

1 **Dietary specializations and diversity in feeding ecology of the earliest stem**
2 **mammals**

3
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22 **The origin and radiation of mammals are key events in the history of life, with fossils**
23 **placing the origin at 220 mya, in the Late Triassic¹. The earliest mammals, representing**
24 **the first 50 my of their evolution and including the most basal taxa, are widely**
25 **considered to be generalized insectivores^{1,2}. This implies that the first phase of the**
26 **mammalian radiation – associated with the appearance in the fossil record of significant**
27 **innovations such as heterodont dentition, diphyodonty, and the dentary-squamosal jaw**
28 **joint^{1,3} – was decoupled from ecomorphological diversification^{2,4}. Finds of exceptionally**
29 **complete specimens of later Mesozoic mammals have revealed greater**
30 **ecomorphological diversity than previously suspected, including adaptations for**
31 **swimming, burrowing, digging and even gliding^{2,5,6}, but such well preserved fossils of**
32 **earlier mammals do not exist¹, and robust analysis of their ecomorphological diversity**
33 **has previously been lacking. Here we present the results of an integrated analysis,**
34 **utilizing synchrotron X-ray tomography and analyses of biomechanics, finite element**
35 **models and tooth microwear textures. We find significant differences in function and**

36 **dietary ecology between two of the earliest mammaliaform taxa, *Morganucodon* and**
37 ***Kuehneotherium*; taxa that are central to the debate on mammalian evolution.**
38 ***Morganucodon* possessed comparatively more forceful and robust jaws and consumed**
39 **‘harder’ prey, comparable to extant small-bodied mammals that eat significant**
40 **amounts of coleopterans. *Kuehneotherium* ingested a diet comparable to extant mixed**
41 **feeders and specialists on ‘soft’ prey such as lepidopterans. Our results reveal**
42 **previously hidden trophic specialization at the base of the mammalian radiation, hence**
43 **even the earliest mammaliaforms were beginning to diversify - morphologically,**
44 **functionally and ecologically. In contrast to the prevailing view^{2,4}, this pattern suggests**
45 **that lineage splitting during the earliest stages of mammalian evolution was associated**
46 **with ecomorphological specialization and niche partitioning.**

47

48 Recently, much progress has been made in understanding the pattern and timing of the
49 radiation of mammals⁷⁻⁹, revealing successive waves of taxonomic and ecomorphological
50 diversification in Mid to Late Jurassic to Palaeogene stem clades and crown groups^{2, 10, 11}.
51 But understanding of early mammaliaforms and the initial radiation of mammals has lagged
52 behind. Here we address this problem by testing the hypothesis that two of the earliest and
53 most basal mammaliaforms were ecomorphologically distinct. *Morganucodon watsoni*¹² and
54 *Kuehneotherium praecursoris*¹³ are central to the debate on mammalian origins and are of
55 fundamental phylogenetic importance (Extended Data Fig. 1). *Morganucodon* is one of the
56 earliest (Late Triassic-Early Jurassic) and best-known Mesozoic mammals, with a global
57 distribution; *Kuehneotherium* is of a similar age and size^{1, 12, 13}. Both taxa are thought to be
58 generalized insectivores¹ and co-existed (see Supplementary Information for discussion of
59 sympatry) on a small landmass present during the Early Jurassic marine transgression
60 (Hettangian–Early Sinemurian, ca. 200 mya), in what is now Glamorgan, South Wales,

61 United Kingdom^{1, 12} (Extended Data Fig. 2). In addition to the apomorphic mammalian jaw
62 joint, both taxa retain the plesiomorphic articular-quadrato jaw joint, as indicated by a well-
63 developed postdentary trough (Fig. 1a, b), thus indicating that the postdentary bones still
64 functioned as part of the jaw joint, rather than being incorporated into a definitive
65 mammalian middle ear (DMME) as in modern mammals^{1-2, 12-14} (*sensu*¹⁵). Curiously,
66 *Kuehneotherium* possesses advanced molars, with cusps arranged in an obtuse-triangle
67 pattern^{13, 16} (Extended Data Fig. 3)

68

69 We tested hypotheses of functional and dietary specialization in these early mammaliaforms
70 by generating digital mandibular reconstructions, and applied a suite of techniques: classical
71 mechanics, finite element modeling and quantitative textural analysis of tooth microwear.
72 The mandible is a good choice for study of feeding adaptations as it is primarily adapted for
73 biting, and is not constrained by sensory systems such as eye or brain size¹⁷. Our null
74 hypothesis was that functional performance did not differ between the two taxa.

