Were early pterosaurs inept terrestrial locomotors?

Mark P Witton

Pterodactyloid pterosaurs are widely interpreted as terrestrially competent, erect-limbed quadrupeds, but the terrestrial capabilities of non-pterodactyloids are thought to have been poor. Common justification for the latter is the absence of a non-pterodactyloid footprint record, suggestions that the expansive uropatagia common to early pterosaurs would restrict hindlimbs in walking or running, and the presence of sprawling forelimbs in some species. Here, these arguments are re-visited and mostly found wanting. Restriction of limb mobility is not a problem faced by extant animals with extensive fight membranes, including species which routinely utilise terrestrial locomotion. The absence of non-pterodactyloid footprints is not necessarily tied to functional or biomechanical constraints. As with other, fully terrestrial clades with poor ichnological records, biases in behaviour, preservation, sampling and interpretation are likely contributing factors to the deficit of early pterosaur ichnites. Suggestions that non-pterodactyloids have slender, mechanically weak limbs are demonstrably countered by the proportionally long and robust limbs of many Triassic and Jurassic species. Details of *Dimorphodon macronyx* and wukongopterid shoulder and forelimb anatomy resemble those of pterodactyloids and suggest fully erect forelimb gaits were possible in these pterosaurs, perhaps indicating proficient terrestriality in at least some non-pterodactyloids. Traditional sprawling models of non-pterodactyloid forelimbs seem appropriate for rhamphorhynchines and campylognathoidids because of their ventrally-restricted glenoid articulations. Antungual sesamoids, which occur in the manus and pes anatomy of many early pterosaur species, may reflect frequent interactions with firm substrates, indicating routine utilisation of terrestrial behaviours in many species. The distribution of characteristics possibly associated with adept terrestriality is complex, but features permitting erect gaits are deeply nested within Pterosauria and not restricted to Pterodactyloidea as previously thought. The 'archetypal' non-pterodactyloid, with sprawling forelimbs and slender hindlimbs, is considered a derived bauplan, with the earliest pterosaurs demonstrating robust, fully erect limbs like their probable ornithodiran ancestors.

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Abstract

Pterodactyloid pterosaurs are widely interpreted as terrestrially competent, erect-limbed quadrupeds, but the terrestrial capabilities of non-pterodactyloids are thought to have been poor. Common justification for the latter is the absence of a non-pterodactyloid footprint record, suggestions that the expansive uropatagia common to early pterosaurs would restrict hindlimbs in walking or running, and the presence of sprawling forelimbs in some species. Here, these arguments are re-visited and mostly found wanting. Restriction of limb mobility is not a problem faced by extant animals with extensive fight membranes, including species which routinely utilise terrestrial locomotion. The absence of non-pterodactyloid footprints is not necessarily tied to functional or biomechanical constraints. As with other, fully terrestrial clades with poor ichnological records, biases in behaviour, preservation, sampling and interpretation are likely contributing factors to the deficit of early pterosaur ichnites. Suggestions that non-pterodactyloids have slender, mechanically weak limbs are demonstrably countered by the proportionally long and robust limbs of many Triassic and Jurassic species. Details of *Dimorphodon macronyx* and wukongopterid shoulder and forelimb anatomy resemble those of pterodactyloids and suggest fully erect forelimb gaits were possible in these pterosaurs, perhaps indicating proficient terrestriality in at least some non-pterodactyloids. Traditional sprawling models of non-pterodactyloid forelimbs seem appropriate for rhamphorhynchines and campylognathoidids because of their ventrally-restricted glenoid articulations. Antungual sesamoids, which occur in the manus and pes anatomy of many early pterosaur species, may reflect frequent interactions with firm substrates, indicating routine utilisation of terrestrial behaviours in many species. The distribution of characteristics possibly associated with adept terrestriality is complex, but features permitting erect gaits are deeply nested within Pterosauria and not restricted to Pterodactyloidea as previously thought. The 'archetypal' non-pterodactyloid, with sprawling forelimbs and slender hindlimbs, is considered a

32 derived bauplan, with the earliest pterosaurs demonstrating robust, fully erect limbs like their probable

33 ornithodiran ancestors.

34

Introduction

36 The terrestrial competency of pterosaurs was keenly debated during the 1980s and 1990s, when the

37 utility of bipedal and quadrupedal gaits, orientation and posture of the extremities, as well as overall

38 terrestriality were discussed at length (Fig. 1, Padian 1983a, b; Padian and Olsen 1984; Wellnhofer

39 1988; Unwin 1988, 1989, 1996a, 1999; Lockley et al. 1995; Bennett 1997a; Clark et al. 1998; see

40 Witton 2013 for a recent overview). A consensus emerged when trackways first identified by Stokes

41 (1957) as pterosaurian, but considered crocodyliform by Padian and Olsen (1984) and Unwin (1989),

42 were convincingly demonstrated as being made by pterodactyloid pterosaurs (Lockley et al. 1995;

43 Unwin 1996a, 1999). This reappraisal made a compelling case for pterodactyloids as erect, terrestrially

44 competent quadrupeds with plantigrade feet, a hypothesis since strengthened not only by more

45 trackway discoveries (e.g. Mazin *et al*. 1995, 2003; Lockley and Wright 2003; Hwang et al. 2002;

46 Padian 2003; Lockley et al. 2008) but also functional analyses of pterosaur anatomy (e.g. Bennett

47 1997a; Clark et al. 1998; Sangster 2000; Wilkinson 2008; Witton and Naish 2008; Fujiwara and

48 Hutchinson 2012; Costa et al. 2013; Hyder et al. 2014).

49

50 It seems that the basic tenets of pterodactyloid terrestrial locomotion are understood, but the same

51 cannot be said for non-pterodactyloids. Research into the terrestrial capacity of early pterosaurs is

52 entirely based on interpretations of their functional anatomy because their trackways remain elusive

53 (Unwin 2005; Lockley et al. 2008). Such considerations are relatively few in number and have reached

54 varying conclusions, either arguing for non-pterodactyloids as terrestrially competent, digitigrade

55 bipeds (Fig. 1a; Padian 1983a, b, 1985); slow, sprawling animals ill-suited to movement on the ground,

56 but possibly adept climbers (Unwin 1987, 1988, 1989, 1999; 2005; Unwin and Bakhurina 1994); or

57 arboreal animals with erect hindlimbs capable of powerful leaping (Bennett 1997b). Support for

58 pterosaur bipedality has not been widespread since the 1980s (but see Bennett 2001; Padian 2003;

59 2008a, b, c) because a suite of evidence suggests their bauplan was ill-suited to bipedal gaits or pedal

60 digitigrady (see Wellnhofer 1988; Bennett 1997b; Clark et al. 1998; Sangster 2000; Fastnacht 2005;

61 Wilkinson 2008; Costa et al. 2013) and a wealth of new trackway data shows routine employment of

62 quadrupedal gaits (e.g. Mazin *et al*. 1995, 2003; Lockley and Wright 2003; Hwang et al. 2002; Padian

63 2003; Lockley et al. 2008). The view of non-pterodactyloids as relatively ineffective terrestrial

64 quadrupeds has since been largely accepted (e.g. Unwin 2005; Ősi 2010; Butler et al. 2013; Benson et

65 al. 2014).

66

67 The concept of grounded non-pterodactyloids as poor terrestrial locomotors relies on three oft-repeated

68 hypotheses. The first concerns the expansive uropatagium which extended between the hindlimbs of

69 non-pterodactyloids, supported distally by long fifth pedal digits (Fig. 2; Sharov 1971; Unwin and

70 Bakhurina 1994; Wild 1994; Kellner et al. 2009). This is reasoned to have restricted independent

71 hindlimb motion and stride length, limited speed and agility, and hindered movement through complex,

72 vegetated environments (e.g. Unwin 1988, 1999; 2005; Ősi 2011). The reduction of fifth toe length in

73 pterodactyloids is interpreted as signifying the loss or reduction of this membrane, as evidenced by a

74 pterodactyloid specimen with reduced hindlimb membranes lacking medial contact (Wellnhofer 1987).

75 This 'decoupling' of the hindlimbs from one another is thought to have permitted longer strides and

76 more effective, faster terrestrial locomotion in pterodactyloids, explaining their relative success in

77 inland settings over their ancestors (e.g. Unwin 1988, 1999, 2005; Ősi 2011).

78

79 The absence of pterosaur trackways from Triassic to Middle Jurassic rocks is a second piece of

80 evidence cited for non-pterodactyloid terrestrial incompetency. The pterosaur body fossil record begins

81 in at least the Norian but, to date, no definitively identified pterosaur trackways occur in rocks pre-

82 dating the Middle-Late Jurassic boundary (Lockley et al. 2008). This coincides with the oldest

83 evidence of pterodactyloids (Andres et al. 2014) and an apparent radiation of 'terrestrialised'

84 pterosaurs, it being assumed that pterodactyloid anatomical nuances allowed exploitation of settings

85 such as tidal flats and lake margins, and creation of a track record (Unwin 2005; Butler et al. 2012;

86 Benson et al. 2014). Non-pterodactyloids, by contrast, are assumed so poorly adapted for walking and

87 running that they scarcely used such forms of locomotion, and thus rarely left footprints (Unwin 2005).

88

89 Both of these concepts are in keeping with a third hypothesis, that non-pterodactyloids had sprawling

90 forelimbs, and perhaps hindlimbs as well (Wellnhofer 1975; Unwin 1988, 1999, 2005; Padian 2008b).

91 It has been argued that these would limit quadrupedal walking speeds and force reliance on other forms

92 of locomotion – bipedal running or flight – to move rapidly (Unwin 1988, 1999, 2005; Padian 2008b).

93 Although some have argued for the hindlimbs of early pterosaurs having both an upright posture and

94 being powerfully muscled (e.g. Padian 1983a, b, 2008b; Bennett 1997b), these observations have

95 largely been ignored in considerations of non-pterodactyloid terrestrial locomotion. Instead, the idea

96 that early pterosaurs were inept terrestrial animals has been presented as an important part of the broad

97 picture of pterosaur evolutionary history, and said to explain patterns within the pterosaur fossil record

98 (Unwin 1999, 2005; Butler et al. 2012; Benson et al. 2014).

99

100 The establishment of these concepts occurs in spite of the low number of dedicated assessments into

101 non-pterodactyloid locomotion. There have been considerably fewer studies into non-pterodactyloid

102 functionality than there are for pterodactyloids, and particularly so in recent years. This probably

103 reflects the larger amount of material available for studies into pterodactyloid mechanics: along with

104 footprints and tracks, many pterodactyloids are known from three-dimensional material which lends

105 itself better to functional studies than the mostly flattened and fragmentary remains forming the non-

106 pterodactyloid record. Nevertheless, some non-pterodactyloid anatomies are well enough known to

107 permit evaluation of arguments suggesting poor terrestriality in these early forms. This is attempted

108 here, with the three principle hypotheses underlying most assessments of non-pterodactyloid

109 terrestriality being considered:

110

111   1. Did the large uropatagium of non-pterodactyloids restrict hindlimb function during terrestrial

112   locomotion?

113   2. Is the absence of non-pterodactyloids trackways related to their terrestrial capabilities?

114   3. Were the limbs of non-pterodactyloids sprawled during terrestrial locomotion?

