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Abstract: The immense size of many pterosaurs is now well known to academics and laymen alike, but truly enormous forms with wingspans more than twice those of the largest modern birds were not discovered until 83 years after the first pterosaur fossils were found. These remains were discovered in an expedition to the Cretaceous chalk deposits of Kansas led by O.C. Marsh in 1870: initially revealing animals with 6.6 m wingspans, Marsh eventually found material from animals estimated to span 7.6 m. Marsh's record breaking pterosaur – the largest flying animal known for nearly 80 years – was equalled by a supposed wing bone described by C.A. Arambourg in 1954, and then surpassed with the discovery of the 10 m span azhdarchid *Quetzalcoatlus northropi* by D. Lawson in 1972. Subsequent fragmentary azhdarchid discoveries suggest even larger forms: reinterpreting Arambourg's 'wing bone' as a cervical vertebra suggests an animal with an 11–13 m wingspan, while the Romanian taxon *Hatzegopteryx thambema* is a particularly large and robust form with a 12 m wingspan. Giant pterosaur footprints are also known, with the largest footprints recording walking azhdarchids of comparable size to those suggested by body fossils.

The spectacular size of many prehistoric animals has almost certainly contributed to their popularity amongst scientists and laymen alike. The Mesozoic seems to have been particularly well stocked with large creatures, bearing enormous dinosaurs on land and gigantic marine reptiles in the seas and oceans. Another Mesozoic group, the pterosaurs, are renowned for not only being the largest Mesozoic vertebrates capable of flight but also the biggest volant animals of all time, with the largest pterodactyloids dwarfing any bird, bat or flying insect known from the past or present (e.g. Buffetaut *et al.* 2002, 2003). Such sizes have ingrained giant pterosaurs into popular culture, and their expansive wingspans have featured prominently in popular books on prehistoric life, television documentaries as well as innumerable films and novels. Their size has captured the imagination of palaeontologists too, and multiple generations of pterosaur workers have felt compelled to estimate the total size of even those animals known from only fragmentary remains (e.g. Marsh 1871; Gilmore 1928; Arambourg 1954; Lawson 1975; Buffetaut *et al.* 2002). Some authors have even openly admitted that they find the size of these pterosaurs so impressive that they are willing to estimate gross proportions of animals not known from even one complete bone, despite the large degree of uncertainty associated with such calculations (Frey & Martill 1996).

The enormous size of pterosaurs was not truly appreciated until their fossils had been known for over 80 years. Prior to 1870, the largest pterosaur fossils known were fragmentary remains from the Cretaceous Chalk of southern England that hinted at forms with wingspans of 3 m (Bowerbank 1854), a wingspan comparable with those of the largest modern birds (see Martill 2010). It was not until pterosaur remains were uncovered outside of Europe in 1870 that their gargantuan sizes were appreciated, while the truly enormous forms we know of today would have to wait another century before discovery. The pterosaur trackway record has also recently been found to record giant forms. There have also been several – sometimes rather unsubstantiated – claims of record pterosaur size, citing the existence of forms that may have defied all understanding of animal flight. The 140-year history of giant pterosaur discoveries are reviewed here, beginning with the discovery of the best known of all giant pterosaurs, *Pteranodon*.

Pteranodon and the discovery of pterosaurs in North America

The first discovery of gigantic pterosaurs is an event synonymous with the first uncovering of pterosaurs in North America, an accolade traditionally credited to O. C. Marsh and his teams working in the Smoky Hill Member of the Niobrara Formation, Kansas, in 1870. However, the story of discovering the first pterosaurs in the New World is not without

