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 Hand and foot morphology maps invasion of terrestrial environments by pterosaurs in the mid-Mesozoic

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Article

Hand and foot morphology maps invasion of terrestrial environments by pterosaurs in the mid-Mesozoic

Highlights

- The hands and feet of pterosaurs were adapted to a broad range of locomotor ecologies

- Early pterosaurs had a scansorial mode of life, which restricted maximum body size

- Anatomical changes in later pterosaurs led to more effective terrestrial ability

- Invasion of terrestrial habitats facilitated diverse feeding ecologies and gigantism

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In brief

Smyth et al. show that pterosaurs exhibit significant disparity in their hand and foot morphologies. This indicates that they occupied a broad range of locomotor ecologies. Early pterosaurs were adapted for climbing, while later forms evolved more effective terrestrial locomotion, which facilitated diversification and the evolution of gigantism.

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Hand and foot morphology maps invasion of terrestrial environments by pterosaurs in the mid-Mesozoic

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SUMMARY

Pterosaurs, the first true flying vertebrates, played a crucial role in Mesozoic terrestrial ecosystems. However, our understanding of their ability to move around on the ground and, more broadly, their terrestrial paleoecology remains limited. Here, we demonstrate an unexpectedly high degree of variation in the hands and feet of pterosaurs, comparable with that observed in extant birds. This suggests that pterosaurs were adapted to a remarkably broad range of non-aerial locomotor ecologies. Small, early, long-tailed pterosaurs (non-pterodactyliforms) exhibit extreme modifications in their hand and foot proportions indicative of climbing lifestyles. By contrast, the hands and feet of later, short-tailed pterosaurs (pterodactyliforms) typically exhibit morphologies consistent with more ground-based locomotor ecologies. These changes in proportions correlate with other modifications to pterosaur anatomy, critically, the separation along the midline of the flight membrane (cruropatagium) that linked the hindlimbs, enabling a much more effective locomotory ability on the ground. Together, these changes map a significant event in tetrapod evolution: a mid-Mesozoic colonization of terrestrial environments by short-tailed pterosaurs. This transition to predominantly ground-based locomotor ecologies did not occur as a single event coinciding with the origin of short-tailed forms but evolved independently within each of the four principal radiations: euctenochasmatians, ornithocheiroids, dsungaripteroids, and azhdarchoids. Invasion of terrestrial environments by pterosaurs facilitated the evolution of a wide range of novel feeding ecologies, while the freedom from limitations imposed by climbing permitted an increase in body size, ultimately enabling the evolution of gigantism in multiple lineages.

INTRODUCTION

Pterosaurs were a key constituent of Earth's terrestrial biotas from the Late Triassic to the end of the Cretaceous (227–66 million years ago [mya]).[1–3] The first vertebrates to achieve active flapping flight, pterosaurs were anatomically and ecologically diverse and distributed worldwide throughout much of their history. Traditionally, pterosaurs have been divided into two groups: "rhamphorhynchoids," a paraphyletic grade characterized by several plesiomorphic features, including a long tail (Figures 1A and 1C), and pterodactyloids, a derived clade with a highly reduced tail (Figures 1B and 1C). Increasingly sophisticated phylogenetic analyses[4–6] and recent additions to the fossil record of species such as *Douzhanopterus zhengi*[7] and *Propterodactylus frankerlae*,[8,9] posited as "transitional" forms, mean that these terms are no longer sufficient to describe the morphological transformations that underpin pterosaur evolutionary

history. Consequently, here we have adopted two additional terms that permit more precise characterization of pterosaur morphological variation, phylogeny, and evolution. Non-pterodactyliforms, a paraphyletic grouping of early pterosaurs (Figure 1D), thrived during the early Mesozoic (Late Triassic to Late Jurassic).[4] This grade group is united by a bauplan comprising a more typically archosaurian skull morphology compared with later pterosaurs, a short neck, an elongated tail, and a well-developed fifth pedal digit that supported a membranous wing panel stretching between the hindlimbs—the cruropatagium (Figures 1A and 1C). Pterodactyliform pterosaurs (*Propterodactylus* + *Douzhanopterus* + pterodactyloids) are distinguished by large, extensively pneumatized skulls, elongated necks, short tails, and reduced fifth pedal digits. These features become even more pronounced among the pterodactyloids, which also develop a bifurcated and significantly reduced cruropatagium (Figures 1B and 1C). Pterodactyloids were the
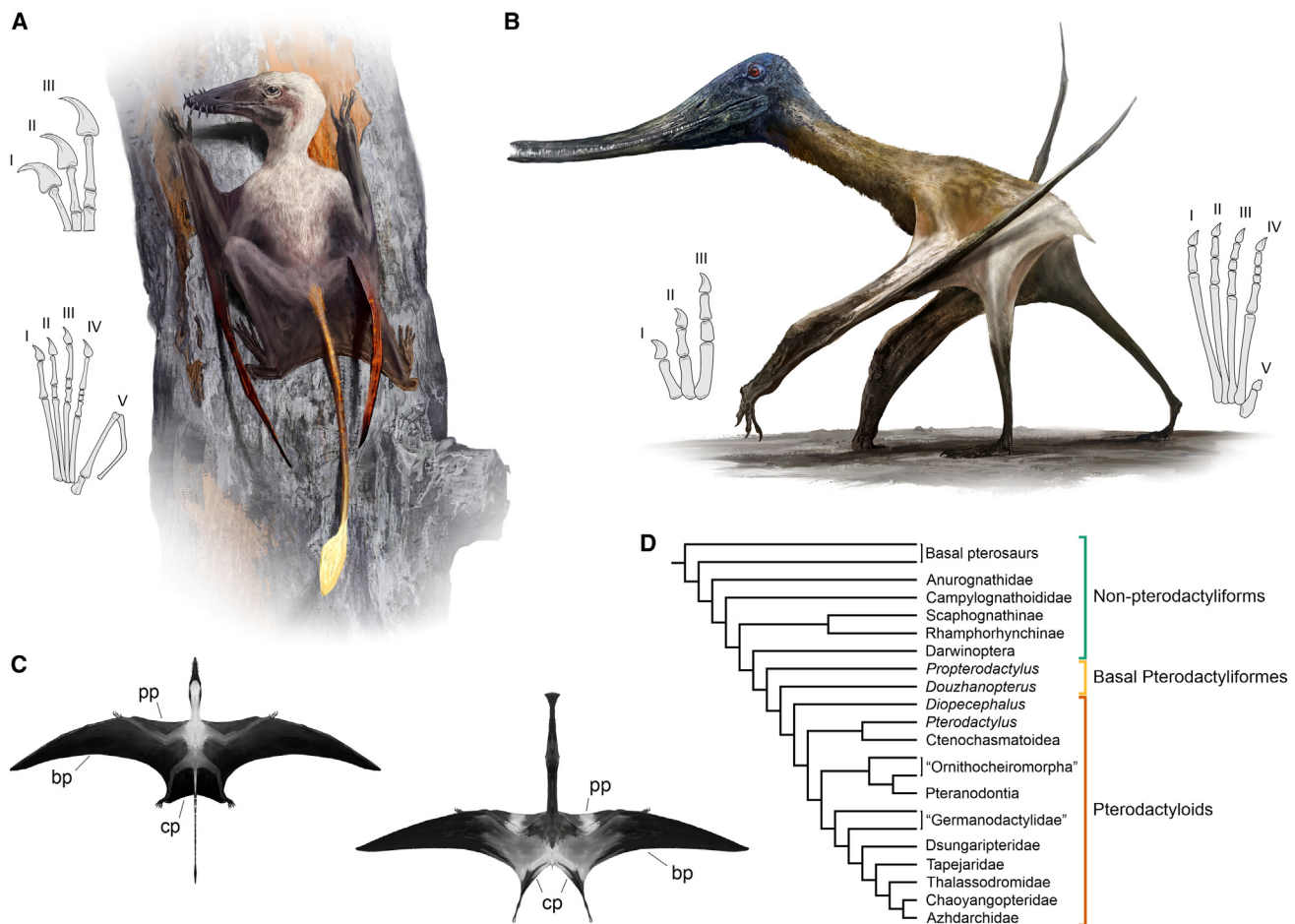
Figure 1. Comparison of autopodial and other anatomical differences between non-pterodactyliform (scaphognathine) and pterodactyliform pterosaurs (derived ctenochasmatoid)

(A) Paleoart reconstruction of the non-pterodactyliform *Scaphognathus crassirostris* (Upper Jurassic) in scansorial mode, with autopodia characterized by short proximal elements and elongated distal elements.

(B) Paleoart reconstruction of the pterodactyliform *Balaenognathus maeuseri* (Upper Jurassic) in terrestrial mode, with autopodia characterized by elongated proximal elements and shortened distal elements.