115

116 *Institutional abbreviations*

117 BSP, Bayerische Staatssammlung für Paläontologie und Geologie, Berlin, Germany; HGM, Henan

118 Geological Museum, Zhengzhou, China; GPIT, Geologisch-Paläontologisches Institut und Museum,

119 Universität Tübingen, Germany; GSM, Geological Survey Museum, Keyworth; UK; IVPP, Institute of

120 Vertebrate Palaeontology and Palaeoanthropology, Beijing, China; JPM, Jehol Paleontological

121 Museum, Chengde, China; MCSNB, Museum Civico di Scienze Naturali di Bergamo, Italy; MFSN.

122 Museo Friulano di Storia Naturale, Udine, Italy; MJML, Museum of Jurassic Marine Life,

123 Kimmeridge, UK; MPUM, Museo Paleontologia Universitá di Milano, Italy; NHMUK, Natural

124 History Museum, London, UK; PIN, Paleontological Institute, Moscow, Russia; SMNS, Staatliches

125 Museum für Naturkunde Stuttgart, Germany.

126

Materials and Methods

128 *Systematic declaration*

129 Pterosaur systematics, and particularly those of early taxa, are currently highly controversial. With so

130 little agreement on multiple aspects of early pterosaur phylogeny including clade content, group

131 definitions, and appropriate nomenclature (e.g. Unwin 2003; Kellner 2003; Wang et al. 2009; Kellner

132 2010; Dalla Vecchia 2009; Lü et al. 2010, 2012; Witton 2013; Andres and Meyers 2013; Andres et al.

133 2014), accurate discussion of pterosaur systematics requires regular citation of the specific taxonomy

134 being followed (e.g. Andres and Meyers 2013) or frequent mentions of conflicting phylogenies (e.g.

135 Witton 2013). Neither approach is practical or makes for compelling reading. Thus, unless otherwise

136 stated, this paper uses the nomenclature and taxonomy of the non-pterodactyloid phylogeny of Lü et al.

137 (2012). Dalla Vecchia (2009), Wang et al. (2010) and Andres and Meyers (2013) offer alternative

138 contemporary schemes.

139

140 *Material*

141 A number of specimens inform the discussion provided here, but key material includes three-

142 dimensionally preserved remains of *Dimorphodon macronyx*, a well-known Sinemurian, Liassic non-

143 pterodactyloid from Dorset, UK. Observations were chiefly made on the holotype NHMUK R1034, a

144 partial skeleton, and the near complete skeleton NHMUK 41412-13. Both specimens, although

145 partially embedded in matrix, are largely three dimensionally preserved and sufficiently prepared to

146 appreciate most aspects of pectoral girdle and limb anatomy, especially when viewed in concert with

147 other, less complete *Dimorphodon* material in the Natural History Museum, London. Additional study

148 was made on a near-complete three-dimensional rhamphorhynchine scapulocoracoid from the

149 Callovian-Oxfordian Oxford Clay, UK, NHMUK R5672. Wellnhofer (1975) referred this specimen to

150 *Rhamphorhynchus* sp., but diagnostic characters for this genus are presently only known in the skull

151 anatomy and limb proportions of this genus (Bennett 1995). While undoubtedly *Rhamphorhynchus*-

152 like, NHMUK R5672 is conservatively considered an indeterminate rhamphorhynchine here, echoing

153 taxonomic suggestions by Unwin (1996b).

154

Results

155

156   *1. Did the large uropatagium of non-pterodactyloids restrict hindlimb function during terrestrial*
157   *locomotion?*

158 The inference that relatively large uropatagia impeded early pterosaur terrestrial habits has received no
159 detailed evaluation, despite its confident presentation in some literature ("There can be no doubt that
160 this shackling of the limbs must have hindered pterosaurs as they sought to move around on the
161 ground" – Unwin 2005, p. 204). It might be presumed that attributes of fossil pterosaur soft-tissues or
162 observations on modern animals with similar membrane structures support assertions of hindlimb-
163 restricting uropatagia in early pterosaurs, but it is only the relatively large size of the membrane which
164 is cited in favour of this idea (e.g. Unwin and Bakhurina 1994; Unwin 2005). While it is difficult to
165 evaluate the effects of soft-tissues on non-pterodactyloid hindlimb kinematics in the absence of
166 footprints, evidence from pterosaur body fossils, and the anatomy and behaviour of modern animals,
167 conflict with proposals that expansive uropatagia impeded early pterosaur terrestriality.

168

169 Many gliding and flying mammals possess large, hindlimb-spanning uropatagia comparable to those of
170 non-pterodactyloids (Fig. 2). A number of these species are terrestrially proficient (e.g. Sollberger
171 1940; Nowark 1994; Stafford et al. 2003; Riskin et al. 2006; Meijaard et al. 2006), some spending
172 considerable amounts of time on the ground in pursuit of food or refuge using fast, complex and
173 sometimes strenuous behaviours (Sollberger 1940; Daniel 1976; Nowark 1994; Pyare and Longland
174 2002; Riskin et al. 2006). These animals are not confined to predator-free environments or the result of
175 reduced competition from other terrestrial creatures, instead living in complex, predator-filled habitats
176 and persisting for many millions of years in some regions (Hand et al. 2009). Examples include the
177 New Zealand lesser short-tailed bat, *Mystacina tuberculata*, which is reported as having 'rodent-like
178 agility on the ground and on trunks, branches, and kiekie vines' by Daniel (1976; p. 397). Common
179 vampires, *Desmodus rotundus*, rely on their terrestrial skills to stealthily stalk hosts or quickly evade
180 danger using forelimb-propelled galloping (Nowark 1994; Riskin and Hermanson 2005; Riskin et al.
181 2006). Flying squirrels, such as *Glaucomys* species, forage on the ground, are capable of running, and
182 have membranes resilient to frequent digging for fungal food sources (Sollberger 1940). Similarly,
183 membranes of *Mystacina* bats withstand crevice-crawling as well as digging (Daniel 1979). Clearly,
184 the grounded activities of these animals are not impeded by their patagia, nor do their membranes snag
185 on obstacles or become easily damaged. Presumably, membrane elasticity plays a role in reducing

186 impedance to terrestrial activity, both allowing the limbs to move freely as well as drawing the

187 membranes close to the body to prevent interference with the environment or limb motion. The extent

188 of such membrane shrinkage can be extreme, rendering them almost indiscernible in some

189 circumstances (Meijaard et al. 2006). Critically, while some membrane-bound modern species are poor

190 terrestrial locomotors, this behaviour is not linked to membrane distribution but instead to aspects of

191 skeletal morphology, limb strength or myology (Riskin et al. 2005).

192

193 Certain bats and flying squirrels show that large uropatagia do not rule out terrestrial potential in volant

194 mammals, but are they suitable models for pterosaurs? Fossils of pterosaur wing membranes show

195 some similarities to those of modern volant mammals in that they were likely elastic in their proximal

196 regions. Pterosaur brachiopatagia are stiffened by structural fibres distally, but other membrane

197 components – including the uropatagium – lack rigid structural fibres and are widely considered to

198 have been compliant (e.g. Unwin and Bakhurina 1994; Bennett 2000; Frey et al. 2003). Unwin and

199 Bakhurina (1994), describing the uropatagium of *Sordes pilosus*, commented specifically on this,

200 stating "…adjacent to the body the [structural] fibres are shorter, more sinuous and loosely packed,

201 indicating that the propatagium, uropatagium and proximal regions of the cheiropatagium were

202 somewhat softer and more elastic" (p. 64). It can be expected that pterosaur membranes would contract

203 significantly when the limbs were not extended to flight position, as occurs in many volant mammals,

204 clearing them of obstacles and permitting stretching of the membranes during walking or running.

205 Some evidence for this contraction may be seen in pterosaur fossils with preserved membranes (Elgin

206 and Hone 2011). Trackways made by running pterodactyloids indirectly demonstrate how elastic their

207 proximal membranes must have been, allowing track makers to take strides of considerable magnitude

208 (Mazin et al. 2003) despite membranes stretching from the distal hindlimb to their hands (Elgin and

209 Hone 2011). The expansion and contraction of brachiopatagia in running pterodactyloids was probably

210 no greater than that experienced by the uropatagia of non-pterodactyloids.

211

212 Even if the hindlimb strides of non-pterodactyloids were restricted by membranes, pterosaurs were

213 likely capable of circumventing this issue by using asymmetrical, bounding gaits (Witton and Habib

214 2010; Witton 2013; Hyder et al. 2014). Indeed, both the fore- and hindlimbs of pterosaurs have been

215 noted for their strength and leaping potential (Padian 1983a, Bennett 1997b; Habib 2008; Witton and

216 Habib 2010), and there are obvious parallels between forelimb-dominated *Desmodus* galloping and

217 recent, compelling hypotheses concerning forelimb use in pterosaur launch (Habib 2008). Pterosaurian

218 bounding locomotion may be countered by exclusive trackway evidence for symmetrical gaits in

219 pterodactyloids (e.g. Stokes 1957; Mazin *et al*. 1995, 2003; Lockley and Wright 2003; Hwang et al.

220 2002), but it remains unclear if these gaits were employed by all pterosaurs, all the time, nor is it clear

221 if interpretations of these tracks are applicable to non-pterodactyloids. Bounding gaits are at least

222 tenable from a functional and biomechanical perspective.

223

224 In light of these observations, the proposal that early pterosaurs were terrestrially hindered by their

225 membranes is peculiar. It relies on the uncertain assumption that the uropatagium was especially

226 restrictive compared to other pterosaur wing membranes and behavioural restrictions – membranes

227 snagging on obstacles and limiting stride length – which have no precedent among modern pterosaur

228 analogues. Clear evidence demonstrating broad uropatagia were barriers to early pterosaur terrestriality

229 has yet to be presented, whereas what we know of pterosaur soft-tissues and modern animal functional

230 anatomy indicates their membranes likely had little, if any, impact on their terrestrial potential.

231

232   *2. Is the absence of non-pterodactyloids trackways related to terrestrial capabilities?*

233 The view that a lack of early pterosaur trackways must equate to their terrestrial ineptitude (e.g. Unwin

234 2005; Butler et al. 2013) relies on a very literal interpretation of the pterosaur fossil record and an

235 assumption that we can distinguish genuine absences of fossil phenomena from biases affecting fossil

236 datasets. There are reasons to consider both these assertions uncertain.

237

238 The non-pterodactyloid body fossil record is not only poorer than that of pterodactyloids, but also

239 many contemporary terrestrial tetrapod groups (e.g. Benton and Spencer 1995; Kielan-Jaworowska et

240 al. 2004). It is particularly impoverished in terrestrial basins (Butler et al. 2013). This is thought to

241 reflect the general lack of inland or near-shore pterosaur-bearing Lagerstätten before the Late Jurassic,

242 the small body sizes and low preservation potential of early pterosaurs, possibly restricted distribution

243 of the group in its early history, or perhaps existence of the first pterosaurs in habitats unconducive to

244 fossilisation and sediment accumulation - inland forests or upland environments (Bennett 1997b;

245 Unwin 2005; Witton 2013; Butler et al. 2013). Regardless of the cause, recent studies have concluded

246 that recorded patterns of Triassic and Jurassic pterosaur diversity – the interval dominated by non-

247 pterodactyloids – have little statistical significance (e.g. Butler et al. 2013; Upchurch et al. 2014), and

248   that our understanding of early pterosaur history remains generally poor. This is difficult to reconcile

249   with suggestions that the lack of an early pterosaur track record is somehow significant. If

250   understanding of the early pterosaur record is demonstrably limited, how can any apparent trends or

251   patterns in that data be confidently interpreted, and especially those reliant on an absence of data?

252

253   It seems unwise to link the absence of a track record to a very specific cause, such as functional

254   anatomy (and especially so given the lack of detailed research into early pterosaur terrestriality) when

255   there are a number of reasons why non-pterodactyloids may not have an ichnological record. If non-

256   pterodactyloids were genuinely rare in terrestrial basins – as their record currently suggests - their

257   likelihood of creating traces must also be low. Likewise, it seems most early pterosaurs were small,

258   with wingspans of 1-2 m (O'Sullivan et al. 2013) and corresponding masses of 0.55-3.26 kg (using

259   data from Witton 2008). Their footprints would thus be small and shallow, without substantial

260   underprinting, and require exceptional conditions for impression, fossilisation and discovery. In

261   contrast, pterodactyloids are generally larger bodied than early pterosaurs (Hone and Benton 2007;

262   Benson et al. 2014), which may constitute creation of deeper, longer-lasting tracks which are better

263   suited to fossilisation and detection. A related problem concerns our ability to distinguish the footprints

264   of pterodactyloids from those expected of non-pterodactyloids (Lockley et al. 2008): all pterosaurs

265   have the same basic manus and pes structure, the only exception being the longer fifth toe in non-

266   pterodactyloids. Given the role of this structure in supporting the uropatagium, it may have been held

267   aloft when walking (Lockley et al. 2008). If so, the tracks of all pterosaurs might look similar, and

268   some alleged upper Jurassic pterodactyloid ichnites may be misidentified.

