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 largely thought to have been poor. This is commonly justified by the absence of a non-pterodactyloid footprint record, suggestions that the expansive uropatagia common to early pterosaurs would restrict hindlimb motion 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 likely contribute 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. Novel assessments of pterosaur forelimb anatomies conflict with notions that all non-pterodactyloids were obligated to sprawling forelimb postures. Sprawling forelimbs seem appropriate for species with ventrally-restricted glenoid articulations (seemingly occurring in rhamphorhynchines and campylognathoidids). However, some early pterosaurs, such as *Dimorphodon macronyx* and wukongopterids, have glenoid arthrologies which are not ventrally restricted, and their distal humeral anatomy resembles those of pterodactyloids. It seems fully erect forelimb stances were possible in these pterosaurs, and may be probable given proposed links between pterodactyloid-like distal humeral morphology and forces incurred through erect forelimb postures. Further indications of terrestrial habits include antungual sesamoids, which occur in the manus and pes anatomy of many early pterosaur species, and only occur elsewhere in terrestrial reptiles, possibly developing through frequent interactions of large claws with firm substrates. It is argued that characteristics possibly associated with terrestriality are deeply nested within Pterosauria and not restricted to Pterodactyloidea as previously thought, and that pterodactyloid-like levels of terrestrial competency may have been possible in at least some early pterosaurs.

2   # Were early pterosaurs inept terrestrial locomotors?

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9   Abstract

10   Pterodactyloid pterosaurs are widely interpreted as terrestrially competent, erect-limbed

11   quadrupeds, but the terrestrial capabilities of non-pterodactyloids are largely thought to have

12   been poor. This is commonly justified by the absence of a non-pterodactyloid footprint record,

13   suggestions that the expansive uropatagia common to early pterosaurs would restrict hindlimb

14   motion in walking or running, and the presence of sprawling forelimbs in some species. Here,

15   these arguments are re-visited and mostly found wanting. Restriction of limb mobility is not a

16   problem faced by extant animals with extensive fight membranes, including species which

17   routinely utilise terrestrial locomotion. The absence of non-pterodactyloid footprints is not

18   necessarily tied to functional or biomechanical constraints. As with other fully terrestrial clades

19   with poor ichnological records, biases in behaviour, preservation, sampling and interpretation

20   likely contribute to the deficit of early pterosaur ichnites. Suggestions that non-pterodactyloids

21   have slender, mechanically weak limbs are demonstrably countered by the proportionally long

22   and robust limbs of many Triassic and Jurassic species. Novel assessments of pterosaur forelimb

23   anatomies conflict with notions that all non-pterodactyloids were obligated to sprawling forelimb

24   postures. Sprawling forelimbs seem appropriate for species with ventrally-restricted glenoid

25   articulations (seemingly occurring in rhamphorhynchines and campylognathoidids). However,

26   some early pterosaurs, such as *Dimorphodon macronyx* and wukongopterids, have glenoid

27   arthrologies which are not ventrally restricted, and their distal humeral anatomy resembles those

28   of pterodactyloids. It seems fully erect forelimb stances were possible in these pterosaurs, and

29   may be probable given proposed links between pterodactyloid-like humeral morphology and

30   forces incurred through erect forelimb postures. Further indications of terrestrial habits include

31   antungual sesamoids, which occur in the manus and pes anatomy of many early pterosaur

32   species, and only occur elsewhere in terrestrial reptiles, possibly developing through frequent

33   interactions of large claws with firm substrates. It is argued that characteristics possibly

34   associated with terrestriality are deeply nested within Pterosauria and not restricted to

35   Pterodactyloidea as previously thought, and that pterodactyloid-like levels of terrestrial

36   competency may have been possible in at least some early pterosaurs.

39   ## Introduction

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

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

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

43   Wellnhofer 1988; Unwin 1988, 1989, 1996a, 1999; Lockley et al. 1995; Bennett 1997a; Clark et

44   al. 1998; see Witton 2013 for a recent overview). The current consensus emerged when

45   *Pteraichnus* trackways, first identified by Stokes (1957) as pterosaurian, but argued to be of

46   crocodylomorph origin by Padian and Olsen (1984) and Unwin (1989), were convincingly

47   demonstrated as belonging to pterodactyloid pterosaurs (Lockley et al. 1995; Bennett 1997a;

48   Unwin 1996a, 1999; also see Kubo 2008). This reappraisal started the construction of a

49   compelling case for pterodactyloids as terrestrially competent quadrupeds with plantigrade feet

50   and parasagittal gaits, a hypothesis now strengthened by numerous trackway discoveries (e.g.

51   Mazin *et al*. 1995, 2003; Lockley and Wright 2003; Hwang et al. 2002; Padian 2003; Lockley et

52   al. 2008) but also functional analyses of pterosaur anatomy (e.g. Bennett 1997a; Clark et al.

53   1998; Sangster 2003; Wilkinson 2008; Witton and Naish 2008; Fujiwara and Hutchinson 2012;

54   Costa et al. 2013; Hyder et al. 2014).

55

56   Although it seems that the basic tenets of pterodactyloid terrestrial locomotion are understood,

57   the same cannot be said for non-pterodactyloids. Research into the terrestrial capacity of early

58   pterosaurs is entirely based on interpretations of their functional anatomy because their

59   trackways remain elusive (Unwin 2005; Lockley et al. 2008; Whyte and Romano 2014). Such

60   considerations are relatively few in number and have reached varying conclusions, either arguing

61   for non-pterodactyloids as terrestrially competent, digitigrade bird-like bipeds which could not

62   easily reach the substrate with their forelimbs (Fig. 1a; Padian 1983a, b, 1985, 2003, 2008); as

63   widely-sprawled quadrupeds, limited to rotatory gaits (as defined by Padian et al. 2010) and ill-

64 suited to movement on the ground, but possibly adept at climbing (Unwin 1987, 1988, 1989,

65 1999; 2005; Unwin and Bakhurina 1994); or as quadrupeds with erect hindlimbs, capable of

66 arboreal locomotion and powerful leaping (Bennett 1997b) or bipedal running (Padian 2008a, b,

67 c).

68

69 To some extent, discussions of non-pterodactyloid terrestriality have been intertwined with

70 debates over pterosaur bipedality, as many of the foundations of this hypothesis were set using

71 non-pterodactyloids (Padian 1983a, b). Pterosaur bipedality has always been controversial

72 (Bennett 1997a, p. 107) and has inspired numerous analyses. Most have suggested that habitual

73 bipedalism – either bird-like or otherwise – is unlikely for any pterosaur. Criticisms of this

74 concept include all pterosaurs having a centre of gravity situated towards the shoulders

75 (Wellnhofer 1988; Bennett 1997a; Sangster 2003; Wilkinson 2008); a pedal morphology ill-

76 suited to digitigrady (Bennett 1997a; Clark et al. 1998); lever arms of proximal hindlimb

77 musculature which perform poorly at postures imposed by bipedality (Fastnacht 2005; Costa et

78 al. 2013); an inability to neatly fold the forelimbs (Wilkinson 2008), and forelimb strength

79 scaling regimes contrasting with those of flying bipeds, but matching those of quadrupeds (Habib

80 2008). The inability of pterosaur forelimbs to reach the ground has also been disputed (Unwin

81 1996a; Bennett 1997a), although Padian (1983b, 2003a, b) maintains that the limb proportions of

82 some species, in concert with perceived limited limb motion at the shoulder, dictates facultative

83 bipedality for some pterosaurs. Functional evidence casting doubt on bipedal postures in

84 pterosaurs is consistent with a wealth of trackway data showing pterosaurs as quadrupedal

85 animals with plantigrade feet (e.g. Mazin *et al*. 1995, 2003; Lockley and Wright 2003; Hwang et

86 al. 2002; Padian 2003; Lockley et al. 2008), and is further bolstered by the unique fit of pterosaur

87 anatomy to these tracks (Lockley et al. 1995; Bennett 1997a; Unwin 1996a). Note that further

88 experimentation with extant crocodilian trackmakers has cast further doubt on perceived

89 similarities between *Pteraichnus* tracks and those of crocodylomorphs (Kubo 2008; contra.

90 Padian and Oslen 1984; Padian 2003).

91

92 Of the several interpretations of non-pterodactyloid terrestrial locomotion outlined above, the

93 proposal that they were relatively ineffective terrestrial quadrupeds has gained the largest

94 acceptance (e.g. Unwin 1987, 1988, 1989, 1999; 2005; Unwin and Bakhurina 1994; Ősi 2010;

95 Butler et al. 2013; Benson et al. 2014; Whyte and Romano 2014). The assumed contrast in

96 terrestrial abilities between non-pterodactyloids and pterodactyloids has influenced

97 considerations of not only non-pterodactyloid palaeobiology (e.g. lifestyle and diets – see Unwin

98 2005; Ősi 2010) but also the evolution of Pterosauria as a whole. Some recent workers have

99 considered the origin of pterodactyloids a 'terrestrialisation' of pterosaurs (Unwin 2005; Butler

100 et al. 2013), and a radical evolutionary departure from the primarily scansorial and volant habits

101 used by earlier members of the group.

102

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

104 repeated hypotheses. The first concerns the expansive uropatagium which extended between the

105 hindlimbs of non-pterodactyloids, supported distally by long fifth pedal digits (Fig. 2; Sharov

106 1971; Unwin and Bakhurina 1994; Wild 1994; Kellner et al. 2009). This is reasoned to have

107 restricted independent hindlimb motion and stride length, limited speed and agility, and hindered

108 movement through complex, vegetated environments (e.g. Unwin 1988, 1999; 2005; Ősi 2011).

109 The reduction of fifth toe length in pterodactyloids is interpreted as signifying the loss or

110 reduction of this membrane, as evidenced by a pterodactyloid specimen with reduced hindlimb

111 membranes lacking medial contact (Wellnhofer 1987). This 'decoupling' of the hindlimbs from

112 one another is thought to have permitted longer strides and more effective, faster terrestrial

113 locomotion in pterodactyloids, explaining their relative success in inland settings over their

114 ancestors (e.g. Unwin 1988, 1999, 2005; Ősi 2011).

115

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

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

118 begins in at least the Norian but, to date, no definitively identified pterosaur trackways occur in

119 rocks pre-dating the Aalenian (Lockley et al. 2008; Whyte and Romano 2014). The oldest

120 occurrence of pterosaur tracks roughly coincides with the oldest evidence of pterodactyloids

121 (Andres et al. 2014; Whyte and Romano 2014) and is seen as evidence for pterosaurs becoming

122 'terrestrialised', it being assumed that pterodactyloid anatomical nuances allowed exploitation of

123 settings such as tidal flats and lake margins, and creation of a track record (Unwin 2005; Butler

124 et al. 2012). Non-pterodactyloids, by contrast, are assumed so poorly adapted for walking and

125 running that they scarcely used such forms of locomotion, and thus rarely left footprints (Unwin

126 2005).