75

76 Applying classical mechanics, we calculated the mechanical advantage (MA) for mid-molar,
77 premolar and canine bites, reflecting the efficiency of the jaw system at transmitting force
78 from the adductor muscles to the bite point. This revealed that *Morganucodon* has a notably
79 larger MA than *Kuehneotherium* (almost 50% greater during mid-molar biting) (Table 1),
80 indicating that the mandible of *Morganucodon* had the potential to generate much larger bite
81 forces than *Kuehneotherium*, and implying that *Kuehneotherium* bites were potentially faster
82 but less forceful. We also determined jaw strength in bending and torsion during biting,
83 treating the mandibular corpus as a beam¹⁸. The pattern of bending strength reveals a very
84 different profile between the two taxa (Fig. 1c, d). *Morganucodon* shows peak resistance to
85 bending at the rear of the tooth row as might be expected, as this region serves as a structural

86 linkage between the tooth row and posterior functional elements of the jaw, such as the jaw
87 joint and muscles¹⁹. However, *Kuehneotherium* shows peak resistance in the region of the
88 anterior molars. Resistance to torsion (J) shows similar patterns (Fig. 1e, f). This different
89 biomechanical profile in *Kuehneotherium* may reflect the importance of resisting bending in
90 the central tooth row, in order to maintain the sharp bladed triangulated molars in precise
91 occlusion¹⁶.

92

93 Finite element analysis (FEA) allowed us to calculate stress, strain and deformation to assess
94 the mechanical behaviour of the jaws²⁰. FEA can provide informative comparative data in the
95 absence of known input parameters¹⁷ and as such the two taxa were loaded with equal
96 adductor muscle forces and constrained at the jaw joint and bite points (Extended Data Fig.
97 4). FEA shows that, during a simulated bite, despite similar length and surface area, the
98 dentary of *Kuehneotherium* experiences greater maximum Von Mises stress and maximum
99 principal strain than *Morganucodon*, regardless of bite position, and higher reaction forces at
100 the jaw joint, despite generating consistently less bite reaction force (Fig. 1g, h; Table 1).

101 *Kuehneotherium* does not possess a robust condyle as in *Morganucodon* (Fig. 1a, b), further
102 reducing its ability to withstand high reaction forces at the jaw joint. We tested whether
103 *Morganucodon* or *Kuehneotherium* could generate enough bite force to pierce ‘hard’ insect
104 cuticle (where ‘hard’ and ‘soft’ refer to the ease with which prey is pierced and chewed²¹).

105 Bite force estimation can circumscribe the range of potential prey, providing a measure of
106 feeding performance and ecological partitioning^{22, 23}. A variety of insect prey was available at
107 the time: the Glamorgan fissures have yielded beetle remains²⁴, and soft bodied insects, such
108 as scorpion flies, were well established in the Early Jurassic²⁵. (See Supplementary
109 Information for discussion of potential prey.) A bite of 2 N is required to pierce the cuticle of
110 a ‘hard’ insect (e.g. beetle) of appropriate prey size for *Morganucodon* or *Kuehneotherium*²⁶,

111 ²⁷. For *Morganucodon* a simulated 2 N bite at mid-molar m2 (see Methods) did not generate
112 excessive stress in the jaw (maximum 54 MPa) (Fig. 1i). For *Kuehneotherium*, increasing
113 muscle loadings (keeping the ratio of muscle recruitment intact), to simulate a bite of 2 N at
114 mid-molar m3, produced higher reaction forces at the dentary condyle (5.45 N compared to
115 2.38 N for *Morganucodon*), and maximum VM stress values up to 134 MPa, which is 2.5
116 times that of *Morganucodon* and close to the tensile stress failure value for bone²⁸. This
117 suggests that *Kuehneotherium* was likely incapable of processing ‘hard’ cuticle, and further
118 illustrates differences in the biomechanical performance of the jaws. Comparative
119 biomechanical data therefore points to morphofunctional and dietary specialization in these
120 two taxa.

121

122 The hypothesis that *Morganucodon* and *Kuehneotherium* consumed different prey was
123 independently tested by comparing their tooth microwear textures to those of extant
124 insectivores with known dietary preferences (specimens listed in Extended Data Table 1).
125 Recent work on insectivorous bats has shown that microwear textural analysis based on 3D
126 roughness parameters discriminates between insectivore species that consume different
127 proportions of ‘hard’ prey (such as beetles) and ‘soft’ prey (such as moths)²⁹. Bats provide a
128 useful comparative dataset for our work because of their well-studied dietary differences and
129 similarity in size to *Morganucodon* and *Kuehneotherium*. We compared the fossil taxa with
130 four species of bats: *Plecotus auritus* (Brown long-eared bat; a specialist on ‘soft’ insects);
131 *Pipistrellus pipistrellus* (Common pipistrelle) and *P. pygmaeus* (Soprano pipistrelle) (more
132 mixed diet, both specialize on Diptera (flies), but *P. pipistrellus* consumes insects with a
133 wider range of cuticle ‘hardness’ and more ‘hard’ prey than *P. pygmaeus*); *Rhinolophus*
134 *ferrumequinum* (Greater horseshoe bat; mixed diet, but including more beetles - prey that is
135 among the ‘hardest’ of insects) (Extended Data Table 2 for dietary details). In the bats, nine

136 roughness parameters differ significantly between species²⁹, and PCA of these parameters
137 (Fig. 2) separates bats according to dietary preferences in a space defined by PC axes 1 and 2
138 (together accounting for 88.3% of variance) with axis 1 strongly correlated with dietary
139 preferences ($r_s = 0.81$, $P < 0.0001$). Increasingly negative values indicate higher proportions
140 of ‘hard’ prey, while increasing positive values indicate increasing proportions of ‘soft’
141 prey²⁹.