(C) Reconstructions of *Scaphognathus* (left) and *Balaenognathus* (right) in dorsal view indicating the principal flight surfaces.

(D) Simplified pterosaur phylogeny indicating the principal taxonomic groups used in this study.

Abbreviations: bp, brachiopatagium; cp, cruropatagium; pp, propatagium. Paleoart by Rudolf Hima.

most successful group of pterosaurs in the later part of the Mesozoic (Late Jurassic and Cretaceous).

Although advances have been made in understanding pterosaur skeletal and soft tissue anatomy,[1–3] phylogeny,[10] flight,[11,12] and ontogeny,[13] their non-aerial locomotor abilities and ecologies are poorly known. It is generally accepted that grounded pterosaurs were quadrupedal, with a functional tridactyl digitigrade manus and functional tetradactyl plantigrade pedes.[14] Uniquely among flying animals, manual digit IV and pedal digit V were exapted from their original functions to become flight structures.[15,16] However, attempts to identify the terrestrial capabilities and feeding ecologies of specific clades have created much controversy,[17,18] and the terrestrial abilities of both non-pterodactyliforms[17] and pterodactyliforms are highly debated.[19–21] Despite these controversies, pterosaur hand and foot morphologies have been largely overlooked,[14,22,23] with little documentation of how these vary across Pterosauria. This

oversight is particularly remarkable considering the fundamental role they play in locomotion. Comparative analysis of manus and pes morphologies could provide important new insights into the ecological roles of pterosaurs within Mesozoic biotas and how this impacted on contemporaneous vertebrate groups, among them a plethora of other volant and gliding Mesozoic amniote groups, including birds.[24–26]

Hands and feet—or autopodia—perform a wide range of functions, facilitating locomotion across various modes, including walking, running, jumping, burrowing, swimming, climbing, and flying.[27] Because the functions of autopodia are so closely tied to specific locomotor modes and ecologies of organisms, the degree to which locomotor modes influence their morphology is often greater than in the rest of the appendicular skeleton.[28–31] Numerous paleontological studies have employed comparative datasets of extant tetrapod autopodia to reconstruct the locomotory modes of extinct animals.[32–36] Until now, the pterosaur

autopodial skeleton (excluding the wing elements) has contributed little to our understanding of their non-aerial locomotor ecology, primarily due to lack of available morphometric data for manual and pedal elements.

In this study, we compiled a comprehensive morphometric dataset for the manus and pes that includes ~64 taxa, representing 18/20 principal pterosaur groups and ranging across their entire history, from the Upper Triassic to Upper Cretaceous (supplemental information). The dataset consists, primarily, of length measurements of phalanges forming digits I–III of the manus (the "claw digits") and pedal rays I–IV of the pes. Statistical analyses of these data (see STAR Methods) generated numerical measures of the morphological disparities of the pterosaur manus and pes that were then framed within a broader context using a comparative dataset for a wide range of amniotes, including reptiles, birds, and mammals (supplemental information). Among these extant groups, phalangeal proportions—most notably the relative proportions of the phalanges of manual and pedal digit III—are strongly correlated with locomotor ecology (see STAR Methods). By comparing this dataset with the same phalangeal proportions for the manus and pes of pterosaurs, we were able to infer their likely non-aerial locomotor ecologies. Finally, we integrated these results with a phylogenetic analysis enabling us to use ancestral reconstruction to position these pterosaur locomotor ecologies within a broader macroevolutionary context. The results of this analysis revealed a macroevolutionary event in which pterodactyloid pterosaurs invaded terrestrial environments in the Middle Jurassic. This transition marked the emergence of proficient terrestrial ability in pterosaurs, triggering a dramatic diversification of dietary ecologies. Additionally, they achieved an extraordinary range of body sizes, unmatched by any other flying animals.[2,37,38]

RESULTS

Disparity in the pterosaurian manus and pes

Morphological patterns of pterosaur autopodial disparity were examined using multivariate analyses of linear measurements of the manual and pedal elements that would have contacted the substrate during non-aerial locomotion. This included the phalanges of manual digits I–III, as well as the metatarsals and pedal phalanges of digits I–IV (see STAR Methods). Manual digits I–III exhibit substantial disparity between non-pterodactyliforms and pterodactyliforms (basal Pterodactyliformes + Pterodactyloidea) in principal component analysis (PCA) (PERMANOVA: p = 1e−6) (Figures 2A and 3A). Principal component 1 (PC 1) reflects differences in the relative proportions of proximal and distal elements of the manual digits, accounting for 65.7% of the total variance in manual disparity across Pterosauria. Linear discriminant analysis (LDA) correctly identified 98.0% of specimens. Non-pterodactyliforms possess shortened proximal phalanges and elongated distal phalanges, while pterodactyloids exhibit a contrasting morphology with elongated proximal phalanges and reduced distal phalanges.

Disparity in pedal proportions (pedal rays I–IV) is also significant (PERMANOVA: p = 0.001) yet shows a high degree of overlap in PCA (Figures 2B and 3B). PC 1 largely reflects the relative length of the metatarsus, with shorter metatarsals corresponding to lower PC 1 scores and elongated metatarsals associated with

higher values. Differences in metatarsal length account for most of the disparity across Pterosauria (66.6%) and LDA correctly classified 96.2% of specimens. Non-pterodactyliforms generally exhibit shorter metatarsals, though exceptions include anurognathids and rhamphorhynchines, which have exceptionally long metatarsals. Several pterodactyloids, including *Diopecephalus*, "ornithocheiromorphs," and tapejarids, have relatively short metatarsals (Figure 3B). PC 2 primarily reflects disparity in pedal digit proportions comparable with those identified in the manus plot, with low PC 2 scores indicating elongated proximal phalanges and shortened distal pedal phalanges and high PC 2 scores indicating the presence of shortened proximal phalanges and elongated distal phalanges. When non-pterodactyliforms and pterodactyliforms are compared, there is no obvious separation (Figure 2B), but this overlap is largely due to a few outlying clades. Most non-pterodactyliform clades exhibit short proximal and elongate distal phalanges, with the exception of Triassic and a few Lower Jurassic taxa (Figure 3B). Most pterodactyloid clades possess more elongate proximal and shorter distal phalanges. The basal pterodactyloid *Diopecephalus*, tapejarids, and the ornithocheiromorph *Zhenyuanopterus* are again unusual in having elongated distal pedal phalanges.

To better understand the scale of this disparity in pterosaur phalangeal proportions, we compared the ratio of pedal phalanx III-3/pedal phalanx III-1 (or penultimate phalanx/proximal phalanx) across a range of digitigrade and plantigrade amniote groups, both extant and extinct (Figure 4A). Pedal proportions were chosen for their persistent use in locomotion, even in bipedal animals. Unexpectedly, pterosaurs show a greater disparity (0.54–3.12) than all other groups except for extant birds (0.25–3.63). Lepidosaurs also exhibit relatively high disparity (0.21–2.07), while mammals generally show low disparity (bats = 0.71–1.01; other mammals = 0.39–1.10), with only the suspensorial sloth (*Choloepus* sp.) as an extreme outlier (3.00). Other archosaurs, including pseudosuchians and non-avian dinosaurs, exhibit markedly conservative ratios (0.20–0.96).

