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

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21 YANG ET AL.—ALLOMETRIC GROWTH OF ANUROGNATHID PTEROSAURS

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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.

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## INTRODUCTION

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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

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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.

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## 93 MATERIALS AND METHODS

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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;

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

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### 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.

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### 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

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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



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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.

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## 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

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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

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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

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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



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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,

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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.

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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

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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).

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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,

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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

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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

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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

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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

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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*,

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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.

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## 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;

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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

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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

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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

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676

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684

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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]