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complications. In actuality, Marsh's bitter rival, E. D. Cope, reported and named supposed American pterosaur material 5 years before Marsh's teams discovered their own. Marsh never mentioned these reports in any of his publications on pterosaurs, suggesting he was either unaware of their existence or simply ignoring them. Unlike Marsh's gigantic pterosaur material from Kansas, Cope's alleged pterosaur remains were of considerably smaller forms sourced from Triassic strata of Pennsylvania, making them the first claims of Triassic pterosaurs anywhere in the world. Cope initially called this material *Pterodactylus longispinis* (Cope 1866), but were placed in his new genus *Rhabdopelix* in his 1870 paper 'Synopsis of the extinct Batrachia, Reptilia and Aves of North America' (Cope 1870; note that the first portion of this paper appeared in 1869: *Rhabdopelix* was erected in the second section, published in 1870 – see Colbert 1966 for more details). The *Rhabdopelix* holotype was reported as being lost five decades later by F. von Huene, but this was supplemented by additional reports of possible pterosaur remains from the same deposit (Huene 1921). Ultimately, however, doubts over the pterosaurian affinities of Cope's finds became apparent. Colbert (1966) noted some similarities between the gliding reptile *Icarosaurus* and the *Rhabdopelix* holotype figured in Cope's 1866 publication, concluding that at least some of the bones identified by Cope as pterosaurian were probably from an *Icarosaurus*-like animal (now recognized as a kuehneosaurid lepidosauromorph – see Gauthier *et al.* 1988), and that *Rhabdopelix longispinis* be considered a *nomen dubium* on account of the fragmentary nature of the holotype and its unknown whereabouts. Wellnhofer (1978) retained *Rhabdopelix* within Pterosauria and referred Huene's (1921) pterosaur discoveries to the same genus, but could only identify them as 'Pterosauria indet.'. Wellnhofer (1991) later questioned the pterosaurian identity of this material and highlighted its possible kuehneosaurid affinities. Dalla Vecchia (2003) was even less confident about the identity of *Rhabdopelix*, stating that all material referred to this taxon could belong to any reptile with slender, hollow bones (e.g. small theropods, protosaurs, kuehneosaurids) and is not necessarily pterosaurian. Thus, while Cope pre-empted Marsh with the first claims of North American pterosaur fossils, his discoveries were apparently insufficient to credit him with the first discovery of pterosaurs on American soil.

Of course, even if Cope had found the first American pterosaurs, he would not have not found the first real pterosaurian giants, whereas Marsh certainly did. Marsh's discoveries were made in the Coniacian–Campanian Smoky Hill Chalk of Kansas, a deposit famous for its rich assemblage of marine reptiles, sharks, bony fishes and marine birds (Everhart 2005). Marsh's expeditions to the Niobrara Chalk found their first pterosaur remains in 1870 and, on their first expedition, uncovered pterosaur remains of unprecedented size. Amongst several pterosaur bones representing two individuals, Marsh's team recovered a wing metacarpal that suggested 'an expanse of wings not less than 20 feet [6.6 m]!' (Marsh 1871, p. 472). This estimate was more than twice that of the largest pterosaurs known at that time in Europe and provided the first indication that pterosaurs grew to wingspans in considerable excess of any modern flying animals. Marsh named these isolated remains '*Pterodactylus Oweni*' in honour of the famed British naturalist Sir Richard Owen (Marsh 1871), and would name another eight pterosaur species from the Niobrara Chalk over the next 11 years. Marsh described the supposed teeth of his first pterosaur species as being 'smooth and compressed', perhaps assuming that teeth associated with the pterosaur remains (Everhart 2005) belonged to the same animal. Given that virtually all pterosaurs known up until this time were toothed, Marsh's assumption that these associated teeth belonged to the pterosaur remains was reasonable. However, and possibly unbeknownst to Marsh, toothless pterosaurs had just been identified in Britain with a reappraisal of the Cambridge Greensand pterosaur *Ornithostoma*, a fragmentary specimen described – as a metacarpal – by Owen (1851) but reinterpreted by Seeley (1871) as the jaw of an edentulous pterosaur. Had Marsh known such pterosaurs existed, he may not have been so confident about allocating the loose teeth he discovered to his first pterosaur finds.

A return to Kansas allowed Marsh to procure additional material of his first pterosaur species (renamed '*Pterodactylus occidentalis*' following the discovery that '*Pterodactylus Oweni*' had already been used by Seeley 1864), including a virtually complete wing that verified his 6.6 m wingspan estimate (Marsh 1872). He also discovered additional specimens that hinted at a species spanning almost 22 ft (7.3 m), and placed these remains in a separate species, *Pterodactylus ingens* (Marsh 1872). Once again, Marsh assumed that this species bore teeth and described them as being relatively slender compared to *Pterodactylus occidentalis*. In fact, it was not until more complete skull remains were found in 1876 that Marsh discovered that the jaws of these pterosaurs were actually edentulous (Marsh 1876*a*) (see Fig. 1a for Marsh's first (1884) reconstruction of the *Pteranodon* skull). Marsh was clearly surprised at this discovery, emphasizing the words 'absence of teeth' in his two 1876 pterosaur papers (Marsh 1976*a*, *b*). Both papers emphasized the difference between the edentulous Niobrara forms and 'all forms known in the

Fig. 1. The giant pterosaur *Pteranodon.* (**a**) Marsh's 1884 reconstruction of the *Pteranodon* skull, his first published figure of any *Pteranodon* material (from Marsh 1884). (**b**) Restoration of a 7.25 m span *Pteranodon longiceps* in flight and standing compared to a human of 1.75 m height (proportions of *Pteranodon* based on FMNH PR 464; see Bennett 2001 for more details).