142

143 Projecting *Kuehneotherium* and *Morganucodon* data onto the axes resulting from the analysis
144 of bats produces clear separation of the two taxa. *Morganucodon* has negative values for
145 PC1, overlapping and extending beyond values for *R. ferrumequinum*. Slightly rougher
146 textures in *Morganucodon* suggest that it consumed a higher proportion of ‘hard’ prey. Most
147 *Kuehneotherium* specimens have positive values for PC1, overlapping the range of the ‘soft’
148 insect specialist *Pl. auritus*. Two specimens have negative PC1 values and plot into a space
149 defined by the mixed feeding *Pipistrellus*. 13 roughness parameters from *Morganucodon* and
150 *Kuehneotherium* are correlated with the bat dietary axis (PC1; Extended Data Tables 3, 4 and
151 5), including 9 of the 10 parameters that in bats are correlated with diet²⁹ and values for PC1
152 differ significantly between the two fossil species ($F = 5.67$; d.f. = 6, 29; $P = 0.0005$).

153 Pairwise tests (Tukey HSD; $P < 0.05$) indicate that microwear textures in *Morganucodon* and
154 *Kuehneotherium* differ from one another, yet *Morganucodon* does not differ from bats with
155 mixed or ‘harder’ diets, and *Kuehneotherium* does not differ from the ‘soft’ insect specialist
156 and mixed feeders. *Kuehneotherium* specimens from different fissure localities do not differ
157 from one another (see Supplementary Information for specimen and fissure details). That
158 *Kuehneotherium* and *Morganucodon* are so clearly separated by application of PCA based on
159 extant bats with different diets provides powerful evidence that the two fossil taxa had diets
160 that differed significantly in terms of prey ‘hardness’, and provides independent validation of

161 distinctive mechanical behavior and function revealed through our standard beam analysis
162 and finite element modeling.

163

164 In summary, our analyses reveal previously hidden trophic diversity and niche partitioning at
165 the base of the mammalian radiation, supporting a hypothesis of coupled lineage splitting and
166 ecomorphological adaptation of the skull and jaws, even during the earliest stages of
167 mammalian evolution. Our approach, combining biomechanical analyses with tooth
168 microtextural validation of dietary differences, does not require exceptionally preserved
169 specimens, and is applicable to fragmentary fossil remains. As such it has the potential to
170 provide direct evidence of ecomorphology and adaptation through a range of vertebrate
171 radiations, utilizing the most commonly preserved fossil elements: teeth and jaws.

172

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239

240 **Supplementary information** is linked to the online version of the paper at

241 www.nature.com/nature.

242

243 **Acknowledgments** We thank G. Armstrong, R. Asher, E. Bernard, P. Brewer, I. Corfe, A.
244 Carrant, A. Gill, T. Goddard, C. Hintermueller, J. Hooker, G. Jones, S. Lautenschlager, M.
245 Lowe, F. Marone, F. Marx, C. Palmer, M. Pound, M. Ruecklin and three anonymous referees.
246 Funded by NERC grants NE/E010431/1 and NE/K01496X/1 to E.J.R and P.G.G; M.A.P.
247 supported by NE/G018189/1. Use of the Swiss Light Source, Paul Scherrer Institut,
248 supported by European Commission 6th Framework Programme (RII3-CT-2004-506008).

249

250 **Author contributions** E.J.R, P.G.G and M.A.P designed the study and wrote the paper;
251 P.G.G., E.J.R, N.J.G and M.S collected the SRXTM data; K.R-B and P.G.G collected the
252 μ CT scan data; P.G.G, created the reconstructions and digital models and analyzed the
253 biomechanical results; P.G.G and E.J.R interpreted the biomechanical results; P.G.G
254 prepared and acquired specimens for microwear analysis, M.A.P and N.C. collected the
255 microwear data, M.A.P. analyzed and interpreted the microwear results.

256

257 **Author information** Reprints and permissions information is available at

258 www.nature.com/reprints. The authors have no competing financial interests.

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261

	<i>Morganucodon</i>		<i>Kuehneotherium</i>	
MA (3D)				
Canine bite	0.51		0.31	
Premolar bite	0.42		0.24	
Molar bite	0.35		0.18	
Max. Von Mises stress (MPa)				
Standard loading canine bite	66		97	
Standard loading premolar bite	61		83	
Standard loading molar bite	54		77	
Max. principal strain (microstrain)				
Standard loading canine bite	3840		5800	
Standard loading premolar bite	3540		5020	
Standard loading molar bite	3100		4440	
Reaction forces (N)				
	Jaw joint	Bite	Jaw joint	Bite
Standard loading canine bite	2.96	1.31	3.45	0.66
Standard loading premolar bite	2.69	1.62	3.30	0.87
Standard loading molar bite	2.38	2.00	3.12	1.14

263

264 **Table 1. Biomechanical analysis results.**

265 Comparative mechanical advantage (MA), maximum Von Mises stress values (in MPa),
266 maximum principal strain values, and reaction forces (in N) for *Morganucodon* and
267 *Kuehneotherium* dentaries. See Methods section for an explanation of the standard loading
268 for muscles. These loads achieve a 2 N reaction bite force at the molar (m2) of
269 *Morganucodon*, sufficient to pierce insect cuticle.

