitate higher biting
245 performance – e.g., piercing, crushing or shearing – without necessitating a more powerful
246 bite.

247 Similarly, drastic reduction in bite force – as a trade-off between force and velocity if
248 jaw closing velocity was under strong selection – would constitute an exceptional rate of
249 adaptation significantly below the expected range of bite force given the universal scaling
250 relationship. However, it is potentially more likely for reductions in bite force to occur over
251 exceptional gains in bite force since muscles are expensive organs to maintain and more so
252 to enlarge. Indeed, we observe more instances of drastic reductions in bite force associated
253 with exceptional rates of adaptive changes than we do exceptional increases in bite force
254 (Figs 2, S5).

255 Despite the overall uniform evolution of bite force relative to body mass, we find
256 evidence for exceptional rates of adaptive changes playing a major role in the evolution of

257 bite force (just not as a tree-wide pattern across all major clades). Since the majority of
258 these exceptional rates of adaptive changes occur as clade-wide rate shifts, it is possible
259 that they are linked to some biological, ecological or environmental features unique to
260 those clades and shared amongst constituent members. For instance: the acquisition of a
261 “key” innovation, which allows such clades to rapidly expand and exploit functional niches; a
262 shift into a new environment, habitat or lifestyle that is associated with new opportunities
263 and resources; or an extrinsic environmental event (such as mass extinction events) that
264 results in an abundance of ecological niches available for exploitation. Determining such
265 factors ultimately responsible for exceptional rates of adaptive changes is theoretically
266 possible. Namely, the VR regression framework allows for the inclusion of extrinsic factors
267 such as dietary preference, feeding strategy, sexual display/conflict, etc., as additional
268 covariates. A covariate can be identified as the extrinsic driver of bite force evolution if its
269 inclusion can explain much of the variation in bite force, thereby reducing or eliminating
270 rate shifts. At present, ecological data associated with biting performance are only available
271 for a handful of species, but we hope that future work will considerably augment
272 information on ecological covariates.

273

274 ***Macroevolutionary Patterns of Exceptional Rates of Adaptive Changes.*** Overall, our results
275 highlight a combination of clade-wise and branch-wise rate shifts occurring across the
276 amniote phylogeny. Clade-wise rate shifts are characterized by an elevated rate that is
277 homogenous across all branches within a given clade and are associated with an increase in
278 trait variation in the constituent taxa given the variance in the other taxa in the data [9].
279 Lineages in such clades continually evolve traits at a faster rate through time compared to
280 other parts of the tree (Fig. 1). This contrasts with a classic description of an adaptive

281 radiation [53], which is characterized by a rapid initial burst of trait evolution followed by a
282 rate slowdown associated with niche saturation [54]; clade-wise rate shifts see continual
283 changes in functional niche occupation. One implication of such patterns in bite force
284 evolution is that evolutionary lineages (sequence of branches leading to terminal taxa) do
285 not stay in the same regions of function-space (pertaining to biting functional variation), but
286 rather, continue to expand out to unoccupied/unexplored regions of function-space.
287 Evolutionary lineages will be moving through various functional niches as their bite force
288 values change through time. An alternative interpretation is that function-space itself
289 changes through time. i.e. functional/ecological niches are dynamic rather than fixed
290 entities, a constantly moving target [55]. Yet another interpretation is that function-space
291 saturates but convergences occur frequently and rapidly – that is, lineages move in and out
292 of occupied/explored regions of function-space. In this context, our results would support
293 the notion that functional adaptations are relatively labile over evolutionary history and
294 remain responsive to changing environmental conditions and ecological demands.

295 Branch-wise rate shifts (rate shifts associated with single branches only) occurring on
296 branches subtending whole clades (Fig. 1), such as that observed at the base of Passeroidea
297 in our dataset, can be interpreted as a mean-shift in bite force after accounting for body
298 mass [9]. In our case, this means that there was a rapid shift in the mean bite force value of
299 Passeroidea from the ancestral maniraptoran mean. The total sum of evolutionary changes
300 accumulating along the branch leading to Passeroidea exceeds that expected from the
301 temporal duration of that branch. This is irrespective of any un-sampled taxa along the
302 lineage – e.g., other perching birds (Passeriformes, e.g. corvids, shrikes) for which bite force
303 data are not available in the literature as far as we are aware.