127

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

129 sprawling forelimbs, and perhaps hindlimbs as well (Wellnhofer 1975; Unwin 1988, 1999, 2005;

130 Padian 2008b). It has been argued that these would limit quadrupedal walking speeds and force

131 reliance on other forms of locomotion – bipedal running or flight – to move rapidly (Unwin

132 1988, 1999, 2005; Padian 2008b). Although some have argued that the hindlimbs of early

133 pterosaurs were erect and powerfully muscled (e.g. Padian 1983a, b, 2008b; Bennett 1997b;

134 Elgin et al. 2011), these observations have not influenced some considerations of non-

135 pterodactyloid terrestrial locomotion (Unwin 1988, 2005). However, even among those

136 proposing erect hindlimbs, the terrestrial prospects of non-pterodactyloids are not considered

137 highly. Padian (2008a, b) has suggested that a combination of erect hindlimbs and sprawled

138 forelimbs would incline early pterosaur torsos anteriorly, and, in concert with limited forelimb

139 reach, render them ill-suited to terrestrial locomotion – at least as quadrupeds (this is considered

140 one line of evidence for bipedal habits). In recent years, views that early pterosaurs were inept

141 terrestrial animals have been presented as established and important parts of the pterosaur

142 evolutionary history, and said to explain patterns within the pterosaur fossil record (Unwin 1999,

143 2005; Butler et al. 2012; Benson et al. 2014).

144

145 These assumptions have become established despite the low number of dedicated assessments

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

147 pterodactyloid functionality than there are for pterodactyloids, and particularly so in recent years.

148 This probably reflects the larger amount of material available for studies into pterodactyloid

149 mechanics: along with footprints and tracks, many pterodactyloids are known from three-

150 dimensional material which lends itself better to functional studies than the mostly flattened and

151 fragmentary remains forming the non-pterodactyloid record. Nevertheless, some non-

152 pterodactyloid anatomies are well enough known to permit evaluation of arguments suggesting

153 poor terrestriality in these early forms. This is attempted here, with the three principle hypotheses

154 underlying most assessments of non-pterodactyloid terrestriality being considered:

155

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

157   terrestrial locomotion?

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

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

160

161   *Institutional abbreviations*

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

163   Henan Geological Museum, Zhengzhou, China; GPIT, Geologisch-Paläontologisches Institut

164   und Museum, Universität Tübingen, Germany; GSM, Geological Survey Museum, Keyworth;

165   UK; IVPP, Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing, China; JPM,

166   Jehol Paleontological Museum, Chengde, China; MCSNB, Museum Civico di Scienze Naturali

167   di Bergamo, Italy; MFSN. Museo Friulano di Storia Naturale, Udine, Italy; MJML, Museum of

168   Jurassic Marine Life, Kimmeridge, UK; MPUM, Museo Paleontologia Universitá di Milano,

169   Italy; NHMUK, Natural History Museum, London, UK; PIN, Paleontological Institute, Moscow,

170   Russia; SMNS, Staatliches Museum für Naturkunde Stuttgart, Germany.

171

Materials and Methods

173   *Systematic declaration*

174   Pterosaur systematics, and particularly those of early taxa, are currently highly controversial.

175   With so little agreement on multiple aspects of early pterosaur phylogeny including clade

176   content, group definitions, and appropriate nomenclature (e.g. Unwin 2003; Kellner 2003; Wang

177   et al. 2009; Kellner 2010; Dalla Vecchia 2009; Lü et al. 2010, 2012; Witton 2013; Andres and

178   Meyers 2013; Andres et al. 2014), accurate discussion of pterosaur systematics requires regular

179   citation of the specific taxonomy being followed (e.g. Andres and Meyers 2013) or frequent

180   mentions of conflicting phylogenies (e.g. Witton 2013). Neither approach is practical or makes

181   for compelling reading. Thus, unless otherwise stated, this paper uses the nomenclature and

182   taxonomy of the non-pterodactyloid phylogeny of Lü et al. (2012). Dalla Vecchia (2009), Wang

183   et al. (2010) and Andres and Meyers (2013) offer alternative contemporary schemes.

184

185   *Material*

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

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

188   non-pterodactyloid from Dorset, UK. Observations were chiefly made on the holotype NHMUK

189   R1034, a partial skeleton, and the near complete skeleton NHMUK 41412-13. Both specimens,

190   although partially embedded in matrix, are largely three dimensionally preserved and sufficiently

191   prepared to appreciate most aspects of limb girdle and limb anatomy, especially when viewed in

192   concert with other, less complete *Dimorphodon* material in the Natural History Museum,

193   London. Additional study was made on a near-complete three-dimensional rhamphorhynchine

194   scapulocoracoid from the Callovian-Oxfordian Oxford Clay, UK, NHMUK R5672. Wellnhofer

195   (1975) referred this specimen to *Rhamphorhynchus* sp., but diagnostic characters for this genus

196   are presently only known in the skull anatomy and limb proportions of this genus (Bennett

197   1995). While undoubtedly *Rhamphorhynchus*-like, NHMUK R5672 is conservatively considered

198   an indeterminate rhamphorhynchine here, echoing taxonomic suggestions by Unwin (1996b).

199

200   Results

201   *1. Did the large uropatagium of non-pterodactyloids restrict hindlimb function during*

202   *terrestrial locomotion?*

203   The inference that relatively large uropatagia impeded early pterosaur terrestrial habits has

204   received no detailed evaluation, despite its confident presentation in some literature ("There can

205   be no doubt that this shackling of the limbs must have hindered pterosaurs as they sought to

206   move around on the ground" – Unwin 2005, p. 204). It might be presumed that attributes of

207   fossil pterosaur soft-tissues or observations on modern animals with similar membrane structures

208   support this assertion, but it is only the relatively large size of early pterosaur uropatagia which is

209   cited in favour of this idea (e.g. Unwin and Bakhurina 1994; Unwin 2005). While it is difficult to

210   evaluate the effects of soft-tissues on non-pterodactyloid hindlimb kinematics in the absence of

211   footprints, evidence from pterosaur body fossils, and the anatomy and behaviour of modern

212   animals, conflict with proposals that expansive uropatagia impeded early pterosaur terrestriality.

213

214   Many gliding and flying mammals possess large, hindlimb-spanning uropatagia comparable in

215   size to those of non-pterodactyloids (Fig. 2). A number of these species are terrestrially

216   proficient (e.g. Sollberger 1940; Nowark 1994; Stafford et al. 2003; Riskin et al. 2006; Meijaard

217 et al. 2006), some spending considerable amounts of time on the ground in pursuit of food or

218 refuge using fast, complex and sometimes strenuous behaviours (Sollberger 1940; Daniel 1976;

219 Nowark 1994; Pyare and Longland 2002; Riskin et al. 2006). These animals are not confined to

220 barren habitats, predator-free environments or the result of reduced competition from other

221 terrestrial creatures. Rather, they inhabit complex, predator-filled habitats and have persisted for

222 many millions of years in some regions (Hand et al. 2009). Examples include the New Zealand

223 lesser short-tailed bat, *Mystacina tuberculata*, which is reported as having "rodent-like agility on

224 the ground and on trunks, branches, and kiekie vines" by Daniel (1976; p. 397). Common

225 vampires, *Desmodus rotundus*, rely on their terrestrial skills to stealthily stalk hosts or quickly

226 evade danger using forelimb-propelled galloping (Nowark 1994; Riskin and Hermanson 2005;

227 Riskin et al. 2006). Flying squirrels, such as *Glaucomys* species, forage on the ground, are

228 capable of running, and have membranes resilient to frequent digging for fungal food sources

229 (Sollberger 1940). Similarly, membranes of *Mystacina* bats withstand crevice-crawling as well

230 as digging (Daniel 1979). Clearly, the grounded activities of these animals are not impeded by

231 their patagia, nor do their membranes snag on obstacles or become easily damaged. Presumably,

232 membrane elasticity plays a role in reducing impedance to terrestrial activity, both allowing the

233 limbs to move freely as well as drawing the membranes close to the body to prevent interference

234 with the environment or limb motion. The extent of such membrane shrinkage can be extreme,

235 rendering them almost indiscernible in some circumstances (Meijaard et al. 2006). Critically,

236 while some membrane-bound extant animals are poor terrestrial locomotors, this has not been

237 linked to membrane size or distribution, but instead to aspects of skeletal morphology, limb

238 strength or myology (Riskin et al. 2005).

239

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

241 volant mammals, but are they suitable models for pterosaurs? Fossils of pterosaur wing

242 membranes show some similarities to those of modern volant mammals in that they were likely

243 elastic in their proximal regions. Pterosaur brachiopatagia are stiffened by structural fibres

244 distally, but other membrane components – including the uropatagium – lack rigid structural

245 fibres and are widely considered to have been compliant (e.g. Padian and Rayner 1993; Unwin

246 and Bakhurina 1994; Bennett 2000; Frey et al. 2003). Unwin and Bakhurina (1994), describing

247 the uropatagium of *Sordes pilosus*, comment specifically on this, stating "…adjacent to the body

248   the [structural] fibres are shorter, more sinuous and loosely packed, indicating that the

249   propatagium, uropatagium and proximal regions of the cheiropatagium were somewhat softer

250   and more elastic" (p. 64). From this, it can be expected that all pterosaur membranes would

251   contract significantly when the limbs were not extended to flight position, as occurs in many

252   volant mammals, clearing them of obstacles and permitting stretching of the membranes during

253   walking or running. Some evidence for this contraction may be seen in pterosaur fossils with

254   preserved membranes (Elgin et al. 2011). Trackways made by running pterodactyloids indirectly

255   demonstrate how elastic their proximal membranes must have been, allowing track makers to

256   take strides of considerable magnitude (Mazin et al. 2003) despite membranes stretching from

257   the distal hindlimb to their hands (Elgin et al. 2011). The expansion and contraction of

258   brachiopatagia in running pterodactyloids was probably no greater than that experienced by non-

259   pterodactyloid uropatagia during terrestrial activity.

260

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

262   were likely capable of circumventing this issue by using asymmetrical, bounding gaits (Witton

263   and Habib 2010; Witton 2013; Hyder et al. 2014). Indeed, both the fore- and hindlimbs of

264   pterosaurs have been noted for their strength and leaping potential (Padian 1983a, Bennett

265   1997b; Habib 2008; Witton and Habib 2010), and there are obvious parallels between forelimb-

266   dominated *Desmodus* galloping and recent, compelling hypotheses concerning forelimb use in

267   pterosaur launch (Habib 2008). Pterosaurian bounding locomotion may be countered by

268   exclusive trackway evidence for symmetrical gaits in pterodactyloids (e.g. Stokes 1957; Mazin *et*

269   *al*. 1995, 2003; Lockley and Wright 2003; Hwang et al. 2002), but it remains unclear if these

270   gaits were employed by all pterosaurs, all the time, nor is it clear if interpretations of these tracks

271   are applicable to non-pterodactyloids. Bounding gaits are at least tenable from a functional and

272   biomechanical perspective.

273

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

275   their membranes is peculiar. It relies on the uncertain assumption that the uropatagium was

276   especially restrictive compared to other pterosaur wing membranes and behavioural restrictions –

277   membranes snagging on obstacles and limiting stride length – which have no precedent among

278   modern pterosaur analogues. Clear evidence demonstrating broad uropatagia were barriers to

279 early pterosaur terrestriality has yet to be presented, whereas what we know of pterosaur soft-

280 tissues and modern animals with similar anatomy indicates that their membranes likely had little,

281 if any, impact on terrestrial potential.

282

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

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

285 Unwin 2005; Butler et al. 2013) relies on a very literal interpretation of the pterosaur fossil

286 record and an assumption that we can distinguish genuine absences of fossil phenomena from

287 biases affecting fossil datasets. There are reasons to consider both these assertions uncertain.