270 **Figure legends.**

271

272 **Fig. 1. Digital reconstructions and biomechanical analyses of *Morganucodon* and**

273 ***Kuehneotherium* jaws. a-b.** Reconstructed left mandibles, medial view. Missing portions in

274 grey. **a.** *Morganucodon watsoni*. **b.** *Kuehneotherium praecursoris*; dentition reconstructed

275 from Gill³⁰. **c-d.** Section moduli (dorsoventral Zx (blue) and mediolateral Zy (red), in mm⁴)

276 for (c) *Morganucodon* and (d) *Kuehneotherium*. **e-f.** Polar moment of inertia (J) in the

277 dorsoventral (Ix) and mediolateral (Iy) planes), for (e) *Morganucodon* and (f)

278 *Kuehneotherium*. **g-i.** Finite element Von Mises stress contour plots for a unilateral molar

279 bite (m2 for *Morganucodon* and m3 for *Kuehneotherium*) with closed jaw: **g.** *Morganucodon*

280 and **h.** *Kuehneotherium*, with standard muscle loading. **i.** *Kuehneotherium* with muscle

281 loading multiplied to give a bite reaction force of 2N. Stress legend and contour plot scale

282 applies to g-i. Single vertical arrows indicate tooth constraints; three grouped arrows indicate

283 jaw joint constraints. (See Supplementary Information for links to scan data and FE model

284 images)

285

286 **Fig. 2. Quantitative textural analysis of microwear in bats and fossil mammaliaforms. a-**

287 **d.** Scale limited roughness surfaces of *Morganucodon* (a; specimen 34), *R. ferrumequinum*

288 (b; specimen 1), *Kuehneotherium* (c; specimen 24), and *Pl. auritus* (d; specimen 12); 146 x

289 110 μm; contour vertical scale in μm. **e.** Principal components analysis of ISO roughness

290 parameters from bats and mammaliaforms. PCA analysis based on data for bats only, with

291 *Morganucodon* (n = 5) and *Kuehneotherium* data (P3 n = 5; P5 n = 6) projected onto the bat

292 PCA axes. There are two anomalous specimens: a single *Kuehneotherium* specimen (29) has

293 PC 1 values similar to *R. ferrumequinum*, and one of the *Morganucodon* specimens (32) plots

294 as an outlier to all other teeth analyzed. P3 = Pontalum 3 and P5 = Pant 5 fissure.

295

296 **Methods.**

297 **Digital models.**

298 Digital mandibular reconstructions (Fig. 1a,b) were generated by combining synchrotron
299 radiation X-ray tomographic microscopy (SRXTM) or micro-computed tomography (μ CT)
300 scans from similar sized, mature individuals of each taxon (Extended Data Figure 3 and
301 Supplementary Information). *Morganucodon* mandibular specimens were scanned using
302 synchrotron radiation X-ray tomographic microscopy (SRXTM) at the Swiss Light Source
303 TOMCAT beamline. The material was scanned at 18keV and a pixel size of 1.85 microns
304 (NHMUK PV M85507) or 22keV and 3.7 microns (UMZC Eo.D.45 and UMZC Eo.D.66) in
305 order to match the size of the sample with the field of view of the microscope. The
306 *Kuehneotherium* mandibular specimens and molar teeth, provided to illustrate the difference
307 in occlusion, were scanned on a Bruker Skyscan 1172 micro-CT system in the Department of
308 Archaeology and Anthropology at the University of Bristol. A lower resolution was adequate
309 for the finite element models (20 microns), although one specimen (NHMUK PV M92779)
310 was also scanned at 3.1 microns for internal detail.

311

312 Processing was performed using Avizo® (Visualization Sciences Group, VSG). For each
313 taxon, the CT data for each specimen were re-oriented and scaled slightly if required, then
314 digitally merged and manually rendered to produce the reconstructions. As all specimens
315 were similar sizes, very limited scaling was required. The final size of the reconstructed jaw
316 was based on scaling all specimens to the size of the most complete specimen. Any empty
317 alveoli were digitally infilled and tooth crowns removed to leave all tooth surfaces at an
318 equivalent level to the tooth neck. Validation studies have shown that edentate finite element
319 models better represent experimental strains than dentate models³¹ and this obviates the need

