

Title	Allometric analysis sheds light on the systematics and ontogeny of anurognathid pterosaurs
Authors	Yang, Zixiao;Benton, Michael J.;Hone, David W. E.;Xu, Xing;McNamara, Maria E.;Jiang, Baoyu
Publication date	2022-03-03
Original Citation	Yang, Z., Benton, M. J., Hone, D. W. E., Xu, X., McNamara, M. E. and Jiang, B. (2021) 'Allometric analysis sheds light on the systematics and ontogeny of anurognathid pterosaurs', Journal of Vertebrate Paleontology. doi: 10.1080/02724634.2021.2028796
Type of publication	Article (peer-reviewed)
Link to publisher's version	https://figshare.com/articles/dataset/Allometric_analysis_sheds_light_on_the_systematics_and_ontogeny_of_anurognathid_pterosaurs/10.1080/02724634.2021.2028796
Rights	© 2022, Taylor & Francis Group, LLC. This is an Accepted Manuscript of an item published by Taylor & Francis in Journal of Vertebrate Paleontology on 03 March 2022, available online: https://doi.org/10.1080/02724634.2021.2028796 - https://creativecommons.org/licenses/by-nc/4.0/
Download date	2024-05-26 15:48:22
Item downloaded from	https://hdl.handle.net/10468/12968



UCC

University College Cork, Ireland
Coláiste na hOllscoile Corcaigh

1 Allometric analysis sheds light on the systematics and ontogeny of anurognathid pterosaurs

2
3 ZIXIAO YANG,¹ MICHAEL J. BENTON,² DAVID W. E. HONE,³ XING XU,⁴ MARIA E.

4 McNAMARA,^{1,5} and BAOYU JIANG^{6,*}

5 ¹School of Biological, Earth and Environmental Sciences, University College Cork, Cork T23

6 TK30, Ireland, zyang@ucc.ie; maria.mcnamara@ucc.ie;

7 ²School of Earth Sciences, University of Bristol, Life Sciences Building, Tyndall Avenue,

8 Bristol BS8 1TQ, UK, mike.benton@bristol.ac.uk;

9 ³School of Biological and Behavioural Sciences, Queen Mary University of London, Mile

10 End Road, London, E1 4NS, UK, d.hone@qmul.ac.uk;

11 ⁴Key Laboratory of Vertebrate Evolution and Human Origins, Institute of Vertebrate

12 Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China,

13 xu.xing@ivpp.ac.cn;

14 ⁵Environmental Research Institute, Lee Road, Cork T23 XE10, Ireland,

15 maria.mcnamara@ucc.ie;

16 ⁶Center for Research and Education on Biological Evolution and Environments, School of

17 Earth Sciences and Engineering, Nanjing University, Nanjing 210023, China,

18 byjiang@nju.edu.cn

19 *Corresponding author.

20
21 YANG ET AL.—ALLOMETRIC GROWTH OF ANUROGNATHID PTEROSAURS

22

23 ABSTRACT—Anurognathids are a clade of non-pterodactyloid pterosaurs with generally
24 conservative morphology, but specializations as insectivores. They are represented by a
25 disparate collection of adult and juvenile specimens that range in wingspan from ca. 0.24–1
26 m. There have been concerns about the extent to which ontogenetic variation might affect
27 phylogenetic inference, and indeed how aspects of their ontogeny might relate to the
28 distinctive anurognathid adult morphology. Here we perform allometric analysis on 23 key
29 skeletal dimensions in 13 anurognathid specimens. Our results show that all anurognathids
30 share a common growth trajectory in most dimensions, and that ontogeny affects variation in
31 a minority of characters commonly used in phylogenetic analysis. Excluding these ontogeny-
32 related characters, a new taxon, *Cascocauda rong* gen. et sp. nov., is established. Based on the
33 ontogenetically corrected dataset, our phylogenetic analysis supports Anurognathidae as the
34 sister-group of Breviquartossa and reveals a general trend of tail reduction in the clade.
35 Allometric growth suggests the anurognathid lifestyle remained consistent throughout
36 ontogeny, maintaining a highly manoeuvrable flight style by near-isometric development in
37 the wing, small prey (i.e., insects), by strong negative allometry in the skull, and an arboreal
38 habit by strong positive allometry in the claws. This specialized lifestyle suggests retention of
39 plesiomorphic juvenile traits into later ontogeny and facilitated morphological stasis by
40 stabilizing selection during over 40 million years of evolution in the group.

41

INTRODUCTION

42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64

Anurognathids lived in Eurasian forests during the Middle Jurassic to Early Cretaceous (Hone, 2020). They shared a distinctive suite of morphological characters consistent being specialized aerial insectivores active in low light conditions. These include (1) a wide mouth with a large gape and a sharp isodont dentition adapted for catching and holding insects (Bennett, 2007a; Ösi, 2011; Hone, 2020), (2) small size, a deep wing with curved wingtip and a short pliable tail, which together facilitated slow and highly manoeuvrable flight in dense forests (Bennett, 2007a; Ösi, 2011; Hone et al., 2015; Hone, 2020) and (3) large, anterolaterally directed eyes that were likely adapted for nocturnal and/or crepuscular predation (Bennett, 2007a; Lü et al., 2018). The gross morphology of anurognathids changed little during their 40-Myr existence, which suggested they had a rather conservative Bauplan (Unwin et al., 2000; Bennett, 2007a; Hone, 2020).

Anurognathids are represented by 13 unequivocal specimens ranging from ca. 0.24 to 1 m in wingspan and of varying ontogenetic status. Nine specimens (including specimens of *Anurognathus*, *Dendrorhynchoides*, *Luopterus*, *Sinomacrops* and *Batrachognathus*, and specimens NJU-57003 and CAGS-Z070 (Dalla Vecchia, 2002; Yang, et al., 2019; Hone, 2020; Wei et al., 2021)) show characteristics of immaturity, e.g., unfused articular bones, scapula-coracoid, pelvis and cranial elements. In contrast, the holotypes of *Jeholopterus* and *Vesperopterylus* show osteological maturity and are thus (sub)adults (Wang et al., 2002; Lü et al., 2018). Two specimens lack detailed descriptions, and their ontogenetic state is unknown (Gao et al., 2009; Jiang et al., 2015).

Inadequate recognition of ontogenetic status in previous studies of anurognathids has

65 raised concerns about confounding ontogenetic variation with systematics (Hone, 2020). In
66 particular, many length ratios used as diagnostic (e.g., Wang et al., 2002; Lü and Hone, 2012;
67 Wei et al., 2021) or in analyzing characters (e.g., Kellner, 2003; Lü et al., 2018) may change
68 greatly during growth (Delfino and Sánchez-Villagra, 2010). Previous statistical studies on
69 ontogenetic changes in other pterosaurs have suggested or prompted taxonomic revisions for
70 some taxa (e.g., Bennett, 1995, 1996, 2006, 2007b, 2013; Jouve, 2004; Vidovic and Martill,
71 2014). The prevalence of immature individuals in the known anurognathid dataset thus
72 creates uncertainty regarding the validity of taxonomic assignments and may bias existing
73 phylogenetic reconstructions.

74 Alternatively, if anurognathids share a common allometric growth pattern for particular
75 elements, the known specimens would constitute a growth series from early juveniles to
76 adults. This growth series would then provide a rare opportunity to explore ontogenetic
77 development of morpho-function and understand the evolution of the distinctive anurognathid
78 morphology. Indeed, studies on pterosaur allometry have already yielded insights into the
79 relationship between skeletal proportions and biomechanics, particularly relating to
80 aerodynamics, across taxa of different body sizes (e.g., Brower and Veinus, 1981; Padian and
81 Warheit, 1989; Witton and Habib, 2010) and through growth of single species (e.g., Tomkins
82 et al., 2010; Hone et al., 2020; Naish et al., 2021).

83 Here, we select skeletal dimensions used in previous diagnoses and phylogenetic analyses
84 to test statistically whether anurognathid specimens share growth trajectories in various
85 dimensions. By revealing which characters related to these dimensions are biased by
86 ontogeny, a new specimen is assessed taxonomically excluding the biased characters.

87 Critically, we compose a refined dataset for phylogenetic analysis by removing the
 88 recognized ontogenetic bias and updating with additional characters from recent studies. Our
 89 goals are to provide a more accurate understanding of anurognathid systematics and to
 90 explore how aspects of their ontogeny might affect the distinctive and conservative
 91 anurognathid adult morphology.

92

93 MATERIALS AND METHODS

94

95 **Institutional Abbreviations**—**BMNHC**, Beijing Museum of Natural History, Beijing;
 96 **BSP**, Bayerische Staatssammlung für Paläontologie und Geologie, Munich; **CAGS**, Chinese
 97 Academy of Geological Sciences, Beijing; **GMV**, National Geological Museum of China,
 98 Beijing; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; **JPM**,
 99 Jinzhou Museum of Paleontology, Jinzhou; **JZMP**, Jinzhou Paleontological Museum,
 100 Jinzhou; **NJU**, Nanjing University, Nanjing; **PIN**, Palaeontological Institute, Russian
 101 Academy of Sciences, Moscow; **SMNS**, Staatliches Museum für Naturkunde Stuttgart,
 102 Stuttgart.

103 **Anatomical Abbreviations**—**aof**, antorbital fenestra; **cd**, caudal vertebrae; **ch**, chevron;
 104 **co**, coracoid; **cv**, cervical vertebrae; **dr**, dorsal rib; **dv**, dorsal vertebrae; **fe**, femur; **fi**, fibula;
 105 **fr**, frontal; **ga**, gastralia; **h**, humerus; **il**, ilium; **is**, ischium; **man**, mandible; **mci–iii**,
 106 metacarpal I–III; **mciv**, metacarpal IV; **mti–iv**, metatarsal I–IV; **mtv**, metatarsal V; **nar**, naris;
 107 **or**, orbit; **pa**, parietal; **pal**, palatine; **pdI–IV**, pedal digits I–IV; **pt**, pteroid; **ppu**, prepubis; **pu**,
 108 pubis; **pdV-1** and **2**, phalanges 1 and 2 of pedal digit V; **q**, quadrate; **r**, radius; **rp**,
 109 retroarticular process; **sc**, scapula; **scr**, sclerotic ring; **t**, tarsal; **th**, tooth; **ti**, tibia; **u**, ulna;

110 **wp1–4**, wing phalanges 1–4; **z**, zygapophysis.