288

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

290 also many contemporary terrestrial tetrapod groups (e.g. Benton and Spencer 1995; Kielan-

291 Jaworowska et al. 2004). It is particularly impoverished in terrestrial basins (Butler et al. 2013).

292 This is thought to reflect the general lack of inland or near-shore pterosaur-bearing Lagerstätten

293 before the Late Jurassic; the small body sizes and low preservation potential of early pterosaurs;

294 a possibly restricted distribution of the group in its early history; or perhaps existence of the first

295 pterosaurs in habitats unconducive to fossilisation and sediment accumulation - inland forests or

296 upland environments (Bennett 1997b; Unwin 2005; Witton 2013; Butler et al. 2013). Regardless

297 of the cause, recent studies have concluded that recorded patterns of Triassic and Jurassic

298 pterosaur diversity – the interval dominated by non-pterodactyloids – have little statistical

299 significance (e.g. Butler et al. 2013; Upchurch et al. 2014), and that our understanding of early

300 pterosaur history remains generally poor. This is difficult to reconcile with suggestions that the

301 lack of an early pterosaur fossils – specifically their track record - is somehow significant. If

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

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

304 data?

305

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

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

308 when there are a number of reasons why non-pterodactyloids may not have an ichnological

309 record. If non-pterodactyloids were genuinely rare in terrestrial basins – as their record currently

310   indicates - their likelihood of creating traces must also be low. Likewise, it seems most early

311   pterosaurs were small, with wingspans of 1-2 m (O'Sullivan et al. 2013) and corresponding

312   masses of 0.55-3.26 kg (using data from Witton 2008). Their footprints would thus be small and

313   shallow, without substantial underprinting, and require exceptional conditions for impression,

314   fossilisation and discovery. In contrast, pterodactyloids are generally larger bodied than early

315   pterosaurs (Hone and Benton 2007; Benson et al. 2014), which may constitute creation of

316   deeper, longer-lasting tracks which are better suited to fossilisation and detection. A related

317   problem concerns our ability to distinguish the footprints of pterodactyloids from those expected

318   of non-pterodactyloids (Lockley et al. 2008): all pterosaurs have the same basic manus and pes

319   structure, the only exception being the longer fifth toe in non-pterodactyloids. Given the role of

320   this structure in supporting the uropatagium, it may have been held aloft when walking (Lockley

321   et al. 2008). If so, the tracks of all pterosaurs might look similar, and some alleged Jurassic

322   pterodactyloid ichnites may be misidentified.

323

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

325   similar track-making potential. The start of the pterosaur footprint record in the Middle Jurassic

326   roughly corresponds with the emergence of pterodactyloid clades predicted to be waders,

327   suspension-feeders and molluscivores (ctenochasmatoid and dsungaripterids - Unwin 2005;

328   Witton 2013). Such animals are expected to routinely patrol lake margins and other habitats

329   suitable to footprint preservation in search of food. Lockley et al. (2003, 2008) note that

330   pterodactyloid tracks are frequently associated with invertebrate traces and occasional feeding

331   marks, which may indicate foraging was a common factor in pterosaur ichnite creation, inferring

332   ecological influences on the delayed start of the pterosaur ichnological record. By contrast, non-

333   pterodactyloids are largely perceived as pelagic piscivores or insectivores (Wellnhofer 1975;

334   Wild 1978; Chatterjee and Templin 2004; Ősi 2010; Witton 2008, 2013), neither of which are

335   habits lending themselves to sustained terrestrial activity on mudflats, water margins or other

336   settings liable to preserving footprints.

337

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

339   The tracks and traces of many fully terrestrial Mesozoic clades are surprisingly poorly known –

340   examples include geographically widespread, long-lived lineages with good body fossil records,

341   such as Mesozoic Mammaliaformes, tyrannosaurids and ceratopsids (Lockley and Hunt 1995;

342   Kielan-Jaworowska et al. 2004; McCrea et al. 2014). Not only are the ichnological records of

343   these groups poor – restricted to single localities in some cases – but many ichnites referred to

344   them are controversially identified (Kielan-Jaworowska et al. 2004; McCrea et al. 2014). This

345   occurs despite these animals seemingly being abundant (as evidenced by their good body fossil

346   records) and fully terrestrial in their habits, thus potentially creating tracks in virtually all of their

347   activities (unlike pterosaurs, which, in being volant, avoided track creation much of the time). In

348   contrast to perceptions of the pterosaur track record however, the sparse trackways of Mesozoic

349   Mammaliaformes or certain dinosaur clades are not interpreted as signs terrestrial ineptitude, but

350   as biases of behaviour, ecology, preservation, sampling or interpretation.

351

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

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

354   Pterosauria, its significance cannot be divorced from a number of factors unrelated to functional

355   morphology. As with any case supported by negative evidence, data deficits can only be

356   interpreted so far, especially when related datasets are demonstrably poor. Considering the

357   absence of early pterosaur tracks as significant requires ignorance of not only statistics on the

358   quality of the pterosaur fossil record, but also data concerning early pterosaur palaeobiology and

359   the broader ichnological record. Other sources of evidence should be pursued for more reliable

360   insights into the development of pterosaur terrestriality.

361

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

363   Postural sprawl and the use of rotatory limb mechanics has been proposed for grounded non-

364   pterodactyloids from assessments of their limb joint arthrology (e.g. Wellnhofer 1975; Unwin

365   1988, 1999; 2005; Padian 2008b). These suggestions have mostly applied to the forelimbs, but

366   some have suggested that both limbsets were constrained to sprawling stances (Unwin 1988,

367   1999, 2005). Unwin (1988) argued that the *Dimorphodon* femoral-pelvic joint projected the

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

369   was capable of twisting medially at the knee, permitting the foot to face forwards. This is said to

370   allow for semi-erect or sprawling stances, which are in accordance with suggested similarities

371   between the pelves of *Dimorphodon* and the sprawling or semi-erect archosauriform *Euparkeria*

372   *capensis* (Unwin 1988). Computer modelling has also predicted entirely sprawling stances and

373   rotatory gaits for non-pterodactyloids through a digital model of *Rhamphorhynchus* (Fig. 1B;

374   Unwin 2005). The methodology behind this has not been presented, but the resultant digital non-

375   pterodactyloid model 'Roborhamphus' shows hindlimbs projecting entirely laterally from the

376   body, similarly-sprawling forelimbs, low clearance from the ground and slow walking speeds

377   (Unwin 2005). The latter is seemingly a consequence of the limited reach afforded by the

378   sprawling limbs.

379

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

381   the assumption that a 'natural articulation' of the hindlimb can be determined from acetabulum

382   and femoral head morphology (Unwin 1988) is problematic. As evidenced by debates over

383   'osteological neutral pose' in fossil animal necks (e.g. Stevens and Parrish 1999, Taylor et al.

384   2009; Taylor and Wedel 2013; Stevens 2013), attempts to determine 'neutral' or 'natural' poses

385   of animal joints rely on arbitrary assignments of optimal joint configurations which often have

386   little or no significance to typical animal postures (Taylor et al. 2009). It is probably unwise to

387   suggest the hindlimb of *Dimorphodon* sprawled based on acetabulum and femoral head

388   morphology alone.

389

390   Secondly, the pelves of *Dimorphodon* and other early pterosaurs are clearly distinguished from

391   those of *Euparkeria* and other sprawling animals in having a well-developed preacetabular

392   process (Unwin 1988; Hyder et al. 2014). In this respect, non-pterodactyloid pelves resemble

393   those of other ornithodirans – including pterodactyloids - and mammals. These taxa are

394   characterised by erect limbs, the preacetabular process anchoring large hip flexors for moving

395   the hindlimb forward in the parasagittal plane (Hyder et al. 2014), and assessments of pterosaur

396   hindlimb muscle mechanics seem to confirm that the pterosaur pelvic and femoral

397   musculoskeletal system is optimally configured for an erect stance (Fastnacht 2006; Costa et al.

398   2013). Furthermore, while arguments for bipedal, pronograde pterosaurs with parasagittal

399   hindlimbs and digitigrade pedes (Padian 1983a, 1985) have been largely criticised in recent years

400   (e.g. Wellnhofer 1988; Bennett 1997a; Clark et al. 1998; Fastnacht 2005 – also see above),

401   observations that their hip, knee and ankle articulations have hallmarks of upright limb

402   functionality have been borne out by further study (Bennett 1997b; Padian 2008a, b; Fastnacht

403   2005; Costa et al. 2013).

404

405   Thirdly, virtually all recent models of pterosaur evolution suggest taxa with erect hindlimbs

406   bracket non-pterodactyloids, with *Scleromochlus taylori* and non-pterosaurian ornithodirans on

407   one side, and pterodactyloids the other (Sereno 1991; Benton 1999, Hone and Benton 2008;

408   Nesbitt 2011; but also see Bennett 2013). This implicates erect hindlimb postures as probably

409   ancestral for Pterosauria and, given the similarity of their pelvic and hindlimb osteology to their

410   nearest probable relatives, there is little reason to assume non-pterodactyloids deviated from this

411   ancestral state (Bennett 1996b; Padian 2008a; Hyder et al. 2014). It seems that multiple lines of

412   evidence indicate erect hindlimbs across Pterosauria, including all known non-pterodactyloids.

413

414   Relatively little has been said on the stature of non-pterodactyloid forelimbs, however.

415   Traditionally, they have been reconstructed as sprawling. Wellnhofer (1975) observed that the

416   glenoid of *Rhamphorhynchus muensteri* projected laterally and permitted anterodorsal and

417   posteroventral motion of the humerus, but that anterior and posterior motion was limited, and

418   that the humerus could not be adducted below the level of the scapula. Padian (1983a) suggested

419   that the glenoid of *Dimorphodon* permitted a 90° arc of rotation, most of it dorsal to the glenoid,

420   also suggested the shoulder joint of *Dorygnathus* permitted little movement below the frontal

421   plane (Fig. 1C; Padian 2008b). This is said to limit *Dorygnathus* to a sprawling forelimb stance

422   during quadrupedal locomotion which could not match pace with the erect hindlimbs during

423   running, for which bipedality was employed (Padian 2008b). This configuration, which Padian

424   (2003, 2008a) considers typical of all 'basal pterosaurs' (presumably non-pterodactyloids), is

425   also thought to limit ventral reach of the forelimb to the extent that bipedal locomotion must be

426   used, as the pectoral region is depressed significantly below that of the hindlimb in a state

427   considered awkward for effective locomotion (Padian 1983b, 2003, 2008a, b). Unwin (2005)

428   showed the digital 'Roborhamphus' forelimbs in a sprawling fashion somewhat consistent with

429   these models (Fig. 1B).

430

431   Notions that non-pterodactyloid forelimbs were confined to sprawling stances by their glenoids

432   are based in part on the pectoral girdles of rhamphorhynchine pterosaurs (e.g. Wellnhofer 1975;

433   Padian 2008b). The glenoids of these animals are typified by the isolated, but well-preserved

434   scapulocoracoid of an Oxford Clay rhamphorhynchine, NHMUK R5672 (Fig. 3D-G, I). Here,

435   the glenoid is a laterally prominent structure with a long axis aligned with the base of the

436   scapula. The anterior and posterior ends are bordered by a prominent lower tubercle and

437   supraglenoidal buttress, respectively, between which occurs a deeply-curved, saddle-shaped

438   articular surface. This wraps almost 90° from the lateral face to the dorsal, suggesting ample

439   humeral motion lateral and dorsal to the glenoid. The articular face is anteroposteriorly broadest

440   in its dorsal region and most constrained laterally. The ventral extent of the glenoid is marked by

441   a laterally-projecting ridge between the posterior buttress and anterior tubercle. This ridge is

442   continuous with the lower extent of the scapula, supraglenoidal buttress and lower tubercle so

443   that the ventral face of the glenoid is a wide, flat surface instead of a saddle shaped-joint like that

444   of the dorsal region. As noted by previous authors (e.g. Wellnhofer 1975; Padian 2008a, b), such

445   glenoids clearly did not permit humeral adduction below the level of the scapula, and likely

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

447   less constrained dorsally, however. Given their marked dorsoventral asymmetry, these glenoids

448   are hereafter referred to as 'asymmetric'.