304 Similarly, the two large-bodied herbivorous taxa, *Stegosaurus* and *Plateosaurus*,
305 have evolved bite force at excessively high rates (~11 and ~35 times background rate,
306 respectively – *Stegosaurus* and *Plateosaurus* have extremely small heads, and thus low bite
307 forces, for their body sizes), but these could potentially represent evolutionary patterns
308 within thyreophoran and sauropodomorph dinosaurs respectively, and not specifically
309 associated with these two species. Using a different measure of size such as head length or
310 width may likely change these results – though, body mass has major benefits over head
311 size for its ecological implications. Nonetheless, major changes in bite force relative to body
312 mass did occur along these lineages so the interpretation remains the same: the amount of
313 change in trait values given the duration of time elapsed is exceptionally high compared to
314 the background rate.

315

316 ***Evolution of Bite Force in Maniraptoran Dinosaurs.*** Maniraptoran theropods are perhaps
317 the most diverse amongst dinosaurs in terms of functional and morphological
318 specializations associated with feeding. Forms like the parrot-like oviraptorosaurs, large
319 herbivorous therizinosaur, hyper-carnivorous dromaeosaurs with recurved teeth (e.g.
320 *Velociraptor*), and toothed and toothless avialans are just some typical examples of
321 maniraptoran morpho-functional diversity. High evolutionary rates in maniraptoran bite
322 force indicate that their morphological and presumed ecological diversity are linked with
323 selection on biting performance. Maniraptoran fossils are predominantly known from
324 Cretaceous rocks but are inferred to have originated by the Middle Jurassic (~168 Myr ago;
325 Fig. 1), with derived members including the avialan *Archaeopteryx* appearing relatively
326 quickly, by the Late Jurassic (~150 Myr ago; Fig. 1). This implies that Maniraptora underwent
327 a rapid diversification (both in species diversity but also in bite force variance) early in their

328 evolutionary history, but that they retained high evolutionary rates in bite force throughout
329 the clade's history.

330 The observation that bite force underwent exceptional rates of adaptive changes in
331 maniraptoran theropods but not uniquely in birds – rates in birds are not distinguishable
332 from those in other non-avian maniraptorans – is consistent with recent findings that the
333 evolution of birds and their immediate close relatives – i.e. paravians – are similar to one
334 another [37], and that many of the features traditionally associated with birds were present
335 in paravians and more broadly in maniraptorans. Here we have demonstrated that this is
336 also the case with bite force evolution (given the available data); the rate of bite force
337 evolution did not change from non-avian maniraptorans to birds. On the other hand, this
338 means that heritable rates of bite force evolution in maniraptoran ancestors possibly
339 contributed to some extent on the subsequent ecological success of birds – the ability to
340 rapidly change bite force in response to changing environmental and ecological pressures
341 would surely have been beneficial for early Cenozoic birds in the post-extinction world.

342 Our identification of an extreme clade-wide rate shift in the Darwin's finches, which
343 is among the highest in the tree (>55 times the background rate; Figs 1, 2, S5; Movies S1-S2;
344 Table S5), is noteworthy for both historical and biological reasons. Darwin's finches are the
345 classic textbook case of 'adaptive radiation', with eco-morphological diversification
346 occurring in a short time interval after the initial colonization of the Galapagos Islands by
347 finches [56-58]. Their diversification in feeding ecology is particularly relevant to the rapid
348 evolution of bite force, as Darwin's finches are well documented to have strong dietary
349 preferences on food types of varying toughness [59] or differences in food manipulations
350 [60]. Within the context of the evolutionary history of amniotes as sampled here (~350
351 Myr), the radiation of Darwin's finches is comparatively recent with some divergences

352 occurring in a geologically instantaneous manner (Fig. 1). Compared to their recent
353 divergence times, bite force variance in Darwin's finches is exceptionally high spanning
354 almost two orders of magnitude (Fig. 2) accounting for their extraordinarily high
355 evolutionary rates.