269

270   It should also not be assumed that early pterosaurs and pterodactyloids occupied ecologies with similar

271   track-making potential. The start of the pterosaur footprint record in the Middle-Late Jurassic roughly

272   corresponds with the emergence of pterodactyloid clades predicted to be waders, suspension-feeders

273   and molluscivores (ctenochasmatoid and dsungaripterids - Unwin 2005; Witton 2013). Such animals

274   are expected to routinely patrol lake margins and other habitats suitable to footprint preservation.

275   Lockley et al. (2003, 2008) note that pterodactyloid tracks are frequently associated with invertebrate

276   traces and occasional feeding marks, which may indicate foraging was a common factor in pterosaur

277   ichnite creation, inferring ecological factors may be related to the delayed start of the pterosaur

278   ichnological record. By contrast, non-pterodactyloids are largely perceived as pelagic piscivores or

279 insectivores (Wellnhofer 1975; Wild 1978; Chatterjee and Templin 2004; Ősi 2010; Witton 2008,

280 2013), neither of which are habits lending themselves to sustained terrestrial activity on mudflats,

281 water margins or other settings liable to preserving footprints.

282

283 Perhaps most importantly, early pterosaurs are not alone in having a very sparse track record. The

284 tracks and traces of many fully terrestrial Mesozoic clades are surprisingly poorly known – examples

285 include geographically widespread, long-lived lineages with good body fossil records, such as

286 Mesozoic Mammaliaformes, tyrannosaurids and ceratopsids (Lockley and Hunt 1995; Kielan-

287 Jaworowska et al. 2004; McCrea et al. 2014). Not only are the ichnological records of these groups

288 poor – restricted to single localities in some cases – but many ichnites referred to them are

289 controversially identified (Kielan-Jaworowska et al. 2004; McCrea et al. 2014). This occurs despite

290 these animals seemingly being abundant (as evidenced by their good body fossil records) and fully

291 terrestrial in their habits, thus potentially creating tracks in virtually all of their daily activities (unlike

292 pterosaurs, which, in being volant, avoided track creation much of the time). In contrast to perceptions

293 of the pterosaur track record however, the sparse trackways of Mesozoic Mammaliaformes or certain

294 dinosaur clades are not interpreted as signs terrestrial ineptitude, but as biases of behaviour, ecology,

295 preservation, sampling or interpretation.

296

297 Ultimately, while the absence of early pterosaur footprints is an intriguing phenomenon of the

298 pterosaur record, and one with possible implications for the development of terrestriality in Pterosauria,

299 its significance cannot be divorced from a number of factors unrelated to functional morphology. As

300 with any case supported by negative evidence, data deficits can only be interpreted so far, especially

301 when related datasets are demonstrably poor. Considering the absence of early pterosaur tracks as

302 significant requires ignorance of not only statistics on the quality of the pterosaur fossil record, but also

303 data concerning early pterosaur palaeobiology and the broader ichnological record. Other sources of

304 evidence should be pursued for more reliable insights into the development of pterosaur terrestriality.

305

306   *3. Were the limbs of non-pterodactyloids sprawled during terrestrial locomotion?*

307 Some degree of postural sprawl has been proposed for grounded non-pterodactyloids from assessments

308 of their limb joint arthrology (e.g. Wellnhofer 1975; Unwin 1988, 1999; 2005; Padian 2008b). It has

309 occasionally been suggested that both limbsets were constrained to sprawling locomotion (Unwin

310   1988, 1999, 2005). Unwin (1988) argued that the *Dimorphodon* femoral-pelvic joint projected the

311   femur anterolaterally and somewhat dorsally when 'naturally articulated', while the tibiotarsus was

312   capable of twisting medially at the knee, permitting the foot to face forwards. This is said to allow for

313   semi-erect or sprawling gaits, which are in accordance with suggested similarities between the pelves

314   of *Dimorphodon* and the sprawling or semi-erect archosauriform *Euparkeria capensis* (Unwin 1988).

315   Computer modelling has also predicted sprawling, ambulatory gaits for non-pterodactyloids using a

316   digital model of *Rhamphorhynchus* (Fig. 1B; Unwin 2005). The methodology behind this has not been

317   presented, but the resultant digital non-pterodactyloid model 'Roborhamphus' shows hindlimbs

318   projecting entirely laterally from the body, similarly-sprawling forelimbs, low clearance from the

319   ground and slow walking speeds (Unwin 2005). The latter is seemingly a consequence of the limited

320   reach afforded by the sprawling limbs.

321

322   There are several reasons to think that the non-pterodactyloid hindlimb did not sprawl. Firstly, the

323   assumption that a 'natural articulation' of the hindlimb can be determined (Unwin 1988) is

324   problematic. As evidenced by debates over 'osteological neutral pose' in fossil animal necks (e.g.

325   Stevens and Parrish 1999, Taylor et al. 2009; Taylor and Wedel 2013; Stevens 2013), attempts to

326   determine 'neutral' or 'natural' poses of animal joints rely on arbitrary assignments of optimal joint

327   configurations which often have little or no significance to typical animal postures (Taylor et al. 2009).

328   It is probably unwise to suggest the hindlimb of *Dimorphodon* sprawled based on acetabulum and

329   femoral head morphology alone.

330

331   Secondly, the pelvis of *Dimorphodon* and other early pterosaurs are clearly distinguished from those of

332   *Euparkeria* and other sprawling animals in having a well-developed preacetabular process (Unwin

333   1988; Hyder et al. 2014). In this respect, non-pterodactyloid pelves resemble those of other

334   ornithodirans – including pterodactyloids - and mammals. These taxa are characterised by erect limbs,

335   the preacetabular process anchoring large hip flexors for moving the hindlimb forward in the

336   parasagittal plane (Hyder et al. 2014). Biomechanical studies confirm that the pterosaur pelvic and

337   femoral musculoskeletal system is optimally configured for an erect gait (Fastnacht 2006; Costa et al.

338   2013). Furthermore, while arguments for bipedal, pronograde pterosaurs with parasagittal hindlimbs

339   and digitigrade pedes (Padian 1983a, 1985) have been largely deconstructed in recent years (e.g.

340   Wellnhofer 1988; Bennett 1997a; Clark et al. 1998; Fastnacht 2005), observations that their hip, knee

341 and ankle articulations have hallmarks of upright limb functionality remain valid (Bennett 1997b;
342 Fastnacht 2005; Costa et al. 2013).

343

344 Thirdly, virtually all recent models of pterosaur evolution suggest taxa with erect hindlimbs bracket
345 non-pterodactyloids, with *Scleromochlus taylori* and non-pterosaurian ornithodirans on one side, and
346 pterodactyloids the other (Sereno 1991; Benton 1999, Hone and Benton 2008; Nesbitt 2011; but also
347 see Bennett 2013). This implicates erect hindlimb postures as ancestral for Pterosauria and, given the
348 similarity of their pelvic and hindlimb osteology to their nearest probable relatives, there is little reason
349 to assume non-pterodactyloids deviated from this ancestral state (Bennett 1996b; Hyder et al. 2014).
350 Multiple lines of evidence indicate upright hindlimb postures across Pterosauria, including all known
351 non-pterodactyloids.

352

353 Relatively little has been said on the stature of non-pterodactyloid forelimbs. Traditionally, they have
354 been reconstructed as sprawling. Wellnhofer (1975) observed that the glenoid of *Rhamphorhynchus*
355 *muensteri* projected laterally and permitted anterodorsal and posteroventral motion of the humerus, but
356 that anterior and posterior motion was limited, and that the humerus could not be adducted below the
357 level of the scapula. Padian (1983a) suggested that the glenoid of *Dimorphodon* permitted a 90° arc of
358 rotation, most of it dorsal to the glenoid, also suggested the shoulder joint of *Dorygnathus* permitted
359 little movement below the frontal plane (Fig. 1C; Padian 2008b). This is said to limit *Dorygnathus* to a
360 sprawling forelimb gait during quadrupedal locomotion which could not match pace with the erect
361 hindlimbs during running, for which bipedal gaits were employed (Padian 2008b). Unwin (2005)
362 showed the digital 'Roborhamphus' forelimbs in a sprawling fashion somewhat consistent with these
363 models (Fig. 1B).

364

365 Notions that non-pterodactyloid forelimbs were confined to sprawling gaits by their glenoids are
366 largely based on the pectoral girdles of rhamphorhynchine pterosaurs (e.g. Wellnhofer 1975; Padian
367 2008b). The glenoids of these animals are typified by the isolated scapulocoracoid of an Oxford Clay
368 rhamphorhynchine, NHMUK R5672 (Fig. 3D-G, I). Here, the glenoid is a laterally prominent structure
369 with a long axis aligned with the base of the scapula. The anterior and posterior ends are bordered by a
370 prominent lower tubercle and supraglenoidal buttress, respectively, between which occurs a deeply-
371 curved, saddle-shaped articular surface. This wraps almost 90° from the lateral face to the dorsal,

372 suggesting ample humeral motion lateral and dorsal to the glenoid. The articular face is

373 anteroposteriorly broadest in its dorsal region and most constrained laterally. The ventral extent of the

374 glenoid is marked by a laterally-projecting ridge between the posterior buttress and anterior tubercle.

375 This ridge is continuous with the lower extent of the scapula, supraglenoidal buttress and lower

376 tubercle so that the ventral face of the glenoid is a wide, flat surface instead of a saddle shaped-joint

377 like that of the dorsal region. As noted by previous authors (Wellnhofer 1975; Padian 2008b), such

378 glenoids clearly did not permit humeral adduction below the level of the scapula, and it also seems

379 fore- and aft-motion of the humerus was limited at maximal adduction. Humeral motion was likely less

380 constrained dorsally, however. Given their marked dorsoventral asymmetry, these glenoids are

381 hereafter referred to as 'asymmetric'.

382

383 A survey of non-pterodactyloid remains suggests asymmetric glenoids occur in a number of taxa,

384 including the Jurassic rhamphorhynchines *Rhamphorhynchus muensteri* (see numerous examples in

385 Wellnhofer 1975), *Dorygnathus banthensis* (see GPIT 1645/1, Padian 2008b), *Sericipterus*

386 *wucaiwanensis* (IVPP V14725, Andres et al. 2010) and the Kimmeridge Clay rhamphorhynchine

387 MJML-K1597 (O'Sullivan, pers. comm. 2014). They thus appear to be typical for rhamphorhynchines,

388 and further occurrences may occur within Campylognathoididae, including the Triassic

389 *Eudimorphodon ranzii* (MCSNB 2888, Wild 1978), and Jurassic *Campylognathoides liasicus* (SMNS

390 11879, Padian 2008c). Asymmetric glenoids may be more widely spread across non-pterodactyloids

391 than this, but establishing their frequency is complicated by not only a deficit of good preservation, but

392 also the requirement for particular scapulocoracoid orientations in flattened specimens. Accordingly,

393 the shape of the glenoid cannot be established for many taxa which may otherwise be considered well-

394 known, such as the Anurognathidae.