449

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

451   including the Jurassic rhamphorhynchines *Rhamphorhynchus muensteri* (see numerous examples

452   in Wellnhofer 1975); the recently-named Kimmeridge Clay *Rhamphorhynchus etchesi* (MJML-

453   K1597, O'Sullivan and Martill, 2015); *Dorygnathus banthensis* (GPIT 1645/1, Padian 2008b);

454   and *Sericipterus wucaiwanensis* (IVPP V14725, Andres et al. 2010). They thus appear to be

455   typical for rhamphorhynchines, and further occurrences may occur within Campylognathoididae,

456   including the Triassic *Eudimorphodon ranzii* (MCSNB 2888, Wild 1978), and Jurassic

457   *Campylognathoides liasicus* (SMNS 11879, Padian 2008c). Asymmetric glenoids may be more

458   widely spread across non-pterodactyloids than this, but establishing their frequency is

459   complicated by a deficit of good preservation and frequently unmet requirements for particular

460   scapulocoracoid orientations in flattened specimens. Accordingly, the shape of the glenoid

461   cannot be established for many taxa which may otherwise be considered well-known, such as the

462   Anurognathidae.

463

464 Asymmetric glenoids are not the only shoulder morph of non-pterodactyloids, however: the well-
465 preserved glenoids on *Dimorphodon macronyx* specimens NHMUK R1034 and 41412-13 are
466 rather differently constructed (Fig. 3A-C, H). Although following the same basic configuration
467 as other non-pterodactyloids, these specimens have a larger supraglenoidal buttress which
468 projects further ventrally than the lower tubercle. The dorsal portion of the glenoid articular face
469 is similar to that described above, but the ventral portion wraps onto the underside of the glenoid
470 until it meets the scapula shaft, instead of terminating at an elevated scapular margin. This gives
471 the glenoid a spool- or hourglass-like appearance in lateral view, and presents no obvious
472 restriction to adducting the humerus to a subvertical position. As with the rest of the glenoid, the
473 ventral articular region is widely open anteroposteriorly (although not as much as the dorsal
474 region) and is estimated to permit 90° of anteroposterior humeral rotation beneath the body. This
475 observation contrasts with previous assessments of *Dimorphodon* glenoid morphology, which
476 suggested anatomy and arthrological range akin to the 'asymmetric' morph outlined above
477 (Padian 1983b, 2003, 2008b). As demonstrated in Fig. 3H-I, the ventral morphologies and likely
478 arthrological ranges of these glenoids are quite distinct.
479
480 Glenoids like those seen in *Dimorphodon* are hereafter referred to as 'symmetric', after their
481 relatively similar dorsal and ventral articular surfaces. It seems such glenoids were rare in non-
482 pterodactyloids: other than *Dimorphodon*, only the wukongopterids *Darwinopterus*
483 *linglongtaensis* (IVPP V16049, Wang et al. 2010) and *Darwinopterus robustodens* (HGM
484 41HIIII-0309A; Lü et al. 2011) seem to possess them, although the caveats mentioned above
485 mean this assessment should not be considered definitive. It is notable that some aspects of
486 pterodactyloid glenoids are similar to this 'symmetric' condition, including the relatively large
487 supraglenoidal buttress, expansive articular face, and absence of an arthrologically prohibitive
488 ventral margin.
489
490 The two non-pterodactyloid glenoid morphologies identified here have different implications for
491 adoption of sprawling or erect postures. Asymmetric glenoids seem to obligate forelimb
492 sprawling, whereas symmetric glenoids could permit either sprawling or upright limb usage. As
493 noted above, relying on a single joint for insight into animal postures can be misleading, and
494 using only glenoid shape to infer forelimb postures in non-pterodactyloids may be unwise.

495   Additional insights on the stances of these animals are afforded by aspects of their distal humeri,

496   however. The morphology of distal humeri seems characteristic of stance in extant quadrupeds,

497   and has been used to predict sprawling or erect limb carriage in extinct animals (Fujiwara and

498   Hutchinson 2012). This is possible because the size of osteological correlates of wrist flexor and

499   extensor muscles, as well as those of elbow extensors, provide insights into primary mechanical

500   loads placed on the distal humerus and, therefore, an insight into habitual forelimb postures

501   (Fujiwara and Hutchinson 2012). This method, grounded and tested in a biometric dataset of 318

502   living taxa, has obvious utility for fossil species where interpreting limb posture based on

503   arthrology alone can be controversial. Fujiwara and Hutchinson (2012) have already applied

504   their technique to a pterodactyloid (*Anhanguera piscator*) humerus and found it met expectations

505   of animals using an upright posture, agreeing with other predictions made from limb bone

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

507   Bennett 1997a; Mazin et al. 2003). Fujiwara and Hutchinson (2012) note that their conclusions

508   likely apply to other pterodactyloids, implying that morphological similarity to *Anhanguera*

509   distal humeri (which are broadly similar to those of other pterodactyloids, even accounting for

510   body size, Fig. 4 G-F) in any pterosaurs might suggest similar forelimb use and stance.

511

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

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

514   glenoids possess markedly reduced medial and lateral epicondyles so that, in anterior view, their

515   distal humeri show relatively little expansion from the diaphyseal shafts. For this reason, the

516   palmar aspect of their distal humeri are dominated by the capitula and trochlea (Fig. 4 D-F). This

517   is seen in at least *Rhamphorhynchus* (Wellnhofer 1975) and *Dorygnathus* (SMNS 51827, SMNS

518   50164, see Padian 2008b), and perhaps also *Eudimorphodon* (MCSNB 2888) and

519   *Campylognathoides* (see examples in Padian 2008c), although the flattened, often oblique

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

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

522   epicondyles in these humeri contrasts with the pterodactyloid condition, in which these structures

523   are prominent and the distal humeri are expanded (Fig. 4 G-F). However, the distal humeri of

524   *Dimorphodon* (NHMUK 42016, YPM 350) and the probable wukongopterid

525   *Archaeoistiodactylus linglongtaensis* (JPM04-0008, see Sullivan et al. 2013 for comments on the

526 phylogenetic position of this species) are much more pterodactyloid-like. In these humeri, well-
527 developed lateral and medial epicondyles create a splayed distal termination much broader than
528 either the humeral diaphysis or the combined width of the capitulum and trochlea (Fig. 4 A-C,
529 Padian 1983a; Lü and Fucha 2010). In *Dimorphodon* at least, the medial condyle is also distally
530 displaced compared to the lateral. This results in the distal ends of *Dimorphodon* and
531 wukongopterid humeri being clearly different to those of rhamphorhynchines and
532 campylognathoidids, but morphologically very similar to those of pterodactyloids (Fig. 4 G-I).
533

534 The correlation between these humeral conditions and glenoid morphology is potentially
535 significant. The similarity of *Dimorphodon* and wukongopterid humeri to those of
536 pterodactyloids implies a similar mechanical regime being experienced at the elbow region
537 which, following Fujiwara and Hutchinson (2012) and other studies on pterodactyloid humeral
538 orientation when walking (e.g. Unwin 1996a; Bennett 1997a; Mazin et al. 2003), might indicate
539 the employment of upright stances. As noted above, portions of the symmetric glenoid articular
540 surface project ventrally in a manner expected for animals with erect forelimbs. The large, open
541 junction between the ventral articular surface, lower extent of the supraglenoidal buttress and the
542 lateral face of the scapula seems capable – perhaps even well-suited - to bolstering a fully
543 adducted forelimb for standing and walking. These anatomies raise the possibility of
544 wukongopterids and *Dimorphodon* being capable of erect forelimb postures. If, as noted by
545 Fujiwara and Hutchinson (2012), pterodactyloid-like distal humeri correlate with an upright
546 forelimb stance, such postures may even be likely. In any case, the assumption that sprawling
547 forelimbs were common to all non-pterodactyloids clearly warrants further investigation.
548 Moreover, the possibility that some early pterosaurs could fully adduct their humeri suggests that
549 reaching the ground in a quadrupedal stance may not have been difficult, as has been proposed
550 (Padian 1983b; 2008a, b).
551

552 The humeral morphology in rhamphorhynchine and campylognathoidid non-pterodactyloids
553 differs from those seen in erect-limbed pterodactyloids (Fujiwara and Hutchinson 2012) and also
554 suits their glenoid morphology. Asymmetric glenoids seem to prohibit humeral adduction into an
555 erect stance, and it would be predicted that correlates for a different set of forelimb muscles –
556 likely those suited to sprawling - would be emphasised at the distal humerus compared to those

557   seen in pterodactyloids. Lack of indications of erect poses suggests these pterosaurs fit

558   'traditional' models of sprawling forelimbs in non-pterodactyloids (e.g. Wellnhofer 1975; Unwin

559   2005; Padian 2008b). It might be predicted that their stance and walking gaits required relatively

560   little wrist motion, as evidenced by their weakly developed epicondyles for muscle attachment

561   related to carpal operation.

562

Discussion

563 Discussion

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

565   The possibility that some non-pterodactyloids were capable of fully upright stances, and

566   unconstrained during terrestrial locomotion by their membranes, might have broad implications

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

568   however, that these are not the only aspects of early pterosaur anatomy indicating greater

569   terrestrial potential than previously anticipated.

570

571   It has been suggested that non-pterodactyloid limbs are too short and slender for effective

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

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

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

575   anurognathids and *Preondactylus bufarinii* possess long, robust, and near-equally sized limbs

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

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

578   and proportionate than those of seemingly terrestrially-competent pterodactyloids, such as

579   azhdarchids (Witton and Naish 2008). It has been noted that several early pterosaur hindlimb

580   skeletons possess features of subcursoriality (Padian 1983b; 2003, 2008a, b), and this is also true

581   of their forelimbs. Subcursorial features include long limbs relative to their bodies, joints with

582   hinge-like mobility, short and massive propodia, slender and distally reduced/fused fibulae,

583   digitigrade manus and elongate metapodia (see Coombs 1978, p. 399 and 402). It bears repeating

584   that the limbs of pterosaurs – including those of non-pterodactyloids - have been frequently

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

586   2003; 2008a, b; Bennett 1997b; Fastnacht 2005; Habib 2008; Witton and Habib 2010), and were

587   therefore likely capable of supporting some grounded activity, perhaps even sustained and

588   energetic terrestrial behaviours. It is likely that the slender, disproportionate limbs of some better

589   known non-pterodactyloids such as *Rhamphorhynchus* have biased opinions on the terrestrial

590   ability non-pterodactyloids as a whole: considered independently, the long, proportionate and

591   robust limbs of genera such as *Dimorphodon*, anurognathids and *Preondactylus* might be

592   considered well-suited to terrestrial locomotion.