356

357 **Evolution of Bite Force in Humans.** The exceptionally high rates of bite force evolution in
358 the hominins excluding *A. anamensis* (Figs 1, 2) – more than 35 times the background rate
359 and ~6 times those for the branches within other anthropoid primates – highlights an
360 important, recent and rapid evolution in our own lineage. In particular, the decrease in bite
361 force in *Homo* species (Fig 2) is contrary to the increase in hominin body size through time
362 (Fig S8) – such a discrepancy between bite force and body mass is indicative of strong
363 directional selection, and coincides with previously documented evolutionary shifts in
364 relative molar sizes, attributed to the reduction in feeding time associated with the
365 introduction of food processing such as cooking [9, 25]. Strikingly, [61] found a rate shift in
366 symphyseal angle in the hominin lineage excluding *A. anamensis*, coinciding with the
367 phylogenetic location where we find a rate shift in bite force (Fig. 1).

368 Additionally, the reduction in bite force in the hominin lineage may have occurred as
369 a consequence of an evolutionary trade-off with increasing brain size in this group [62-64]
370 (see ESM; Figs S9-S10). As brain size increases relative to skull size, the temporal fossa
371 (defined as the opening between the braincase and the zygomatic arch) is reduced in
372 dimension, thereby decreasing the amount of space available to house the temporal
373 muscles [63, 64], which are critical for achieving hard biting in most animals. This reduction
374 in temporal muscle can be seen in the changing predominance of the sagittal crest (ridge of
375 bone running along the midline of the skull) where the temporal muscles attach through

376 hominin evolution (Fig. S10). Strikingly, molecular evidence supports the hypothesis that a
377 drastic reduction in the temporal muscle occurred along the lineage to *H. sapiens* after its
378 divergence from chimpanzees owing to a frameshifting mutation, causing inactivation of the
379 predominant myosin heavy chain expression in masticatory muscles [63]. The mutation has
380 been inferred to have coincided approximately with the enlargement of the brain,
381 presumably concurrent with the origin of the genus *Homo* [63] – though the timing has
382 been contested [65, 66]. Furthermore, *H. sapiens* relies less on the temporal muscles and
383 more on the masseter muscles to generate bite force [67]. Thus, such a trade-off between
384 temporal muscle size and brain size is a reasonable explanation for the evolutionary
385 reduction in bite force in the hominin lineage through time, with the advent of cooking
386 further accelerating the loss of reliance on high bite force for food processing.

387 Indeed, an auxiliary phylogenetic regression modelling [68] of bite force on brain size
388 (endocranial volume) [69-71] accounting for body mass on hominids (*Pongo*, *Gorilla*, *Pan*,
389 and hominins), shows that bite force scales negatively with brain size (ESM; Fig. S9). The
390 reduction in bite force is statistically associated with an increase in brain size.

391 Alternatively, the reduction in bite force may owe to neoteny, whereby the jaw
392 muscles arrest in development along the hominin lineage. However, neoteny in humans has
393 also been interpreted as being associated with brain enlargement so the precise cause of
394 the reduction in jaw adductor musculature and thus bite force is up for debate.

395

396 **CONCLUSIONS**

397 Taken together, our results reveal that the evolution of bite force in amniotes occurred as
398 bursts of accelerated changes across multiple clades, and as the product of repeated and
399 nested pulses of progressively higher rates of change, representing instances of exceptional

400 functional adaptations. Using a phylogenetic evolutionary framework, on a dataset
401 representing the largest taxonomic sample to date, enables us to statistically detect
402 instances of adaptations in biomechanical metrics, not only along specific branches, but also
403 through time, paving the way to better understand how specific ecological niches (feeding
404 ecologies) are occupied. In order to determine whether species' bite force underwent
405 instances of exceptional rates of adaptive changes, it is necessary to demonstrate an
406 exceptionally high rate of evolution associated with that species in a phylogenetic context
407 after accounting for size and the expected evolutionary change associated with divergence
408 time.