320 to reconstruct missing teeth in the original scan data. A 2D surface mesh generated in Avizo
321 (VSG) was exported to *Hypermesh* (part of the *Hyperworks* suite from Altair, MA, USA),
322 where the digital jaws were converted into finite element (FE) models. Two-dimensional
323 mesh optimization was performed and a 3D FE-mesh generated of linear four-noded
324 tetrahedral (C3D4) elements (115,213 for *Morganucodon* and 68,555 for *Kuehneotherium*).
325 Four-noded tetrahedra may be stiffer than 10-noded tetrahedral and may slightly
326 underestimate strain³² but our models are comparative, and tetrahedral elements are useful for
327 modeling complex and intricate morphologies. The dentary and tooth roots were created as
328 separate parts with shared mesh boundaries. In the case of fossil material, where it is
329 impossible to validate predictions of bite force with *in vivo* experimental data, it is possible to
330 compare the relative performance of finite element models if the models are properly scaled.
331 Scaling to equal force: surface area ratio provides a comparison of stress-strength
332 performance based solely on shape³³. The linear dimensions (canine to condyle) of the
333 mandibles are 17.5 mm and 20.0 mm for *Morganucodon* and *Kuehneotherium* respectively.
334 The surface area ratio of *Morganucodon: Kuehneotherium*, calculated from Avizo, is 1.02:1
335 and, as there is very slightly more coronoid process and incisors missing from the
336 *Kuehneotherium* model, the models are taken to be equal in surface area for the purpose of
337 this analysis. In this case it was therefore not necessary to scale the applied muscle forces,
338 and the models could be directly compared using the same loadings. The models were
339 converted to SI base unit linear dimensions (metres) when imported into Abaqus/CAE for
340 finite element analysis (FEA).

341

342 The dentary bone was assigned isotropic and homogenous material properties: Young's
343 modulus of 18 GPa and Poisson's ratio of 0.3. Those for the tooth roots were as for dentine,
344 Young's modulus of 25 GPa and Poisson's ratio of 0.3. It is possible that the actual jaw

345 material properties were not isotropic, but in the absence of data otherwise, we assume
346 isotropy for the sake of this analysis. Likewise we will never know the elastic properties of
347 Mesozoic mammaliaform jaws, yet recent nanoindentation studies on the jaws of rats,
348 squirrels and guinea pigs have revealed a range of 10-30 GPa for the Young's modulus of
349 bone, and 15-25 GPa for incisor dentine³⁴ and our chosen values encompass this range.

350

351 The orientation (line of action) of the mammaliaform anterior and posterior temporalis and
352 superficial and deep masseter adductor muscles were reconstructed (Extended Data Fig. 4a,
353 b). The medial pterygoid was omitted as, if present, it was small³⁵. Adductor muscle
354 orientation was deduced by estimating the position of the point of origination on the skull,
355 coupled with study of the insertion areas on the mandibular fossae of the fossil specimens.
356 The detailed description of the skull of *Morganucodon*³⁶ was used as reference for the muscle
357 origins for *Morganucodon*. There is no skull material for *Kuehneotherium*, but, the gross
358 morphology of the lower jaw of the slightly older Brazilian eucynodont *Brasilitherium*^{37, 38} is
359 very similar to *Kuehneotherium* (PGG pers. obs.) and so the general skull shape of
360 *Brasilitherium* was used, with caution, as a proxy for the position of the *Kuehneotherium*
361 muscle origins (Extended Data Figure 4c, d). The temporalis has its origin on the parietal
362 bones of the skull, with development of a sagittal crest in *Morganucodon*, although this latter
363 is not known for *Kuehneotherium*. The temporalis inserts both medially and laterally in the
364 temporal fossae on either side of the coronoid process, with the muscles divided into anterior
365 and posterior vectors³⁵. The anterior temporalis (AT) insertions on the lateral and medial
366 sides of the jaws were represented by a predominantly vertical vector and were coupled to a
367 single point in space representing their origin on the skull. The posterior temporalis (PT)
368 component was dealt with by applying a posteriorly directed load, as from the posterodorsal
369 portion of the coronoid process. The coronoid hook of *Morganucodon*¹² and posterodorsal

370 portion of the coronoid process in *Kuehneotherium* are missing in the reconstructions, so a
371 means to simulate the missing portions of the coronoid processes for the muscle attachment
372 had to be devised. A multi-point rigid body was created, from the broken edge of the
373 coronoid process to the position of the coronoid hook; in effect completing the coronoid
374 process and producing a point in space for the posterior temporalis origin (Extended Data
375 Fig. 4 insert). The masseter in mammals is divided into superficial and deep components,
376 with their origins on the zygomatic arch³⁵; the superficial masseter (SM) at the anterior end
377 on the jugal and the deep masseter (DM) posteriorly on the squamosal³⁶. They insert laterally
378 on the jaw behind the tooth row. In *Morganucodon*, the two mandibular fossae are distinct
379 and that of the superficial masseter is adjacent to the angular process of the jaw. There is no
380 angular process in *Kuehneotherium*, but the masseteric fossa is well developed. The lines of
381 action of muscles defined here were used to calculate mechanical advantage, and for the
382 finite element analysis.