111

112 **Measurements for Allometric Analysis**

113 Twenty-three skeletal variables were measured from 13 anurognathid specimens (Fig. 1A
114 and Supplemental Data 1): 1, skull length; 2, skull width; 3, scapula length; 4, coracoid
115 length; 5, humerus length; 6, ulna or radius length; 7, pteroid length; 8, wing metacarpal
116 length; 9, manual claw length; 10–13, length of first, second, third and fourth phalanx of wing
117 finger, respectively; 14, femur length; 15, tibia length; 16, fibula length; 17, metatarsal length;
118 18, length of pedal digit III; 19, foot length = (metatarsal length + pedal digit III length); 20–
119 21, length of first and second phalanx of pedal digit V, respectively; 22, length of pedal claw;
120 23, wingspan = (humerus + ulna/radius + metacarpal IV + wp1–4) × 2.1 (Lü et al., 2011).

121 Measurements were taken from the literature, photographs and, where possible, directly
122 from specimens (see Supplemental Data 1 for details). Measurements from photographs were
123 obtained using the image processing freeware ImageJ (available at <http://rsbweb.nih.gov/ij/>)
124 and those from specimens were taken using a digital caliper; in both cases measurements were
125 taken twice to ensure accuracy. Mean values were used for left and right elements when
126 possible.

127

128 **Tests for Allometric Correlation**

129 All measurements were logarithmically transformed to evaluate the bivariate allometric
130 relationship ($y = a \cdot x^b$) in the linearized form ($\log y = \log a + b \log x$). The standardized
131 major axis (SMA) line-fitting method was applied to determine the allometric equation, and
132 coefficients of determination (R^2) and probability values (p) were calculated to evaluate the

133 strength and statistical significance of the correlation.

134 If the correlation was statistically significant ($p < 0.05$), we further tested the null
135 hypothesis of isometry ($b = 1$). On account of the small sample size and unknown distribution
136 of the allometric scaling coefficient (b), a bootstrap method (Plotnick, 1989) was applied with
137 1000 iterations to generate a one-tailed 95% confidence interval for b . We rejected the null
138 hypothesis if the 95% confidence interval of b lay entirely above or below 1, i.e., positive or
139 negative allometry, respectively. Otherwise, isometry was assumed. These were calculated in
140 R v. 3.5.1 using the “smatr” (Warton et al., 2012), “dplyr” (Wickham et al., 2015) and “purrr”
141 (Henry and Wickham, 2020) packages, using code given in the Supplemental Content.

142 As pterosaurs are forelimb-dominated launchers and fliers, humerus length has been used
143 as a proxy for body mass and size (e.g., Wellnhofer, 1970; Wellnhofer, 1975; Wang et al.,
144 2017). Here, humerus length was thus compared with most other variables in our pairwise
145 bivariate analysis. Additional pairs yielding diagnostic length ratios in previous studies were
146 also included (listed in Supplemental Data 2) and were tested, in the same way as those
147 involving humerus length, for proportional change during growth in order to identify
148 ontogenetic bias.

149 The data were further explored using principal components analysis (PCA) to assess
150 whether humerus length is an appropriate body size proxy and the compatibility between
151 allometric patterns resulting from bivariate and multivariate methods. Skeletal variables that
152 did not return statistically significant allometric correlations in bivariate analysis were
153 excluded from the PCA, since in these dimensions anurognathids show strong interspecific
154 variation in growth trajectory. For the remaining skeletal variables, a covariance matrix of the

155 log-transformed measurements was subjected to PCA to extract the first principal component
156 (PC1) as an internally defined size variable; this accounted for every skeletal variable
157 involved and allowed calculation of the allometric scaling coefficient for each skeletal
158 variable (Jolicoeur, 1963; Klingenberg, 1996). Missing data were imputed using the iterative
159 PCA method (Kiers, 1997), also known as the EM-PCA algorithm (Josse and Husson, 2012);
160 this is suitable for small datasets and provides better estimates than other imputation
161 techniques when variables are highly correlated (Dray and Josse, 2015). The null hypothesis
162 of isometry was then tested using the same scheme as in the bivariate analysis. The PCA was
163 performed in R v. 3.5.1 using the “missMDA” (Josse and Husson, 2016) and “boot” (Canty
164 and Ripley, 2021) packages, using code provided in the Supplemental Content.

165

166 **Character Matrices**

167 The data compiled for phylogenetic analysis were based largely on the character-taxon
168 matrix from Longrich et al. (2018), which comprises 134 taxa and 271 characters and was
169 copied and pasted into a Microsoft Excel file for editing. Considering that the present study
170 focuses only on the phylogeny of Anurognathidae, we excluded non-pterodactyloid species
171 with > 50% missing data and pterodactyloid species with > 25% missing data, leaving 36
172 species in the matrix. We added five anurognathids, *Luopterus mutoudengensis* (Lü and Hone,
173 2012; Hone, 2020), *Vesperopterylus lamadongensis* (Lü et al., 2018; Hone, 2020),
174 *Sinomacrops bondei* (Wei et al., 2021), CAGS-Z070 (Ji and Yuan, 2002) and NJU-57003
175 (Yang et al., 2019), yielding a total of 41 taxa in the matrix.

176 Concerning the character (Char.) list, Char. 54 from Longrich et al. (2018) was deleted

177 because the character description is likely incorrect: “Palate_anterior_end_shape: absent
178 present”; Char. 122 was deleted as it is a repetition of Char. 115. Further, we used the ratio of
179 skull : humerus length for Char. 1 instead of skull : dorsal vertebra length as in the original
180 dataset (Longrich et al., 2018). This is because (1) dorsal vertebrae are either missing or
181 preserved with poorly defined boundaries in specimens of *Anurognathus*, *Luopterus*,
182 *Sinomacrops*, *Dendrorhynchoides*, CAGS-Z070 and NJU-57003, (2) the skull : single
183 vertebra length ratio is sensitive to measurement error, and (3) simply adding the skull :
184 humerus length ratio to the character list would overweight the skull length in the analysis.
185 The skull : humerus length ratio for non-anurognathid taxa was calculated by dividing the
186 value for Char. 1 by that of Char. 28 in Longrich et al. (2018).

187 In order to incorporate as many characters as possible that were phylogenetically
188 informative for anurognathid taxa, we evaluated each character in the original diagnosis and
189 additional characters in Hone (2020) and Wei et al. (2021) (Supplemental Data 2) prior to
190 inclusion in the character list (Supplemental Content). Characters were omitted if (1) they are
191 uninformative (i.e., same states in all anurognathids), (2) the corresponding skeletal elements
192 are poorly preserved, (3) they already exist in Longrich et al. (2018), or (4) they show
193 allometric growth bias. The final character list (Supplemental Content) comprises 286
194 characters, including 17 newly added characters.

195 The original continuous characters (Longrich et al., 2018) were also checked for potential
196 allometric growth bias, but the biased characters were not omitted from the character list
197 because they are useful for determining phylogenetic relationships outside Anurognathidae.
198 For each of the ontogeny-biased characters, we coded each anurognathid (with the

199 corresponding anatomy preserved) with the same state as the largest specimen in order to
200 remove the impact of such characters on taxonomy within Anurognathidae (Supplemental
201 Data 3). An ontogenetically uncorrected matrix (i.e., using original states for each
202 anurognathid) was compiled for comparison (Supplemental Data 4).

203 We recoded all four anurognathid taxa in the original dataset based on published
204 specimen-specific descriptions and figures. The coding of *Jeholopterus ningchengensis* was
205 based on the holotype specimen IVPP V12705 (Wang et al., 2002) alone and the referred
206 *Jeholopterus* specimen CAGS-Z070 (Ji and Yuan, 2002; Lü and Hone, 2012; Yang et al.,
207 2019) was coded separately since its species assignment remains unclear. The coding of
208 *Anurognathus ammoni* was based on the holotype BSP 1922 I 42 (Wellnhofer, 1975); a
209 second specimen assigned to this species is from a private collection but has a cast specimen
210 (SMNS 81928) available (Bennett, 2007a). The coding of *Batrachognathus volans* was based
211 on the holotype PIN 52-2 (Bakhurina and Unwin, 1995; Unwin and Bakhurina, 2000) and a
212 second specimen PIN 2585/4a (Costa et al., 2013) assigned to this species. The coding of
213 *Dendrorhynchoides curvidentatus* was based on the holotype specimen of GMV 2128 (Ji and
214 Ji, 1998). Codings of the recently named taxa, *Luopterus mutoudengensis*, *Vesperopterylus*
215 *lamadongensis* and *Sinomacrops bondei* were based on their respective holotype specimens
216 JZMP-04-07-3 (Lü and Hone, 2012), BMNHC-PH-001311 (Lü et al., 2018) and JPM-2012-
217 001 (Wei et al., 2021), respectively.

218 Concerning the problematic tail in the holotype of *Dendrorhynchoides curvidentatus*, we
219 agree with previous observations by Unwin et al. (2000) and Hone (2020) that only the
220 proximal portion of the tail is genuine, where six disk-like vertebrae remain articulated and in

221 contact with the sacrum, and that, based on the tapering of the proximal portion, the tail
222 overall is short as in other short-tailed anurognathids and consists of fewer than 15 vertebrae.
223 The distal portion of the tail, separated from the proximal portion by a gap, shows distinctly
224 different morphology more typical of long-tailed pterosaurs and is considered artificial.
225 Therefore codings for caudal morphology were based on the proximal portion (Chars. 24, 25,
226 208, 209, 210) and the tail : humerus length ratio was coded as unknown (Char. 49).