395

396 Asymmetric glenoids are not the only shoulder morph of non-pterodactyloids. The well-preserved

397 glenoids on *Dimorphodon macronyx* specimens NHMUK R1034 and 41412-13 are rather differently

398 constructed (Fig. 3A-C, H). Although following the same basic configuration as other non-

399 pterodactyloids, these specimens have a larger supraglenoidal buttress which projects further ventrally

400 than the lower tubercle. The dorsal portion of the glenoid articular face is similar to that described

401 above, but the ventral portion wraps onto the underside of the glenoid until it meets the scapula shaft,

402 instead of terminating at an elevated scapular margin. This gives the glenoid a spool- or hourglass-like

403 appearance in lateral view, and presents no obvious restriction to adducting the humerus to a vertical

404 position. As with the rest of the glenoid, the ventral articular region is widely open anteroposteriorly

405 (although not as much as the dorsal region) and is estimated to permit 90° of anteroposterior humeral

406 rotation beneath the body. This observation contrasts with previous assessments of *Dimorphodon*

407 glenoid morphology, which suggested anatomy and arthrological range akin to the 'asymmetric' morph

408 outlined above (Padian 1983b). As demonstrated in Fig. 3H-I, the ventral morphologies and likely

409 functionality of these glenoids are quite distinct. *Dimorphodon*-like glenoids are hereafter referred to as

410 'symmetric', after their relatively similar dorsal and ventral articular surfaces. It seems such glenoids

411 were rare in non-pterodactyloids: other than *Dimorphodon*, only the wukongopterids *Darwinopterus*

412 *linglongtaensis* (IVPP V16049, Wang et al. 2010) and *Darwinopterus robustodens* (HGM 41HIIII-

413 0309A; Lü et al. 2011) seem to possess them, although the caveats mentioned above mean this

414 assessment should not be considered definitive. It is notable that some aspects of pterodactyloid

415 glenoids are similar to this 'symmetric' condition, including the relatively large supraglenoidal

416 buttress, expansive articular face, and absence of an arthrologically prohibitive ventral margin.

417

418 The two non-pterodactyloid glenoid morphologies identified here have different implications for

419 adoption of sprawling or erect postures. Asymmetric glenoids seem to obligate forelimb sprawling,

420 whereas symmetric glenoids could permit either sprawling or upright limb usage. As noted above,

421 relying on a single joint for insight into animal postures can be misleading, and using only glenoid

422 shape to infer erect forelimb postures in some non-pterodactyloids may be unwise. Additional insights

423 on the gaits in these animals are afforded by aspects of their distal humeri, however. The morphology

424 of distal humeri are characteristic of sprawling and erect limb carriage in extant quadrupeds (Fujiwara

425 and Hutchinson 2012), allowing the potential for erect forelimbs in early pterosaurs to be identified by

426 these elements. Fujiwara and Hutchinson (2012) noted that the size of osteological correlates of wrist

427 flexor and extensor muscles, as well as those of elbow extensors, provide insights into mechanical

428 loads placed on the distal humerus and, therefore, predominant forelimb postures. This method,

429 grounded and tested in a biometric dataset of 318 living taxa, is useful for fossil species where

430 interpreting limb posture based on arthrology alone can be controversial. Applying this technique to a

431 pterodactyloid (*Anhanguera piscator*) humerus suggested it met expectations of animals using an

432 upright posture (Fujiwara and Hutchinson 2012), agreeing with other predictions made from limb bone

433 arthrology and trackway data concerning erect forelimb use in pterodactyloids (e.g. Unwin 1996a;

434   Bennett 1997a; Mazin et al. 2003; Fujiwara and Hutchinson 2012). Fujiwara and Hutchinson (2012)

435   note that their conclusions likely apply to other pterodactyloids, implying that morphological similarity

436   to *Anhanguera* distal humeri (which are broadly similar to those of other pterodactyloids, even

437   accounting for body size, Fig. 4 G-F) in any pterosaurs might suggest similar forelimb use and

438   carriage.

439

440   A survey of non-pterodactyloid humeri shows variation in their distal ends that correlate with

441   distinctions in their glenoid shape (Fig. 4). The distal humeri of pterosaurs with asymmetric glenoids

442   possess markedly reduced medial and lateral epicondyles so that, in anterior view, their distal humeri

443   show relatively little expansion from the diaphyseal shafts. For this reason, the palmar aspect of their

444   distal humeri are dominated by the capitula and trochlea (Fig. 4 D-F). This is seen in at least

445   *Rhamphorhynchus* (Wellnhofer 1975) and *Dorygnathus* (SMNS 51827, SMNS 50164, see Padian

446   2008b), and perhaps also *Eudimorphodon* and *Campylognathoides*, although the flattened, often

447   oblique preservation of humeri in specimens of the latter species prohibits full confidence in this

448   observation (Wild 1978; Padian 2008c). The lack of well-developed lateral and medial epicondyles in

449   these humeri contrasts with the pterodactyloid condition, in which these structures are prominent and

450   the distal humeri are expanded (Fig. 4 G-F). However, the distal humeri of *Dimorphodon* (NHMUK

451   42016, YPM 350) and the probable wukongopterid *Archaeoistiodactylus linglongtaensis* (JPM04-

452   0008, see Sullivan et al. 2013 for comments on the phylogenetic position of this species) do present a

453   pterodactyloid-like condition. In these humeri, well-developed lateral and medial epicondyles create a

454   splayed distal termination much broader than either the humeral diaphysis or combined width of the

455   capitulum and trochlea (Fig. 4 A-C, Padian 1983a; Lü and Fucha 2010). In *Dimorphodon* at least, the

456   medial condyle is also distally displaced compared to the lateral. This results in the distal ends of

457   *Dimorphodon* and wukongopterid humeri being clearly different to those of rhamphorhynchines and

458   campylognathoidids, but being morphologically very reminiscent to those of pterodactyloids (Fig. 4 G-

459   I).

460

461   The correlation between these humeral conditions and glenoid morphology is potentially significant.

462   The similarity of *Dimorphodon* and wukongopterid humeri to those of pterodactyloids implies a similar

463   mechanical regime being experienced at the elbow region which, following Fujiwara and Hutchinson

464   (2012) and other studies on pterodactyloid humeral orientation when walking (e.g. Unwin 1996a;

465 Bennett 1997a; Mazin et al. 2003), might be related to the employment of upright gaits. As noted

466 above, portions of the symmetric glenoid articular surface project ventrally in a manner predicted for

467 animals using erect gaits. The large, open junction between the ventral articular surface, lower extent of

468 the supraglenoidal buttress and the lateral face of the scapula seems capable – perhaps even well-suited

469 - to bolstering a fully adducted forelimb for standing and walking. These pterodactyloid-like anatomies

470 raise the possibility of wukongopterids and *Dimorphodon* being capable of erect forelimb postures. If,

471 as noted by Fujiwara and Hutchinson (2012), pterodactyloid-like distal humeri are indicate of upright

472 limbs, such postures may even be likely. In any case, the assumption that sprawling forelimbs were

473 common to all non-pterodactyloids clearly warrants further investigation.

474

475 By contrast, the humeral morphology in rhamphorhynchine and campylognathoidid non-

476 pterodactyloids differs from those seen in erect-limbed pterodactyloids (Fujiwara and Hutchinson

477 2012). This also correlates well with their glenoid morphology, as asymmetric morphs seem to prohibit

478 humeral adduction and imply correlates for a different set of forelimb muscles – likely those suited to

479 sprawling - would be emphasised at the distal humerus. Lack of indications of erect poses suggests

480 these pterosaurs fit 'traditional' models of sprawling forelimbs in non-pterodactyloids (e.g. Wellnhofer

481 1975; Unwin 2005; Padian 2008b). It might be predicted that their stance and walking gaits required

482 relatively little wrist motion, as evidenced by their weakly developed epicondyles for muscle

483 attachment related to carpal operation.

484

485 ## Discussion

486 *Other indications of terrestrial competency in non-pterodactyloids*

487 The potential for some non-pterodactyloids as fully upright terrestrial animals might have broad

488 implications for our perception of their palaeobiology and role in pterosaur evolutionary history. Note,

489 however, that this is not the only aspect of early pterosaurs indicating greater terrestrial potential than

490 previously anticipated. It has been suggested that non-pterodactyloid limbs are too short and slender for

491 effective terrestrial locomotion (Fig. 5, Ősi 2011). This is probably an over-generalisation: early

492 pterosaur anatomy is quite disparate in many respects (Witton 2013). Several well-known taxa do

493 possess short and/or slender limbs (e.g. Fig. 5E-F), but Triassic and Jurassic taxa such as

494 *Dimorphodon*, anurognathids and *Preondactylus bufarinii* possess long, robust, and near-equally sized

495 limbs with well-developed extremities (Fig. 5A-D; Owen 1870; Dalla Vecchia 1998; Bennett 2007;

496   Padian 2008a). Indeed, the limbs of some non-pterodactyloids are more substantially developed and

497   proportionate than those of terrestrially-competent pterodactyloids, such as azhdarchids (Witton and

498   Naish 2008). Several early pterosaurs possess features of subcursoriality including long limbs relative

499   to their bodies, joints with hinge-like mobility, short and massive propodia, slender and distally

500   reduced/fused fibulae, digitigrade manus and elongate metapodia (Coombs 1978, p. 399 and 402). It

501   bears repeating that the limbs of pterosaurs – including those of non-pterodactyloids - have been

502   frequently identified as powerfully muscled and strongly built for leaping and flying (Padian 1983a, b;

503   Bennett 1997b; Fastnacht 2005; Habib 2008; Witton and Habib 2010), and were therefore likely

504   capable of supporting some grounded activity, perhaps even sustained and energetic terrestrial

505   behaviours. It is likely that the slender, disproportionate limbs of some better known non-

506   pterodactyloids such as *Rhamphorhynchus* have influenced opinions on the terrestrial ability non-

507   pterodactyloids as a whole. Considered independently, the long, proportionate and robust limbs of

508   genera such as *Dimorphodon*, anurognathids and *Preondactylus* might be considered well-suited to

509   terrestrial locomotion. .

510

511   The digits of several non-pterodactyloid species are also adorned with features which may betray

512   routine terrestrial habits: antungual sesamoids (Fig. 6). These small, round bones are situated on the

513   dorsal surfaces of the penultimate manual phalanges of many Triassic and Lower Jurassic pterosaur

514   specimens, including the Triassic taxa *Eudimorphodon ranzii* (MCSNB 2888), *Carniadactylus*

515   *rosenfeldi* (MFSN 1797), *Peteinosaurus zambellii* (MCSNB 2887), the "*Eudimorphodon*" specimen

516   MCSNB 8950, the "*Peteinosaurus*" specimen MCSNB 3359 (Wild 1978, 1994; Dalla Vecchia 2009)

517   as well as the Jurassic pterosaurs *Dorygnathus* (e.g. Fig. 6C, BSP 1938 I 49; see also Padian 2008b)

518   and *Dimorphodon* (Fig. 6A, NHMUK 41212; NHMUK R1034; see Padian 1983a, Unwin 1988).

519   *Dimorphodon* is unusual in also bearing pedal antungual sesamoids, spreading their distribution across

520   all clawed digits (Fig. 6B, GSM 1546; Unwin 1988). Antungual sesamoids are present in an

521   osteologically immature specimen of *Eudimorphodon* (MPUM 6009; Wild 1978), suggesting they are

522   not confined to gerontic, well-ossified adults.

523

524   Pterosaur antungual sesamoids are consistently preserved dorsally adjacent to the articular condyles of

525   penultimate phalanges and were presumably situated within the tendons of the digit extensors (Bennett

526   2008). Their function has not been explored in detail, but two studies (Unwin 1988 and Bennett 1997b)

527   cite them as part of a suite of characters important to pterosaur grasping and climbing capabilities.

528   Anatomies related to grasping and climbing are relatively well explored (see Sustaita et al. 2013 for a

529   recent review) but, to this author's knowledge, extension of the ungual is not generally associated with

530   this ability. Perhaps the only exceptions are the actions of some climbing geckos, which retract

531   adhesive pads situated on the distal ends of their digits before each step (Zaaf et al. 1999; Russel and

532   Higham 2009). However, these geckos famously adhere themselves to substrates via manipulation of

533   molecular forces, not with claws, and their climbing methods are unlikely to mirror those used by

534   pterosaurs.