Phalangeal proportions and their relationship to locomotor modes

Differences in the relative lengths of the proximal and penultimate phalanges of digit III are closely correlated with preferred scansorial, arboreal, or terrestrial locomotor modes in amniotes (Figure 4B).[39] Phalanx III-3/III-1 ratios serve as a reliable indicator that differentiates between grasping/gripping locomotor ecologies (scansorial and arboreal) and terrestrial locomotor ecologies (Figure S1). Scansorial and arboreal animals typically possess short proximal phalanges and elongated penultimate phalanges, with the principal loading aligned with the long axis of the digits.[40,41] This arrangement of phalanges facilitates extended reach, enhanced grasping capability, and heightened gripping forces through elongation of the lever arm, particularly in the penultimate phalanges.[40,41] The adaptive pressures imposed by terrestrial locomotion, in which the principal axis of loading is perpendicular to the digits, favors the development of elongated proximal phalanges and shortened penultimate phalanges. Configurations of this kind, typical for the manus and pes of most, but not all, pterodactyloids, aid terrestrial locomotion by improving weight-bearing and stability, reducing loading
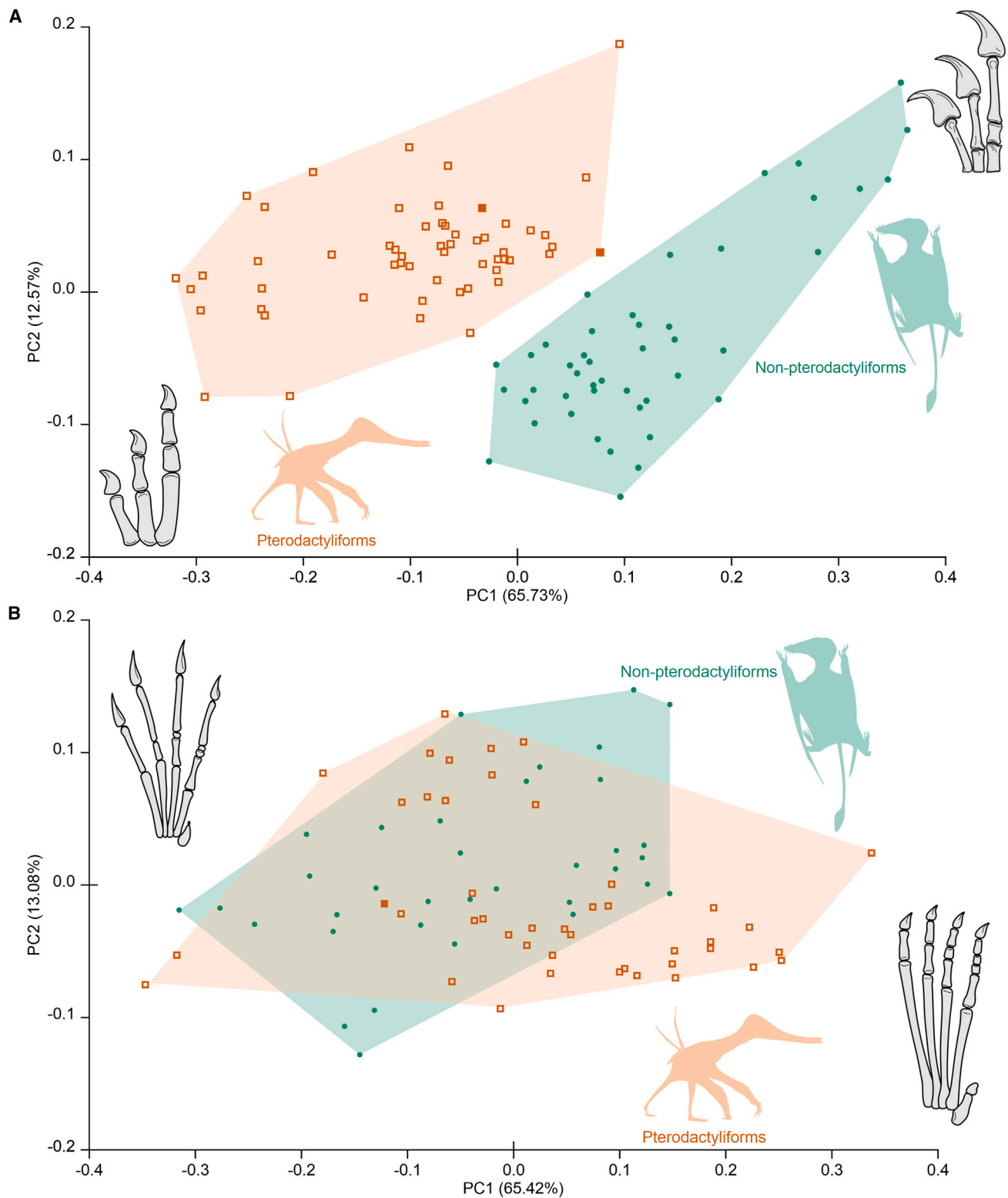
Figure 2. Autopodial morphospace across major pterosaur baupläne

(A) Biplot showing the first two axes of variation (PC1 and PC2) in the clawed digits of the pterosaur manus (digits I–III).

(B) Biplot showing the first two axes of variation (PC1 and PC2) in the metatarsus and clawed digits of the pterosaur pes (metatarsals and digits I–IV). Green circles, non-pterodactyliforms; orange squares, pterodactyliforms; Filled squares, basal Pterodactyliformes; open squares, pterodactyloids.

See also Data S1.
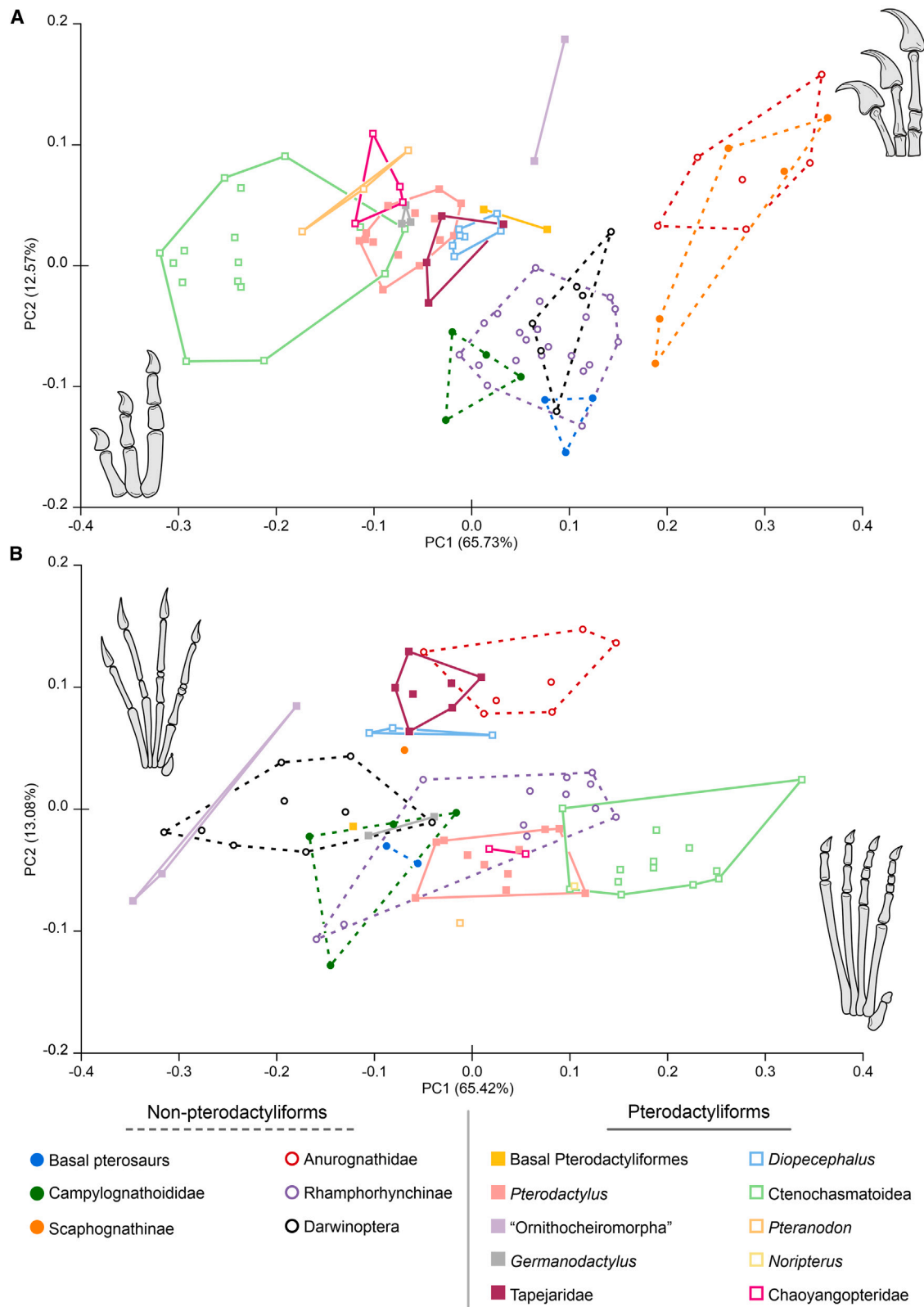
regimes within successive phalanges, and increasing stride efficiency.[27,42]

These relationships between phalangeal proportions and locomotor ecologies permit broad inferences to be drawn regarding the dominant locomotor ecologies of grounded pterosaurs, with extant birds chosen as the primary comparator for likely pterosaur locomotor modes (Figure 5). There are several arguments in favor of this approach. Birds are the closest extant relatives of pterosaurs and, more importantly, are the only group that spans a comparable range of phalangeal proportions to those exhibited by pterosaurs. Most birds retain the plesiomorphic autopodial phalangeal formula across pedal digits I–IV (2-3-4-5). In mammals and several lepidosaur lineages, the total number of phalanges in both the manus and pes is reduced; consequently, their phalangeal formulas differ from those of birds and pterosaurs. While the manual digits of birds are among the most heavily modified of any tetrapod group, their digitigrade, often-functional tridactyl pedal anatomy is, in many ways, the closest analog to the pterosaurian manus.