227 Concerning the controversial configuration of the external naris and antorbital fenestrae
228 (i.e., separated vs. confluent) in anurognathids (e.g., Andres et al. 2010; Wei et al., 2021), this
229 was coded as separated for NJU-57003 (based on present study) and *Anurognathus* (based on
230 description by Bennett (2007a)), and as unknown for other anurognathids (Supplemental Data
231 3 and 4). For comparison, we composed a second matrix (Supplemental Data 5), based on the
232 ontogenetically corrected data in Supplemental Data 3, in which NJU-57003 was coded as
233 separated, *Batrachognathus volans*, *Sinomacrops bondei* and CAGS-Z070 as confluent (Wei
234 et al., 2021), and as unknown for other anurognathids.

235 Phylogenetic matrices (Supplemental Data 3–5) in tnt format can also be found on the
236 Morphobank page of this study (project 4151).

237 **Phylogenetic Analysis**

238 Phylogenetic analysis was conducted using TNT v1.5 (Goloboff and Farris, 2008), with
239 the settings used in Longrich et al. (2018): ordered and unordered characters were used and
240 equally weighted; continuous characters were rescaled to unity using the “nstates stand”
241 command; basic tree searches of 2,000 random addition sequence replicates were conducted
242 with and without the parsimony ratchet; ambiguous branch support was not used; zero-length

266 of other specimens (Fig. 2L). This probably explains its unusual tibia : femur length ratio, a
267 diagnostic trait (Wei et al., 2021); its tibia length is similar to that of other specimens (Fig.
268 2M). The third exception is the scapula-coracoid pair ($p = 0.064$; Table 1), which also
269 represents strong interspecific variation: scapula : coracoid length ratio ranges from 2 in the
270 *Jeholopterus ningchengensis* holotype to less than 1 in *Vesperopterylus lamadongensis*.

271 Among the dimensions with shared growth trajectories, those from the skull have the
272 largest deviations from isometry, with both length and width showing strong negative
273 allometry relative to the humerus (Figs. 1A, 2A–B, Table 1). The relatively low R^2 values
274 (0.845 and 0.812 for skull length and width, respectively) probably reflect a combination of
275 interspecific variation and the effect of dorsal-ventral compaction commonly seen in these
276 specimens. In addition, skull length exhibits negative allometry relative to width (Fig. 2C),
277 suggesting that the shape of the skull becomes proportionally broader with growth.

278 In the limbs, only the femur shows slight negative allometry relative to the humerus,
279 while the pteroid, both manual and pedal claws, wp3–4 and wingspan exhibit positive
280 allometry and the remaining elements (ulna/radius, metacarpal IV and wp1–2) grow
281 isometrically (Figs. 1A, 2, Table 1). Wingspan shows only slight positive allometry, despite
282 relatively strong positive allometry in wp3–4, because the latter account for < 10% of the
283 wingspan. Similarly, although the pedal claw shows relatively strong positive allometry to the
284 humerus (Figs. 1A, 2P), the growth of foot length overall is isometric (Figs. 1A, 2N).

285 In some cases, the recovered allometric scaling coefficients suggest allometry, but are
286 interpreted here as evidence of isometry based on the bootstrapping results. These cases
287 include humerus-metacarpal IV, humerus-tibia, ulna/radius-metacarpal IV, pdIII-pdV,

288 metatarsal-metacarpal IV and tibia-fibula (Fig. 2, Table 1). This conflict between allometric
289 scaling coefficients and bootstrapping results probably reflects relatively higher interspecific
290 variation in these elements (e.g., pdV : pdIII length ratio ranges from 2.1 to 1.5 among
291 anurognathids), and/or the small sample size, preventing discrimination of the allometric
292 scaling coefficient from 1 (isometry).

293 In the PCA, length data of scapula and coracoid were excluded from the analysis due to
294 the strong interspecific variation detected (Table 1). *Batrachognathus volans* and
295 *Sinomacrops bondei* were included but with respective skull length and femur length treated
296 as missing data, given the interspecific variations in these dimensions (Fig. 2A, L) and that
297 the other studied dimensions follow the growth trajectories in other anurognathids.

298 PC1 captures 95.9% of total variance with high scores for large specimens, supporting
299 PC1 as a size factor (Table 2). The resulting allometric pattern is largely compatible with the
300 bivariate analysis using humerus length as a body size proxy (Fig. 1). PCA recovered the
301 humerus with only slight negative allometry, and as such, the allometric status of many
302 skeletal variables identified by PCA (including skull length and width, manual and pedal
303 claws, pteroid, wp3–4 and femur) is the same as that suggested by the bivariate analysis (Fig.
304 1). Further, in both analyses the skeletal variables rank similarly using the allometric scaling
305 coefficients (Tables 1 and 3): pedal claw > manual claw > pteroid > metacarpal IV >
306 wingspan > foot > wp2 > wp1 > ulna/radius > femur > tibia > skull width > skull length. The
307 only discrepancy is the ranking of wp3–4 and pedal claw, which is wp3–4 > pedal claw in
308 bivariate analysis and the reverse in PCA; nonetheless in both analyses the coefficient values
309 are similar and indicate positive allometry.

310 Notably, the humerus allometric scaling coefficient recovered by PCA is slightly below 1
311 (negative allometry), unlike in bivariate analysis where it is assumed to equal 1 (isometry). In
312 summary, our results show that for each skeletal variable bivariate analysis consistently
313 produces higher allometric scaling coefficient values than PCA (Tables 1, 3). As a result,
314 bivariate analysis recovered ulna/radius, wp1 and tibia with allometric scaling coefficients < 1
315 (albeit statistically indistinguishable from 1), whereas PCA indicates negative allometry in
316 these dimensions. Similarly, wingspan growth is recovered as slightly positively allometric
317 using bivariate analysis, but isometric using PCA.

318

319 **Biases in Diagnoses and Character Matrices**

320 According to the allometric analysis, seven characters previously used to diagnose
321 anurognathid taxa (see Supplemental Data 2 for the full list) are biased by allometric growth:
322 (1) wingspan (Bakhurina and Unwin, 1995; Wang et al., 2002); (2) skull size (Lü and Hone,
323 2012; Lü et al., 2018); (3) skull aspect ratio (Wang et al., 2002; Lü and Hone, 2012; Lü et al.,
324 2018), except for *Batrachognathus volans*; (4) length ratio of (femur + tibia) to humerus
325 (Unwin and Bakhurina, 2000); (5) length ratio of humerus to femur (Kellner, 2003; Wang et
326 al., 2005; Wei et al. 2021), except for *Sinomacrops bondei*; (6) length ratio of metacarpal IV
327 to metatarsal I–III (Lü et al., 2018); and (7) length ratio of metacarpal IV to lower arm (Wang
328 et al., 2002). These were omitted in the taxonomic study (below) of the new anurognathid
329 taxon.

330 Further, nine characters in the character list (Supplemental Content) use length ratios that
331 can be biased by ontogenetic variation in anurognathid proportions, including Chars. 1 (skull :

332 humerus ratio of 0.452–0.823 except for *Batrachognathus*), 32 (pteroideum : ulna ratio of 0.098–
333 0.166), 33 (metacarpal IV : humerus ratio of 0.282–0.407), 37 (wp2 : wp1 ratio of 0.796–
334 0.915), 38 (wp3 : wp1 ratio of 0.423–0.769), 39 (wp4 : wp1 ratio of 0.100–0.183), 43 (femur :
335 humerus ratio of 0.645–0.778 with the exclusion of *Sinomacrops*), 45 (fibula : tibia ratio of
336 0.408–0.666) and 46 (metatarsal III : tibia ratio of 0.399–0.532). Excepting *Batrachognathus*
337 and *Sinomacrops*, which were coded using their unique length ratio for Chars. 1 and 43,
338 respectively, specimens were assigned the ontogenetically corrected states for these characters
339 (see Character Matrices in MATERIALS AND METHODS).

340

341 SYSTEMATIC PALEONTOLOGY

342

343 PTEROSAURIA Kaup, 1834

344 ANUROGNATHIDAE Kuhn, 1937

345 *CASCOCAUDA RONG* gen. et sp. nov.

346 (Figs. 3–6, S1)

347 **Holotype**—The holotype is NJU-57003, preserving a well-articulated and nearly
348 complete skeleton with extensive preserved soft tissues (Figs. 3–6, S1). The specimen
349 comprises two fragmented slabs (main slab and counter slab), which are housed in Nanjing
350 University, Nanjing, China.

351 **Etymology**—The generic name is composed of the Latin ‘cascus’ meaning ‘ancient,
352 primitive’, and ‘cauda’ meaning ‘tail’. The specific name is from Chinese character róng (绒),
353 as used in the phrase máo róng róng, meaning ‘a fluffy appearance’, which refers to the
354 extensive integumentary covering (Yang et al., 2019).

355 **Locality and Horizon**—The holotype was recovered from Mutoudeng, Qinglong County
356 in Hebei Province, China, from the Middle–Late Jurassic Tiaojishan Formation (Xu et al.,
357 2016).

358 **Diagnosis**—A new anurognathid pterosaur that differs from other anurognathids by the
359 following combination of diagnostic features: at least 20 caudal vertebrae with elongate
360 zygapophyses and chevrons (different from *Jeholopterus*, *Anurognathus*, *Dendrorhynchoides*
361 and *Vesperopterylus*), scapula slightly longer than coracoid with a length ratio of 1.2 (different
362 from *Luopterus*, *Jeholopterus* and *Vesperopterylus*), second phalanx of pedal digit V curved
363 (different from *Luopterus* and *Jeholopterus*), long and thin teeth with distal curvature
364 (different from *Anurognathus* and *Vesperopterylus*), humerus subtriangular deltopectoral crest
365 (different from *Batrachognathus* and *Sinomacrops*) and skull wider than long (different from
366 *Batrachognathus*).