593

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

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

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

597   pterosaur specimens, including the Triassic taxa *Eudimorphodon ranzii* (MCSNB 2888),

598   *Carniadactylus rosenfeldi* (MFSN 1797), *Peteinosaurus zambellii* (MCSNB 2887), the

599   "*Eudimorphodon*" specimen MCSNB 8950, the "*Peteinosaurus*" specimen MCSNB 3359 (Wild

600   1978, 1994; Dalla Vecchia 2009) as well as the Jurassic pterosaurs *Dorygnathus* (e.g. Fig. 6C,

601   BSP 1938 I 49; see also Padian 2008b) and *Dimorphodon* (Fig. 6A, NHMUK 41212; NHMUK

602   R1034; see Padian 1983a, Unwin 1988). *Dimorphodon* is unusual in also bearing pedal

603   antungual sesamoids, spreading their distribution across all clawed digits (Fig. 6B, GSM 1546;

604   Unwin 1988). Antungual sesamoids are present in an osteologically immature specimen of

605   *Eudimorphodon* (MPUM 6009; Wild 1978), suggesting they are not just confined to gerontic,

606   well-ossified adults.

607

608   Pterosaur antungual sesamoids are consistently preserved dorsally adjacent to the articular

609   condyles of penultimate phalanges and were presumably situated within the tendons of the digit

610   extensors (Bennett 2008). Their function has not been explored in detail, but two studies (Unwin

611   1988 and Bennett 1997b) cite them as part of a suite of characters important to pterosaur

612   grasping and climbing capabilities. Anatomies related to grasping and climbing are relatively

613   well explored (see Sustaita et al. 2013 for a recent review) but, to this author's knowledge,

614   extension of the ungual is not generally associated with this behaviour. An exception might be

615   climbing geckos, which retract adhesive pads situated on the distal ends of their digits before

616   each step (Zaaf et al. 1999; Russel and Higham 2009). However, these geckos famously adhere

617   themselves to substrates via manipulation of molecular forces, not with claws, and their climbing

618   methods are unlikely to mirror those used by pterosaurs.

619

620 Antungual sesamoids are currently only known from three tetrapod groups: pterosaurs, and

621 terrestrial reptiles: several squamate lineages (Haines 1969; Jerez et al. 2009; Otero and Hoyos

622 2013) and the semiaquatic 'bottom walking' Triassic turtle *Proganochelys* (Gaffney 1990).

623 Gaffney (1990) proposed that antungual sesamoids confer functions typical of other reptile

624 sesamoids: increasing tendon moment arm lengths around joints, ensuring nutrient delivery to

625 tendons by limiting strain or pressure on joints articulated to their extremes (Haines 1969), or

626 strengthening tendons (Nussbaum 1982). High mechanical stresses on the dorsal side of

627 phalangeal-ungual joints seem to be the most likely catalyst for antungual sesamoid

628 development. Perhaps the only shared functional attributes between pterosaurs, squamates and

629 *Proganochelys* are large unguals and the potential to walk on firm substrates. It may be that these

630 two factors alone can account for antungual sesamoid development. One possibility is that

631 deflection of large, curving unguals by hard surfaces induce pressure on the extensor tendon,

632 promoting the development of a sesamoid to maintain tendon nutrient flow during sustained

633 bouts of standing and walking (Fig. 6Dii). Alternatively, deliberate hyperextension of claws may

634 promote antungual sesamoid development as means to increase the extensor tendon moment

635 arm, and thus improve efficiency of claw retraction (Fig. 6Diii). It is notable that pterosaurs with

636 antungual sesamoids possess expanded, deeply grooved penultimate phalangeal terminations and

637 large ungual extensor tubercles (Fig. 6A-C), similar to the phalanges of animals with

638 hyperextensible digits, such as cats, dromaeosaurids and schizotherine chalicotheres (Coombs

639 1983; Gonyea and Ashworth 1975; Parsons and Parsons 2009). By contrast, pterosaurs lacking

640 antungual sesamoids have relatively small, weakly developed phalangeal-ungual joints (e.g.

641 Wellnhofer 1975; Clark et al. 1998), suggesting limited potential for hyperextension. Ungual

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

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

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

645 1999; Russel and Higham 2009): the possibility it occurred in pterosaurs is not unreasonable.

646 Indeed, claw retraction has been proposed as an explanation for the lack of ungual traces in some

647 pterodactyloid ichnites (Frey et al. 2003).

648

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

650   pressure for antungual sesamoid development. Sustained activity in terrestrial settings is perhaps

651   the most likely cause of this interaction, and congruent with the seemingly-exclusive

652   development of antungual sesamoids in terrestrialised taxa such as squamates and

653   *Proganochelys*. If antungual sesamoids do represent such adaptations, their development in non-

654   pterodactyloids may represent further evidence of terrestrial habits in early pterosaurs.

655

656   *The terrestrial proficiency of early pterosaurs*

657   The considerations of early pterosaur limb and limb girdle functions offered here suggest views

658   of non-pterodactyloid palaeobiology may warrant more detailed consideration. Existing models

659   of pterosaur locomotory mechanics, where pterodactyloids are adaptable, 'terrestrialised'

660   pterosaurs and their forebears were confined to climbing and flying, are perhaps over-simplistic.

661   Not only are common arguments for terrestrially-inept early pterosaurs problematic, but

662   anatomies consistent with fully erect stances and other possible hallmarks of competent

663   terrestriality seem to be deeply nested within Pterosauria. These findings are the latest in a series

664   showing that pterosaur palaeobiology is much richer, more diverse and complex than previously

665   anticipated (see Witton 2013 for an overview).

666

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

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

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

670   Andres et al. 2014). Some tentative conclusions may be drawn, however. The distribution of

671   glenoid and humeral morphologies identified above is complicated, with no set of features

672   limited to specific clades or 'grades' of pterosaurs (Fig. 7). Potential signatures of erect postures

673   appear early in pterosaur evolution: *Dimorphodon* indicates that symmetric glenoids and

674   pterodactyloid-like humeral features had developed by the Sinemurian at the latest, and

675   pterosaurs with elongate, robust limbs (e.g. *Peteinosaurus*, "*Eudimorphodon*" specimen MCSNB

676   3359, *Preondactylus*) represent some of the oldest known pterosaurs (Carnian/Norian). Given

677   that likely pterosaur outgroups such as dinosauromorphs and *Scleromochlus* bore strong, erect

678   limbs (e.g. Sereno 1991; Benton 1999), it is possible that these early pterosaurs retained

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

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

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

682   before spreading to marine habitats (Andres et al. 2014). Taxa likely utilising sprawling

683   forelimbs tend to occur further from the pterosaur root however, suggesting this 'traditional'

684   stance might be a derived feature of clades such as Rhamphorhynchinae and

685   Campylognathoididae, and perhaps associated with the development of increasingly pelagic

686   lifestyles (see below).

687

688   How the development of these features relates to possible evidence for fully erect limbs in the

689   pterodactyloid sister group, Wukongopteridae, is intriguing. Their Callovian/Oxfordian (Lü et al.

690   2010) appearance in the fossil record approximates the appearance of pterosaur footprints as well

691   as the first pterodactyloids (Andres et al. 2014), making questions about distinguishing

692   pterodactyloid tracks from those of non-pterodactyloids all the more pertinent (Lockley et al.

693   2008). Were wukongopterids involved in an upper Jurassic 'terrestrial radiation' of pterosaurs,

694   and was this part of a separate 'terrestrialisation event' to that potentially indicated by earlier,

695   *Dimorphodon*-like pterosaurs? Do wukongopterids represent a lineage of pterosaurs which

696   retained plesiomorphic glenoid and humeral morphologies from much earlier pterosaurs, or were

697   these reversed from sprawling ancestors? Future discoveries of Jurassic and Triassic pterosaurs

698   in terrestrial basins and further resolution on the phylogeny of early pterosaurs may shed light on

699   these questions.

700

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

702   of early pterosaurs as forelimb-sprawling terrestrial locomotors (e.g. Wellnhofer 1975; Padian

703   2008b) seems appropriate for at least rhamphorhynchines and campylognathoidids (Fig. 8A),

704   although how limiting their sprawled or crouched forelimbs were to walking and running

705   remains to be determined. Padian's (1983b, 2008a, b) suggestion that the torsos of quadrupedal

706   pterosaurs with sprawling forelimbs would be anteriorly inclined, and thus ill-suited to terrestrial

707   locomotion, is questionable. As demonstrated by the alternative reconstructions of such

708   pterosaurs provided in Fig. 5, torso inclination seems reliant on assumptions made when

709   restoring pterosaur skeletons – such as enhancement of hindlimb height through elevated

710   (digitigrade) ankles (compare Fig. 5E-F with Padian's 2008b *Dorygnathus* illustration in Fig.

711   1C). In any case, the fact that numerous fossil and extant quadrupedal animals have anteriorly-

712   sloping backs and variable limb girdle heights when standing and walking (examples include

713   protorosaurs, modern and fossil crocodylomorphs, several dinosaur clades (diplodocoids,

714   stegosaurids, ceratopsids), and many small mammals lagomorphs, rodents, certain bats)

715   questions what significance this observation has on terrestriality. Other views that sprawling

716   gaits are inherently 'primitive' or inferior to erect ones, or somehow limit movement speed

717   (Unwin 2005) are problematic, as demonstrated by the tremendous success of sprawling

718   tetrapods both today and in Deep Time (Russell and Bels 2001). Although perhaps ill-suited to

719   sustained terrestrial locomotion, sprawling can be an effective, perhaps superior locomotory

720   kinematic for rapid acceleration, sprinting and climbing (Russell and Bels 2001). Indeed,

721   specialist lifestyles promote the retention or development of sprawling limbs in many species

722   (McElroy et al. 2008). Thus, the sprawling forelimbs of rhamphorhynchines and

723   campylognathoidids are not necessarily means to assume low terrestrial competency, and

724   arguments that sprawling pterosaurs would be limited to slow, ponderous locomotion do not

725   reflect the sometimes explosive and powerful abilities of modern sprawling amphibians, reptiles

726   and mammals (contra. Unwin 2005, Padian 2008b). Note that the limbs of galloping vampire

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

728   rhamphorhynchines and campylognathoidids required bipedal stances for rapid terrestrial

729   movement (e.g. Padian 2008b, c).