Admittedly, there are some regards in which the hands and feet of lepidosaurs are more comparable with those of pterosaurs, as both groups are quadrupedal and share a plantigrade pes. However, the combination of small average body size and a sprawling posture has profound implications for their locomotor functions. Even among those lepidosaurs that we would characterize as terrestrial, many exhibit manual and pedal proportions that are more typical of grasping than propulsive locomotor modes. This is because small size, coupled with sprawled posture, renders many terrestrial environments complex and three-dimensional, necessitating a degree of climbing proficiency that is not required of larger animals with erect postures and, critically, in the case of both birds and pterosaurs, the ability to fly.

DISCUSSION

Evolution of pterosaur terrestrial locomotion
Non-pterodactyliforms
All non-pterodactyliforms are characterized by manual phalanx III-3/III-1 ratios that indicate an effective grasping and gripping ability and align with those of extant scansorial amniotes (Figures 5 and 6). Seemingly at odds with this, basal-most forms, dimorphodontids, campylognathoidids, and the basal rhamphorhynchine *Dorygnathus* exhibit pedal proportions that are only slightly less "terrestrialized" than those of other archosaurs (Figures 5 and 7). This disparity most likely reflects retention of a plesiomorphic archosaurian condition in the pes of early pterosaurs. That scansorial adaptations of the manual digits appeared earlier and to a greater degree than in the pedal digits is not surprising. Arboreal/scansorial quadrupeds typically require greater dexterity, grip, and manoeuvrability from their manual digits compared with their pedal digits.[43] The latter primarily function as stable, weight-bearing supports during climbing.[44] Moreover, in

pterosaurs, the proportionately larger and more powerful skeleto-muscular system of the forelimbs compared to the hind limbs is consistent with forelimb-dominated locomotion (Figure 1A). During non-pterodactyliform evolution, pedal phalangeal proportions become more scansorial, decreasing the disparity between the manus and pes (Figure 7).

Among non-pterodactyliforms, two clades became highly specialized for hyper-scansoriality: anurognathids and scaphognathines. Each independently evolved exceptionally high manual and pedal phalangeal ratios reflecting extreme scansorial adaptations (Figures 5, 6, and 7). Phalangeal proportions of this kind are rare among extant amniotes, found only in suspensorial sloths, scansorial birds and lizards, and the specialized constricting feet of owls.[45] Lacking corollary raptorial or suspensorial characters, scansorial birds, such as swifts (Apodidae), offer the closest extant analogs for anurognathids and scaphognathines, exhibiting pedal morphologies adapted for clinging to vertical surfaces.[46] Moreover, the highly modified pamprodactyl foot morphology of swifts closely resembles the functionally tetradactyl feet of these pterosaurs (Figure 1A).[2,47] Extreme adaptation for scansoriality in both the manus and pes demonstrates that anurognathids and scaphognathines were likely among the least terrestrially adept of all pterosaurs.

Our data indicate that arboreality/scansoriality was the ancestral non-aerial locomotor mode for pterosaurs and was retained by all non-pterodactyliforms (Figures 5 and 6). This interpretation is consistent with the nature of the flight apparatus of non-pterodactyliforms where, in all cases, the fore and hind limbs were connected via the brachiopatagia and the hind limbs were linked together by the cruropatagium, supported along its rear margin by the highly elongate pedal digit V.[15,16] As in bats and colugos, this configuration structurally and functionally forms a single locomotor module that significantly restricts terrestrial locomotion, in particular limiting the direction and range of the hind limb movement.[48] By contrast, when adopting a scansorial posture, the hind limbs only need to flex within the plane of the wings, effectively serving as props or supports without requiring them to be positioned beneath the body (Figure 1A).

Widespread scansoriality may also help explain the relatively restricted size of non-pterodactyloids (wingspan 0.2–2.5 m) compared with pterodactyloids (wingspan 0.2–10 m) (Figure S2).[49,50] Scansoriality is among the most mass-restrictive of tetrapod locomotor ecologies, imposing various mechanical, energetic, and environmental demands that limit the maximum body size. These demands favor smaller sizes that can efficiently navigate and exploit vertical habitats (Figure S3).[51,52]

Pterodactyliformes
Two basal pterodactyliforms, *Propterodactylus*[8,9] and *Douzhanopterus*,[7] shed light on the evolutionary transition that led to the pterodactyloid body plan and more-terrestrial locomotor ecologies. *Propterodactylus* retains limb proportions and autopodial characteristics typical of earlier non-pterodactyliforms, while the more derived form, *Douzhanopterus*, exhibits a closer

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Figure 3. Autopodial morphospace across principal pterosaur clades
(A) Biplot showing the first two axes of variation (PC1 and PC2) in the clawed digits of the pterosaur manus (digits I–III).
(B) Biplot showing the first two axes of variation (PC1 and PC2) in the metatarsus and clawed digits of the pterosaur pes (metatarsals and digits I–IV). Circles and dashed-line hulls, non-pterodactyliforms; squares and solid-line hulls, pterodactyliforms.
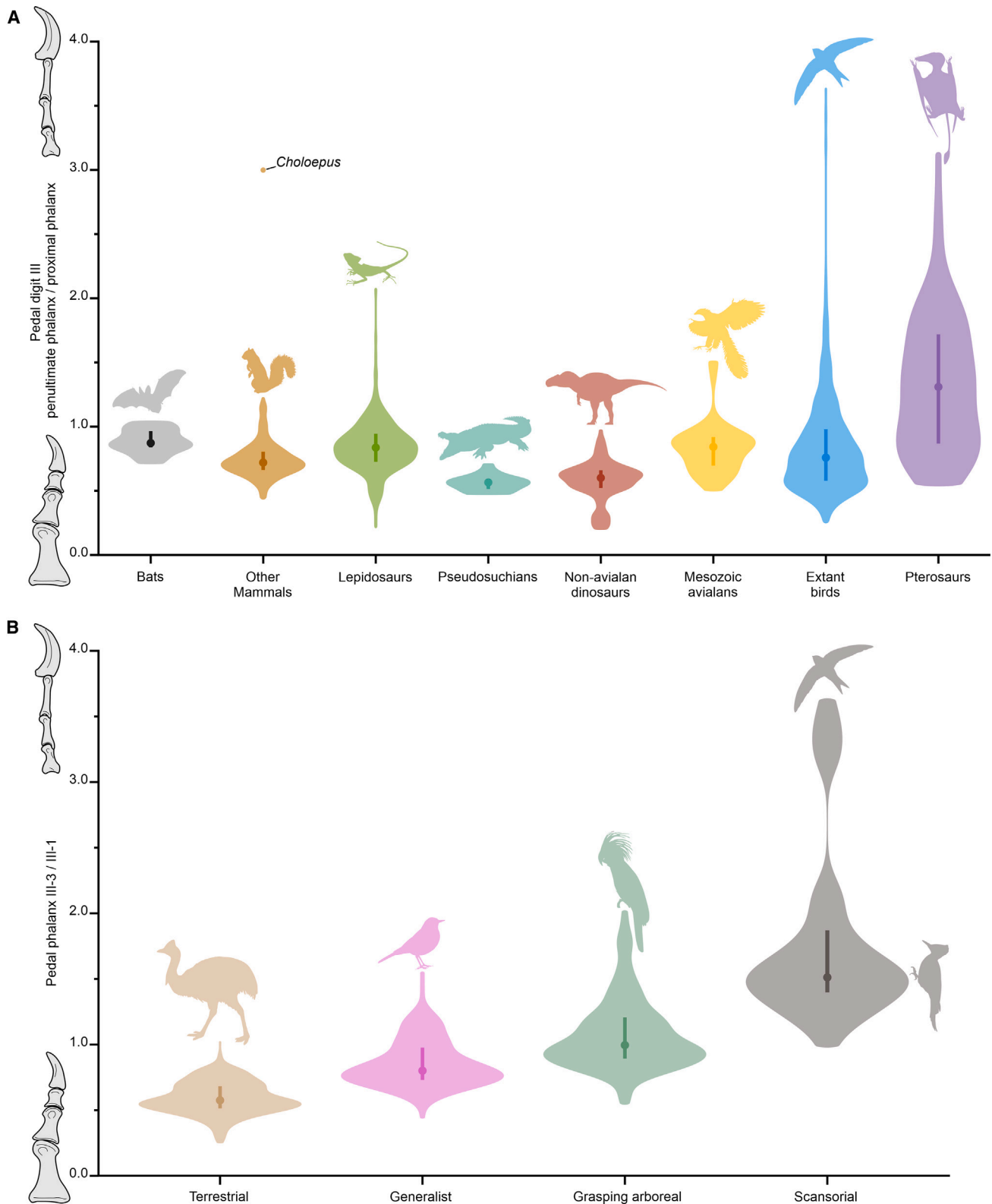See also Data S1.