535

536   Antungual sesamoids analogous to those of pterosaurs are currently only known from terrestrial

537   reptiles: several squamate lineages (Haines 1969; Jerez et al. 2009; Otero and Hoyos 2013) and the

538   semiaquatic 'bottom walking' Triassic turtle *Proganochelys* (Gaffney 1990). Gaffney (1990) proposed

539   that antungual sesamoids confer functions typical of other reptile sesamoids: increasing tendon

540   moment arm lengths around joints, ensuring nutrient delivery to tendons by limiting strain or pressure

541   on joints articulated to their extremes (Haines 1969), or strengthening tendons (Nussbaum 1982). High

542   mechanical stresses on the dorsal side of phalangeal-ungual joints seem to be the most likely catalyst

543   for antungual sesamoid development.

544

545   Perhaps the only shared functional attributes between pterosaurs, lepidosaurs and *Proganochelys* are

546   large unguals and the potential to walk on firm substrates. It may be that these two factors alone can

547   account for antungual sesamoid development. One possibility is that deflection of large, curving

548   unguals by hard surfaces induce pressure on the extensor tendon, promoting the development of a

549   sesamoid to maintain tendon nutrient flow during sustained bouts of standing and walking (Fig. 6Dii).

550   Alternatively, deliberate hyperextension of claws may promote antungual sesamoid development as

551   means to increase the extensor tendon moment arm, and thus improve efficiency of claw retraction

552   (Fig. 6Diii). It is notable that pterosaurs with antungual sesamoids possess expanded, deeply grooved

553   penultimate phalangeal terminations and large ungual extensor tubercles (Fig. 6A-C), similar to the

554   phalanges of animals with hyperextensible digits, such as cats, dromaeosaurids and schizotherine

555   chalicotheres (Coombs 1983; Gonyea and Ashworth 1975; Parsons and Parsons 2009). By contrast,

556   pterosaurs lacking antungual sesamoids have relatively small, weakly developed phalangeal-ungual

557   joints (e.g. Wellnhofer 1975; Clark et al. 1998), suggesting limited potential for hyperextension.

558   Ungual hyperextension has evolved repeatedly within terrestrial tetrapods to avoid claw blunting (e.g.

559   Gonyea and Ashworth 1975; Coombs 1983) or to release strong grips, as demonstrated by many

560   modern geckos which, when walking, retract the ends of their digits before each step (Zaaf et al. 1999;

561   Russel and Higham 2009): the possibility it occurred in pterosaurs is not unreasonable. Indeed, claw

562   retraction has been proposed as an explanation for the lack of ungual traces in some pterodactyloid

563   ichnites (Frey et al. 2003).

564

565   These hypotheses share frequent ungual interaction with hard substrates as the chief adaptive pressure

566   for antungual sesamoid development. Sustained activity in terrestrial settings is perhaps the most likely

567   cause of this interaction, and congruent with the seemingly-exclusive development of antungual

568   sesamoids in terrestrialised taxa such as squamates and *Proganochelys*. If antungual sesamoids do

569   represent such adaptations, their development in non-pterodactyloids may represent further evidence of

570   terrestrial habits.

571

572   *The terrestrial proficiency of early pterosaurs*

573   The considerations of early pterosaur limb and limb girdle functions offered here suggest views of non-

574   pterodactyloid palaeobiology may warrant more detailed consideration. Existing models of pterosaur

575   locomotory mechanics, where pterodactyloids are adaptable, 'terrestrialised' pterosaurs and their

576   forebears were confined to climbing and flying, are perhaps over-simplistic. Not only are common

577   arguments supporting terrestrially-inept early pterosaurs problematic, but pterodactyloid-like anatomies

578   consistent with fully erect gaits and other possible hallmarks of competent terrestriality seem to be

579   deeply nested within Pterosauria. These findings are the latest in a series showing that pterosaur

580   palaeobiology is much richer, more diverse and complex than previously anticipated (see Witton 2013

581   for an overview).

582

583   Assessing the evolutionary pathways of the anatomies described here is complicated by the lack of

584   consensus over non-pterodactyloid phylogeny (Unwin 2003; Kellner 2003; Wang et al. 2009; Kellner

585   2010; Dalla Vecchia 2009; Lü et al. 2010, 2012; Witton 2013; Andres and Meyers 2013; Andres et al.

586   2014). Some tentative conclusions may be drawn, however. The distribution of anatomies permitting

587   erect and sprawling gaits is complicated, with no set of features limited to specific clades or 'grades' of

588   pterosaurs (Fig. 7). Potential signatures of erect postures appear early in pterosaur evolution:

589   *Dimorphodon* indicates that some pterodactyloid-like features of pterosaur limbs occurred by the

590   Sinemurian at latest, and pterosaurs with elongate, robust limbs (e.g. *Peteinosaurus*, "*Eudimorphodon*"

591   specimen MCSNB 3359, *Preondactylus*) represent some of the oldest known pterosaurs

592   (Carnian/Norian). Given that likely pterosaur outgroups such as dinosauromorphs and *Scleromochlus*

593   bore strong, erect limbs (e.g. Sereno 1991; Benton 1999), it is possible that these early pterosaurs

594   retained characteristics of efficient terrestriality from immediate pterosaur ancestors. This might be in

595   keeping with models of pterosaurs evolving from terrestrially- or scansorially-adapted ancestors in

596   inland environments (Padian 1985, 2008a; Bennett 1997b; Witton 2013; Andres et al. 2014), before

597   spreading to marine habitats (Andres et al. 2014). Taxa likely utilising sprawling forelimbs tend to

598   occur further from the pterosaur root however, suggesting this 'traditional' gait might be a derived

599   feature of clades such as Rhamphorhynchinae and Campylognathoididae, and perhaps associated with

600   the development of increasingly pelagic lifestyles (see below).

601

602   How this relates to possible evidence for erect gaits in the pterodactyloid sister group,

603   Wukongopteridae, is intriguing. Their Callovian/Oxfordian (Lü et al. 2010) appearance in the fossil

604   record coincides with the appearance of pterosaur footprints as well as the first pterodactyloids (Andres

605   et al. 2014), making questions about distinguishing pterodactyloid tracks from those of non-

606   pterodactyloids all the more pertinent (Lockley et al. 2008). Were wukongopterids involved in the

607   upper Jurassic 'terrestrial radiation' of pterosaurs, and was this part of a separate 'terrestrialisation

608   event' to possible earlier terrestrialisation indicated by *Dimorphodon*-like pterosaurs? Do

609   wukongopterids represent a lineage of pterosaurs which retained plesiomorphic glenoid and humeral

610   morphologies from much earlier pterosaurs, or were these reversed from sprawling ancestors? Future

611   discoveries of Jurassic and Triassic pterosaurs in terrestrial basins and further resolution on the

612   phylogeny of early pterosaurs may shed light on these questions.

613

614   Concerning the specifics of terrestrial locomotion in different non-pterodactyloid taxa: the view of

615   early pterosaurs as partially-sprawling terrestrial locomotors (e.g. Wellnhofer 1975; Padian 2008b)

616   seems to hold true for at least rhamphorhynchines and campylognathoidids (Fig. 8A), although how

617   limiting their sprawled or crouched forelimbs were to walking and running remains to be determined.

618   Views that sprawling gaits are inherently 'primitive' or inferior to erect ones are problematic, as

619   demonstrated by the tremendous success of sprawling tetrapods both today and in Deep Time (Russell

620 and Bels 2001). Although perhaps ill-suited to sustained terrestrial locomotion, sprawling can be an

621 effective, perhaps superior locomotory kinematic for rapid acceleration, sprinting and climbing

622 (Russell and Bels 2001). Indeed, specialist lifestyles promote the retention or development of

623 sprawling limbs in many species (McElroy et al. 2008). Thus, the sprawling forelimbs of

624 rhamphorhynchines and campylognathoidids are not necessarily means to write off their terrestrial

625 competency, and assumptions that sprawling pterosaurs would be limited to slow, ponderous

626 locomotion do not reflect the sometimes explosive and powerful abilities of modern sprawling

627 amphibians, reptiles and mammals (contra. Unwin 2005, Padian 2008b). Note that the limbs of

628 galloping vampire bats are sprawled (Riskin et al. 2006), a fact worth considering when arguing that

629 rhamphorhynchines and campylognathoidids required bipedal stances for rapid terrestrial movement

630 (e.g. Padian 2008b, c).

631

632 Nevertheless, because sustained terrestrial locomotion seems better served by erect gaits, the indication

633 that rhamphorhychines and campylognathoidids had sprawling forelimbs is consistent with predictions

634 that these pterosaurs were relatively flight-reliant, seabird-like species (see functional and

635 palaeoecological evidence discussed by Wellnhofer 1975; Wild 1978; Chatterjee and Templin 2004;

636 Witton 2008, 2013, etc.). Like some seabirds, these pterosaurs may have relied on flight for long-

637 distance movement rather than terrestrial locomotion (e.g. Kaiser 2007; Abourachid and Höfling 2012),

638 and parallels may be drawn between the restricted shoulder arthrology of asymmetric glenoids and the

639 energy-saving arthrological 'locks' found in the shoulders of modern soaring birds (e.g. Meyers and

640 Stakebake 2005). If antungual sesamoids are, as proposed here, indicators of routine claw interaction

641 with the ground, their presence in *Dorygnathus*, *Carniadactylus* and *Eudimorphodon* still suggest

642 frequent terrestrial activities however. It may be that these pterosaurs routinely landed to forage or

643 roost but performed only limited walking or running activities when grounded, while other habits –

644 perhaps hanging or climbing – necessitated large, trenchant claws and associated sesamoids. The

645 sprawling stance of their forelimbs is well suited to climbing behaviour (Russell and Nels 2001), as are

646 the particularly large and robust third manual digits of *Dorygnathus* (Fig. 6C; Padian 2008b)

647

648 With symmetrical glenoids and pterodactyloid-like distal humeri, it is possible *Dimorphodon* and

649 wukongopterids could utilise fully upright gaits and had pterodactyloid-like terrestrial capabilities.

650 *Dimorphodon* particularly embodies many 'subcursorial' features (long, robust limbs; stout propodia,

651   reduced fibulae, etc.) and it may have been capable of not only sustained, but also relatively fast

652   terrestrial activity (Fig. 8B). Especially well-developed appendages and possession of antungual

653   sesamoids on all clawed digits might signify that *Dimorphodon* was not unduly reliant on flight, as do

654   data suggesting it was particularly heavy for its wingspan and a relatively ineffective, perhaps short-

655   distance flier (Brower and Veinus 1980; Witton 2008, 2013). Scansorial features of the *Dimorphodon*

656   skeleton (e.g. elongate penultimate phalanges, asymmetrical pes structure, claw curvature – see Unwin

657   1988, Clark et al. 1998; Witton 2013) marry with conclusions drawn here to present it as a terrestrial

658   generalist, able to run, walk and climb as well as fly. Many extant terrestrial animals with mobile limb

659   joints and long limbs - such as rodents, bovids, carnivorans, etc. – are as adept at climbing as they are

660   walking and running, to the extent that some measures of their ecomorphospace overlap significantly

661   with scansorial animals (e.g. Samuels et al. 2013). The suggested diet of insects and small vertebrates

662   for *Dimorphodon*, based on its tooth shape and wear patterns (Ősi 2010), is concordant with generally

663   terrestrial habits (Fig. 8B). Wukongopterid pterosaurs may have also been capable terrestrial

664   locomotors, although their limbs are not as powerfully built as those of *Dimorphodon* and some aspects

665   of their flight anatomy, such as their pteroids, are more substantially developed (Witton 2013). Like

666   many small modern birds, wukongopterids may have been proficient enough to move through

667   terrestrial settings without flight – perhaps in search of insect prey (Lü et al. 2011; Witton 2013) – but

668   seem more aerially capable and flight-ready than the heavyset *Dimorphodon*.