730

731   Nevertheless, because sustained terrestrial locomotion seems better served by erect limbs, the

732   indication that rhamphorhychines and campylognathoidids had sprawling forelimbs might be

733   consistent with predictions that these pterosaurs were relatively flight-reliant, seabird-like

734   species (see functional and palaeoecological evidence discussed by Wellnhofer 1975; Wild 1978;

735   Chatterjee and Templin 2004; Witton 2008, 2013, etc.). Like some seabirds, these pterosaurs

736   may have relied on flight for long-distance movement rather than terrestrial locomotion, and

737   their anatomy may reflect adaptive biases towards the former (e.g. Kaiser 2007; Abourachid and

738   Höfling 2012). For instance, parallels may be drawn between the restricted shoulder arthrology

739   of asymmetric glenoids and the energy-saving arthrological 'locks' found in the shoulders of

740   modern soaring birds (e.g. Meyers and Stakebake 2005). If antungual sesamoids are, as proposed

741   here, indicators of routine claw interaction with the ground, their presence in *Dorygnathus*,

742   *Carniadactylus* and *Eudimorphodon* still suggest frequent terrestrial activities however. It may

743   be that these pterosaurs routinely landed to forage or roost but performed only limited walking or

744   running activities when grounded, while other habits – perhaps hanging or climbing –

745   necessitated large, trenchant claws and associated sesamoids. The sprawling stance of their

746   forelimbs is well suited to climbing behaviour (Russell and Nels 2001), as are the particularly

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

748

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

750   wukongopterids could utilise fully upright gaits and had pterodactyloid-like terrestrial

751   capabilities. *Dimorphodon* particularly embodies many 'subcursorial' features (long, robust

752   limbs; stout propodia, reduced fibulae, etc.) and it may have been capable of not only sustained,

753   but also relatively fast terrestrial activity (Fig. 8B). Especially well-developed appendages and

754   possession of antungual sesamoids on all clawed digits might signify that *Dimorphodon* was not

755   unduly reliant on flight, as do data suggesting it was particularly heavy for its wingspan and a

756   relatively ineffective, perhaps short-distance flier (Brower and Veinus 1980; Witton 2008, 2013,

757   in prep.; Henderson 2010). Scansorial features of the *Dimorphodon* skeleton (e.g. elongate

758   penultimate phalanges, asymmetrical pes structure, claw curvature – see Unwin 1988, Clark et

759   al. 1998; Witton 2013) marry with conclusions drawn here to present it as a terrestrial generalist,

760   capable of running, walking and climbing as well as flight. Many extant terrestrial animals with

761   mobile limb joints and long limbs - such as rodents, bovids, carnivorans, etc. – are as adept at

762   climbing as they are walking and running, to the extent that some measures of their

763   ecomorphospace overlap significantly with scansorial animals (e.g. Samuels et al. 2013): the

764   identification of climbing adaptations in some early pterosaurs does preclude terrestrial

765   proficiency. The suggested diet of insects and small vertebrates for *Dimorphodon*, based on its

766   skull morphology, tooth shape and dental wear patterns (Ősi 2010), is concordant with generally

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

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

769   aspects of their flight anatomy, such as their pteroids, are more substantially developed (Witton

770   2013). Like many small modern birds, wukongopterids may have been proficient enough to

771   move through terrestrial settings without flight – perhaps in search of insect prey (Lü et al. 2011;

772   Witton 2013) – but seem more aerially capable and flight-ready than the heavyset *Dimorphodon*.

773

Concluding remarks

775 The assessment of non-pterodactyloid terrestrial locomotion offered here demonstrates that our
776 understanding of functionality and locomotory mechanics in early pterosaurs is limited to the
777 extent that basic differences in limb skeleton construction have yet to be noted in detail. It is
778 hoped this work will inspire further investigation into the functionality of these animals. As here,
779 such studies will likely be hampered by the quality of non-pterodactyloid fossils, where even
780 complete specimens can be too extensively crushed or poorly preserved to show the anatomies
781 needed for functional interpretation. However, there is clearly greater potential for understanding
782 early pterosaur functionality than currently realised and, until this has been researched more
783 thoroughly, caution is urged against making generalisations about the terrestrial competency of
784 non-pterodactyloids, and its role in the evolution of Pterosauria.

785

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794

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1091   Figure 1. Select hypotheses for non-pterodactyloid poses made in the last 35 years. A, Padian's

1092   (1983a) bipedal *Dimorphodon macronyx*; B, redrawn lateral view of the 'Roborhamphus' model

1093   discussed by Unwin (2005); C, quadrupedal *Dorygnathus banthensis* with sprawling forelimbs,

1094   reversed from Padian (2008b).

1095

1096   Figure 2. Pterosaur and bat uropatagia compared. A, line drawing of hindlimb region of *Sordes*

1097   *pilosus* specimen PIN 2885/3, showing extensive, toe-supported uropatagium (dark shading) and

1098   associated brachiopatagia (light shading); B, skeletal reconstruction of *Rhamphorhynchus*

1099   *muensteri* showing distribution of membranes in non-pterodactyloid pterosaurs based on fossil

1100   remains (see Elgin et al. 2011); C, line drawing of hanging common vampire bat *Desmodus*

1101   *rotundus*, a terrestrially-competent species with an extensive uropatagium analogous to those of

1102   non-pterodactyloid pterosaurs. Note *Desmodus* has a small uropatagium compared to other,

1103   terrestrially-adept bat species. Scale bar of A represents 10 mm, other images not to scale.

1104   Abbreviations: Brachio, brachiopatagium; CV, caudal vertebrae; Ep, epiphysis, Fem, femur; Fib,

1105   fibula; Pel, pelvis; Pro, propatagium; Ta, tarsals; Tib, tibia; Uro, uropatagium; WP, wing phalanx

1106   (numerals denote phalanx number); i-v denote pedal digit numbers. A, modified from Unwin and

1107   Bakhurina 1994; B, modified from Witton 2013; C, redrawn from photograph in Nowark 1994.

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1109   Figure 3. Non-pterodactyloid glenoid morphology. A-C, line drawings of NHMUK R1034

1110   *Dimorphodon macronyx* left scapulocoracoid in anterodorsal (A), lateral (B) and ventrolateral

1111   (C) aspect; D-G, NHMUK R5672, indeterminate rhamphorhynchine right scapulocoracoid in

1112   dorsal (D), ventral (E), lateral (F) and anterior (G) aspects; H, photograph of the NHMUK R1034

1113   glenoid ('symmetric' morph), in posteroventral aspect; I, photograph of NHMUK R5672

1114   ('asymmetric' morph) in posteroventral aspect; J, schematic reconstruction of a non-

1115   pterodactyloid torso with a symmetric (i) and asymmetric (ii) glenoid conditions, where green

1116   shading approximates articulatory range of the humerus in the vertical plane based on extent of

1117   articular surface. Scapulocoracoids in J reconstructed based on specimens illustrated herein and

1118   models of pectoral anatomy presented for other early pterosaurs (Wellnhofer 1975; 1991;

1119   Bennett 2003). Note this is only approximate for *Dimorphodon* because its sternum remains

1120   unknown. ac, acromion process; ar, articular face of glenoid; cor, coracoid, lt, lower tubercle; sc,

1121   scapula; sb, supraglenoidal buttress. Scale bars represent 10 mm. J, modified from Wellnhofer

1122   (1991).

1123

1124   Figure 4. Pterosaur humeri in anterior view, showing development of lateral and medial

1125   epicondyles adjacent to the capitula and trochleae (shaded grey) in non-pterodactyloids (A-F)

1126   and pterodactyloids (G-I). A, NHMUK 42016, *Dimorphodon macronyx*; B, YPM 350 F, *Di.*

1127   *macronyx* ; C, JPM04-0008, *Archaeoistiodactylus linglongtaensis*; D, Wellnhofer's (1975)

1128   *Rhamphorhynchus muensteri* humerus; E, SMNS 51827, *Dorygnathus banthensis*; F, SMNS

1129   50164, *Do. banthensis*; G, YPM 1164, *Pteranodon* sp; H, MOR 691, *Montanazhdarcho minor*; I,

1130   IVPP V.2777, *Dsungaripterus weii*. Note the relatively poorly developed epicondyles in D-F,

1131   and how the distal humeri of A-C resemble those of pterodactyloids more than other non-

1132   pterodactyloids. Ca, capitulum; LE, lateral epicondyle; ME, medial epicondyle; Tr, trochlea.

1133   Scale bars represent 10 mm, except for G and H, which equal 50 mm. B, after Padian (1983a); D,

1134   after Wellnhofer (1975); E, after Padian (2008b); G, modified from Bennett (2001); H, after

1135   McGowen et al. (2002); I, after Young (1964). D, E and H are reversed from their sources to

1136   enhance comparability.

1137

1138   Figure 5. Are non-pterodactyloids ubiquitously equipped with short, slender limbs? Skeletal

1139   reconstructions of taxa such as *Preondactylus bufarini* (A), *Dimorphodon macronyx* (B) and

1140   *Anurognathus ammoni* (C and D, in erect and crouched poses respectively, acknowledging the

1141   poorly known glenoid condition of anurognathids) show they have proportionally long, robust

1142   limbs. Only some non-pterodactyloids, including the Early Jurassic campylognathoidid

1143   *Campylognathoides liasicus* (E) and Late Jurassic rhamphorhynchine *Rhamphorhynchus*

1144   *muensteri* (F) have proportionally short and slender hindlimbs. *Preondactylus* has been

1145   reconstructed with erect forelimbs based on its grossly similar humeral morphology to

1146   *Dimorphodon*, although it remains to be established that this similarity extends to more detailed

1147   forelimb anatomy. Scale bars represent 100 mm, except for C and D, which represent 50 mm.

1148   Skeletal reconstructions modified from Witton (2013).

1149

1150   Figure 6. Antungual sesamoids in pterosaurs. A, manus and pes of NHMUK 41212

1151   *Dimorphodon macronyx*; B, partial pes skeleton of GSM 1546 *Di. macronyx*; C, manus of BSP

1152   1938 I 49 *Dorygnathus banthensis*; D, proposed interactions of pterosaur unguals with hard

1153   substrates, and utilisation of antungual sesamoids (extensor tendon shown in grey shading). Di,

1154   terminal phalanges of *Dimorphodon* manual digit 2 show as resting on a hard substrate without

1155   loading; Dii, passive hyperextension of the ungual, where pulling or depressing the phalanges

1156   (force vectors shown with arrows) retract the ungual to contact the sesamoid; Diii, active

1157   hyperextension of the ungual, where the extensor tendon is pulled to clear the ungual tip of the

1158   ground using the additional lever arm length afforded by the sesamoid. A-C, shading and

1159   numbers denote identification of clawed digits (Arabic numerals for manual digits, unary for

1160   pedal). Some skeletal elements present on the illustrated specimens are omitted for clarity. mc1-

1161   3, metacarpals 1-3; mt1-4, metatarsals 1-4; mt5, metatarsal 5; pd v, pedal digit 5; r, dorsal rib; s,

1162   sesamoids; wmc, wing metacarpal; wp, wing finger proximal phalanx. Scale bars represent 10

1163   mm.

1164   Figure 7. Complex distribution of characteristics linked to terrestrial capabilities in non-

1165   pterodactyloids in a simplified pterosaur phylogeny (based on Lü et al. 2012). Other pterosaur

1166   phylogenies suggest different arrangements of non-pterodactyloid taxa (see text for details), but

1167   the distribution of these characteristics would be as complex, if not more so, in competing

1168   arrangements.