Figure 4. Variation in phalangeal proportions for principal groups of extant and extinct amniotes
(A) Pedal digit III ratio (penultimate phalanx/proximal phalanx).
(B) Pedal phalanx ratio across bird ecomorphs. See Figure S1 for expanded ecological categories.
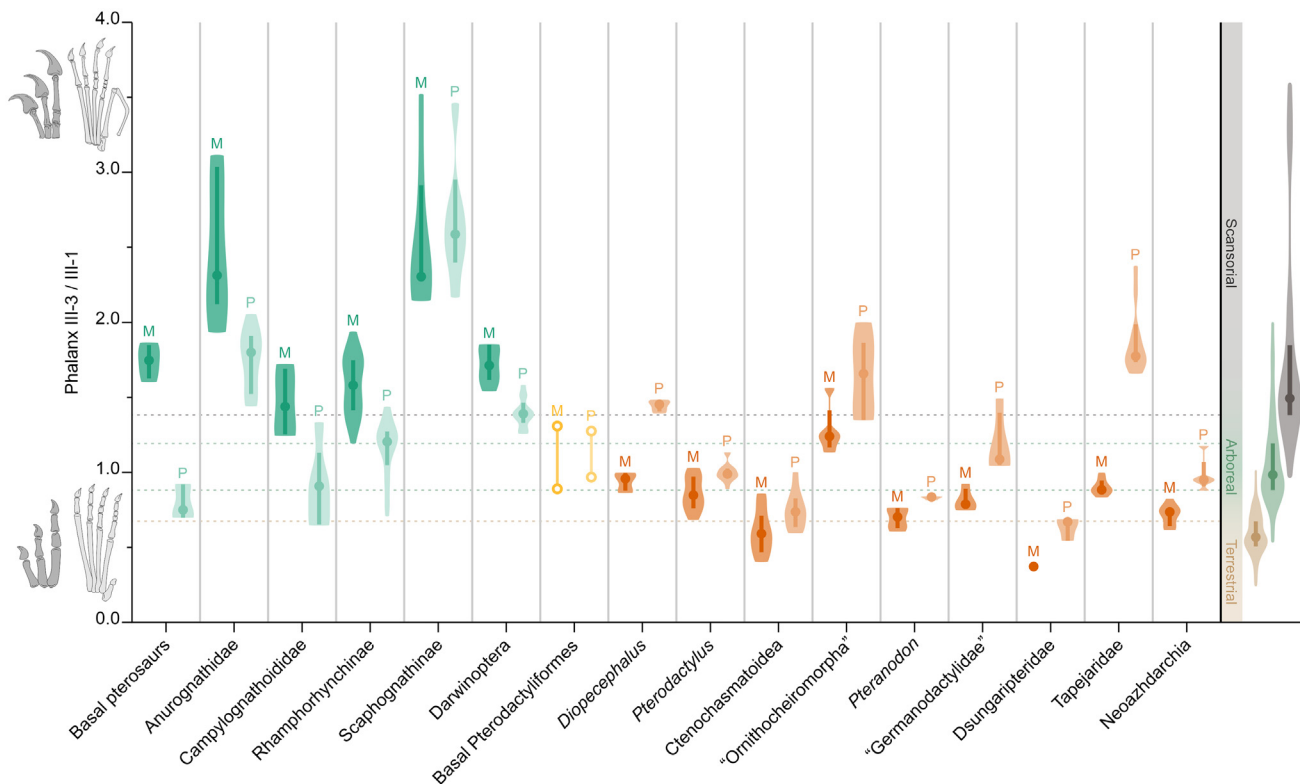See also Data S1.

Figure 5. Manual phalanx ratio (Mph III-3/III-1) and pedal phalanx ratio (Pph III-3/III-1) across principal pterosaur groups compared with extant bird ectomorphs

M, manual phalanx ratio; P, pedal phalanx ratio. Manual phalanx ratio values always exceed those for the pes in non-pterodactyliforms, whereas the reverse is the case for all pterodactyliforms except for *Propterodactylus*.

See also Data S1.

resemblance to pterodactyloids, particularly in its phalangeal proportions (Figures 5 and 6). *Douzhanopterus* displays significantly lower manual and pedal phalangeal ratios compared with other Late Jurassic non-pterodactyloids. These generalized proportions indicate a degree of locomotor versatility not present among non-pterodactyliforms. Although the hands and feet of *Douzhanopterus* indicate that it was incapable of sustaining a scansorial lifestyle, its generalized phalangeal proportions are consistent with a variety of locomotor ecologies, from grasping arboreality to partial terrestriality.

Manual phalanx III-3/III-1 ratios of approximately 1.0 or lower distinguish the clade containing *Douzhanopterus* and Pterodactyloidea from other non-pterodactyloids (excluding "ornithocheiromorphs"). In contrast to more basal forms, members of this group also exhibit consistently lower manual phalanx ratios than pedal ratios (Figure 5). These modifications reflect a shift in pterosaur locomotor ecology away from predominantly arboreal/scansorial locomotor modes toward generalist and, ultimately, terrestrial modes (Figures 5 and 6). Consistently lower manual phalanx ratios imply that the manual digits were better adapted for propulsion-dominated terrestrial locomotion than were the pedal digits. Although this may seem unusual, it is a predictable consequence of the pterosaur bauplan. Just as the non-pterodactyloid manus shows greater scansorial adaptation, the pterodactyloid manus shows greater adaptation to terrestriality.

During terrestrial locomotion, pterodactyloids used a digitigrade stance on their forelimbs. Due to their notably "front-heavy" build (Figure 1B), this stance exerted greater stress on their manual digits compared with the plantigrade stance of their hind limbs. This is evidenced by the deeper impressions of manus prints compared with pes prints in pterosaur trackways.[53]

The shift to terrestrial locomotor modes in pterodactyloids is not only evidenced by changes in hand and foot morphology but also by a suite of other morphological transformations that characterize the pterodactyloid bauplan. A major reduction in the extent of the cruropatagium is evidenced by both the atrophy of pedal digit V and, critically, the bifurcation of the cruropatagium along the midline, as revealed by fossilized soft tissues.[2,12] This resulted in two structurally and functionally independent locomotor modules wherein the limbs on the left side could be swung forward and backward, independently of the limbs on the right side.