383

384 **Classical mechanics.**

385 The digital models were used for calculation of mechanical advantage and beam theory to
386 measure strength in bending. Mechanical advantage (MA), as a measure of the efficiency of
387 the jaw system to transfer input muscle force from the adductor musculature to the point of
388 biting, is frequently used as a metric of jaw function³⁹ and correlates with prey choice and
389 feeding ecology in organisms such as fish^{40, 41}. MA is calculated here as the length of the in-
390 lever, the moment arm of the adductor musculature, divided by the length of the out-lever,
391 the moment arm of the bite, i.e. the distance from the jaw joint to the bite point. The moment
392 arms were calculated by taking scaled screen images of the jaws in Abaqus, in both lateral
393 and dorsal orientations to calculate the in-lever arm for each of the four muscles (anterior
394 temporalis; posterior temporalis; deep masseter and superficial masseter). A central point

395 was chosen within the muscle insertion area, in each case, to give the line of action of each
396 muscle. The four muscle vectors were resolved to give a single adductor muscle vector, and
397 the in-lever arm calculated.

398

399 Beam theory has been applied to the mandibular corpus in a number of studies^{18, 22, 35, 42} and
400 is related to dietary specialization in small mammals such as bats⁴³. A measure of strength in
401 bending is estimated from the section modulus Z , calculated at specific intervals along the
402 jaw. The section modulus Z is the second moment of area (I) divided by the distance from the
403 neutral axis to the outer edge, in the plane of bending, so the orientation considered affects
404 the value of the bending strength. In this case the section modulus was measured in the
405 dorsoventral (Z_x) and mediolateral planes (Z_y). We follow Therrien¹⁸ in measuring Z at
406 interdental gaps along the tooth row to the canine, plus a further section just posterior to the
407 ultimate molar. The reconstructed hemimandibles were digitally sliced perpendicular to the
408 long axis of the mandible to produce cross sectional images at the interdental gaps. Each
409 cross section image was loaded into ImageJ⁴⁴ and Z_x and Z_y calculated using the plugin
410 MomentMacro. We measured all interdental gaps, with postcanine numbers of eight and 12
411 for *Morganucodon* and *Kuehneotherium* respectively. The polar moment of inertia (J), the
412 beam's ability to resist torsion, is calculated from the addition of the second moment of area,
413 I , in the dorsoventral (I_x) and mediolateral (I_y) planes.

414

415 **Finite element analysis (FEA).**

416 Boundary constraints were applied to the condyle and at three bite points; canine, final
417 premolar and mid molar. The anterior incisor bite point could not be included, as there are no
418 specimens of this portion of the mandible in *Kuehneotherium*. The ultimate premolar is the
419 largest of the premolars in both taxa. In *Morganucodon*, the largest (second) molar was

420 chosen as the ‘mid molar’ and in *Kuehneotherium* a mid row (third) molar was used. Both
421 single node⁴⁵ and distributed area (stiff beam elements) constraints⁴⁶ have been used to
422 estimate bite forces (discussion in Tseng *et al.*¹⁷), but we used multipoint constraints (MPC),
423 with master and slave nodes to minimise artificial stress concentrations⁴⁷. There were
424 approximately 22 nodes constrained for each tooth and 30 nodes constrained at the jaw joint.
425 Boundary conditions should never restrict deformations allowed by the represented
426 environment⁴⁷, so the bite points were appropriately constrained in four degrees of freedom
427 (DOF) ($U1=U2=UR2=UR3=0$), and the dentary condyle in four DOF ($U1=U2=U3=UR3=0$).
428 (N.B. U1 is the mesiodistal axis; U2 is the dorsoventral axis and U3 is the axis along the
429 length of the jaw, U refers to translational movement, UR refers to rotational movement).
430
431 As the true muscle loadings for *Morganucodon* and *Kuehneotherium* are not known, we
432 utilized a comparative approach, assuming an equal muscle load applied to each taxon^{48, 49}.
433 Given the equivalence of surface area between the two models, this was appropriate³³. For
434 the initial models the relative contribution of each muscle to overall bite force was based on
435 muscle ratios assigned to *Morganucodon* by Crompton and Hylander³⁵. These authors assign
436 unit values of muscle forces to the jaw of *Morganucodon*: anterior temporalis, 10; posterior
437 temporalis, 8; superficial masseter, 8; deep masseter, 8. The values are arbitrary but reflect
438 the relative proportions each muscle contributes to bite force production. The actual loading
439 forces we used were: anterior temporalis, 2N; posterior temporalis, 1.6N; superficial
440 masseter, 1.6N; deep masseter, 1.6N. We call this the initial loading regime. Contracting
441 together at 100% activation, these muscles generate a bite reaction force of 2N at the mid-
442 molar of the *Morganucodon* FE-model, sufficient to pierce insect cuticle (see below).
443 Crompton & Hylander’s calculations³⁵ are based on a unilateral bite, but with adductors
444 active on both sides, so allowance is made for the balancing side. Both *Morganucodon* and

445 *Kuehneotherium* have a mobile symphysis^{12,30} and, as this current study is a comparative one
446 of single lower jaws, it does not make assumptions about the forces on the balancing side,
447 and the loads above are applied to the individual mandibular rami.