old world', suggesting that Marsh was still unaware of *Ornithostoma*. Marsh used the edentulousness of these forms, along with a distinctive posterodorally directed cranial crest, to establish a new genus, *Pteranodon*, and erected a third species, *Pteranodon longiceps*, as its type (Marsh 1876*a*). In the same publication Marsh placed all of his other Niobrara pterosaur species in the same genus and also commented on the enormous size of some *Pteranodon* skulls, with some fragments indicating skull lengths of over 4 ft (1.3 m). The same year saw Marsh report *Pteranodon* with wingspans of 7.6 m (Fig. 2c) and reallocate a previously named species of *Pteranodon*, *P. gracilis*, to a new genus of Niobrara pterosaur, *Nyctosaurus* (Marsh 1876*b*; note that Marsh (1881) renamed this genus *Nyctodactylus* following presumption that his first name was preoccupied; this was shown to be erroneous by Williston 1903). His description of this 'eight to ten feet' (2.4–3 m) span taxon as 'medium size' (Marsh 1876*b*, p. 480) demonstrates that the definition of a 'giant pterosaur' had shifted significantly in the 6 years since Marsh first reported *Pteranodon*.

Following Marsh's (1876*a*) claim of 7.6 m span *Pteranodon*, no pterosaur remains were found that could challenge it for the title of largest flying animal for almost a century, despite Eaton (1910) downsizing *Pteranodon* to a wingspan of 6.8 m. This reduced estimate was, in part, attributable to Eaton (1910) factoring flexion between wing bones into his span estimates, giving a more realistic wingspan of the living animal than simply adding the lengths of the wing bones and shoulder width. However, he provided no methodological details as to how he factored this flexion into his wingspan estimates, making his accuracy against other *Pteranodon* size estimates difficult to fathom. Larger pterosaurs were reported in 1966 when an almost complete skull of a new *Pteranodon* species, *Pteranodon sternbergi*, was described and suggested to belong to an individual spanning 30 ft (9.1 m) across the wings (Fig. 2e) (Harksen 1966).

This species, along with *Pteranodon longiceps*, are the only *Pteranodon* taxa still considered valid (Bennett 1994), but a reappraisal of the *Pteranodon* wingspan in a comprehensive review of all *Pteranodon* material by Bennett (2001) suggests that its size estimates have fared better than its taxonomy. Bennett (2001) agreed with Eaton (1910) that estimates of pterosaur wingspans should allow for flex in the wing joints and suggested that the wing bone lengths be added without the shoulder girth, the absence of which from the span-total accounting for the flexion between wing bones. Bennett (2001) did not consider the wingspan of the individual represented by the *Pteranodon sternbergi* skull as the largest *Pteranodon* known, instead suggesting that the biggest *Pteranodon* individual known is represented by an isolated radius and ulna that give an estimated wingspan of 7.25 m (Fig. 1b). This specimen is not from the Niobrara Formation, however, but the overlying Pierre Formation: the largest Niobrara individual, and also the largest *Pteranodon* recorded by relatively complete remains, suggests a wingspan of 6.25 m. These dimensions have been eclipsed in recent decades by the discovery of larger pterosaurs, but with almost 140 years of research history, over 1100 specimens known and comprehensive descriptions of its entire osteology (Eaton 1910; Bennett 2001), the status of *Pteranodon* as the most completely known giant pterosaur has yet to be challenged.

Azhdarchidae: long-necked giants

No pterosaur remains were discovered that indicated animals larger than *Pteranodon* for the first seven decades of the twentieth century. The average wingspans of Cretaceous pterosaurs, however, rose so that spans of 2–5 m became appreciated as typical for pterodactyloids (e.g. Hooley 1913; Gilmore 1928; Swinton 1948; Young 1964; Miller 1971). A potential record of a giant pterosaur was mentioned in a 1936 *Time* article (entitled 'Diggers' published 16 November) in which T. A. Stoyanow was reported to have discovered an enormous pterosaur in Jurassic deposits of Arizona. With a reported 10 m wingspan (Fig. 2d), this find would have been significant in not only being larger than *Pteranodon* but also in being three being times larger than any Jurassic pterosaur known, even today (see Carpenter *et al.* 2003). The find, however, was never documented beyond the *Time* article and was never followed up by other pterosaur workers. This lull in discoveries of giant pterosaurs was broken when C. A. Arambourg recovered the first evidence of non-American pterosaurs that rivalled *Pteranodon* in size around 1940. This 500 mm-long bone from Campanian phosphate mines in Jordan was interpreted as a wing metacarpal (Fig. 3a) and was suggested to represent an animal spanning 7 m, a size equal to the wingspan of *Pteranodon* (Arambourg 1954). The specimen was named *Titanopteryx philidelphiae* 5 years later (Arambourg 1959), but its affinities and significance would not become clear for several more decades.