367 **Remarks**—The differences in many skeletal proportions among anurognathids are related
368 to growth based on their shared allometry. However, NJU-57003 is unique in two skeletal
369 proportions of taxonomic significance and several non-ratio diagnostic traits (see above),
370 which warrants the erection of a new taxon notwithstanding its immaturity. Further, excluding
371 the growth-related characters in the diagnoses of existing anurognathid species, the unbiased
372 characters are diagnostic and therefore the seven species previously erected remain valid. In
373 addition to the eight established species, CAGS-Z070 appears to represent another
374 unrecognized species yet to be formally named. It has been referred to the genus *Jeholopterus*
375 (Kellner et al., 2010) but differs from the holotype specimen of that taxon in scapula :
376 coracoid length ratio (1.1 rather than 2), tooth morphology (striated rather than smooth

377 texture, and short teeth rather than both long and short teeth), pteroid shape (straight rather
378 than curved; although this could be due to the preserved orientation in which a curved
379 element can appear straight) and pdV-2 shape (curved rather than straight).

380

381 **Description**

382 The holotype specimen of *Cascocauda rong* has a wingspan of 434 mm and is preserved
383 in dorsal view on the main slab, with wings folded on both sides of the body and hindlimbs
384 flexed (Figs. 3, S1). The skeleton is near complete and well-articulated, with extensive
385 preservation of pycnofibers and wing membranes.

386 **Ontogenetic Status**—The specimen represents a juvenile based on the unfused articular
387 bones, such as carpals, scapula and coracoid (Fig. 5E–F), and the pitted and rough articular
388 surfaces of limb bones (Fig. 5C–D) indicative of incomplete ossification.

389 **Skull**—The skull is wider than long (22.2 mm long and 31.7 mm wide) with a typical
390 anurognathid frog-like jaw (Figs. 4A–B and S2). Most of the cranial bones are highly
391 compressed and poorly defined, with frontal, palatine, teeth and the retroarticular process
392 being barely discernible. On the right side, two processes extending from the anterior portion
393 of the upper jaw towards the frontal probably represent the ascending processes of maxilla
394 and jugal/nasal, respectively; these separate the naris, antorbital fenestra and orbit (Figs. 4C
395 and S2). On the left, the ascending process of the maxilla is partially preserved and part
396 impression, while the ascending processes of the jugal/nasal is not preserved (Figs. 4C and
397 S2). Nineteen widely spaced teeth are visible; these are 2.2–2.7 mm long, about 0.5 mm wide
398 at the midpoint and distally curved with smooth surfaces (Fig. 5A–B).

399 **Vertebral Column**—The cervical, dorsal and sacral vertebrae are crushed or partially
400 covered, so the exact number of vertebrae is uncertain (Fig. 3). The neck is represented by
401 short and robust cervical vertebrae. No evidence of cervical ribs is preserved, suggesting they
402 were highly reduced or absent. At least ten dorsal vertebrae are preserved. Dorsal ribs are
403 straight or slightly curved in the anterior portion of the body, while the more posterior ribs are
404 distinctly curved posteriorly. Sacral vertebrae are short, broad, and articulated with the caudal
405 vertebrae, and bear posterolaterally directed ribs and/or transverse processes. Three rows of
406 gastralia are preserved and become progressively shorter caudally. Caudal vertebrae are well-
407 preserved and -articulated. Although the boundaries between several caudal vertebrae are
408 obscured by compression, there are at least 20 vertebrae with a total length of 42 mm (Fig.
409 6A). A single caudal vertebra is ca. 2 mm long at the base of the tail, and becomes more
410 elongate posteriorly, reaching a maximum length of 3.4 mm near the midpoint, and then
411 shortens towards the distal tip. Elongate zygapophyses and chevrons (exposed by the absence
412 of some caudal vertebrae) are best preserved in the middle portion of the tail, where they are
413 at least twice the length of the vertebral centrum (Fig. 6A–B); the paired appearance of
414 chevrons probably reflects superposition of vertebrae rather than bifurcation of the structure.

415 **Pectoral Girdles**—The scapulae are unfused to, and longer than the slightly curved
416 coracoids. They are preserved in articulation on the left, where they meet in a ‘V’ shape at an
417 angle of approximately 60° (Figs. 3, 5E–F).

418 **Forelimbs**—The humerus is robust, with a sub-triangular deltopectoral crest (Fig. 5C–
419 D). The shaft of the humerus is slightly curved and the articular surfaces are pitted and rough
420 (Figs. 3, 5C–D). Ulna and radius are both straight and significantly longer than the humerus,

421 only slightly shorter than the first wing phalanx, and subequal in length to the second wing
422 phalanx (Fig. 3). No epiphysis is discernible due to extensive fragmentation during burial.
423 Carpals are poorly preserved and difficult to discern individuals. The pteroid is short, curved
424 and blunt at the distal end. The four metacarpals are subequal in length and less than one
425 quarter the length of the radius. The wing metacarpal is much more robust than the other
426 three. The manual claws are strongly curved, sharp and similar in shape to the pedal claws,
427 but the manual claws are larger and more robust (Fig. 6C–D). The wing consists of four
428 phalanges that exhibit a rapid reduction in length proceeding distally, although the lengths of
429 the first two phalanges are similar (Fig. 3).

430 **Pelvic Girdles**—The bones of the pelvic girdle are articulated with the hindlimb (Figs. 3,
431 6E–F) and although crushed, are separated, indicating an unfused state. The ilia have long and
432 slender anterior processes, but the shape of the posterior processes is unclear. The ischia are
433 broad plates that approach each other closely at the posterior end. The shape of the pubis is
434 difficult to discern. The left prepubis bears a distinct proximal shaft and an asymmetrically
435 fan-shaped distal portion (Fig. 6E–F).

436 **Hindlimbs**—The femur is straight and oriented nearly perpendicular to the vertebral
437 column. The fibula is not fused to the tibia, tapering out at less than half the length of the
438 tibia. Metatarsals I–IV are straight and parallel to each other with nearly equal lengths. The
439 fifth metatarsal is slightly more robust but significantly shorter than metatarsals I–IV. The
440 phalangeal formula is 2-3-4-5-2. The first digit of the pes is not reversed, and in pedal digits
441 II–IV the penultimate phalanges are longer than the more proximal phalanges (Figs. 3, 6D).
442 Pedal digit V consists of two long phalanges, of which the first phalanx is robust and straight,

443 while the second is slender and slightly curved (Fig. 6G–H).

444

445 PHYLOGENETIC ANALYSIS

446

447 By using ontogenetically corrected codings and treating only *Cascocauda* and
448 *Anurognathus* as having separated naris and antorbital fenestrae (with the character coded as
449 unknown for all other specimens; Supplemental Data 3), our analysis produced a single most
450 parsimonious and fully resolved tree (Fig. 7), with 850.283 steps, consistency index (CI) of
451 0.442 and retention index (RI) of 0.708. Most major clades are recovered, among which the
452 Anurognathidae, supported by 42 synapomorphies (see Supplemental Results for details), is
453 placed as the sister group of Breviquartossa. Within Anurognathidae, *Cascocauda rong* is the
454 sibling group to (*Batrachognathus volans* + *Sinomacrops bondei*), which together form the
455 Batrachognathinae (sensu Kellner et al., 2010). Alongside Batrachognathinae, the
456 Anurognathinae (sensu Wei et al., 2021) comprises all other anurognathids. The number of
457 synapomorphies supporting each internal node of Anurognathidae varies from 3 to 13
458 (Supplemental Results). Bremer support and bootstrap scores indicate high stability (>1 for
459 the former and over 50 for the latter) for Anurognathidae, Batrachognathinae and
460 *Batrachognathus volans* + *Sinomacrops bondei* (Fig. S3). Anurognathinae and the clades
461 within are less stable: only two clades, (*Dendrorhynchoides* + *Anurognathus* +
462 (*Vesperopterylus* + (*Jeholopterus* + CAGS-Z070))) and (*Jeholopterus* + CAGS-Z070), have
463 Bremer support scores of 1, and only the clade (*Jeholopterus* + CAGS-Z070) has a bootstrap
464 score higher than 50.

465 Ontogenetically uncorrected codings (Supplemental Data 4) produced an identical tree

466 topology with a slightly longer tree length (852.302 steps) and similar Bremer support and
467 bootstrap scores (Fig. S4A). The phylogenetic analysis is thus subject to limited allometric
468 growth bias, probably because (1) the number of biased characters is small compared to the
469 total number of informative characters, and (2) growth-related variations are coded as
470 continuous characters and thus caused relatively small step changes (always <1 by each
471 character) compared to the informative discrete characters.

472 We also ran the analysis using ontogenetically corrected codings but under a different
473 scenario for the configuration states of naris and antorbital fenestrae (Supplemental Data 5),
474 i.e., treating *Cascocauda* as separated, *Batrachognathus volans*, *Sinomacrops bondei* and
475 CAGS-Z070 as confluent (Wei et al., 2021), and the rest of anurognathids as unknown. The
476 analysis produced an identical tree topology to the original and “ontogenetically uncorrected”
477 analyses, although with an even longer tree length (853.227 steps) than the latter, and similar
478 Bremer support and bootstrap scores (Fig. S4B). The Bremer support for Batrachognathinae
479 reduced to 1, probably because the analysis recovered the configuration of naris and antorbital
480 fenestrae of Batrachognathinae as ambiguous (Fig. S5).