The effectiveness of this pivotal development was further enhanced by additional adaptations toward terrestrial locomotor efficiency. Although efficient scansorial locomotion benefits from shorter limbs and short distal elements, elongating the limbs, particularly the distal elements, is favored for effective terrestrial movement.[27] This phenomenon is evident within pterodactyloids. These modifications to the limb proportions improve stride efficiency by improving limb leverage.
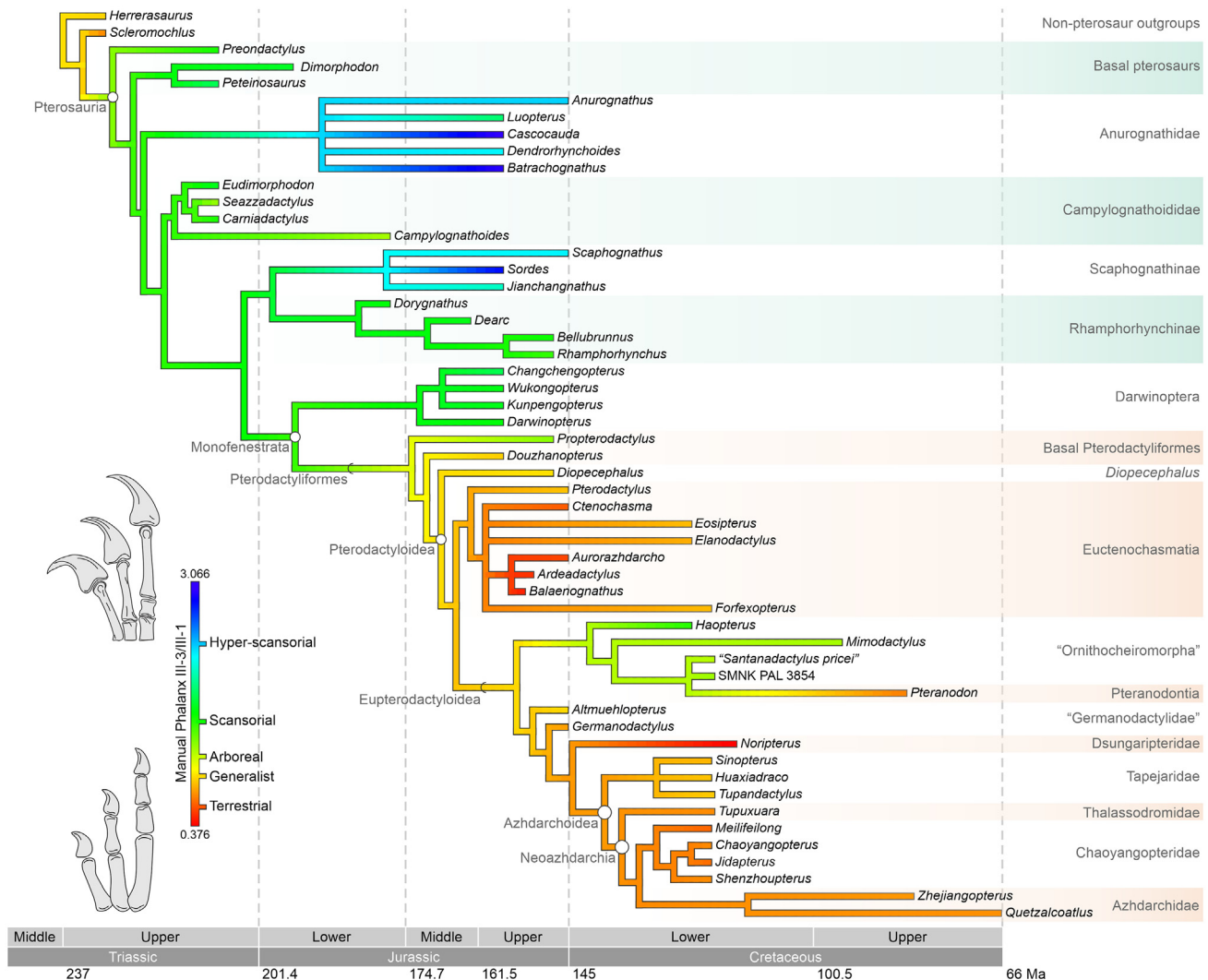
Figure 6. Ancestral character-state reconstruction of pterosaur manual proportions
Changes in phalangeal proportions for the pterosaur manus exemplified by the manual phalanx ratio (Mph III-3/III-1), mapped onto a time-calibrated reduced strict consensus tree.
See also Data S1.

Additionally, positioning limb musculature closer to the body's center of mass reduces the moment of inertia and decreases the energy required for limb oscillation. This is most apparent in the pterosaur forelimb, where a clear correlation exists between scansorial manual phalangeal proportions and a relatively shorter metacarpus, as well as increasingly terrestrial manual phalangeal proportions and elongation of the distal forelimb (Figure S4). Although pterosaur forelimb morphology is widely considered to be primarily adapted for flight, this trend emphasizes the extent to which non-aerial locomotion played an important role in shaping the morphology of the pterosaur forelimb.

The transition from a scansorial to a terrestrial locomotor mode also facilitated a fundamental change in pterodactyloid take-off. Scansorial non-pterodactyliforms could simply launch into the air from elevated positions, allowing them to initiate flight without generating significant thrust. During take-off from the ground, however, pterodactyloids would have needed to

generate considerably more thrust to become airborne. One likely consequence of this was selection for autopodia that showed a greater degree of terrestrialization, mitigating the impact of large stresses, particularly upon the manus.

Radiation of pterodactyloids into a broader range of locomotor ecologies seems to have begun in the Middle Jurassic (Figures 6 and 7), as highly specialized forms are already present in the earliest Upper Jurassic.[54] Although the first pterodactyloids inherited locomotor versatility, including some degree of facultative terrestrial behavior, predominant, or obligate, terrestriality did not arise from a singular terrestrialization event early in their evolution. Our results suggest that the earliest pterodactyloids experimented with a variety of autopodial morphologies. For example, *Diopecephalus* combines generalist manual proportions comparable with *Douzhanopterus*, with scansorial pedal proportions reminiscent of *Propterodactylus*. As with many other major evolutionary transitions, it is likely that the pterodactyloid
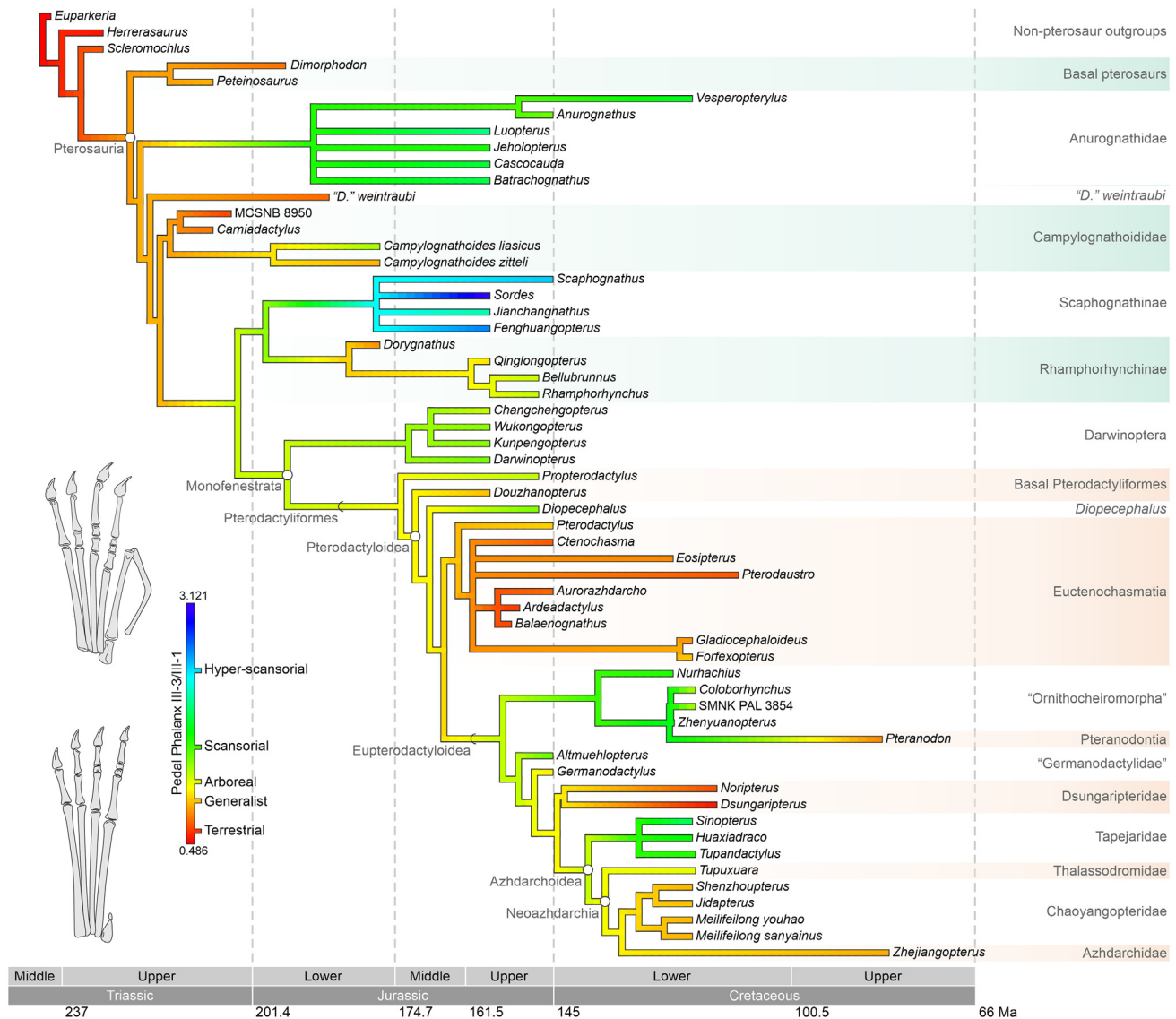
Figure 7. Ancestral character-state reconstruction of pterosaur pedal proportions

Changes in phalangeal proportions across the pterosaur pes exemplified by the pedal phalanx ratio (Pph III-3/III-1), mapped onto a time-calibrated reduced strict consensus tree.

See also Data S1.

transition was complex and did not follow a simple linear narrative. Moreover, the evolution of predominantly terrestrial locomotor ecologies occurred later, and independently, within each of the four principal pterodactyloid radiations: Euctenochasmatia, Ornithocheiroidea, Dsungaripteridae, and Azhdarchoidea (Figure 7).