669

Concluding remarks

671   The assessment of non-pterodactyloid terrestrial locomotion offered here demonstrates that our

672   understanding of functionality and locomotory mechanics in early pterosaurs is limited, perhaps

673   echoing suggestions that early pterosaur history is generally poorly known (e.g. Butler et al. 2013). It is

674   hoped this work will inspire further investigation into the functionality of these animals. As here, such

675   studies will likely be hampered by the quality of non-pterodactyloid fossils, where even complete

676   specimens can be too extensively crushed or poorly preserved to show the anatomies needed for

677   functional interpretation. However, there is clearly greater potential for understanding early pterosaur

678   functionality than currently realised and, until this has been researched more thoroughly, caution is

679   urged against making generalisations about the terrestrial competency of non-pterodactyloids, and its

680   role in the evolution of Pterosauria.

681

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688

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948 Young, C. C. (1964). On a new pterosaurian from Sinkiang, China. *Vertebrate Palasiatica*, 8, 221-225.

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953 Padian (2008b).

954

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956 specimen PIN 2885/3, showing extensive, toe-supported uropatagium (dark shading) and associated

957 brachiopatagia (light shading); B, skeletal reconstruction of *Rhamphorhynchus muensteri* showing

958 distribution of membranes in non-pterodactyloid pterosaurs based on fossil remains (see Elgin and

959 Hone 2011); C, line drawing of hanging common vampire bat *Desmodus rotundus*, a terrestrially-

960 competent species with an extensive uropatagium analogous to those of non-pterodactyloid pterosaurs.

961 Note *Desmodus* has a small uropatagium compared to other, terrestrially-adept bat species. Scale bar of

962 A represents 10 mm, other images not to scale. Abbreviations: Brachio, brachiopatagium; CV, caudal

963 vertebrae; Ep, epiphysis, Fem, femur; Fib, fibula; Pel, pelvis; Pro, propatagium; Ta, tarsals; Tib, tibia;

964 Uro, uropatagium; WP, wing phalanx (numerals denote phalanx number); i-v denote pedal digit

965 numbers. A, modified from Unwin and Bakhurina 1994; B, modified from Witton 2013; C, redrawn

966 from photograph in Nowark 1994.

967

968 Figure 3. Non-pterodactyloid glenoid morphology. A-C, line drawings of NHMUK R1034

969 *Dimorphodon macronyx* left scapulocoracoid in anterodorsal (A), lateral (B) and ventrolateral (C)

970 aspect; D-G, NHMUK R5672, indeterminate rhamphorhynchine right scapulocoracoid in dorsal (D),

971 ventral (E), lateral (F) and anterior (G) aspects; H, photograph of the NHMUK R1034 glenoid

972 ('symmetric' morph), in posteroventral aspect; I, photograph of NHMUK R5672 ('asymmetric' morph)

973 in posteroventral aspect; J, schematic reconstruction of a non-pterodactyloid torso with a symmetric (i)

974 and asymmetric (ii) glenoid conditions, where green shading approximates articulatory range of the

975 humerus in the vertical plane based on extent of articular surface. Scapulocoracoids in J reconstructed

976 based on specimens illustrated herein and models of pectoral anatomy presented for other early

977 pterosaurs (Wellnhofer 1975; 1991; Bennett 2003). Note this is only approximate for *Dimorphodon*

978 because its sternum remains unknown. ac, acromion process; ar, articular face of glenoid; cor,

979 coracoid, lt, lower tubercle; sc, scapula; sb, supraglenoidal buttress. Scale bars represent 10 mm. J,

980 modified from Wellnhofer (1991).

981

982   Figure 4. Pterosaur humeri in anterior view, showing development of lateral and medial epicondyles

983   adjacent to the capitula and trochleae (shaded grey) in non-pterodactyloids (A-F) and pterodactyloids

984   (G-I). A, NHMUK 42016, *Dimorphodon macronyx*; B, YPM 350 F, *Di. macronyx* ; C, JPM04-0008,

985   *Archaeoistiodactylus linglongtaensis*; D, Wellnhofer's (1975) *Rhamphorhynchus muensteri* humerus;

986   E, SMNS 51827, *Dorygnathus banthensis*; F, SMNS 50164, *Do. banthensis*; G, YPM 1164,

987   *Pteranodon* sp; H, MOR 691, *Montanazhdarcho minor*; I, IVPP V.2777, *Dsungaripterus weii*. Note the

988   relatively poorly developed epicondyles in D-F, and how the distal humeri of A-C resemble those of

989   pterodactyloids more than other non-pterodactyloids. Ca, capitulum; LE, lateral epicondyle; ME,

990   medial epicondyle; Tr, trochlea. Scale bars represent 10 mm, except for G and H, which equal 50 mm.

991   B, after Padian (1983a); D, after Wellnhofer (1975); E, after Padian (2008b); G, modified from Bennett

992   (2001); H, after McGowen et al. (2002); I, after Young (1964). D, E and H are reversed from their

993   sources to enhance comparability.

994

995   Figure 5. Are non-pterodactyloids ubiquitously equipped with short, slender limbs? Skeletal

996   reconstructions of taxa such as *Preondactylus bufarini* (A), *Dimorphodon macronyx* (B) and

997   *Anurognathus ammoni* (C and D, in erect and crouched poses respectively, acknowledging the poorly

998   known glenoid condition of anurognathids) show they have proportionally long, robust limbs. Only

999   some non-pterodactyloids, including the Early Jurassic campylognathoidid *Campylognathoides liasicus*

1000   (E) and Late Jurassic rhamphorhynchine *Rhamphorhynchus muensteri* (F) have proportionally short

1001   and slender hindlimbs. *Preondactylus* has been reconstructed with erect forelimbs based on its grossly

1002   similar humeral morphology to *Dimorphodon*, although it remains to be established that this similarity

1003   extends to more detailed forelimb anatomy. Scale bars represent 100 mm, except for C and D, which

1004   represent 50 mm. Skeletal reconstructions modified from Witton (2013).

1005

1006   Figure 6. Antungual sesamoids in pterosaurs. A, manus and pes of NHMUK 41212 *Dimorphodon*

1007   *macronyx*; B, partial pes skeleton of GSM 1546 *Di. macronyx*; C, manus of BSP 1938 I 49

1008   *Dorygnathus banthensis*; D, proposed interactions of pterosaur unguals with hard substrates, and

1009   utilisation of antungual sesamoids (extensor tendon shown in grey shading). Di, terminal phalanges of

1010   *Dimorphodon* manual digit 2 show as resting on a hard substrate without loading; Dii, passive

1011   hyperextension of the ungual, where pulling or depressing the phalanges (force vectors shown with

1012   arrows) retract the ungual to contact the sesamoid; Diii, active hyperextension of the ungual, where the

1013   extensor tendon is pulled to clear the ungual tip of the ground using the additional lever arm length

1014   afforded by the sesamoid. A-C, shading and numbers denote identification of clawed digits (Arabic

1015   numerals for manual digits, unary for pedal). Some skeletal elements present on the illustrated

1016   specimens are omitted for clarity. mc1-3, metacarpals 1-3; mt1-4, metatarsals 1-4; mt5, metatarsal 5;

1017   pd v, pedal digit 5; r, dorsal rib; s, sesamoids; wmc, wing metacarpal; wp, wing finger proximal

1018   phalanx. Scale bars represent 10 mm.

1019   Figure 7. Complex distribution of characteristics linked to terrestrial capabilities in non-pterodactyloids

1020   in a simplified pterosaur phylogeny (based on Lü et al. 2012). Other pterosaur phylogenies suggest

1021   different arrangements of non-pterodactyloid taxa (see text for details), but the distribution of these

1022   characteristics would be as complex, if not more so, in competing arrangements.

1023

1024   Figure 8. Potential variation in terrestrial locomotion gait in non-pterodactyloid pterosaurs. A, life

1025   restoration of the Early Jurassic rhamphorhynchine *Dorygnathus banthensis* with obligated crouching,

1026   somewhat sprawled forelimbs; B, life restoration of the Early Jurassic *Dimorphodon macronyx* with

1027   fully adducted humeri and completely erect gait, shown here facilitating subcursorial, rapid terrestrial

1028   locomotion in pursuit of sphenodontian prey. Both animals are restored with retracted claws on digits

1029   possessing antungual sesamoids.

1

Select hypotheses for non-pterodactyloid poses made in the last 35 years

Figure 1. Select hypotheses for non-pterodactyloid poses made in the last 35 years . A, Padian's (1983a) bipedal *Dimorphodon macronyx*; B, redrawn lateral view of the 'Roborhamphus' model discussed by Unwin (2005); C, quadrupedal *Dorygnathus banthensis* with sprawling forelimbs, reversed from Padian (2008b).

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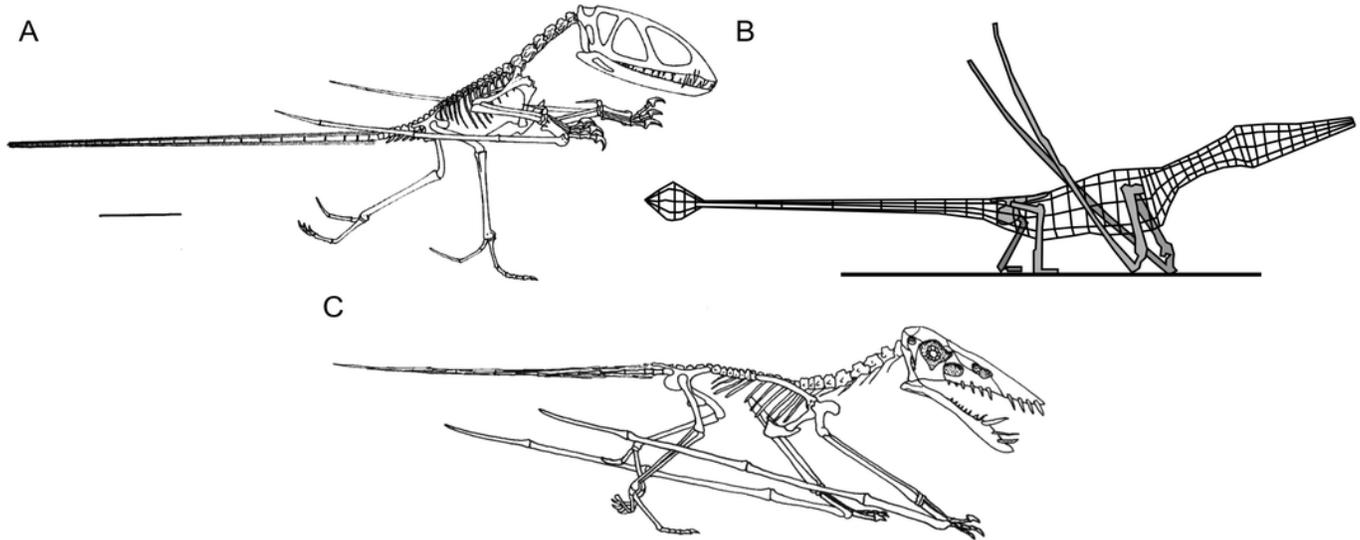
Pterosaur and bat uropatagia compared

Figure. 2. Pterosaur and bat uropatagia compared. A, line drawing of hindlimb region of *Sordes pilosus* specimen PIN 2885/3, showing extensive, toe-supported uropatagium (dark shading) and associated brachiopatagia (light shading); B, skeletal reconstruction of *Rhamphorhynchus muensteri* showing distribution of membranes in non-pterodactyloid pterosaurs based on fossil remains (see Elgin and Hone 2011); C, line drawing of hanging common vampire bat *Desmodus rotundus*, a terrestrially-competent species with an extensive uropatagium analogous to those of non-pterodactyloid pterosaurs. Note *Desmodus* has a small uropatagium compared to other, terrestrially-adept bat species. Scale bar of A represents 10 mm, other images not to scale. Abbreviations: Brachio, brachiopatagium; CV, caudal vertebrae; Ep, epiphysis, Fem, femur; Fib, fibula; Pel, pelvis; Pro, propatagium; Ta, tarsals; Tib, tibia; Uro, uropatagium; WP, wing phalanx (numerals denote phalanx number); i-v denote pedal digit numbers. A, modified from Unwin and Bakhurina 1994; B, modified from Witton 2013; C, redrawn from photograph in Nowark 1994. _