481

482 DISCUSSION

483

484 **Allometry-related Biases in Anurognathid Systematics**

485 Our analysis demonstrates that anurognathids share the same growth trajectory in most
486 skeletal dimensions and that seven characters in existing anurognathid diagnoses relate to
487 allometric growth rather than interspecific variations. Similar studies of other pterosaur
488 clades, on skeletal proportional changes during growth, have suggested or led to taxonomic

489 revisions, including synonymization of multiple species based on shared growth curves (e.g.,
490 Bennett, 1995, 1996, 2007b, 2013; Jouve, 2004) and recognition of the outliers of the curves
491 as separate taxa (e.g., Bennett 2006; Vidovic and Martill, 2014). In Anurognathidae, however,
492 excluding the biased characters, the rest of the diagnosis remains sufficient to discriminate
493 among existing species, which are thus considered valid here. Our analysis also recognizes
494 two outliers among the shared growth trajectories, i.e., the proportionally longer skull of
495 *Batrachognathus volans* and the shorter femur of *Sinomacrops bondei*, further supporting the
496 validity of these two species.

497 Concerning phylogenetic analysis, although the detected allometry-related biases have
498 not affected tree topology in the present study, they might have a more discriminatory effect if
499 the number of informative characters (and consequently synapomorphies) is small. In
500 pterosaur phylogenies, nodes usually have few supporting characters (Lü and Hone, 2012);
501 this is particularly true for interpretations of anurognathid systematics that have relied on
502 limited available information (see discussion in Hone, 2020 and Wei et al., 2021). For
503 instance, the position of *Anurognathus* as the earliest-diverging member of Anurognathidae is
504 typically supported by a single character: the proportional size of the humerus compared to
505 the femur (Kellner, 2003; Wang et al., 2005). According to our results, however (Fig. 2L),
506 this character arises from ontogenetic rather than phylogenetic variation, and thus the
507 proposed phylogenetic position is not valid.

508

509 **Phylogeny of Anurognathids**

510 The phylogenetic position of Anurognathidae and the interrelationships of anurognathid
511 taxa have historically been contentious. Six hypotheses have been proposed for the position of

512 Anurognathidae, where the clade is viewed as: the basal-most pterosaur group (e.g., Kellner,
513 2003; Lü and Ji, 2006; Bennett, 2007a; Wang et al., 2008; Lü et al., 2018); the sister-group of
514 Novialoidea (Unwin, 2003b; Lü et al., 2010); the sister-group of Breviquartossa (Viscardi et
515 al., 1999; Britt et al., 2018; Dalla Vecchia, 2019); belonging to the Scaphognathidae (Vidovic
516 and Martill, 2018); the sister-group of Pterodactyloidea (Dalla Vecchia, 2009; Andres et al.,
517 2010, 2014); or a basal monofenestran group (Wei et al., 2021). Interspecific relationships
518 within Anurognathidae are also inconsistent with numerous different topologies having been
519 proposed (Kellner, 2003; Unwin, 2003a; Lü and Ji, 2006; Andres et al., 2014; Wang et al.,
520 2017; Lü et al., 2018; Vidovic and Martill, 2018; Wei et al., 2021).

521 Given ongoing discoveries of new anatomical traits and species of anurognathids,
522 particularly in recent years (e.g., Jiang et al., 2015; Lü et al., 2018; Hone 2020; Wei et al.,
523 2021), we compare our phylogenetic results primarily with the most recent and species-
524 inclusive phylogenetic study by Wei et al. (2021), albeit with reference to others.

525 Our phylogenetic placement of Anurognathidae, outside Monofenestrata and as the sister-
526 group of Breviquartossa (Fig. 7), differs from the suggestion by Wei et al. (2021) that the
527 clade is the basal-most branch in Monofenestrata. One key factor is that we code
528 anurognathids as either having separate external nasal and antorbital fenestrae (*Cascocauda*
529 and *Anurognathus*) or unknown (other anurognathids), whereas the group was considered to
530 have a confluent nasoantorbital fenestra (a feature typical of the Monofenestrata and coded as
531 present in *Batrachognathus*, *Sinomacrops* and CAGS-Z070) by Wei et al. (2021). This
532 difference in reconstructions arises from the poor preservation of the ascending processes of
533 the maxilla, either undiscernible or isolated from the maxilla, that, if present, would have

534 separated the naris and antorbital fenestra (Andres et al., 2010; Wei et al., 2021). The newly
535 described holotype of *Cascocauda rong*, however, preserves two distinct processes rising
536 from the anterior portion of the upper jaw towards the frontal (Fig. 4C), which are most likely
537 the ascending processes of the maxilla and jugal/nasal, respectively. The absence of the
538 ascending process of the maxilla in holotypes of *Batrachognathus* and *Sinomacrops* and
539 specimen CAGS-Z070 (Wei et al., 2021) is not necessarily evidence for its anatomical
540 absence but that this structure is fragile and prone to displacement during fossilization. As
541 such, we consider that available evidence supports the traditional view of separate nasal and
542 antorbital fenestrae in anurognathids (Bennett, 2007a; Hone, 2020).

543 If we code *Batrachognathus*, *Sinomacrops* and CAGS-Z070 as having a confluent
544 nasoantorbital fenestra following Wei et al. (2021), and code only *Cascocauda* as having
545 separate external naris and antorbital fenestrae and the rest as unknown, the resulting tree
546 topology is identical to that produced by our original codings (Fig. S4B). Further, our
547 phylogenetic placement of Anurognathidae is consistent with the position proposed by
548 Viscardi et al. (1999), Britt et al. (2018) and Dalla Vecchia (2019); all coded the confluent
549 nasoantorbital fenestra as present or unknown. These results further support the position of
550 the Anurognathidae outside Monofenestrata as a sister-group of Breviquartossa and suggest
551 that except for the configuration of the external naris and antorbital fenestrae, anurognathid
552 anatomy is non-monofenestratan.

553 In terms of relationships within Anurognathidae, our results are largely congruent with
554 Wei et al. (2021) in placing *Batrachognathus* and *Sinomacrops* as a clade and members of
555 Batrachognathinae (with the inclusion of *Cascocauda* in the present study), placing the other

556 anurognathids as Anurognathinae and recognizing the clade (*Anurognathus* + *Vesperopterylus*
557 + *Jeholopterus*). Only two discrepancies occur, namely whether *Luopterus* or
558 *Dendrorhynchoides* is the sister group to the clade (*Anurognathus* + *Vesperopterylus* +
559 *Jeholopterus*) and relationships within the latter clade.

560 Wei et al. (2021) placed *Luopterus* as sister to the clade (*Anurognathus* + *Vesperopterylus*
561 + *Jeholopterus*) based on the synapomorphy of a straight last phalanx of pedal digit V.
562 However, this phalanx is described as curved in both the holotype (Wellnhofer, 1970) and the
563 referred specimen (Bennett, 2007a) of *Anurognathus*, yet coded as straight by Wei et al.
564 (2021). Our analysis, on the basis of six synapomorphies (see Supplemental Results for
565 details), recovered *Dendrorhynchoides* as more closely related to the clade (*Anurognathus* +
566 *Vesperopterylus* + *Jeholopterus*), which together constitute a clade containing all short-tailed
567 anurognathids, i.e., having fewer than 15 caudal vertebrae with disk-like morphology and
568 short zygapophyses, and tail : humerus length ratio < 0.5.

569 Interestingly, according to our results, this clade of short-tailed anurognathids is
570 immediately preceded by *Luopterus* with an elongated tail (tail : humerus length ratio of
571 0.67), which is further preceded by other long-tailed species with much longer tails (tail :
572 humerus length ratio of 1.47 for *Batrachognathus volans*, 1.50 for *Cascocauda rong* and > 2
573 for *Sinomacrops bondei*). Although positive allometric growth in the tail has been observed in
574 *Pterodaustro* (Codorníu, 2007) and *Kunpengopterus* (Jiang et al., 2021), i.e., the tail becomes
575 proportionally longer during ontogeny, this is probably not the case here. For instance,
576 *Luopterus* has a similar humerus length (near isometry to body size in growth) to
577 *Cascocauda*, but its tail is less than half as long as the latter; compared to *Sinomacrops*,

578 *Luopterus* has a longer humerus and yet a much shorter tail length. The observed difference in
579 tail length is therefore best explained as interspecific variation. The stepwise shortening of the
580 tail from the Batrachognathinae to *Luopterus* and then to the clade (*Dendrorhynchoides* +
581 *Anurognathus* + *Vesperopterylus* + *Jeholopterus*) probably reflects a general evolutionary
582 trend of tail reduction in Anurognathinae.

583 Wei et al. (2021) recovered a sister-group relationship between *Anurognathus* and
584 *Vesperopterylus* based on one synapomorphy: the complete loss of mid-cervical ribs.
585 Although this trait characterizes *Anurognathus* and *Vesperopterylus* and has been included in
586 our character matrix (Char. 202), our analysis found *Jeholopterus* to be more closely related
587 to *Vesperopterylus* than *Anurognathus* based on four synapomorphies (see Supplemental
588 Results for details). Among these four synapomorphies, while the number of teeth may be
589 uncertain from preservational bias (loss or covered by other bones or matrix), *Vesperopterylus*
590 and *Jeholopterus* share (1) the length to mid-width ratio of 0.9 for the third phalanx of pedal
591 digit IV (2.3 in *Anurognathus*), (2) distinctly curved dorsal ribs in the anterior portion of the
592 body (straight ribs in *Anurognathus*) and (3) robust first phalanx of pedal digit V (absent in
593 *Anurognathus*). The latter two traits were not included in the analysis by Wei et al. (2021), but
594 had been noted previously by Hone (2020), probably leading to the different results.

595 Support for relationships within Anurognathidae (especially Anurognathinae) will
596 improve with incorporation of additional diagnostic features following future discovery of
597 new specimens.