It was not until the 1970s that relatively frequent discoveries of giant pterosaurs began again and the concept of giant pterosaur size was heightened further. A 544-mm long humerus (Fig. 3b) and other elements of a huge wing were recovered by D. Lawson in the Maastrichtian Javelina Formation of Texas in 1972, revealing that pterosaurs with wingspans far greater than 7 m once existed. The humerus of this giant is twice the size of even the largest *Pteranodon* humerus and suggested that this pterosaur, named *Quetzalcoatlus northropi* in 1975, had a wingspan of between 11 and 21 m, depending on which pterosaurs were used to extrapolate its size (Lawson 1975). A medial figure of 15.5 m was provisionally accepted until work on several smaller, more complete, *Quetzalcoatlus* skeletons (designated *Quetzalcoatlus* sp.) found at the same time as their giant brethren, but 40 km distant, indicated that an 11–12 m wingspan

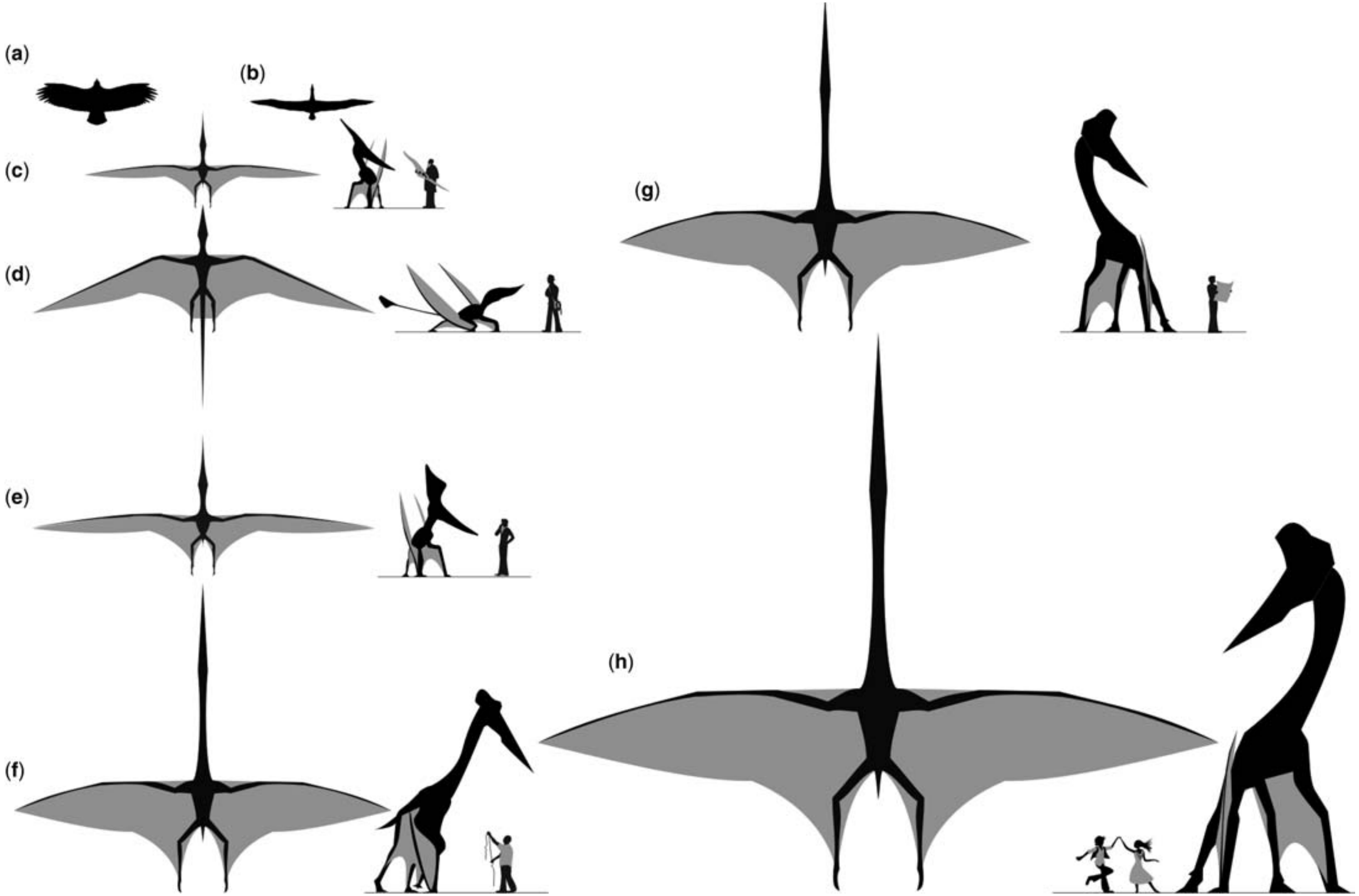