409 DATA ACCESSIBILITY

410 Data are available on the Dryad Digital Repository (provisional DOI:

411 doi:10.5061/dryad.q12c06f). Temporary review link is as follows:

412 <https://datadryad.org/review?doi=doi:10.5061/dryad.q12c06f>

413

414 ETHICS STATEMENT

415 Not applicable

416

417 COMPETING INTERESTS

418 We have no competing interests.

419

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424 AUTHOR CONTRIBUTIONS

425 MS, MR and CV conceived of the study, designed the study, coordinated the study and draft

426 the manuscript. MS collected and analysed the data. All authors gave final approval for

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643

644 **FIGURE LEGENDS**

645 **Figure 1. Evolution of bite force and its relationship with body mass**

646 Exceptional rates of bite force evolution are shown as a colour gradient (green to gold) on
647 corresponding branches of the phylogenetic tree used in this study, while branches in which
648 no exceptional rates of adaptive changes are detected are in black. Silhouettes highlight
649 clades of interest coloured according to corresponding rates: *Deinonychus antirrhopus*,
650 Maniraptora; *Platyspiza*, branch subtending Passeroidea; *Geospiza fuliginosa*, Thraupidae;
651 Papionin monkey, Anthropeidea; and *Homo sapiens*, hominin lineage. Inset, the fitted
652 regression lines from a 5-Group variable-rate regression model accounting for bite point (5-
653 Group+BitePoint VR model) across all MCMC runs are shown in colours corresponding to
654 the five groups of interest: bats, blue; mammals excluding bats, grey; finches, red; dinosaurs
655 excluding finches, turquoise; and reptiles excluding dinosaurs, orange. Significant
656 differences in slopes do not exist between bats and finches as well as between mammals,
657 reptiles and dinosaurs, but significant differences exist between the two sets of groups –
658 i.e., bats/finches and mammals/reptiles/dinosaurs (Table S3). Similarly, slopes in bats and
659 finches are significantly different from the theoretical slope of 0.67 but those in mammals,
660 reptiles and dinosaurs are not (Table S4).

661

662 **Figure 2. Ancestral reconstruction of bite force across phylogeny and through time**

663 Evolution of bite force with respect to body size while accounting for variable rates show
664 branches and clades with higher amount of change in bite force than expected given
665 ancestral body sizes and phylogenetic positions. Exceptional rates along the branches of the
666 whole tree are shown as a colour gradient (green to gold), with the two clades exhibiting
667 the highest rates (Darwin's finches and hominins) indicated with silhouettes coloured

668 according to corresponding rates (a). Clades in which exceptional rates were detected are
669 highlighted: b, Dinosauria (turquoise) with maniraptorans (skyblue), finches (red) and
670 Darwin's finches (brown); and c, Anthropeida (teal) and hominins (bright green). Insets
671 show subclades of interest (node denoted by a white circle in the whole tree): Darwin's
672 finches amongst the Passeroidea (b) and hominins amongst Hominidae – i.e., great apes (c).
673