Euctenochasmatians were the earliest-branching pterodactyloid radiation and rapidly diversified into a broad range of terrestrial niches. The basal-most member of the group, *Pterodactylus*, exhibits generalized autopodial proportions, but all more-derived ctenochasmatoids are strongly terrestrialized, suggesting that they were among the most terrestrially competent of all known pterosaurs. This interpretation is consistent with traditional interpretations of ctenochasmatoids as occupying a range

of dietary niches closely associated with marginal aquatic environments.[1–3,18]

By contrast, ornithocheiroids appear to have reverted toward a scansorial mode of life. Most ornithocheiroids possess autopodial proportions comparable to those of non-pterodactyloids. The greatly atrophied pes in most ornithocheiroid taxa suggests that non-aerial locomotion played a relatively minor role in their overall ecological strategies. This aligns with the traditional paleoecological view of the group as specialized soarers adapted for scavenging or aerial piscivory.[18,55] However, highly terrestrially adapted autopodia evolved in the toothless ornithocheiroid *Pteranodon*. This is unexpected, as traditionally *Pteranodon* and its closest relatives have been interpreted as some of the least-adept terrestrial locomotors among all

pterosaurs.[3] Our results suggest that this is not the case, although the implications of our finding for their overall ecology remain to be determined.

"Germanodactylids" (*Altmuehlopterus* and *Germanodactylus*), differ significantly in their autopodial anatomy. *Altmuehlopterus*, the least-derived form, retains proportions similar to those of the basal pterodactyloid *Diopecephalus*, with a significant discrepancy between manual and pedal proportions. The autopodial proportions of *Germanodactylus* are more consistent, typical of a generalist or limited arboreal locomotor ecology. It seems that although these animals appear quite similar, they likely occupied different ecological roles.

Dsungaripterids are characterized by remarkably low phalangeal ratios, ranking among the lowest of any pterosaurs. This characteristic suggests a predominantly terrestrial locomotor ecology, which aligns with their notably terrestrial fore- and hindlimb proportions. Moreover, this interpretation is consistent with the widely accepted notion that these pterosaurs were specialized shellfish feeders.[1–3]

Azhdarchoids show considerable diversity in manual and pedal morphology. Similar to ornithocheiroids, tapejarids appear to have reverted to an arboreal/scansorial mode of life, re-evolving highly derived autopodial proportions characterized by a generalized manus and a strongly scansorial pes. The more generalized manual proportions of tapejarids compared with other scansorial pterosaurs may reflect a transition to a grasping form of arboreality, necessitated by large body size, or a biomechanical compromise that facilitated both arboreal/scansorial locomotion and terrestrial locomotion.

Neoazhdarchians (thalassodromeids, chaoyangopterids, and azhdarchids) show a trend toward increasing terrestrialization. All neoazhdarchians exhibit manual proportions similar to those of other large ground-based pterosaurs and typical of terrestrial locomotors. The degree of terrestrial adaptation in the neoazhdarchian pes, particularly in *Tupuxuara*, is more generalized and less strongly terrestrialized compared with most other large ground-dwelling pterosaurs. Among this group, azhdarchids and chaoyangopterids appear to be most strongly adapted for terrestrial locomotion. These clades are generally interpreted as being ground-based feeders, and this is consistent with their autopodial morphology.[20]

Pterosaurs and their roles in Mesozoic terrestrial ecosystems

The evolution of flight opened up new modes of life for the first pterosaurs but, even before taking to the air, they were already pioneering new ecological niches. Evolving from as-yet-unknown gliding ancestors in the Triassic, non-pterodactyliform pterosaurs were the first, and only, group of archosaurs to effectively exploit arboreal/scansorial niches in the early- to mid-Mesozoic. Instead of expanding into terrestrial habitats, most non-pterodactyliform clades consolidated their foothold in arboreal/scansorial locomotor ecologies and, over time, became more mechanically proficient at climbing on inclined and vertical substrates. Their remarkable success lay in extending typical archosaurian feeding ecologies—such as invertivory, carnivory, and piscivory—into new scansorial and aerial habitats.

In the Middle Jurassic, pterosaurs underwent a significant shift in their non-aerial locomotor abilities as basal pterodactylforms began acquiring adaptations conducive to more versatile locomotor modes, including facultative terrestriality. Some pterodactyloid lineages extended terrestrial adaptations even further, becoming reliant on terrestrial ecosystems. By achieving greater locomotor proficiency on the ground, pterosaurs once again expanded into unexploited ecospace accessible only to animals adept in both terrestrial locomotion and flight. This interpretation is reinforced by diversification in the pterodactyloid craniodental morphology, much of which was unlike anything found among non-pterodactyliforms.

Many pterodactyloid lineages were highly successful during the latter half of the Mesozoic. Ctenochasmatoids, competent terrestrial locomotors, occupied a broad range of niches within shoreline ecosystems for at least 60 million years. Other clades, such as pteranodontians, dsungaripterids, and neoazhdarchians, diversified in the Late Jurassic and Early Cretaceous. In particular, neoazhdarchians achieved remarkable morphological and ecological diversity, persisting for approximately 80 million years, through to the end of the Cretaceous. Terrestrial adaptation enabled pterosaurs to achieve some of their most enduring and spectacular successes, as freedom from size constraints imposed by scansoriality allowed pterodactyloids to become much larger, attaining giant size across multiple lineages.

Evidence from the ichnological record strongly supports this proposed history of pterosaur locomotor ecology. No pterosaur tracks occur in the first half of the Mesozoic prior to the evolution of pterodactyloids[37], and footprints of non-pterodactyliforms are entirely absent from the record.[56] Pterodactyloid tracks first appear in the Middle-Late Jurassic, soon after the appearance of the group (Figures 6 and 7), and quickly become widespread.[37] Pterodactyloid footprints remain a persistent feature of the late Mesozoic terrestrial ecosystems until the end of the Cretaceous.[37]

Non-pterodactyliforms appear to have become extinct by the end of the Jurassic, with only a single putative Cretaceous representative (Figure 7). Despite this, some of their ecologies persisted, with ornithocheiroids replacing certain non-pterodactyloids as aerial piscivores. Tapejarids re-evolved arboreal/scansorial autopodial proportions, enabling them to exploit entirely novel ecological niches by combining scansoriality with a potentially herbivorous diet.[3,57]

This study shows that disparity in autopodial morphology across Pterosauria is much higher than has been previously appreciated, much greater than that in other groups of Mesozoic archosaurs, and comparable with that in extant birds. Such diversity strongly suggests a wide array of non-aerial ecological roles within the group, challenging previous conservative assumptions that pterosaurs occupied a relatively restricted range of niches in Mesozoic ecosystems. Non-pterodactyloids were typically highly specialized for scansorial lifestyles and were likely largely absent from terrestrial ecosystems. From the Middle Jurassic to the Late Cretaceous, pterodactyloids diversified into more generalized and ultimately terrestrial locomotor modes, evolving diverse and, in some cases, unprecedented feeding strategies. Throughout their 160-million-year history, pterosaurs continually innovated new ecological niches. The shift from predominantly scansorial to primarily terrestrial ecologies in pterosaurs occurred during the Middle Jurassic. This period also saw several amniote groups, such as scansoriopterygids, avialans, volaticotherins, and gliding eleutherodontids,

evolving toward more arboreal and aerial lifestyles. To understand how pterosaurs may have interacted with these emerging clades, it is crucial to gain a deeper understanding of their non-aerial ecologies in addition to their flight capabilities.

AUTHOR CONTRIBUTIONS

Conceptualization, R.S.H.S., B.H.B., R.J.B., P.L.F., and D.M.U.; methodology; R.S.H.S., R.J.B., and D.M.U.; investigation, R.S.H.S., R.J.B., and D.M.U.; formal analysis and data curation, R.S.H.S., R.J.B., and D.M.U.; visualization, R.S.H.S.; supervision, B.H.B., R.J.B., P.L.F., and D.M.U.; writing—original draft, R.S.H.S., B.H.B., R.J.B., P.L.F., and D.M.U.; writing—review & editing, R.S.H.S., and D.M.U.; funding acquisition, R.S.H.S., B.H.B., R.J.B., P.L.F., and D.M.U.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2024.09.014.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Software and algorithms		
ImageJ v1.53u	Schneider et al.[58]	https://imagej.net/ij/
MorphoSource.org	MorphoSource	https://www.morphosource.org/
Past v4.17	Hammer et al.[59]	https://www.nhm.uio.no/english/research/resources/past/
TNT 1.6	Goloboff and Catalano[60]	http://www.lillo.org.ar/phylogeny/tnt/
R package strap, version 1.6-0	Bell and Lloyd[61]	https://doi.org/10.1111/pala.12142
R	R Development Core Team[62]	https://cran.r-project.org/

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Comparative data from extant taxa was retrieved from the published literature and from the 3D data repository MorphoSource. Additional data for extant birds was collected by R.S.H.S. from the bird skeleton collections in the Natural History Museum at Tring, UK. See data collection section below and Data S1 for more information.