Fig. 2. Record claims of pterosaur wingspans and equivalent standing heights compared to (**a**) a 3 m span Andean condor (*Vultur gryphus*) and (**b**) a 3 m span wandering albatross (*Diomedea exulans*). (**c**) Marsh's (1876*a*) 7.6 m span *Pteranodon longiceps*. (**d**) Stoyanow's (16 November 1936, *Time Magazine*) apocryphal 10 m span Jurassic pterosaur. (**e**) Harksen's (1966) 9.1 m span *Pteranodon sternbergi*. (**f**) Lawson's (1975) 11 m span *Quetzalcoatlus northropi*. (**g**) The Buffetaut *et al.* (2002) 12 m span *Hatzegopteryx thambema*. (**h**) The erroneously reported BA Festival of Science 20 m span pterosaur. Humans used for scale are 1.75 m tall.

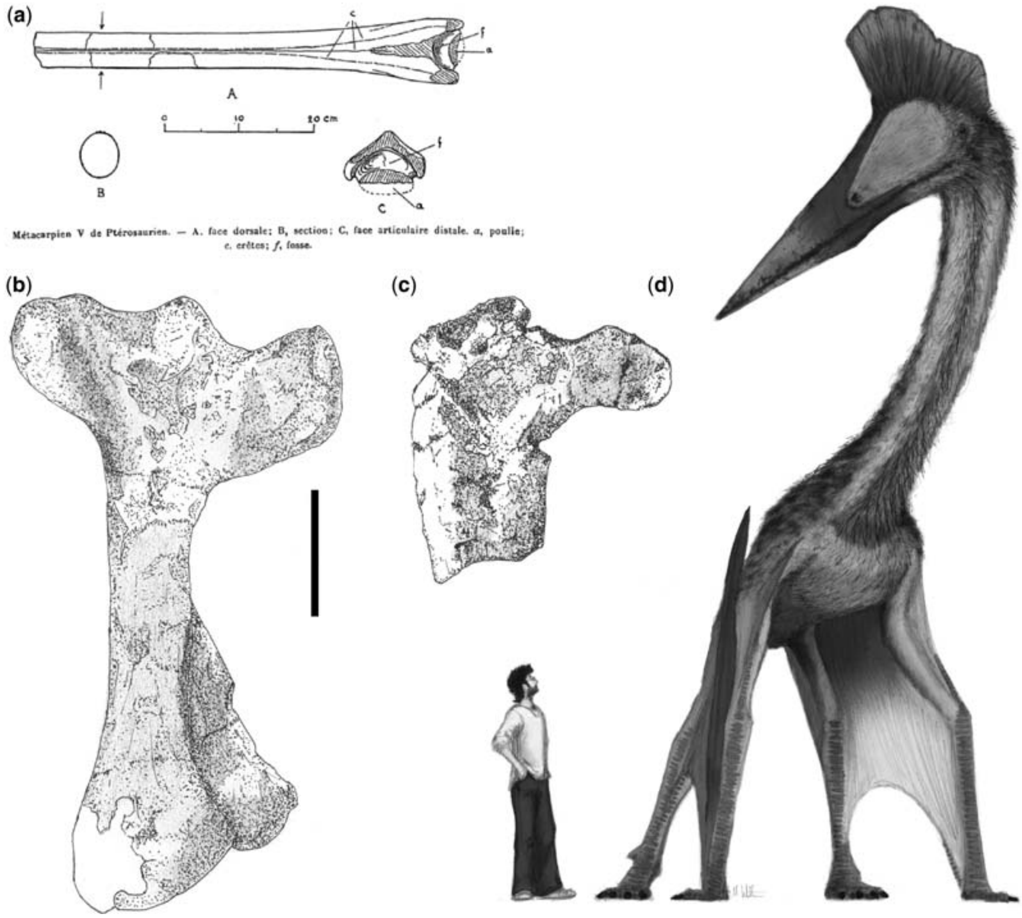

Fig. 3. Giant azhdarchids. (**a**) The earliest figured azhdarchid material: Arambourg's 1954 figure and figure caption of the *Arambourgiania* 'wing metacarpal', later revealed to be a cervical vertebra (modified from Arambourg 1954). (**b**) The 544 mm-long *Quetzalcoatlus northropi* left humerus (TMM 41450-3; drawn from Wellnhofer 1991). (**c**) Proximal left humerus fragment of *Hatzegopteryx thambema* (FGGUB R 1083; drawn from Buffetaut *et al.* 2002). Scale bar of (b) and (c) represents 100 mm. (**d**) Life restoration of 12 m span *Hatzegopteryx* next to a 1.75 m tall human.