598

599 **Ontogeny and Evolution of Anurognathids**

600 The gross morphology—and presumably ecology—of anurognathids varies little both in
601 space, across much of Eurasia (known at least from Germany, Kazakhstan, China and North
602 Korea) and time, over an interval of > 40 million years (Unwin et al., 2000; Bennett, 2007a;
603 Hone, 2020). They are widely interpreted as having been specialized aerial insectivores active
604 in low light conditions based on their anatomy, including a frog-like large gape and sharp
605 isodont dentition (Bennett, 2007a; Ósi, 2011; Hone, 2020), small size, deep wing with curved
606 wingtip, short flexible tail (Bennett, 2007a; Ósi, 2011; Hone et al., 2015; Hone, 2020) and
607 large eyes (Bennett, 2007a; Lü et al., 2018). Limited variation among anurognathids does,
608 however, suggests adaptations to slightly different niches. For example, variations in the
609 number and shape of teeth indicate different prey types (Wang et al., 2002); the reversed first
610 toe in some anurognathids suggests enhanced gripping ability, and by extension arboreality
611 (Lü et al., 2018); variations in the proportions of scapula and coracoid and the shape of the
612 humerus deltopectoral crest reflect different musculature constructions and thereby flight
613 styles (Frey et al., 2003; Hone, 2020); and reduction of the tail suggest reduction of drag,
614 leading to higher maneuverability during flight (Evans and Thomas, 1992; Bennett, 2007a).

615 Our recovered allometric growth pattern suggests that the lifestyle of anurognathids
616 changed very little in ontogeny as well as through space and time. The (near-)isometric
617 growth in most of the wing elements and wingspan (Fig. 1) indicates that juvenile
618 anurognathids, as small as only 0.24 m in wingspan, have very similar wing shape and
619 relative size to adults. This indicates precocial flight capability, as has been suggested for
620 many other pterosaurs with similar isometric growth (e.g., Unwin, 2005; Bennett, 2017;

621 Unwin and Deeming, 2019; Hone et al., 2020; Naish et al., 2021). Given the faster (cubic)
622 increase in body mass than isometric growth of the skeletal lengths and (squared) increase of
623 wing area, juveniles may have had lower wing loading than adults and therefore different
624 flight performance (Hone et al., 2020). This difference, however, may have been relatively
625 small due to the overall low body mass and could have been offset at least partially by
626 increasing pneumaticity during growth (Schepelmann, 1990; Wedel, 2003; Benson et al.,
627 2012; Hone et al., 2020). Further, rather than reflecting a different flight style, a lower wing
628 loading in juveniles may reflect foraging with a reduced flight cost (Shaw, 2011). Indeed,
629 both juveniles and adults shared a suite of characters that would have allowed slow and highly
630 maneuverable flight, critical for aerial insectivores, including a deep wing chord, curved
631 wingtips, a flexible tail and likely voluntarily flexed interphalangeal joints (Unwin, 2005;
632 Bennett, 2007a; Witton, 2008; Hone et al., 2015).

633 The strong negative allometry in both skull length and width (Fig. 1B, C) confirms
634 Bennett's (2007a) suggestion that the skull became smaller relative to body size during
635 growth. Although this is common among vertebrates from strong negative allometry of brain
636 growth (Dodson, 1975), this is not seen in at least some other pterosaurs (Bennett, 2006; Hone
637 et al., 2020). In the case of anurognathids, it may arise from specialization on a particular size
638 class of prey items (i.e., insects) during ontogeny, which is consistent with the stability
639 through ontogeny of anurognathid feeding-related characters of the skull (Ősi, 2011).

640 Further, the robust and sharply curved manual and pedal claws of anurognathids are well
641 adapted for quadrupedal climbing on vertical surfaces (Bennett, 1997; Unwin, 2005; Hone,
642 2020); the observed strong positive allometry in these elements (Fig. 1P, Q) probably reflects

643 retention of climbing despite increasing bodyweight. This is consistent with other evidence
644 for a predominantly arboreal lifestyle, including the unique, highly compact resting posture
645 observed in both juveniles and adults, presumably for concealment in trees (Bennett, 2007a;
646 Hone, 2020), small size (Hone, 2020) and co-occurrence of tree-dwelling animals indicative
647 of a forest environment (Chen et al., 2019).

648 The retention of the juvenile lifestyle into adulthood by anurognathids may have led to
649 their highly conserved morphology. Most other pterosaurs (Bennett, 2017) and many other
650 reptiles (Werner and Gilliam, 1984) exhibit distinct ontogenetic niche shifts, and occupy
651 different ecological niches to support larger body size during growth. As such, many aspects
652 of their ecomorphology change significantly during growth, and their adult traits, divergent
653 from plesiomorphic juvenile traits, become exaggerated in the process. In contrast, the
654 specialized and consistent lifestyle of anurognathids during ontogeny may have caused
655 retention of plesiomorphic juvenile traits, such as their characteristic large eyes, short skull
656 and small size. Consequently, this may have restricted anurognathid morphospace and
657 prevented further morphological divergence by stabilizing selection, as has been hypothesized
658 for some closely related cryptic species of modern bats (Mayer and Helversen, 2001).

659

660

CONCLUSION

661

662 Allometric analysis on 23 skeletal dimensions from the skull, pectoral girdle and limbs of
663 13 anurognathid specimens reveals an ontogenetic trajectory for this clade that affects a
664 minority of characters that have been used to assess their taxonomy and phylogenetic
665 position. Excluding the ontogeny-related characters, a new taxon, *Cascocauda rong* gen. et

666 sp. nov., is erected, which displays clear evidence for separated external naris and antorbital
667 fenestrae. Phylogenetic analysis on an ontogenetically corrected dataset supports the
668 hypothesis that Anurognathidae is sister of Breviquartossa, and that there was a general trend
669 of tail reduction in the family. The recovered allometric growth pattern suggests little change
670 through ontogeny in their lifestyle as arboreal, aerial insectivores and perhaps even a
671 consistent prey size. This specialized and ontogenetically consistent lifestyle may have
672 retained plesiomorphic juvenile traits to later ontogeny, and confined anurognathids in certain
673 area of morphospace despite their broad geographical and temporal distribution.

674

675 ACKNOWLEDGMENTS

676

677 We thank Q. Ji, S. Ji and H. Huang for access to specimen CAGS-Z070 and N. MacLeod
678 for suggestions. This work is supported by the National Natural Science Foundation of China
679 (41688103 and 41672010) and Strategic Priority Research Program (B) of the Chinese
680 Academy of Sciences (XDB26000000) to B.J., and the China Scholarship Council (No.
681 201906190142) and the program A for Outstanding PhD candidate of Nanjing University
682 (202002A028) to Z.Y. We also thank the referees and editor for their comments which helped
683 improve the manuscript.

684

685 LITERATURE CITED

686

687 Andres, B., J. M. Clark, and X. Xu. 2010. A new rhamphorhynchid pterosaur from the Upper
688 Jurassic of Xinjiang, China, and the phylogenetic relationships of basal pterosaurs.

-
- 689 Journal of Vertebrate Paleontology 30:163–187.
- 690 Andres, B., J. M. Clark, and X. Xu. 2014. The earliest pterodactyloid and the origin of the
691 group. *Current Biology* 24:1011–1016.
- 692 Bakhurina, N. N., and D. M. Unwin. 1995. A survey of pterosaurs from the Jurassic and
693 Cretaceous of the former Soviet Union and Mongolia. *Historical Biology* 10:197–245.
- 694 Bennett, S. C. 1995. A statistical study of *Rhamphorhynchus* from the Solnhofen Limestone of
695 Germany: year-classes of a single large species. *Journal of Paleontology* 69:569–580.
- 696 Bennett, S. C. 1996. Year-classes of pterosaurs from the Solnhofen Limestone of Germany:
697 taxonomic and systematic implications. *Journal of Vertebrate Paleontology* 16:432–444.
- 698 Bennett, S. C. 1997. The arboreal leaping theory of the origin of pterosaur flight. *Historical*
699 *Biology* 12:265–290.
- 700 Bennett, S. C. 2006. Juvenile specimens of the pterosaur *Germanodactylus cristatus*, with a
701 review of the genus. *Journal of Vertebrate Paleontology* 26:872–878.
- 702 Bennett, S. C. 2007a. A second specimen of the pterosaur *Anurognathus ammoni*.
703 *Paläontologische Zeitschrift* 81:376–398.
- 704 Bennett, S. C. 2007b. A review of the pterosaur *Ctenochasma*: taxonomy and ontogeny. *Neues*
705 *Jahrbuch für Geologie und Paläontologie, Abhandlungen* 245:23–31.
- 706 Bennett, S. C. 2013. New information on body size and cranial display structures of
707 *Pterodactylus antiquus*, with a revision of the genus. *Paläontologische Zeitschrift*
708 87:269–289.
- 709 Bennett, S. C. 2017. New smallest specimen of the pterosaur *Pteranodon* and ontogenetic
710 niches in pterosaurs. *Journal of Paleontology* 92:1–18.

-
- 711 Benson, R. B., R. J. Butler, M. T. Carrano, and P. M. O'Connor. 2012. Air-filled postcranial
712 bones in theropod dinosaurs: physiological implications and the 'reptile'–bird transition.
713 *Biological Reviews* 87:168–193.
- 714 Brower J.C., and J. Veinus. 1981. Allometry in pterosaurs. University of Kansas
715 *Paleontological Contributions*, Paper 105:1–32.
- 716 Britt, B. B., F. M. Dalla Vecchia, D. J. Chure, G. F. Engelmann, M. F. Whiting, and R. D.
717 Scheetz. 2018. *Caelestiventus hanseni* gen. et sp. nov. extends the desert-dwelling
718 pterosaur record back 65 million years. *Nature Ecology & Evolution* 2:1386–1392.
- 719 Canty, A., and B. Ripley. 2021. boot: bootstrap R (S-Plus) functions. R package version 1.3-
720 27. Available at <https://cran.r-project.org/package=boot>.
- 721 Chen, M., C. A. Strömberg, and G. P. Wilson. 2019. Assembly of modern mammal
722 community structure driven by Late Cretaceous dental evolution, rise of flowering
723 plants, and dinosaur demise. *Proceedings of the National Academy of Sciences, USA*
724 116:9931–9940.
- 725 Codorniú, L. 2007. Evidencias de cambios alométricos en las cervicales de *Pterodaustro*
726 *guinazui* (Pterosauria, Pterodactyloidea). *Ameghiniana* 44:10.
- 727 Costa, F., V. Alifanov, F. Dalla Vecchia, and A. W. A. Kellner. 2013. On the presence of an
728 elongated tail in an undescribed specimen of *Batrachognathus volans* (Pterosauria:
729 Anurognathidae: Batrachognathinae). In *Rio Ptero 2013-International Symposium on*
730 *Pterosaurs, Short Communications* 54–56.
- 731 Dalla Vecchia, F. M. 2002. Observations on the non-pterodactyloid pterosaur *Jeholopterus*
732 *ningchengensis* from the Early Cretaceous of northeastern China. *Natura Nascosta*