METHOD DETAILS

Data collection

Metric data for pterosaurs was obtained by direct measurement of specimens, from scaled photographs using ImageJ v.1.53u[58] and from the published literature. Most metric data for other amniote groups were compiled from existing publications.[24,32,63–65] To enhance their phylogenetic and locomotor representativeness these datasets were augmented by additional data from museum collections, recent literature, and the 3D data repository MorphoSource.org.

Autopodial function and locomotor assignment

The primary autopodial function in extant tetrapods was assigned based on ecologies presented in the datasets, as well as literature review. Occasionally, traditional ecological categorisations were found to be inappropriate for autopodial function. For instance, the marine iguana (*Amblyrhynchus cristatus*) is commonly assigned a semi-aquatic ecology, yet this designation does not align with its primary autopodial function. Among lepidosaurs, aquatic locomotion primarily relies upon tail propulsion, with the autopodia performing a secondary and relatively minor role. In the case of the marine iguana, autopodial morphology is adapted for a saxicolous (rock-traversing) function, so shows morphology typical of a grasping (climbing) rather than a propulsive (aquatic) mode. Likewise, many birds are characterised as possessing an aerial hawking ecology, but this locomotor ecology is largely independent from the function of the pedal digits.

Differences in phalangeal proportions serve as a reliable indicator that differentiates between grasping/gripping autopodial functions (scansorial, raptorial, and arboreal) and propulsive functions (terrestrial, wading, and aquatic). However, it can be difficult to distinguish between some functions within the grasping and propulsive groups, as it is important to consider that these functions are far from exclusive. Autopodia that show propulsive adaptations are rarely limited to a single locomotor mode. For example, waders (a specialized form of walking) and foot-propelled swimmers are generally adept terrestrial locomotors, with rare exception. Similarly, autopodia adapted for grasping are not necessarily limited to a single function. For example, almost all raptorial birds are also arboreal, with similar underlying mechanics involved in grasping both prey and perches. Thus, the high degree of overlap between these two categories is not surprising.

It would be overly artificial and unrepresentative to exclude aquatic and wading birds from the terrestrial locomotor group, or raptorial birds from the arboreal locomotor group, simply because their feet perform additional functions. As such, two figures are used to illustrate both reduced and expanded ecological categories (Figures 4B and S1). To illustrate the differences in body size range among these expanded avian locomotor ecologies, especially the restricted size distribution in scansorial and arboreal taxa, we use femur length as a proxy for overall body size (Figure S3).

To demonstrate that proportional changes in pterosaur autopodial morphology align with other indicators of locomotor ecology in the limb skeleton, manual phalanx ratio (Mph III-3 / III-1) was plotted against the degree of distal forelimb elongation (MC IV / (humerus + radius)). This analysis reveals a distinct correlation between scansorial manual phalangeal proportions and a shorter metacarpus, which is linked to enhanced climbing efficiency. Conversely,[27] more terrestrial manual phalangeal proportions are associated with an elongated distal forelimb, contributing to greater walking efficiency (Figure S4).

QUANTIFICATION AND STATISTICAL ANALYSIS

Morphometric data and analyses

The pterosaur manus multivariate dataset includes 101 pterosaur specimens, representing 43 taxa, while the pedal dataset contains 38 taxa based on 79 specimens. A secondary dataset, containing only the phalanges of manual and pedal digit III was created for several reasons. First, consistent patterns in phalangeal proportions are observed across all digits in pterosaurs, such that the morphological patterns in digit III are representative of the other digits. This observation allowed us to include all taxa wherein manual and/or pedal digit III are complete, irrespective of the completeness of other digits, significantly expanding the taxonomic breadth of the secondary data set. Secondly, extensive datasets for manual and pedal digit III are available for extant groups, enabling direct comparison with pterosaurs. The non-pterosaur comparative dataset contains the following taxa: 187 extant mammals (240 specimens); 377 extant lepidosaurs (401 specimens); 11 extant and 12 extinct pseudosuchians (65 specimens); 166 non-avialan dinosaurs (359 specimens); 57 Mesozoic avialans (100 specimens); 855 extant birds (942 specimens).

Morphometric analyses were conducted in Past 4.17,[59] using a set of linear measurements of the autopodia that would have contacted the substrate during non-aerial locomotion. This included the phalanges of manual digits I-III, as well as the metatarsals and pedal phalanges of digits I-IV. Manual digit IV (the wing-finger) and the fifth metatarsal, along with its pedal digit, were excluded from analyses as these elements, heavily modified and incorporated within the flight apparatus, were not used during non-aerial locomotion.

Variation in the relative proportions of the lengths of the proximal and penultimate phalanges is a major source of disparity in both the pterosaur manus and pes. The functional and ecological underpinnings of this variation are well-documented, and large datasets exist for digit III across a wide range of extant groups with known primary autopodial functions and locomotor ecologies, allowing for direct comparison.[24,32,63–65] This pattern is consistent across all digits, so the morphology of a single digit can be adopted as representative of other digits. Consequently, restricting data collection to manual and pedal digit III permitted the compilation of a more comprehensive dataset for pterosaurs. Manual phalanx III-3/III-1 ratios were calculated for 134 pterosaur specimens representing approximately 53 taxa, and pedal phalanx III-3/III-1 ratios for 148 specimens representing approximately 56 taxa. In both cases taxon sampling included representatives from 18/20 principal pterosaur groups, with the exceptions of Lonchodectidae and Nyctosauridae, clades for which the autopodia are entirely unknown or very poorly preserved (see Phylogenetic analysis and taxonomy).

While relative metatarsus length is the primary source of disparity in the pterosaur pes, the possible correlates between metatarsal length and locomotor ecology are less clearly constrained than those relating to phalangeal proportions, especially concerning flying vertebrates,[66] with similar increases or decreases in relative length occurring across disparate locomotor ecologies. Metatarsal proportions are also heavily influenced by stance and gait, which likely has a confounding influence on any ecological comparison made across taxa.[27,67] For these reasons, disparity and ecomorphological comparisons between pterosaurs and other groups of amniotes were restricted in this study to variation in phalangeal proportions.

To minimise the impact of collection bias when comparing the distribution of phalanx ratios across amniote groups, a mean value was used for those taxa represented by multiple individuals. In multivariate analyses, morphometric data was normalised to mitigate the influence of absolute body size on the results. Individual elements from manual digits I–III were divided by the total length of manual digit III (MPh III-1 + III-2 + III-3 + III-4), while pedal elements were divided by the total length of pedal ray III (MT III + PPh III-1 + III-2 + III-3 + III-4) (Smyth and Unwin, unpublished data).

Change in pterosaur body size through time was estimated using humerus length as a proxy (Figure S2). Each taxon is represented by the largest known humerus. Taxa represented only by highly immature individuals were excluded. The plotted age for each taxon was the midpoint calculated from maximum and minimum ages obtained from a literature search.

Phylogenetic analysis and ancestral reconstruction

To locate changes in autopodial morphology within an evolutionary framework, we analysed a modified version of the pterosaur morphological character matrix (Smyth & Unwin, under review), which was expanded to include as many pterosaur OTUs as possible in which the manual or pedal digits are preserved. This resulted in 95 active taxa with *Euparkeria capensis* designated as the outgroup. The matrix contains 187 characters, 41 of which were treated as ordered. The analysis was performed in TNT version 1.6[60] using a two-phase tree searching procedure.[5] See supplemental information for more details.

The resulting strict consensus tree (Figure S5) was time-calibrated using the DatePhylo function of the R package strap, version 1.6-0,[61] R version 4.3.0.[62] First and last appearance dates were obtained from a literature search. Branches were scaled using the 'equal' method which eliminates zero-length branches by sharing duration from the more basal non-zero-length branches.[61] The time-scaled tree was pruned in R to produce two trees that include only those pterosaurs for which manus data are available and only those pterosaurs for which pes data are available. Ancestral character-state reconstructions were performed by mapping manus and pes data onto the pruned time-calibrated phylogenies using the contMap function in phytools.[68]

Taxonomic definitions

Pterosauria: the most inclusive clade exhibiting fourth metacarpal and digit hypertrophied to support wing membrane synapomorphic with that in *Pterodactylus antiquus*.[69,70] Monofenestrata: the most inclusive clade exhibiting confluent external naris and antorbital fenestra synapomorphic with that in *Pterodactylus antiquus*.[71] Pterodactyliformes the most inclusive clade containing *Pterodactylus antiquus* but not *Darwinopterus modularis*.[4] Pterodactyloidea: the most inclusive clade exhibiting metacarpus at least 80% the length of the humerus synapomorphic with *Pterodactylus antiquus*.[70,72]