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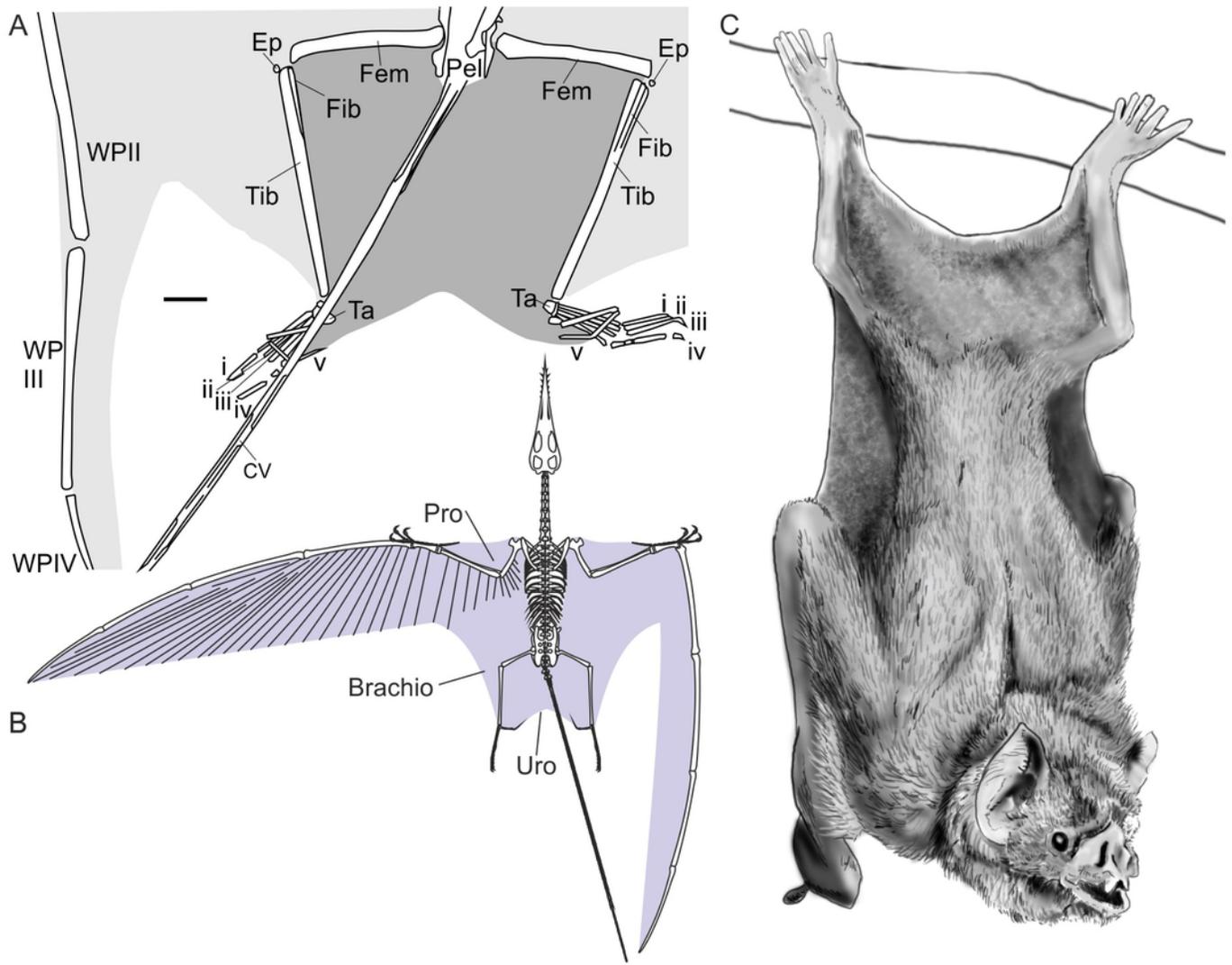
Non-pterodactyloid glenoid morphology

Figure 3. Non-pterodactyloid glenoid morphology. A-C, line drawings of NHMUK R1034 *Dimorphodon macronyx* left scapulocoracoid in anterodorsal (A), lateral (B) and ventrolateral (C) aspect; D-G, NHMUK R5672, indeterminate rhamphorhynchine right scapulocoracoid in dorsal (D), ventral (E), lateral (F) and anterior (G) aspects; H, photograph of the NHMUK R1034 glenoid ('symmetric' morph), in posteroventral aspect; I, photograph of NHMUK R5672 ('asymmetric' morph) in posteroventral aspect; J, schematic reconstruction of a non-pterodactyloid torso with a symmetric (i) and asymmetric (ii) glenoid conditions, where green shading approximates articulatory range of the humerus in the vertical plane based on extent of articular surface. Scapulocoracoids in J reconstructed based on specimens illustrated herein and models of pectoral anatomy presented for other early pterosaurs (Wellnhofer 1975; 1991; Bennett 2003). Note this is only approximate for *Dimorphodon* because its sternum remains unknown. ac, acromion process; ar, articular face of glenoid; cor, coracoid, lt, lower tubercle; sc, scapula; sb, supraglenoidal buttress. Scale bars represent 10 mm. J, modified from Wellnhofer (1991).

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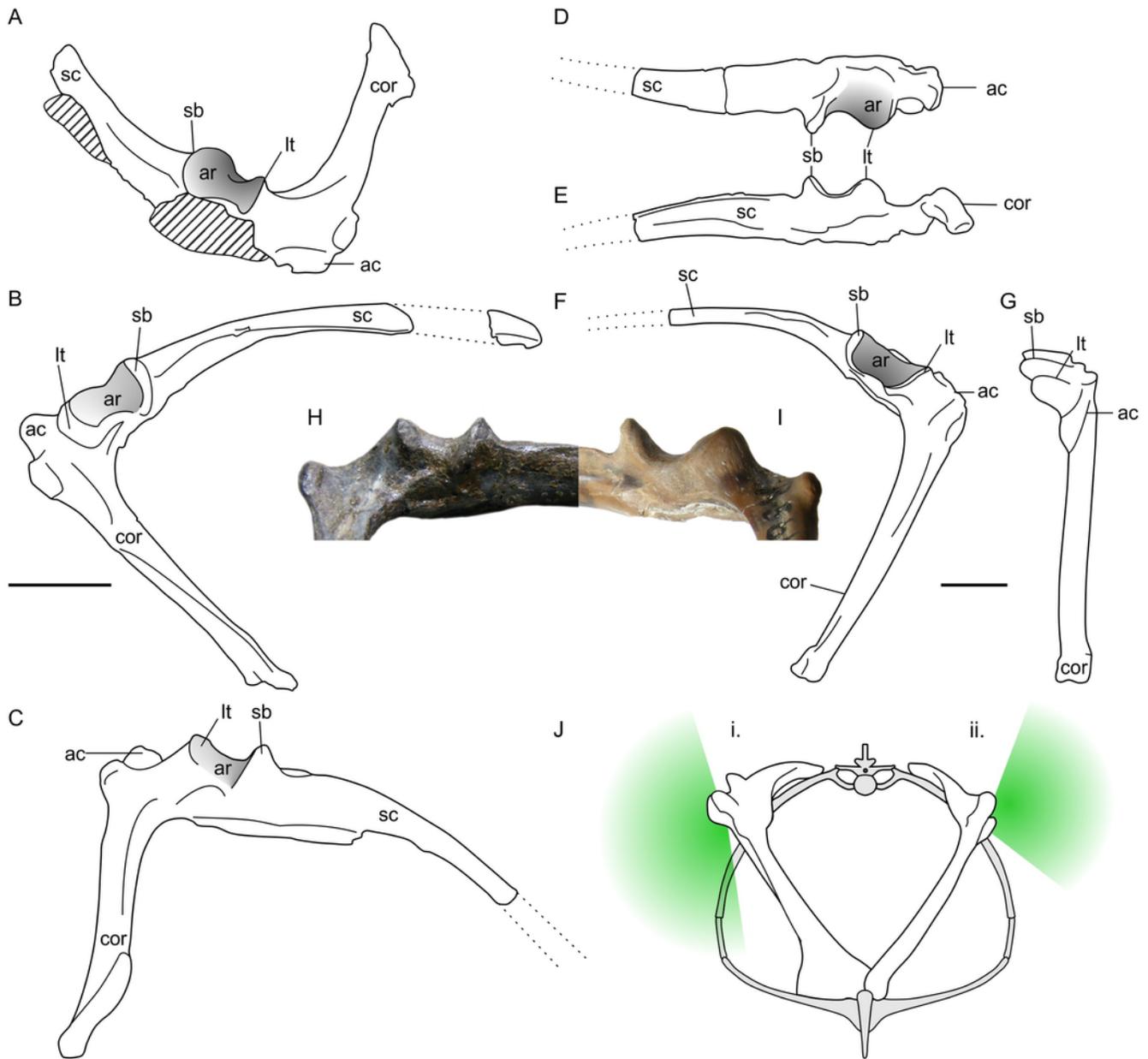
Pterosaur humeri in anterior view

Figure 4. Pterosaur humeri in anterior view, showing development of lateral and medial epicondyles adjacent to the capitula and trochleae (shaded grey) in non-pterodactyloids (A-F) and pterodactyloids (G-I). A, NHMUK 42016, *Dimorphodon macronyx*; B, YPM 350 F, *Di. macronyx* ; C, JPM04-0008, *Archaeoistiodactylus linglongtaensis*; D, Wellnhofer's (1975) *Rhamphorhynchus muensteri* humerus; E, SMNS 51827, *Dorygnathus banthensis*; F, SMNS 50164, *Do. banthensis*; G, YPM 1164, *Pteranodon* sp; H, MOR 691, *Montanazhdarcho minor*; I, IVPP V.2777, *Dsungaripterus weii*. Note the relatively poorly developed epicondyles in D-F, and how the distal humeri of A-C resemble those of pterodactyloids more than other non-pterodactyloids. Ca, capitulum; LE, lateral epicondyle; ME, medial epicondyle; Tr, trochlea. Scale bars represent 10 mm, except for G and H, which equal 50 mm. B, after Padian (1983a); D, after Wellnhofer (1975); E, after Padian (2008b); G, modified from Bennett (2001); H, after McGowen et al. (2002); I, after Young (1964). D, E and H are reversed from their sources to enhance comparability. �I? ? 0<~�Tm
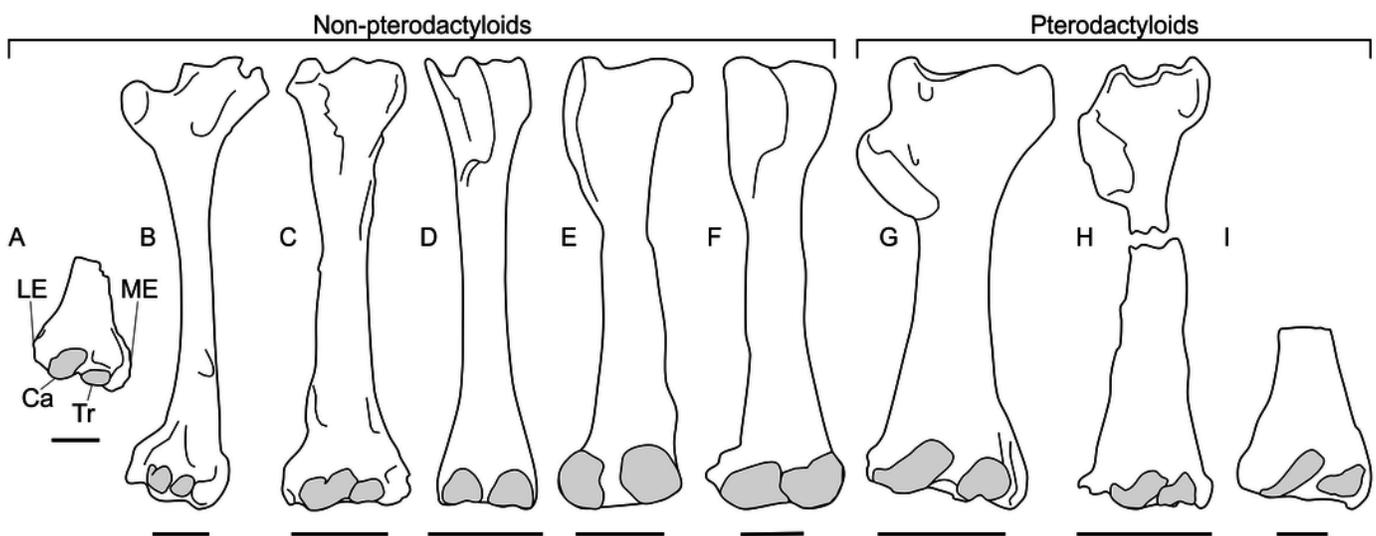
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Skeletal reconstructions of non-pterodactyloid pterosaurs