-
- 733 24:8–27.
- 734 Dalla Vecchia, F. M. 2009. Anatomy and systematics of the pterosaur *Carniadactylus* gen. n.
735 *rosenfeldi* (Dalla Vecchia, 1995). *Rivista Italiana di Paleontologia e Stratigrafia*
736 115:159–188.
- 737 Dalla Vecchia, F. M. 2019. *Seazzadactylus venieri* gen. et sp. nov., a new pterosaur (Diapsida:
738 Pterosauria) from the Upper Triassic (Norian) of northeastern Italy. *PeerJ* 7:e7363.
- 739 Delfino, M., and M. R. Sánchez-Villagra. 2010. A survey of the rock record of reptilian
740 ontogeny. *Proceedings Seminars in Cell & Developmental Biology* 21:432–440.
- 741 Dodson, P. 1975. Functional and ecological significance of relative growth in *Alligator*.
742 *Journal of Zoology* 175:315–355.
- 743 Dray, S., and J. Josse. 2015. Principal component analysis with missing values: a comparative
744 survey of methods. *Plant Ecology* 216:657–667.
- 745 Evans, M.R. and A.L. Thomas. 1992. The aerodynamic and mechanical effects of elongated
746 tails in the scarlet-tufted malachite sunbird: measuring the cost of a handicap. *Animal*
747 *Behaviour* 43:337–347.
- 748 Frey, E., M.-C. Buchy, and D. M. Martill. 2003. Middle-and bottom-decker Cretaceous
749 pterosaurs: unique designs in active flying vertebrates. Geological Society, London,
750 *Special Publications* 217:267–274.
- 751 Gao, K., Q. Li, M. Wei, H. Pak, and I. Pak. 2009. Early Cretaceous birds and pterosaurs from
752 the Sinuiju Series, and geographic extension of the Jehol Biota into the Korean
753 Peninsula. *Journal of the Paleontological Society of Korea* 25:57–61.
- 754 Goloboff, P., and J. S. Farris. 2008. TNT, a free program for phylogenetic analysis. *Cladistics*

-
- 755 24:774–786.
- 756 Gradstein, F. M., J. G. Ogg, M. D. Schmitz, and G. M. Ogg. 2012. *The Geologic Time Scale*
- 757 2012. Elsevier, Oxford, U.K., 1176 pp.
- 758 Henry, L., and H. Wickham. 2020. Purrr: functional programming tools. R package version
- 759 0.3.4. Available at <https://cran.r-project.org/package=purrr>.
- 760 Hone, D. W. E. 2020. A review of the taxonomy and palaeoecology of the Anurognathidae
- 761 (Reptilia, Pterosauria). *Acta Geologica Sinica* 94:1676–1692.
- 762 Hone, D. W. E., M. Van Rooijen, and M. Habib. 2015. The wingtips of the pterosaurs:
- 763 anatomy, aeronautical function and ecological implications. *Palaeogeography,*
- 764 *Palaeoclimatology, Palaeoecology* 440:431–439.
- 765 Hone, D. W. E., J. M. Ratcliffe, D. K. Riskin, J. W. Hermanson, and R. R. Reisz. 2020.
- 766 Unique near isometric ontogeny in the pterosaur *Rhamphorhynchus* suggests hatchlings
- 767 could fly. *Lethaia* 54:106–112.
- 768 Ji, Q., and C. Yuan. 2002. Discovery of two kinds of protofeathered pterosaurs in the
- 769 Mesozoic Daohugou Biota in the Ningcheng region and its stratigraphic and biologic
- 770 significances. *Geological Review* 48:221–224.
- 771 Ji, S., and Q. Ji. 1998. A new fossil pterosaur (Rhamphorhynchoidea) from Liaoning. *Jiangsu*
- 772 *Geology* 22:199–206. [Chinese]
- 773 Jiang, S., X. Wang, X. Cheng, F. R. Costa, J. Huang, and A. W. A. Kellner. 2015. Short note
- 774 on an anurognathid pterosaur with a long tail from the Upper Jurassic of China.
- 775 *Historical Biology* 27:718–722.
- 776 Jiang, S., X. Wang, X. Zheng, X. Cheng, J. Zhang, and X. Wang. 2021. An early juvenile of

-
- 777 *Kunpengopterus sinensis* (Pterosauria) from the Late Jurassic in China. *Anais da*
778 *Academia Brasileira de Ciências* 93:e20200734.
- 779 Jolicoeur, P. 1963. The multivariate generalization of the allometry equation. *Biometrics*
780 19:497–499.
- 781 Josse, J., and F. Husson. 2012. Handling missing values in exploratory multivariate data
782 analysis methods. *Journal de la Société Française de Statistique* 153:1–21.
- 783 Josse, J., and F. Husson. 2016. missMDA: a package for handling missing values in
784 multivariate data analysis. *Journal of Statistical Software* 70:1–31.
- 785 Jouve, S. 2004. Description of the skull of *Ctenochasma* (Pterosauria) from the latest Jurassic
786 of eastern France, with a taxonomic revision of European Tithonian Pterodactyloidea.
787 *Journal of Vertebrate Paleontology* 24:542–554.
- 788 Kaup, S. S. 1834. Versuch einer Eintheilung der Säugethiere in 6 Stämme und der Amphibien
789 in 6 Ordnung. *Isis von Oken* 1834:311–324.
- 790 Kellner, A. W. A. 2003. Pterosaur phylogeny and comments on the evolutionary history of the
791 group. *Geological Society, London, Special Publications* 217:105–137.
- 792 Kellner, A. W. A., X. Wang, H. Tischlinger, D. de A. Campos, D. W. E. Hone, and X. Meng.
793 2010. The soft tissue of *Jeholopterus* (Pterosauria, Anurognathidae, Batrachognathidae)
794 and the structure of the pterosaur wing membrane. *Proceedings of the Royal Society B*
795 277:321–329.
- 796 Kiers, H. 1997. Weighted least squares fitting using ordinary least squares algorithms.
797 *Psychometrika* 62:251–266.
- 798 Klingenberg, C. P. 1996. Multivariate allometry; pp. 23–49 in L. F. Marcus, M. Corti, A. Loy,

-
- 799 G. J. P. Naylor and D. E. Slice (eds.), *Advances in Morphometrics*. Plenum Press, New
800 York.
- 801 Kuhn, O. 1937. *Die fossilen Reptilien*. Gebrüder Borntraeger, Berlin, 121 pp.
- 802 Longrich, N.R., D.M. Martill, and B. Andres. 2018. Late Maastrichtian pterosaurs from North
803 Africa and mass extinction of Pterosauria at the Cretaceous-Paleogene boundary. *PLoS*
804 *Biology* 16:e2001663.
- 805 Lü, J., and D. W. E. Hone. 2012. A new Chinese anurognathid pterosaur and the evolution of
806 pterosaurian tail lengths. *Acta Geologica Sinica* 86:1317–1325.
- 807 Lü, J., and Q. Ji. 2006. Preliminary results of a phylogenetic analysis of the pterosaurs from
808 western Liaoning and surrounding areas. *Journal of the Paleontological Society of*
809 *Korea* 22:239–261.
- 810 Lü, J., D. M. Unwin, X. Jin, Y. Liu, and Q. Ji. 2010. Evidence for modular evolution in a
811 long-tailed pterosaur with a pterodactyloid skull. *Proceedings of the Royal Society B*
812 277:383–389.
- 813 Lü, J., Q. Meng, B. Wang, D. Liu, C. Shen, and Y. Zhang. 2018. Short note on a new
814 anurognathid pterosaur with evidence of perching behaviour from Jianchang of
815 Liaoning Province, China. *Geological Society, London, Special Publications* 455:95–
816 104.
- 817 Lü, J., D. M. Unwin, D. C. Deeming, X. Jin, Y. Liu, and Q. Ji. 2011. An egg-adult association,
818 gender, and reproduction in pterosaurs. *Science* 331:321–324.
- 819 Mayer, F., and O. v. Helversen. 2001. Cryptic diversity in European bats. *Proceedings of the*
820 *Royal Society B* 268:1825–1832.