1169

1170   Figure 8. Potential variation in terrestrial locomotion gait in non-pterodactyloid pterosaurs. A,

1171   life restoration of the Early Jurassic rhamphorhynchine *Dorygnathus banthensis* with obligated

1172   crouching, somewhat sprawled forelimbs; B, life restoration of the Early Jurassic *Dimorphodon*

1173   *macronyx* with fully adducted humeri and completely erect gait, shown here facilitating

1174   subcursorial, rapid terrestrial locomotion in pursuit of sphenodontian prey. Both animals are

1175   restored with retracted claws on digits 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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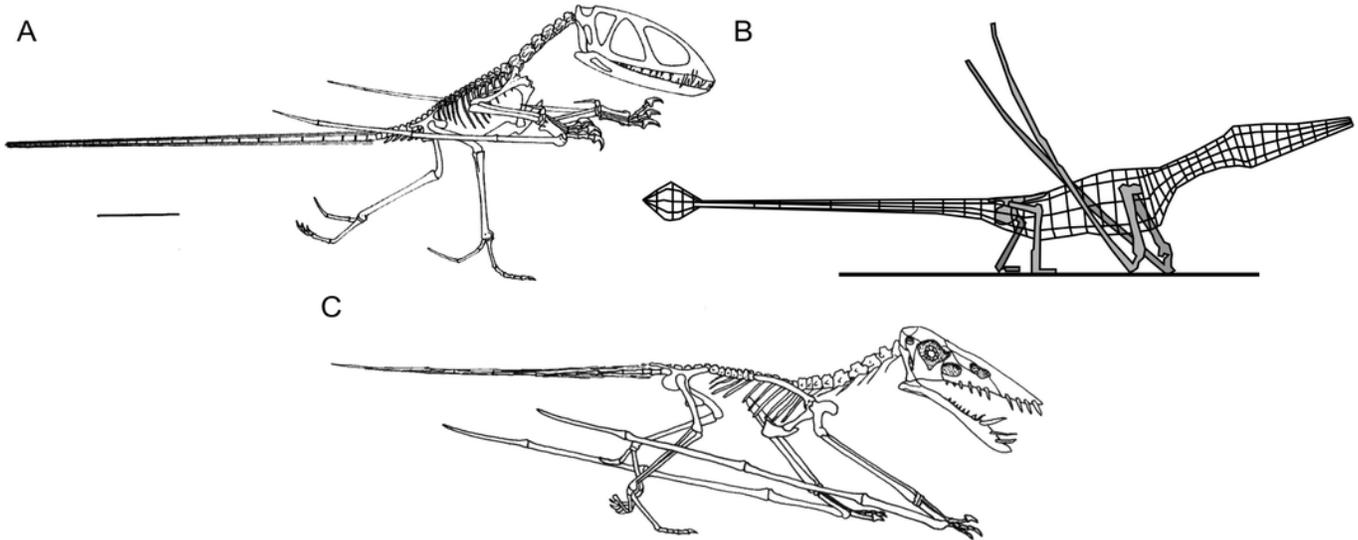
Pterosaur and bat uropatagia compared

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. _

A — WPII, WP III, WPIV, Ep, Fem, Pel, Fib, Tib, Ta, i, ii, iii, iv, v, Cv

B — Pro, Brachio, Uro

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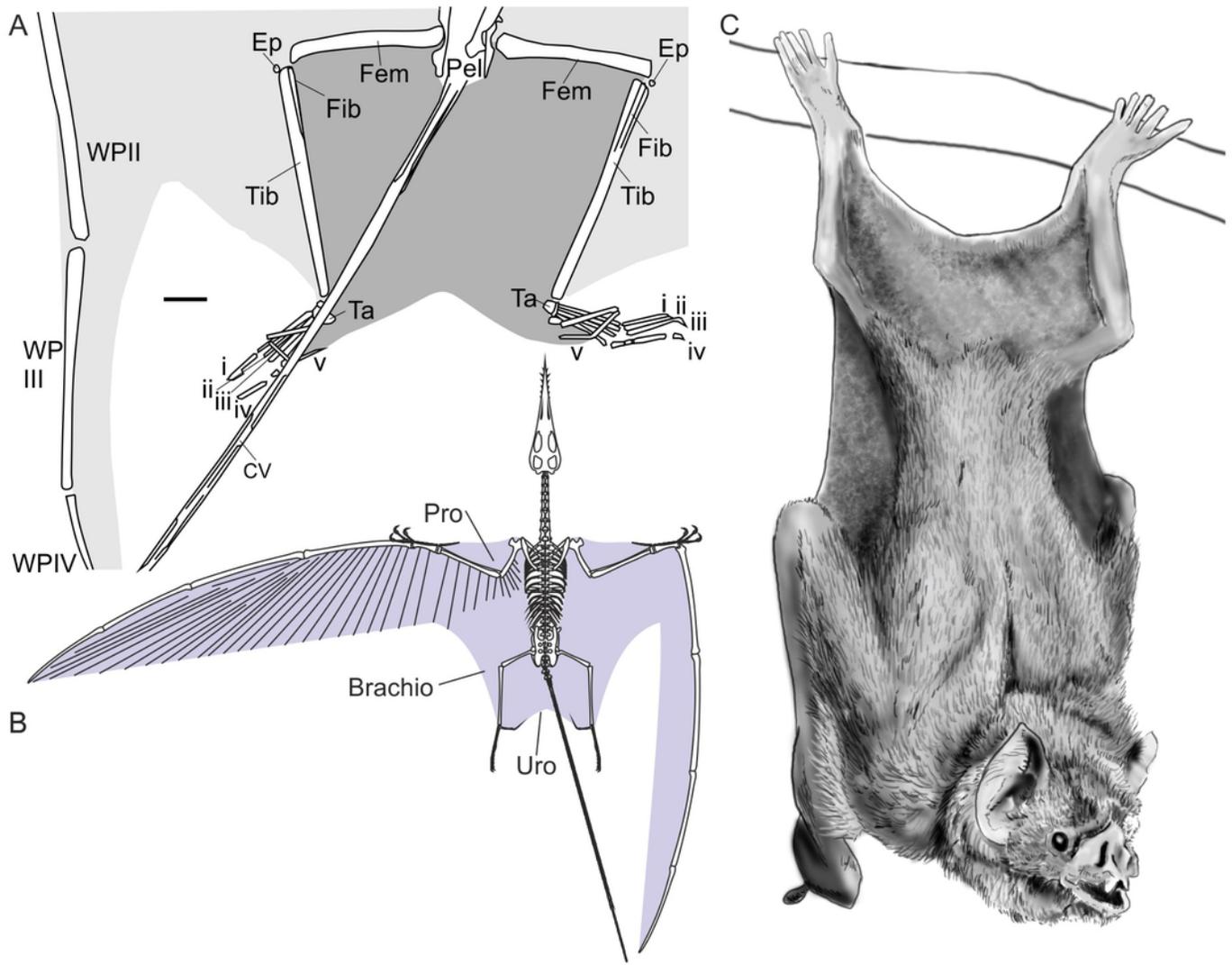
Non-pterodactyloid glenoid morphology

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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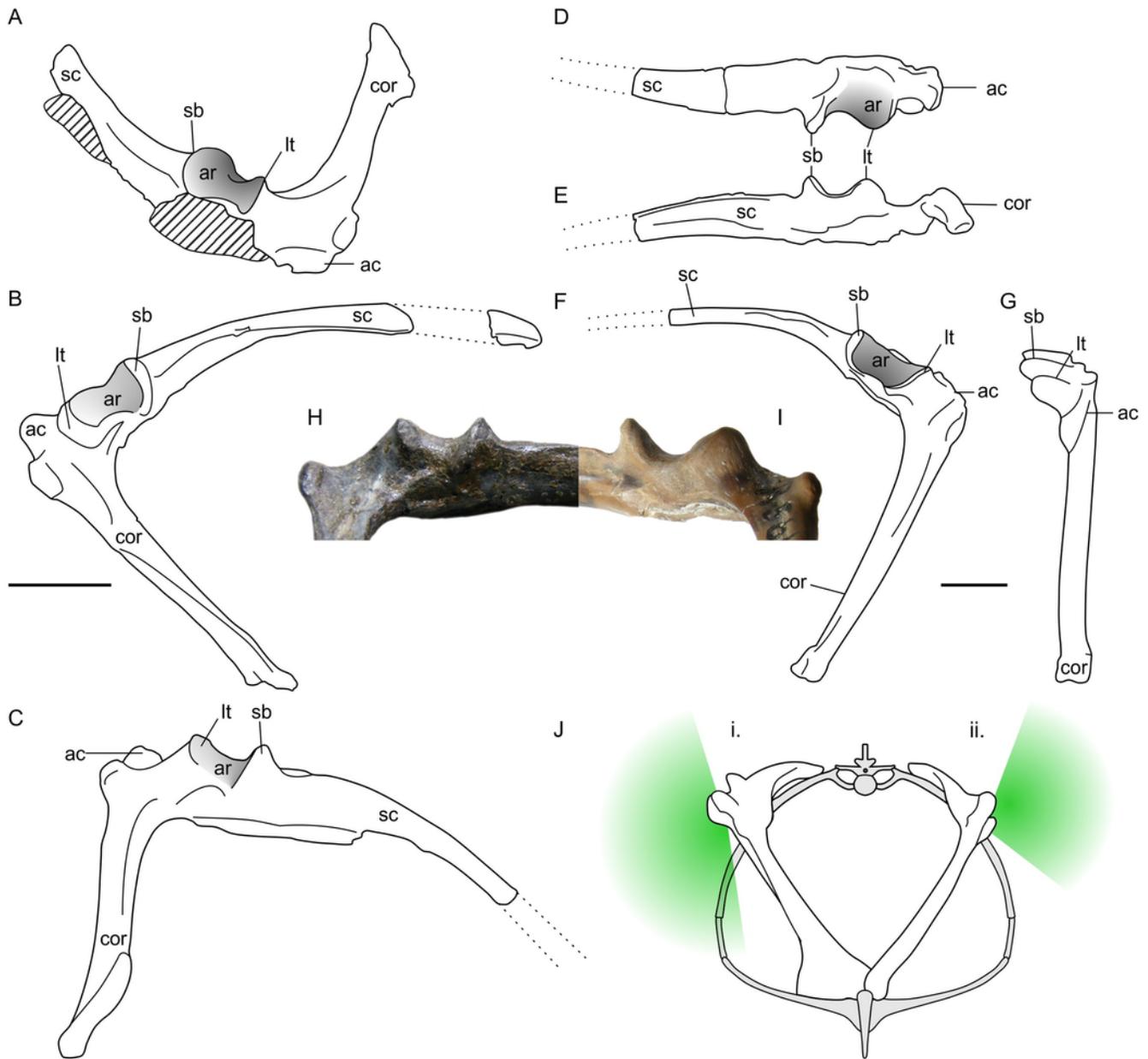
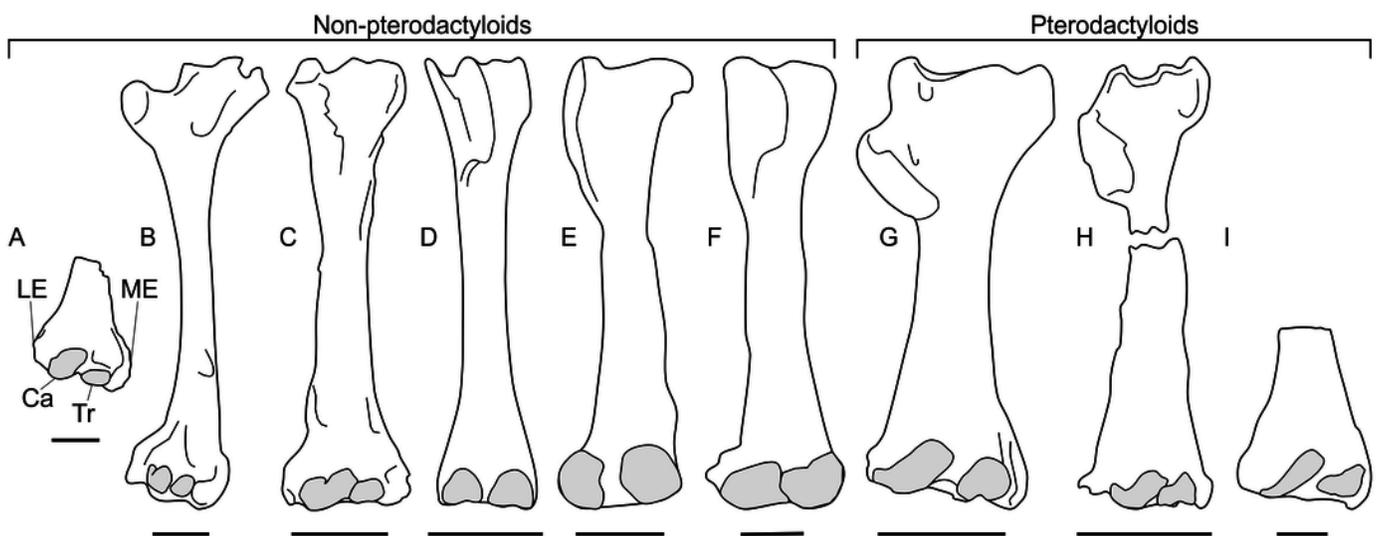