estimate for *Quetzalcoatlus northropi* was more accurate (Langston 1981). This revision also appears to have incorporated arguments from aeronautical engineers who proposed that the skeleton of a 15–20 m span pterosaur would suffer overwhelming stresses during flight, a point with which Bakker (1986) argued strongly against. Stating that too little was known of the *Q. northropi* wing joints to curb wingspan estimates on account of engineering pitfalls, Bakker suggested that the original 15 m wingspan estimate should be accepted until there was good evidence to the contrary. However, given that a complete wing of the smaller *Quetzalcoatlus* species indicates that their wing fingers were proportionally short (Langston 1981), an 11 m wingspan seems more in keeping with *Quetzalcoatlus* anatomy than 15 or 20 m span estimates. Later discoveries of complete skeletons from smaller but closely related forms such as *Zhejiangopterus* (Cai & Wei 1994) add further confidence to the lower wingspan estimate of *Quetzalcoatlus northropi*. These estimates suggest that *Quetzalcoatlus northropi* had a wingspan almost 40% larger than that of *Pteranodon* (Fig. 2f), and it remains one of the largest known flying animals.

The long neck of *Quetzalcoatlus* generated almost as much interest upon its discovery as its large size and short wings. With several elongate, sub-cylindrical vertebrae – the longest of which is 8 times its width – the neck of *Quetzalcoatlus* provided an insight to the real identity of the

Titanopteryx holotype: Lawson (1975) re-identified Arambourg's pterosaur metacarpal as a cervical vertebra from a *Quetzalcoatlus*-like animal, and one with similar proportions to *Quetzalcoatlus northropi*. The following decade revealed another form similar to *Quetzalcoatlus* and *Titanopteryx*; *Azhdarcho* (Nessov 1984), and a new pterosaur group, Azhdarchinae, was erected to house them. Contemporaneously, Padian (1984) acknowledged the similarities between *Quetzalcoatlus* and *Titanopteryx*, and erected Titanopterygiidae as a group containing these taxa. Despite exclusively containing the world's largest pterosaurs, Padian (1984) stated of his Titanopterygiidae that '[g]reat size is not a diagnostic character' (p. 522) and used only features of the cervical vertebrae to qualify his group. By contrast, Nessov (1984) suggested that gigantic size was apomorphic for Azhdarchinae, a puzzling statement considering that *Azhdarcho* was not particularly large, with typical wingspans of 4–5 m and only rare individuals reaching 6 m (Bakhurina & Unwin 1995). Realizing that Azhdarchinae had precedence over Titanopterygiidae, Padian (1986) elevated the former to 'familial' rank – Azhdarchidae, and, again, defined the group exclusively by their elongate cervical vertebrae. More recent analyses have identified other azhdarchid characters (e.g. Unwin 2003), but their vertebrae remain highly diagnostic and are still used in determining the relationships of azhdarchids to other pterosaurs (e.g. Howse 1986; Bennett 1994; Unwin 2003; Kellner 2003; Andres & Ji 2008).

With the discovery of *Quetzalcoatlus* redefining the term 'giant pterosaur' from the 1970s onwards, the remains of a large Cretaceous pterosaur from Montana received little hyperbole despite indicating an animal of enormous size (wingspan 7.5–9 m; Padian 1984). A fragmentary femur from the Campanian Judith River Formation of Alberta (now the Oldman Formation of the Judith River Group: see Eberth 2005) was suggested to indicate an animal with a wingspan of 13 m (Currie & Russell 1982), providing the first evidence of an azhdarchid significantly larger than *Quetzalcoatlus*. This material has since been re-examined and is probably an ulna (Bennett pers. comm. 2009), suggesting the wingspan cited for this specimen by Currie & Russell (1982) is too high. A reappraisal of *Titanopteryx* provided alternative evidence for 13 m span pterosaurs, however, despite the misplacing of the *Titanopteryx* holotype by the late 1980s. Nessov & Jarkov (1989) saw fit to rename this pterosaur *Arambourgiania* after it became apparent that *Titanopteryx* was preoccupied by a blackfly, and a re-description of the specimen as a cervical vertebra by Frey & Martill (1996) was performed using plaster casts deposited in European and American museums. The holotype was later rediscovered in Jordan and additional descriptions of features not observable on the plaster cast were made by Martill *et al.* (1998). Comparing the incomplete *Arambourgiania* vertebra with those of *Quetzalcoatlus* sp. suggested that the former spanned 11–13 m: thus, Arambourg's *c.* 1940 discovery makes it the earliest find of a pterosaur larger than *Pteranodon*, albeit one that took 60 years to appreciate.