-
- 821 Naish, D., M. P. Witton, and E. Martin-Silverstone. 2021. Powered flight in hatchling
822 pterosaurs: evidence from wing form and bone strength. *Scientific Reports* 11:1–5.
- 823 Ósi, A. 2011. Feeding-related characters in basal pterosaurs: implications for jaw mechanism,
824 dental function and diet. *Lethaia* 44:136–152.
- 825 Padian, K., and K. I. Warheit. 1989. Morphometrics of the pterosaur wing: one sharp division,
826 few trends. *Journal of Vertebrate Paleontology* 9:35A.
- 827 Plotnick, R. E. 1989. Application of bootstrap methods to reduced major axis line fitting.
828 *Systematic Biology* 38:144–153.
- 829 Schepelmann, K. 1990. Erythropoietic bone marrow in the pigeon: development of its
830 distribution and volume during growth and pneumatization of bones. *Journal of*
831 *Morphology* 203:21–34.
- 832 Shaw, J. B. 2011. Evolution and development of wing form, body size and flight in large-and
833 small-bodied fruit bats (*Artibeus jamaicensis* and *Carollia perspicillata*). Ph.D.
834 dissertation, University of Northern Colorado, Greeley, Colorado, 253 pp.
- 835 Tomkins, J. L., N. R. LeBas, M. P. Witton, D. M. Martill, and S. Humphries. 2010. Positive
836 allometry and the prehistory of sexual selection. *American Naturalist* 176:141–148.
- 837 Unwin, D. M. 2003a. *Eudimorphodon* and the early history of pterosaurs. *Rivista del Museo*
838 *Civico di Scienze Naturali “Enrico Caffi”* 22:39–46.
- 839 Unwin, D. M., 2003b, On the phylogeny and evolutionary history of pterosaurs. *Geological*
840 *Society, London, Special Publications* 217:139–190.
- 841 Unwin, D. M. 2005. *The pterosaurs from deep time*. Pi Press, New York, 347 pp.
- 842 Unwin, D. M., and N. N. Bakhurina. 2000. *Pterosaurs from Russia, Middle Asia and*

-
- 843 Mongolia; pp. 420–433 in M. J. Benton, M.A. Shishkin, D. M. Unwin, and E. N.
844 Kurochkin (eds.), *The age of dinosaurs in Russia and Mongolia*. Cambridge University
845 Press, Cambridge.
- 846 Unwin, D. M., and D. C. Deeming. 2019. Prenatal development in pterosaurs and its
847 implications for their postnatal locomotory ability. *Proceedings of the Royal Society B*
848 286:20190409.
- 849 Unwin, D. M., J. Lü, and N. N. Bakhurina. 2000. On the systematic and stratigraphic
850 significance of pterosaurs from the Lower Cretaceous Yixian Formation (Jehol Group)
851 of Liaoning, China. *Fossil Record* 3:181–206.
- 852 Vidovic, S. U., and D. M. Martill. 2014. *Pterodactylus scolopaciceps* Meyer, 1860
853 (Pterosauria, Pterodactyloidea) from the Upper Jurassic of Bavaria, Germany: the
854 problem of cryptic pterosaur taxa in early ontogeny. *PLoS ONE* 9:e110646.
- 855 Vidovic, S. U., and D. M. Martill. 2018. The taxonomy and phylogeny of *Diopecephalus*
856 *kochi* (Wagner, 1837) and ‘*Germanodactylus rhamphastinus*’ (Wagner, 1851).
857 Geological Society, London, Special Publications 455:125–147.
- 858 Viscardi, P., G. Dyke, M. Wilkinson, and J. Rayner. 1999. Missing data and the phylogeny of
859 the Pterosauria. *Journal of Vertebrate Paleontology* 19:83A.
- 860 Wang, X., A. W. A. Kellner, Z. Zhou, and D. A. Campos. 2005. Pterosaur diversity and faunal
861 turnover in Cretaceous terrestrial ecosystems in China. *Nature* 437:875–879.
- 862 Wang, X., A. W. A. Kellner, Z. Zhou, and D. A. Campos. 2008. Discovery of a rare arboreal
863 forest-dwelling flying reptile (Pterosauria, Pterodactyloidea) from China. *Proceedings*
864 *of the National Academy of Sciences, USA* 105:1983–1987.

-
- 865 Wang, X., Z. Zhou, F. Zhang, and X. Xu. 2002. A nearly completely articulated
866 rhamphorhynchoid pterosaur with exceptionally well-preserved wing membranes and
867 “hairs” from Inner Mongolia, northeast China. *Chinese Science Bulletin* 47:226–230.
- 868 Wang, X., S. Jiang, J. Zhang, X. Cheng, X. Yu, Y. Li, G. Wei, and X. Wang. 2017. New
869 evidence from China for the nature of the pterosaur evolutionary transition. *Scientific*
870 *Reports* 7:42763.
- 871 Warton, D. I., R. A. Duursma, D. S. Falster, and S. Taskinen. 2012. *smatr* 3—an R package for
872 estimation and inference about allometric lines. *Methods in Ecology and Evolution*
873 3:257–259. R package version 3.4-8. Available at [https://cran.r-](https://cran.r-project.org/package=smatr)
874 [project.org/package=smatr](https://cran.r-project.org/package=smatr).
- 875 Wedel, M. J. 2003. The evolution of vertebral pneumaticity in sauropod dinosaurs. *Journal of*
876 *Vertebrate Paleontology* 23:344–357.
- 877 Wei, X., R.V. Pêgas, C. Shen, Y. Guo, W. Ma, D. Sun and X. Zhou. 2021. *Sinomacrops*
878 *bondei*, a new anurognathid pterosaur from the Jurassic of China and comments on the
879 group. *PeerJ* 9:e11161.
- 880 Wellnhofer, P. 1970. Die Pterodactyloidea (Pterosauria) der Oberjura-Plattenkalke
881 Süddeutschlands. Bayerische Akademie der Wissenschaften, Mathematisch-
882 Wissenschaftlichen Klasse, Abhandlungen 141:1–133.
- 883 Wellnhofer, P. 1975. Die Rhamphorhynchoidea (Pterosauria) der Oberjura-Plattenkalke
884 Süddeutschlands. *Palaeontographica A* 148:1–33, 148:132–186, 149:1–30.
- 885 Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size-
886 structured populations. *Annual review of Ecology and Systematics* 15:393–425.

-
- 887 Wickham, H., R. Francois, L. Henry, and K. Müller. 2015. dplyr: a grammar of data
888 manipulation. R package version 0.8.1. Available at [https://cran.r-](https://cran.r-project.org/package=dplyr)
889 [project.org/package=dplyr](https://cran.r-project.org/package=dplyr).
- 890 Witton, M. P. 2008. A new approach to determining pterosaur body mass and its implications
891 for pterosaur flight. *Zitteliana B* 28:143–158.
- 892 Witton, M. P., and M. B. Habib. 2010. On the size and flight diversity of giant pterosaurs, the
893 use of birds as pterosaur analogues and comments on pterosaur flightlessness. *PLoS*
894 *ONE* 5:e13982.
- 895 Xu, X., Z. Zhou, C. Sullivan, Y. Wang, and D. Ren. 2016. An updated review of the Middle-
896 Late Jurassic Yanliao Biota: chronology, taphonomy, paleontology and paleoecology.
897 *Acta Geologica Sinica* 90:2229–2243.
- 898 Yang, Z., B. Jiang, M. E. McNamara, S. L. Kearns, M. Pittman, T. G. Kaye, P. J. Orr, X. Xu,
899 and M. J. Benton. 2019. Pterosaur integumentary structures with complex feather-like
900 branching. *Nature Ecology & Evolution* 3:24–30.
- 901
- 902 Submitted December 21, 2020; revisions received Month DD, YYYY; accepted Month DD,
903 YYYY.

904 FIGURE 1. Allometric growth in anurognathids. **A**, line drawing of a generalized
905 anurognathid showing measured skeletal dimensions and their allometric growth pattern
906 relative to humerus. **B**, allometric growth pattern recovered by PCA. ~~Orange, grey and blue~~
907 ~~colors represent negative allometry, isometry and positive allometry, respectively.~~ Allometric
908 scaling coefficients were indicated next to the corresponding elements. Negative allometry,
909 isometry and positive allometry are indicated by orange, grey and blue, respectively, in the
910 online version of this article. [planned for page width]

911
912 FIGURE 2. Allometric growth of various skeletal dimensions relative to humerus (**A–B** and
913 **D–P**) and to skull width (**C**). ~~Orange, grey and blue trendlines indicate negative allometry,~~
914 ~~isometry and positive allometry, respectively.~~ Both x and y axes were log-transformed and the
915 values were in millimeters, and slope of the thick black lines corresponds to isometry ($b = 1$).
916 Trendlines of negative allometry, isometry and positive allometry are indicated by orange,
917 grey and blue, respectively, in the online version of this article. In **A–C** and **L–M**, the white
918 circles indicate specimens of *Batrachognathus volans*, white triangles indicate the holotype of
919 *Sinomacrops bondei*, and the black squares indicate the other anurognathids. [planned for
920 page width]

921
922 FIGURE 3. Holotype specimen of *Cascocauda rong* (NJU-57003). **A**, overview of the main
923 slab. **B**, line drawing of the holotype with skeletal element identification. Dark grey shading
924 represents partial losses of original bones inferred from remaining impressions. Scale bars
925 equal 10 mm. [planned for page width]

926

927 FIGURE 4. Close-up photographs and line drawings of the skull of holotype specimen of
928 *Cascocauda rong* (NJU-57003). **A–B**, short and broad skull with widely spaced teeth. **C**,
929 close-up on the anterior portion of the skull showing separated naris and antorbital fenestrae.
930 Scale bars equal 5 mm (**A**) and 1 mm (**C**). [planned for page width]

931

932 FIGURE 5. Close-up photographs and line drawings of holotype specimen of *Cascocauda*
933 *rong* (NJU-57003). **A–B**, long, thin teeth with distal curvature. **C–D**, humerus with
934 subtriangular deltopectoral crest and pitted and rough surface at proximal end (shaded area in
935 **D**). **E–F**, unfused scapula and coracoid. Scale bars equal 1 mm (**A**) and 2 mm (**C** and **E**).
936 [planned for page width]

937

938 FIGURE 6. Close-up photographs and line drawings of the holotype specimen of *Cascocauda*
939 *rong* (NJU-57003). **A–B**, completely preserved tail with elongated rod-like structures
940 interpreted as zygapophyses and chevrons. **C**, large curved manual claws. **D**, curved pedal
941 claws (counter slab). **E–F**, pelvic girdle (counter slab) showing a long and slender iliac
942 anterior process and a fan-shaped prepubis, and in articulation with the left femur
943 (impression; original bone preserved on the main slab). **G–H**, ankle region showing unfused
944 tibia and tarsal, metatarsal i–v similar in robustness, and pedal digit V with a long and gently
945 curved phalange 2. Scale bars equal 2 mm (**A**, **C–E**, and **G**) and 1 mm (**B**). [planned for page
946 width]

947

948 FIGURE 7. Single most parsimonious trees recovered from the phylogenetic analysis using
949 ontogenetically corrected codings. [planned for page width]