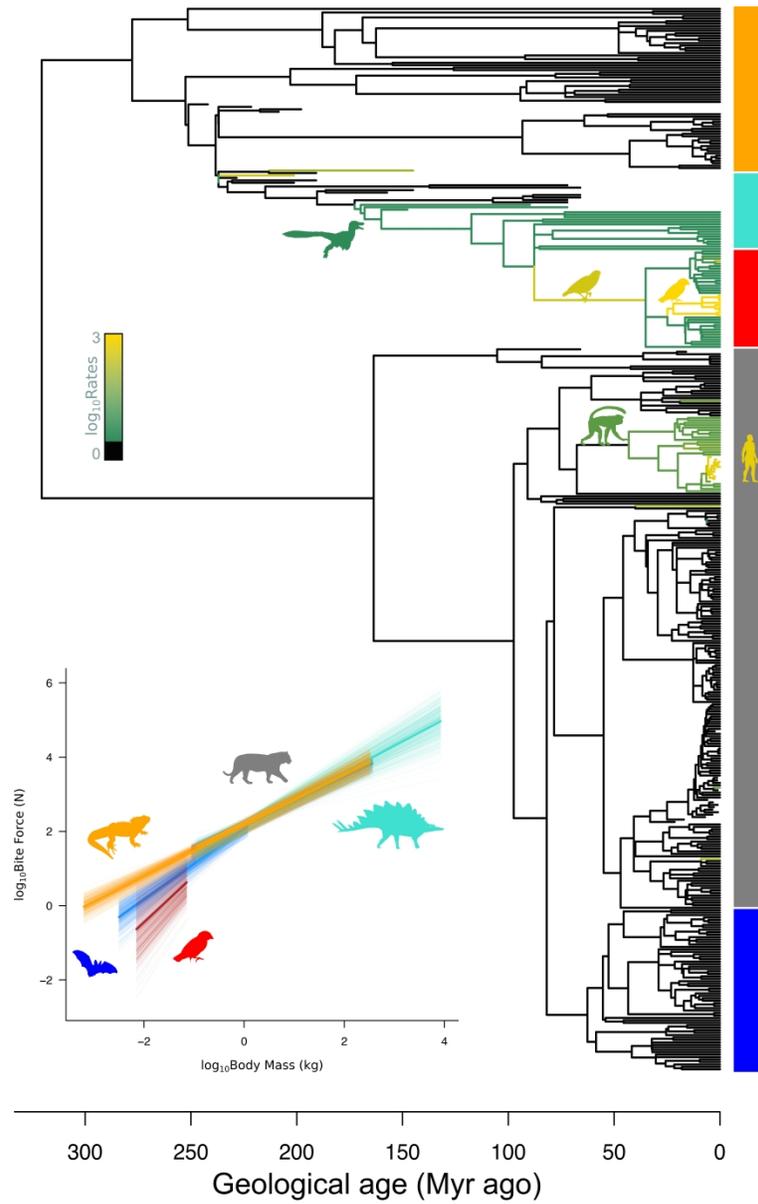


Figure 1. Evolution of bite force and its relationship with body mass

434x687mm (600 x 600 DPI)

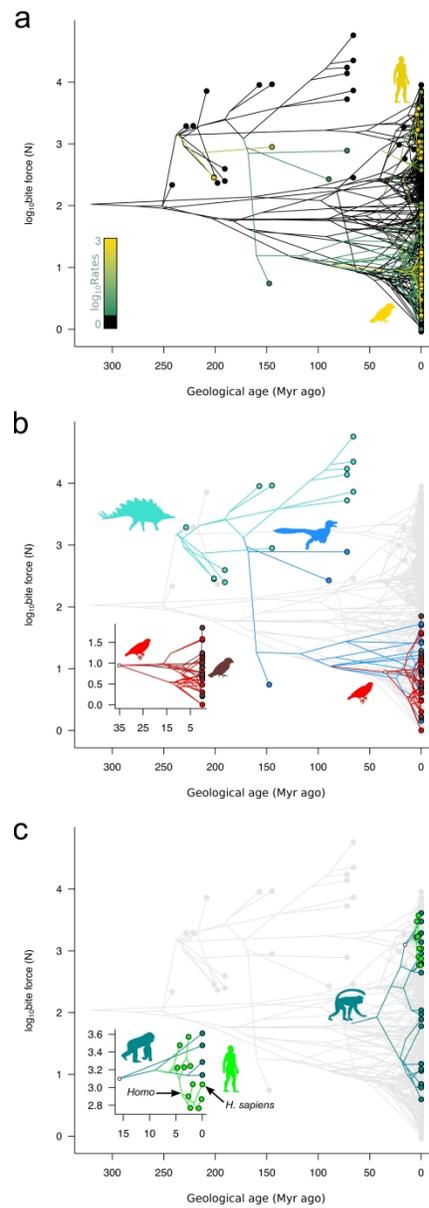


Figure 2. Ancestral reconstruction of bite force across phylogeny and through time

216x609mm (300 x 300 DPI)