While work on *Arambourgiania* was underway, European deposits began to yield their first remains of giant pterosaurs. Martill *et al.* (1996) reported on a wing-finger fragment from a giant pterosaur found in Barremian–Aptian shales of the Isle of Wight, southern England, and suggested it may have spanned 9 m. The taxonomic position of this specimen could not established, but it remains noteworthy as the geologically oldest record of a giant pterosaur. Buffetaut *et al.* (1997) reported an azhdarchid cervical vertebra from Maastrichtian deposits of the French Pyrenees that indicated an animal of a similar size, while Company *et al.* (2001) reported a larger azhdarchid from the Maastrichtian of Valencia, Spain, with a wingspan of over 12 m. Recently, fragmentary remains of the largest pterosaur yet reported were recovered from the Maastrichtian Haţeg Basin of Romania (Buffetaut *et al.* 2002, 2003). The remains, named *Hatzegopteryx thambema*, include the only skull material known from a giant azhdarchid and are noteworthy for their unusually robust construction. The fragmentary skull bones indicate a jaw width of 500 mm (Buffetaut *et al.* 2003): if a 'typical' neoazhdarchian jaw length/width ratio (averaged to 0.2 across seven taxa: see Witton 2008, table 2) is assumed for *Hatzegopteryx*, its jaws may have been around 2.5 m long. Such a figure grants *Hatzegopteryx* with one of the longest skulls of any non-marine vertebrate, an accolade made all the more remarkable when it is considered that most non-marine animals with atypically large skulls – such as ceratopsian dinosaurs – only achieve comparable lengths through 'accessory' structures such as supraoccipital frills and spikes. If *Hatzegopteryx* has a skull like those of other azhdarchids, the estimated 2.5 m length would represent the jaws alone, granting it a larger gape than even the biggest theropod dinosaurs (see Dal Sasso *et al.* 2005). The *Hatzegopteryx* humerus (Fig. 3c) is also more robust than that of *Quetzalcoatlus*, suggesting it had a minimum wingspan of 12 m (Fig. 2g) and, when standing, a shoulder height of 3 m (Fig. 3d).

Grounded giants: giant pterosaur footprints

The 1952 discovery of pterosaur footprints in Upper Jurassic deposits of Arizona by W. L. Stokes (Stokes 1957) was integral to understanding pterodactyloid terrestrial locomotion. Controversy reigned over the identification and interpretation of these tracks for several years, and, although a rough consensus has since been reached, some arguments remain to be settled (see Lockley *et al.* 1995; Bennett 1997; Unwin 1997, 2005; Mazin *et al.* 2003; Padian 2003). Stokes' pterosaur tracks were made by pterosaurs of moderate size, with 76 mm-long pes prints and 83 mm-long manus prints, and most pterosaur prints found subsequently are of comparable size or smaller (e.g. Mazin *et al.* 1995; Lockley & Wright 2003; Padian 2003; Rodriguez-de la Rosa 2003). Two possible pterosaur track sites contain prints considerably larger than those in Stokes' (1957) trackway, however, and suggest that larger pterosaurs – perhaps even giants – also have an ichnological record. *Purbeckopus pentadactylus* was first described by J. B. Delair (1963) from Lower Cretaceous deposits of the Purbeck Group, southern England, and later interpreted as a pterosaur trace by Wright *et al.* (1997). With 150 mm-long manus prints and 200 mm-long pes prints (Fig. 4b and c), *Purbeckopus* records a large pterosaur with an estimated 5–6 m wingspan: while this size may not constitute a 'giant' pterosaur as known from the pterosaur body fossil record, *Purbeckopus* is a relatively enormous pterosaur track with prints roughly twice those of other pterosaur footprints. A more specific identification of the *Purbeckopus*-trackmaker is not clear, but possible 'beakprod' marks made by the *Purbeckopus* trackmaker suggest it bore at least partially edentulous jaws. Note, however, that the identification of *Purbeckopus* as a pterosaur track has recently been questioned: Billon-Bruyat & Mazin (2003) argued that crucial details of the *Purbeckopus* tracks are indeterminable, and that there is no clear association between alleged pes and manus prints, suggesting further work is needed to confirm its status as a pterosaur trace.

