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Foot posture in a primitive pterosaur

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The nature of the hindlimb posture and gait of pterosaurs has been controversial^{1–16}, partly because most of the pterosaur skeletons that have been found were flattened in thin-bedded rocks, therefore obscuring three-dimensional anatomy. A major controversy concerns the extent to which pterosaurs move on the ground; they have been variously interpreted as ranging from sprawling, quadrupedal walkers to erect, bird-like bipedal cursors¹. Study of pelvis and femur material from the derived group Pterodactyloidea^{11–13} has resolved which movements are possible at the hip, but the lack of three-dimensional, articulated pterosaur feet has prevented examination of all of the movements that are possible within the foot. We have found a large, uncrushed, partial skeleton of a new species of the basal pterosaur *Dimorphodon* in thick-bedded deposits of Tamaulipas, Mexico; this material includes such a three-dimensional foot. The nature of this skeleton contradicts an important part of the cursorial interpretation, that is, that only the toes contacted the ground during terrestrial locomotion^{2–7}. The flattened metatarsal-phalangeal joint at the base of the first four toes of this specimen would not allow such a digitigrade posture without separating

most of the joints. A flat-footed stance is consistent with presumed footprints of pterosaurs^{8–10} that show impressions of the entire sole of the foot.

Monophyletic hierarchy⁶: Diapsida, Archosauria, Ornithodira, Pterosauria,

Dimorphodontidae

Dimorphodon weintraubi, sp. nov.

Etymology. *weintraubi*: after the late Dr Robert L. Weintraub.

Holotype. Universidad Nacional Autónoma de México Instituto Geología de México (IGM) 3494, an articulated partial skeleton including the posterior part of the skull and first four cervical vertebrae, left and right scapulocoracoids, left humerus, second phalanx of left wing finger, right wing distal to mid-humerus, and right leg distal to mid-tibiotarsus.

Locality and horizon. Lower part of the La Boca Formation in Huizachal Canyon, Tamaulipas, Mexico, from a 1-metre-thick volcanoclastic siltstone deposited as a subaerial, waterlain debris flow^{17,18}. The fauna indicates a late Early or early Middle Jurassic age¹⁷.

Diagnosis. *D. weintraubi* differs from *D. macronyx* (Buckland 1829), the only other species in the genus¹⁹, in that its first wing phalanx is not significantly shorter than the ulna¹⁴. A sesamoid at the base of pedal claws, reported for *D. macronyx*¹⁴, is also not seen. The holotype is larger than the largest specimens of

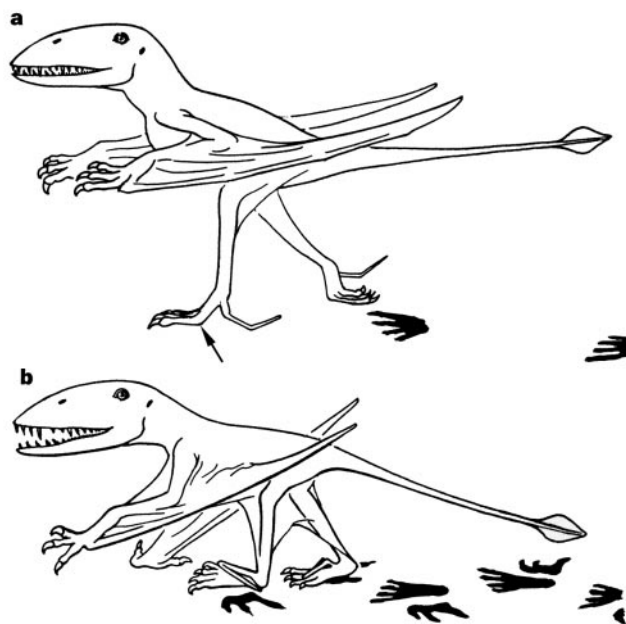


Figure 1 Alternative reconstructions of locomotor posture and trackways of *D. macronyx*. **a**, *D. macronyx* reconstructed as a bipedal digitigrade runner (redrawn from ref. 13, adapted from ref. 2) in which substantial hyperextension occurs at the metatarsal-phalangeal (MP) joints (arrow) when the foot contacts the ground. **b**, *D. macronyx* as a quadrupedal, plantigrade walker, in which the entire plantar surface of the foot contacts the ground and only slight hyperextension occurs at the MP joints at the end of the propulsive phase. In **a**, the hindlimb moves in a parasagittal plane and the footprints are close to the animal's midline, as dictated by the bipedal-running hypothesis. In **b**, the forelimbs and hindlimbs may have been more sprawling than indicated here and the footprints may have been further from the midline. The reconstruction of the flight membrane in **b** is based on the interpretation of *Sordes pilosus*¹⁶; the depiction of the folding of the fifth pedal digit over the foot is based on preservation seen in *D. weintraubi* and other primitive pterosaurs^{14,23,24}. The footprints in **a** are hypothetical: the spacing and orientation of the footprints in **b** are based on a trackway of *Pteraichnus cf. saltwashensis*⁹.