Pterosaur humeri in anterior view

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

5

Skeletal reconstructions of non-pterodactyloid pterosaurs

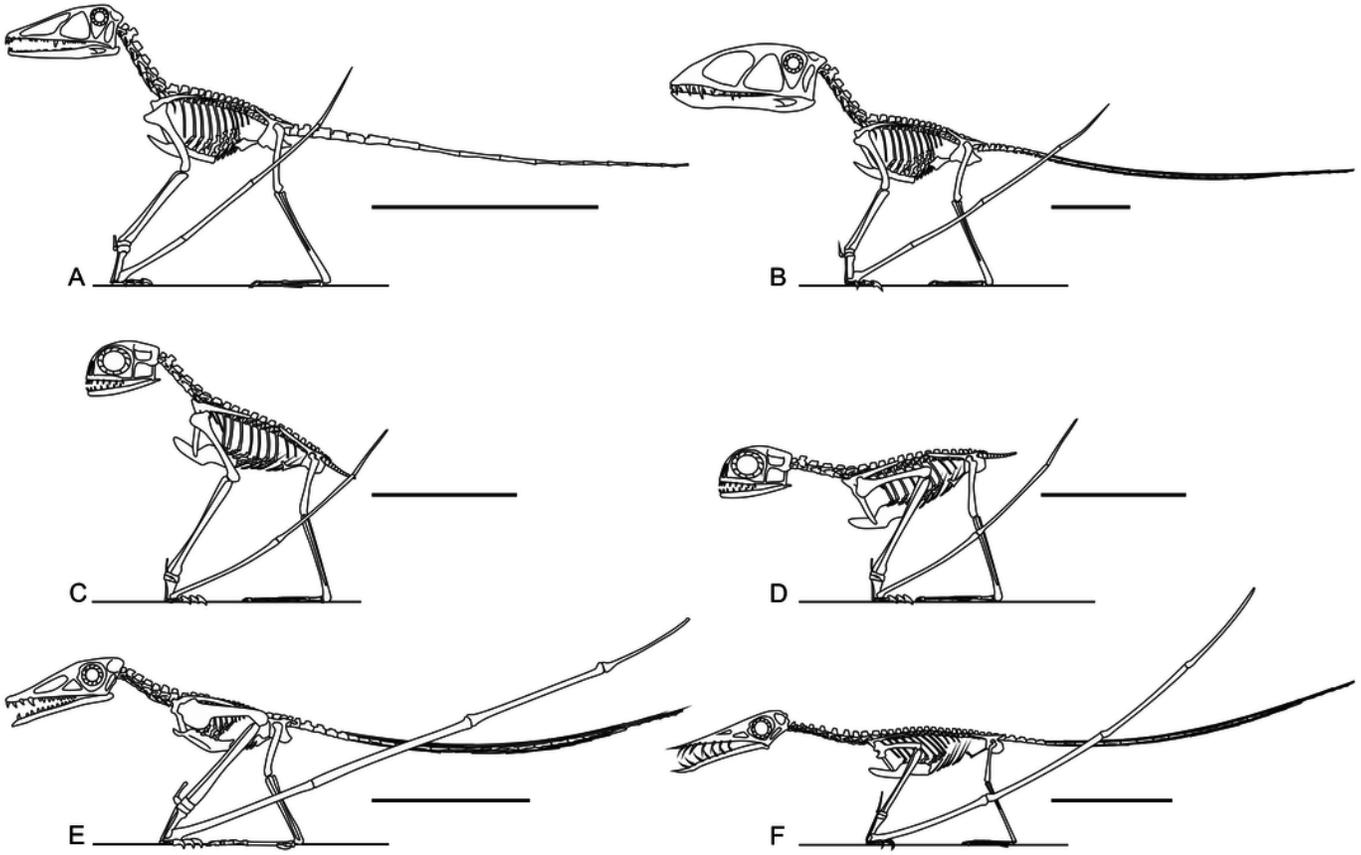
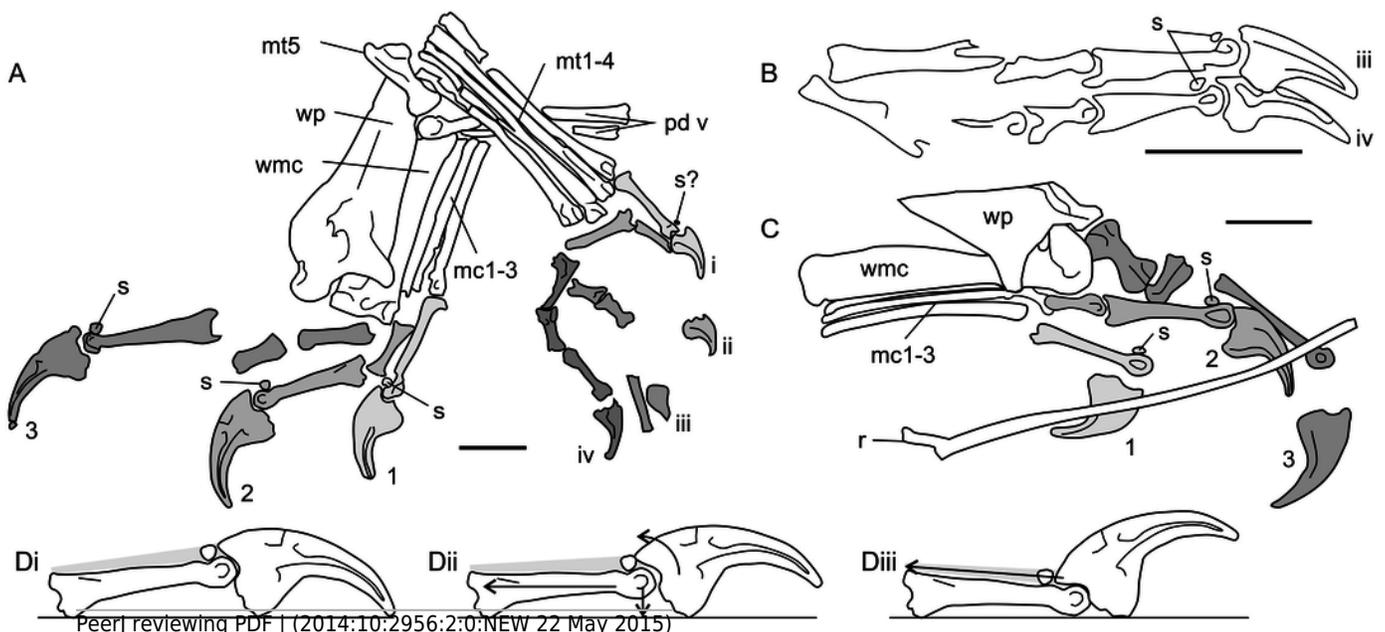
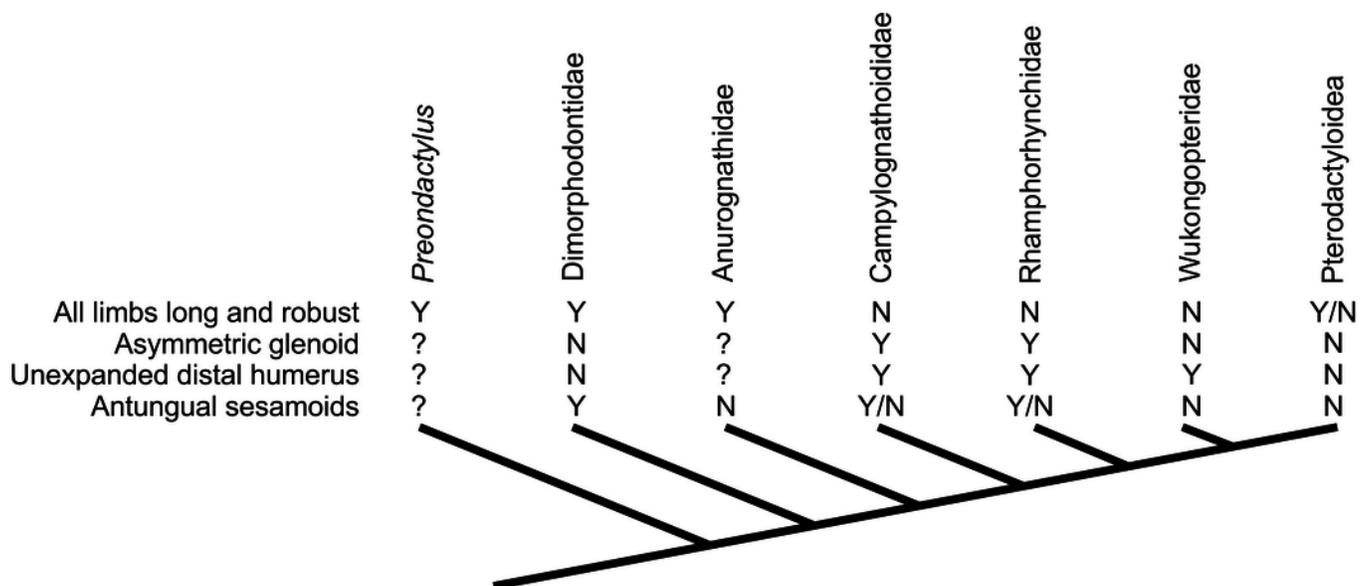
Figure 5. Are non-pterodactyloids ubiquitously equipped with short, slender limbs? Skeletal reconstructions of taxa such as *Preondactylus bufarini* (A), *Dimorphodon macronyx* (B) and *Anurognathus ammoni* (C and D, in erect and crouched poses respectively, acknowledging the poorly known glenoid condition 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]

Antungual sesamoids in pterosaurs

Figure 6. Antungual sesamoids in pterosaurs. A, manus and pes of NHMUK 41212 *Dimorphodon macronyx*; B, partial pes skeleton of GSM 1546 *Di. macronyx*; C, manus of BSP 1938 I 49 *Dorygnathus banthensis*; D, proposed interactions of pterosaur unguals with hard substrates, and utilisation of antungual sesamoids (extensor tendon shown in grey shading). Di, terminal phalanges of *Dimorphodon* manual digit 2 show as resting on a hard substrate without loading; Dii, passive hyperextension of the ungual, where pulling or depressing the phalanges (force vectors shown with arrows) retract the ungual to contact the sesamoid; Diii, active hyperextension of the ungual, where the extensor tendon is pulled to clear the ungual tip of the ground using the additional lever arm length afforded by the sesamoid. A-C, shading and numbers denote identification of clawed digits (Arabic numerals for manual digits, unary for pedal). Some skeletal elements present on the illustrated specimens are omitted for clarity. mc1-3, metacarpals 1-3; mt1-4, metatarsals 1-4; mt5, metatarsal 5; pd v, pedal digit 5; r, dorsal rib; s, sesamoids; wmc, wing metacarpal; wp, wing finger proximal phalanx. Scale bars represent 10 mm.

7

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