More confidently identified and considerably larger pterosaur tracks were described in 2002. The prints, including several isolated footprints and trackways from Santonian–Campanian age deposits of South Korea, were placed in the new ichnotaxon *Haenamichnus*, with some particularly large specimens placed in the new ichnospecies *Haenamichnus uhangriensis* (Hwang *et al.* 2002). Unlike most pterosaur trackways, the distinctive form of *Haenamichnus* has allowed for a more precise identification of its maker to be established, with several aspects of their morphology showing similarities with what is known of azhdarchid feet. Although only known from few specimens, azhdarchids seem to bear slender but robust pedes, metatarsals of almost equal length, digits approximately half the metatarsal length and reduced pedal claws (Hwang *et al.* 2002). Because many of these details are demonstrated by the *Haenamichnus* prints, it is likely that they record the movements of azhdarchids, and their size and age corroborate this hypothesis. Thus far, only large *Haenamichnus* prints are known: virtually all pes prints are over 150 mm long and most are over 200 mm. A trackway comprised of 14 footprint pairs (average pes print length of 228 mm) constitute the longest continuous pterosaur trackway known at 7.3 m long. Scaling these prints with complete azhdarchid skeletons suggest a pterosaur with an 8 m wingspan and standing shoulder height of 2 m. However, the largest *Haenamichnus* pes prints are up to 350 mm in length with only marginally shorter manus prints (Fig. 4d and e): scaling these prints suggests animals standing 3 m tall at their shoulders and wingspans comparable with those predicted for the largest azhdarchid body fossils.

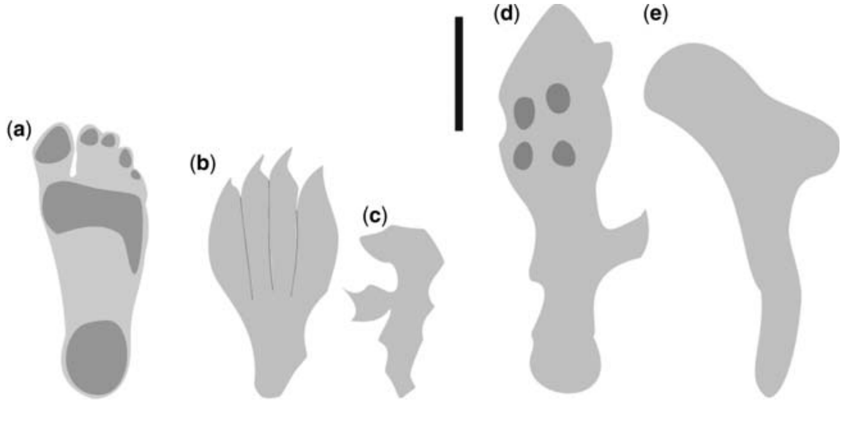

Fig. 4. Giant pterosaur footprints compared to a human (280 mm-long) footprint (**a**). (**b**) and (**c**) *Purbeckopus pentadactylus* right pes and left manus print (drawn from Wright *et al.* 1997). (**d**) and (**e**) *Haenamichnus uhangriensis* right pes and manus prints (drawn from Hwang *et al.* 2002). Scale bar represents 100 mm.

Even larger?

Since the discovery of the 10 m span *Quetzalcoatlus*, evidence of pterosaurs of equal or larger proportions have been reported in relatively quick succession (e.g. Padian 1984; Frey & Martill 1996; Martill *et al.* 1996; Buffetaut *et al.* 1997, 2002; Company *et al.* 2001; Hwang *et al.* 2002). Even these giants, however, were dwarfed by the claim of a 20 m span pterosaur made in 2005 (Fig. 2h). Tales of enormous pterosaur footprints in Mexico and a huge wing bone from Israel were revealed in a press conference at the 2005 British Association Festival of Science prior to any formal publication of either find, and an excited media quickly widely reported this announcement in newspapers, magazines and numerous websites around the world (for examples of coverage in the British press, see 9 September 2005 editions of *The Guardian* (p. 9) and *The Daily Mail* (p. 25). However, subsequent reappraisals of the alleged discoveries suggest that the footprints belong to a large theropod dinosaur and the 'wing bone' is, in fact, a particularly large piece of fossil wood (Frey pers. comm. 2007). Clearly, the claims of 20 m flying reptiles were made somewhat prematurely. It is intriguing to speculate, however, whether or not such a pterosaur *could* exist. Several lines of biomechanical evidence suggest that known pterosaur skeletal morphology may not permit them to obtain such sizes: any pterosaur with a wingspan above 12 or 13 m is likely to have considerable difficulty in becoming airborne, and would render its wing long bones and joints highly vulnerable to buckling and torsional forces once in flight (Cunningham & Habib pers. comm. 2008). Hence, although the fossil record has repeatedly confounded vertebrate palaeontologists and biomechanists who have attempted to speculate on the maximum size of extinct animals, a 20 m span pterosaur would be a surprise to any pterosaur researcher and would need to be a wholly different beast to any flying reptile currently known.

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