D. macronyx, and is the largest known nonpterodactyloid pterosaur; its 60.5-mm-long metacarpal IV is longer than the 57.5-mm element of the largest previously reported basal pterosaur²⁰.

This species is similar to *D. macronyx* from the Lower Jurassic of England^{2,14,19} in nearly all skeletal features known for both taxa. Although the cranial material of *D. macronyx* and *D. weintraubi* has few elements in common, the unusually deep, vertical basiptyergoid processes of the basiphenoid of *D. weintraubi* indicate that the pterygoid and quadrate extended well below the occipital condyle, and that the temporal region was similar to that of *D. macronyx* in being significantly deeper than in other pterosaurs. In both taxa, the second phalanx of pedal-digit V is unusually long and straight²¹, and the first pedal digit diverged medially at least 15° (although the distribution of these features among pterosaurs is incompletely known). *Dimorphodon* is at present considered to be a basal pterosaur that is more distantly related to pterodactyloids than are some other 'rhamphorhynchoid'-grade taxa^{21,22}.

Specimens of *D. macronyx* have been important in interpreting primitive pterosaurs as highly cursorial bipeds², and were the only specimens directly cited in support of digitigrady³. Hindlimbs were proposed to have moved with an erect, parasagittal gait, and with a digitigrade foot posture (Fig. 1). In a fully digitigrade gait, the ankle and metatarsus are raised above the ground and only the digits contact the substrate. It was argued^{2,3}, on the basis of comparisons with birds and dinosaurs, that dorsiflexion (hyperextension) occurred at the metatarsal–phalangeal (MP) joints of digits I–IV. The shape of these joints² and the symmetry of the foot on either side of the long third toe³ were used to support this hypothesis.

The MP joints of digits I–IV of *D. weintraubi* (Figs 2 and 3) indicate, however, that little rotation, far less than in birds, was possible. The articular surfaces on the distal end of the avian tarsometatarsus (Figs 3d and 4) extend in a broad arc over 180° in lateral view. This surface forms a trochlea (a pulley-shaped structure) that articulates with a ridge on the proximal phalanx. In *D.*

weintraubi, however, the articular surface on the distal end of each metatarsal extends to only a limited extent onto the dorsal surface of the shaft (Figs 3a, e and 4), and a complementary groove and ridge are absent from the articular surfaces. In *D. macronyx*, a broad groove present on the ventral surface of the distal end of metatarsals I–IV was interpreted to be a trochlea², but in *D. weintraubi* and *D. macronyx* (Natural History Museum, London) the proximal phalanx does not articulate within this groove, and it was presumably occupied by flexor tendons that were inserted on more distal phalanges.

Most important, the distal joint surfaces on the metatarsals of *D. weintraubi* are only slightly convex and those of the opposing phalanges only slightly concave (Figs 2 and 3b, c and e), forming an unusually flat MP joint compared with those in members of the two groups of living archosaurs. When articulated with the joint surfaces flush, the shaft of each phalanx of *D. weintraubi* would be directly in line with that of the metatarsus (except for the first toe, which diverged medially). Even a small amount of hyperextension of the phalanx on the metatarsal (as little as 5°) would disarticulate a large portion of the joint surface (Fig. 3e).

When the foot is considered as a whole, the interphalangeal joint surfaces also allow little hyperextension. The joint between the ungual and penultimate phalanx in the three digits in which the ungual is preserved allows for no hyperextension, indicating that an unguigrade posture (walking on unguals) was impossible. The remaining interphalangeal joints allow differing degrees of dorsiflexion among the digits, with the amount of dorsiflexion increasing from medial to lateral digits, as in plantigrade reptiles but not in birds. In digit I, the single interphalangeal joint allows for no hyperextension, whereas the four interphalangeal joints of digit IV together allow for elevation of the metatarsus approximately 50° above the ground (assuming its claw to be similar to those of other digits). As digit I is deflected medially by its oblique MP joint, it may not have reached the ground in a digitigrade posture. However, a