448

449 The reaction forces were queried in ABAQUS at the bite points and condyle and the
450 maximum Von Mises (VM) stress patterns recorded. VM stress is calculated as it indicates
451 regional deformation as a function of the three principal stresses σ_1 , σ_2 , and σ_3 ⁵⁰. Maximum
452 principal strain values were also recorded (Table 1). Muscle loadings were then manipulated
453 to obtain a bite reaction force sufficient to pierce appropriately sized beetle carapace. *Myotis*
454 bats are a similar size to *Morganucodon* and *Kuehneotherium* (skull length ca. 14mm) and
455 beetles in their stomachs range in length from 1-10 mm, with a 10 mm beetle requiring 2-3N
456 of force to pierce the insect²⁷. This is corroborated by *Myotis velifer* bats recorded as having a
457 bite force of 2.2N²⁶. The initial muscle loads in *Morganucodon* produced a bite reaction force
458 of 2N at the molar bite, but in *Kuehneotherium* it was necessary to increase the muscle
459 loadings by 1.75x to give a 2N reaction force at the constrained molar tooth.

460

461 **Microtextural analysis of tooth microwear.**

462 Recent work has shown that quantitative microtextural analysis of tooth wear is a powerful
463 tool for dietary discrimination and investigation of trophic resource exploitation in a range of
464 extant and fossil vertebrates⁵¹⁻⁵⁶. Our analysis compared the values for ISO 25178-2 areal
465 texture parameters⁵⁷ for worn tooth surfaces in *Morganucodon* and *Kuehneotherium* with the
466 results of analysis of the relationship between texture and diet in extant insectivorous bats²⁹.
467 3D microtextural analysis is entirely independent of our other functional and biomechanical
468 analyses and thus provides effective validation of our results.

469

470 Material used for microwear analysis is listed in Extended Data Table 1. Fossil specimens
471 were recently prepared at the School of Earth Sciences, University of Bristol by immersing
472 dried blocks of matrix in hot water, with the addition of dilute hydrogen peroxide only if
473 required. The exception is two Pontalun 3 *Kuehneotherium* molars, prepared at University
474 College London (UCL) in the 1970s, with added sodium hexametaphosphate (TM Calgon) to
475 aid dissolution of the matrix. No acetic acid was used on any specimens. Bat specimens were
476 all wild-found, acquired from UK sources (Extended Data Table 1) and assumed to be
477 natural-deaths. Specimens were fixed in either ethanol (UOB, NLBG) or 10% formalin
478 solution (VLA). Taxa were selected in order to include insectivores with well-constrained
479 differences in their diets⁵⁸⁻⁵⁹. See Extended Data Table 2 and Purnell *et al.*²⁹ for details.

480

481 Our methods for capture of 3D microwear data follow those developed by Purnell *et al.*⁶⁰ (for
482 full details see Purnell *et al.*²⁹). 3D surface data were captured from tooth wear facets (distal
483 protoconid facet of M₂ for bats, distobuccal wear facet of the main cusp of m₂ for
484 *Morganucodon* and a mid-row molar for *Kuehneotherium*) using an Alicona Infinite Focus
485 microscope G4b (IFM; software version 2.1.2, field of view 145 x 110 µm, lateral optical
486 resolution 0.35 - 0.4 µm, vertical resolution 20 µm; lateral resolution factor for the IFM set at
487 0.3) (see Purnell *et al.*²⁹). All 3D data were edited to delete dirt and dust particles from the
488 surface (using Alicona IFM software) and exported as .sur files. All subsequent processing of
489 data used SurfStand (version 5.0.0). Data were leveled, and a 5th order robust polynomial
490 and a robust Gaussian wavelength filter ($\lambda_c = 0.025$ mm) applied to remove gross surface
491 form and long wavelength features of the tooth surface. This generates a scale-limited
492 roughness surface (Fig. 2) from which we derived ISO 25178-2 standard roughness
493 parameters⁵⁷. Sample sizes used in this study are relatively small, but as demonstrated by
494 Purnell *et al.*²⁹ this does not prevent detection of dietary signals through microtextural

495 analysis. Data were explored using ANOVA, correlations, and Principal Components (on
496 correlations; PCA). All statistical analysis of microtextural data was carried out using JMP 9.
497 The results of Shapiro-Wilk tests indicated that some roughness parameters were non-
498 normally distributed ($p > 0.05$), but for almost all parameters we were unable to reject the
499 null hypothesis of normality for log-transformed data, so log-transformed data were used for
500 analysis. Where homogeneity of variance tests revealed evidence of unequal variances,
501 Welch ANOVA was used.

502

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585

586 **Extended Data Legends**

587 **Extended Data Figure 1 | Phylogenetic relationships of major Mesozoic mammal**

588 **lineages.** Relative tree positions of *Morganucodon* and *Kuehneotherium* in red. Based on Fig.