Figure 5. Are non-pterodactyloids ubiquitously equipped with short, slender limbs? Skeletal reconstructions of taxa such as *Preondactylus bufarini* (A), *Dimorphodon macronyx* (B) and *Anurognathus ammoni* (C and D, in erect and crouched poses respectively, acknowledging the poorly known glenoid condition of anurognathids) show they have proportionally long, robust limbs. Only some non-pterodactyloids, including the Early Jurassic campylognathoidid *Campylognathoides liasicus* (E) and Late Jurassic rhamphorhynchine *Rhamphorhynchus muensteri* (F) have proportionally short and slender hindlimbs. *Preondactylus* has been reconstructed with erect forelimbs based on its grossly similar humeral morphology to *Dimorphodon*, although it remains to be established that this similarity extends to more detailed forelimb anatomy. Scale bars represent 100 mm, except for C and D, which represent 50 mm. Skeletal reconstructions modified from Witton (2013). <!--? 0[b]

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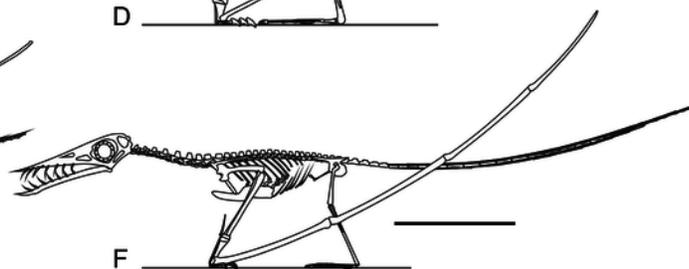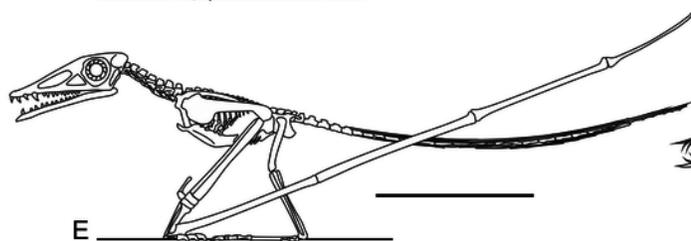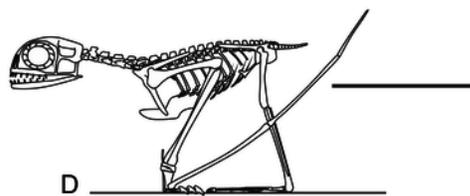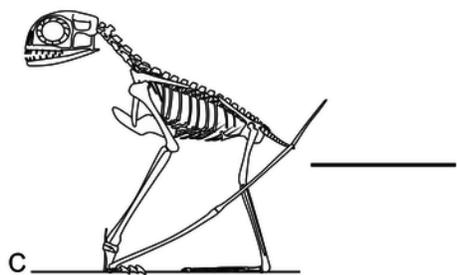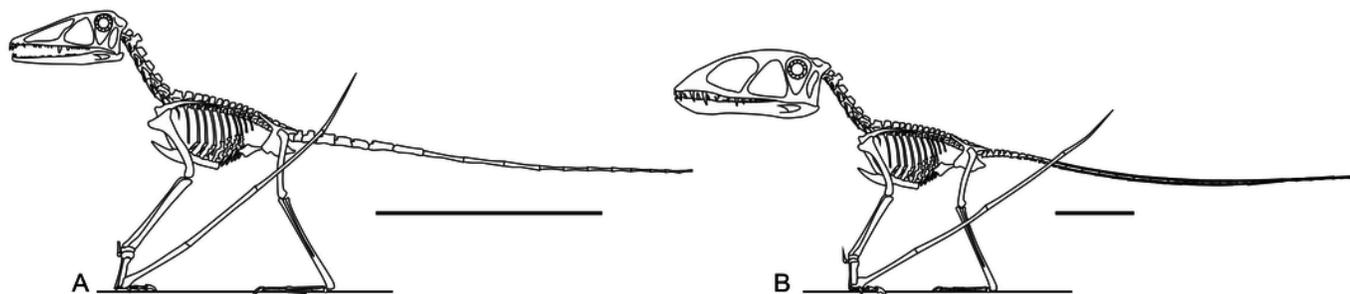
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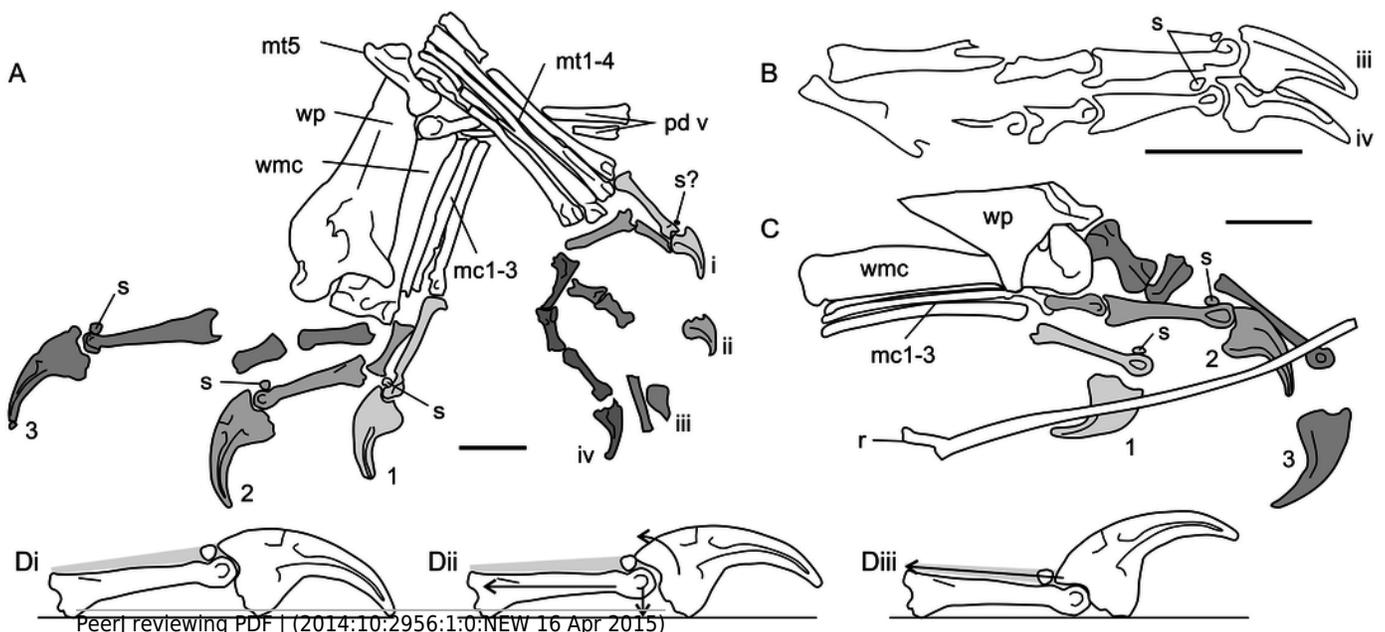
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Distribution of characteristics linked to terrestrial capabilities in non-pterodactyloids in a simplified pterosaur phylogeny

Figure 7. Complex distribution of characteristics linked to terrestrial capabilities in non-pterodactyloids in a simplified pterosaur phylogeny (based on Lü et al. 2012). Other pterosaur phylogenies suggest different arrangements of non-pterodactyloid taxa (see text for details), but the distribution of these characteristics would be as complex, if not more so, in competing arrangements.
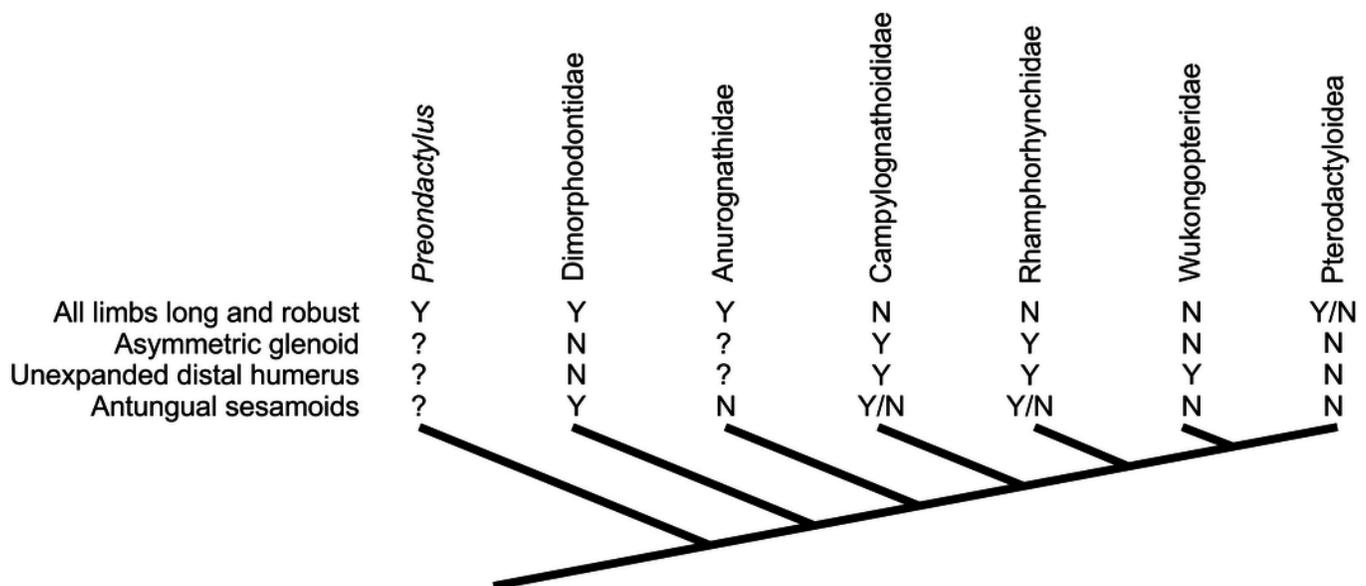
8

Potential variation in terrestrial locomotion gait in non-pterodactyloid pterosaurs

Figure 8. Potential variation in terrestrial locomotion gait in non-pterodactyloid pterosaurs. A, life restoration of the Early Jurassic rhamphorhynchine *Dorygnathus banthensis* with obligated crouching, somewhat sprawled forelimbs; B, life restoration of the Early Jurassic *Dimorphodon macronyx* with fully adducted humeri and completely erect gait, shown here facilitating subcursorial, rapid terrestrial locomotion in pursuit of sphenodontian prey. Both animals are restored with retracted claws on digits possessing antungual sesamoids. ml> 0