589 1 in Luo *et al.*⁶¹. The filled green circle denotes the node for the mammalian crown group.

590

591 **Extended Data Figure 2 | Pontalun 3 fissure locality. a,** Map to show location of the

592 Glamorgan quarries in Wales, UK. The black square denotes the area of the map shown in b.

593 Map attribution; Jhamez84. CC-BY-SA-3.0 (<http://creativecommons.org/licenses/by-sa/3.0>).

594 **b,** Location of the Glamorgan quarries yielding tetrapod remains, with white arrow marking

595 Pontalun quarry. Carboniferous Limestone upland areas in grey. Modified from Evans and
596 Kermack⁶².

597

598 **Extended Data Figure 3 | Molar form and specimens scanned to create the digital**
599 **reconstructions of the dentaries of *Morganucodon* and *Kuehneotherium*.** **a**, NHMUK PV
600 M92538, an isolated *Morganucodon watsoni* right lower molar (identified as m4) in lingual
601 view **b**, NHM NHMUK PV M9277, an isolated *Kuehneotherium praecursoris* right lower
602 molar (mid row) in lingual view; note the triangulation of the cusp arrangement. Both molars
603 digitally reconstructed from uCT scans and reversed to fit with views of the dentaries. **c-e**,
604 Specimens used for the digital reconstruction of *Morganucodon watsoni*. **c**, UMZC Eo.D.61
605 with m4 in situ; **d**, UMZC Eo.D.45 with p4, m1, m3 and m4 in situ; **e**, NHMUK PV M85507
606 with i1-4. (N.B. the only Glamorgan specimen known with complete incisors in situ). **f-i**,
607 Specimens used for the digital reconstruction of *Kuehneotherium praecursoris*: **f**, NHMUK
608 PV M19766 (paratype C865 in Kermack *et al.*¹³) with coronoid process and condylar region;
609 **g**, NHMUK PV M19749 (paratype C864 in Kermack *et al.*¹³) postdentary trough region; **h**,
610 UMZC Sy.97 with complete alveoli for m5-6 and partial alveoli for m3-4; **i**, NHMUK PV
611 M92779 with alveoli for p1-m4 (U73 in Gill⁶³). All from Pontalun 3 fissure, except f and g
612 from Pontalun 1 fissure, which Gill³⁰ assigned to the same hypodigm. All images show
613 medial view. All are left dentaries, except c and d which are reversed for ease of reference to
614 the reconstructions in Fig. 1.

615

616 **Extended Data Figure 4 | Static loaded FE models to represent the jaw at the moment of**
617 **biting.** Right mandible models in lateral view of **a**, *Morganucodon* and **b**, *Kuehneotherium*
618 to show muscle loading, constraints and bite points. Inset in a, shows modeled rigid body
619 used to simulate missing coronoid process, for posterior temporalis loading. Muscle

620 abbreviations: AT, anterior temporalis; PT, posterior temporalis; SM, superficial masseter;
621 DM, deep masseter. Constraints indicated at the jaw joint and three individual bite points at
622 the mid molar (m2 in *Morganucodon* and m3 in *Kuehneotherium*), ultimate premolar (p4 in
623 *Morganucodon* and p6 in *Kuehneotherium*) and canine. The muscle origin positions are
624 shown for **c**, *Morganucodon* and **d**, *Kuehneotherium*. *Morganucodon* skull reconstruction
625 from Kermack *et al.*³⁶ and *Brasilitherium* skull, used as a proxy for the unknown
626 *Kuehneotherium* skull, from Bonaparte *et al.*³⁷. The teeth have been removed for consistency
627 with the mandible models. See Methods for explanations.

628

629 **Extended Data Table 1 | Specimens used for the microtextural analysis of tooth**

630 **microwear.** Abbreviations: LEIUG, University of Leicester Geology collections; UOB,
631 University of Bristol; VLA, Veterinary Laboratory Agencies; NLB, North Lancashire Bat
632 Group.

633

634 **Extended Data Table 2 | Trophic categorization and diets of British bat species used for**

635 **validation of microtextural analysis of early mammal teeth.** Table from Purnell *et al.*²⁹
636 modified from Vaughan⁵⁸ and references therein, and Barlow⁵⁹.

637

638 **Extended Data Table 3 | Correlations between roughness parameters from**

639 *Morganucodon* and *Kuehneotherium* teeth and PC axes 1 and 2 derived from analysis of

640 **the nine roughness parameters that differ between bat species.** * indicates significant

641 correlations ($P < 0.05$). See **Extended Date Table 5** for definitions of parameters.

642

643 **Extended Data Table 4 | Loadings (eigenvectors) for roughness parameters onto PC**

644 **axes 1 and 2 for the PCA analysis of bat species.** From Purnell *et al.*²⁹.

645

646 **Extended Data Table 5 | Short definitions and categorization of 3D areal surface**

647 **texture parameters.** For further explanation see Purnell *et al.*²⁹, figs S1 and S2.