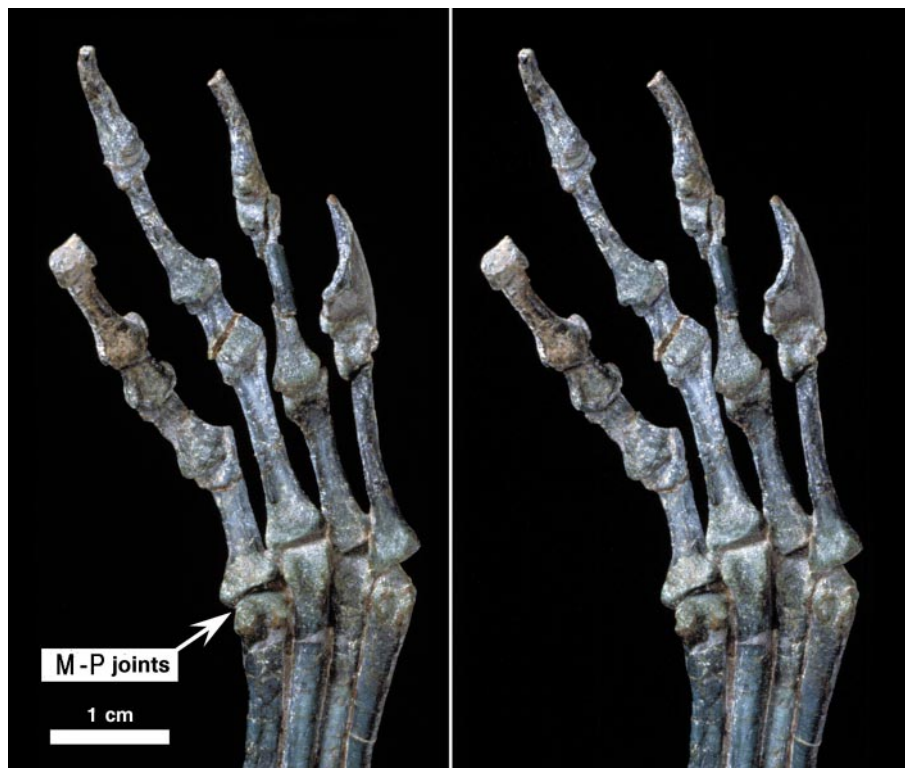


Figure 2 Stereophotographs of the right foot of *D. weintraubi* in ventral view. The toes have been hyperextended and dislocated slightly to the right (left side of photograph), exposing the flat articulation surfaces on both sides of the

metatarsal–phalangeal joints (MP Jts.). Digit IV, without a claw, is slightly flexed; when extended it would have reached beyond the level of the end of the preungual phalanges of digit III.

limit to digital hyperextension on the medial side of the foot is set by digit II, which was capable of a maximum of 20° of dorsiflexion. A parasagittal stride would begin with the digits parallel to the ground, and maximum dorsiflexion would have occurred at the end of the stride. This limited degree of hyperextension on the inner side of the foot is not consistent with a wholly digitigrade, parasagittal stride, in which digits II–IV support the weight of the body throughout the contact phase of the foot.

It has been argued³ that the symmetry of the pterosaur pes, with the third digit being the longest, supports the idea that pterosaurs moved rapidly and displayed obligate bipedality. However, the pes is not symmetrical in *D. weintraubi*. Assuming that the missing claw of digit IV is as long as that of digit III, digit IV is longer than digit III. Although the third toe is the longest in pterodactyls and rhamphorhynchids²³, in the basal pterosaurs *Peteinosaurus*²⁴ and *Eudimorphodon*¹⁵ and in *D. macronyx*¹⁴ (J.A.H., unpublished observations) the toes increase in length from digit I to digit IV. Thus, the digits of basal pterosaurs have proportions that are similar to those of the sprawling feet of ambulatory, plantigrade reptiles rather than those of the cursorial, digitigrade feet of bipedal reptiles.

The phalanges of the slender, elongated fifth digit, to which the wing membrane may have been attached¹⁶, apparently did not participate in supporting the foot. The robust metatarsal is positioned posterolaterally to the other metatarsals, and its plantar surface would contact the substrate in a plantigrade stance. How-

ever, the nature of the MP joint does not indicate that the proximal phalanx was capable of projecting much further ventrally than metatarsals I–IV, and its length and slenderness would have provided little mechanical advantage in supporting the rest of the foot.

Other features of digits I–IV of the *D. weintraubi* foot indicate a capacity for grasping that is consistent with an ability to climb but is unexpected in an obligate cursor. The claws are moderately curved (nearly as strongly as the claws of the manus); all phalanges except the most proximal have well developed flexor tubercles for the insertion of digital flexors (Fig. 2); and all of the IP joints allow for extensive flexion of the digits (as exhibited by digit IV; Fig. 2). Furthermore, the phalangeal proportions of the digits of *Dimorphodon* and other basal pterosaurs are similar to those of birds with grasping feet (that is, perching, climbing, and raptorial species) and unlike those of primarily ground-living birds, bipedal dinosaurs and the primitive dinosauromorphs *Lagerpeton* and *Marasuchus* (Fig. 5).

The similarity of the foot of *D. weintraubi* to that of other basal pterosaurs^{15,24} suggests that the features outlined here are primitive features of the group. The lack of cursorial adaptations in the foot of *D. weintraubi* contradicts the reconstruction of basal pterosaurs as rapidly moving, digitigrade cursors^{2,3}. On the contrary, the capacity for grasping exhibited by this foot and the similarity of its phalanges to those of birds with grasping feet indicates that basal pterosaurs may have been scansorial and, perhaps, arboreal^{1,14,15}. □

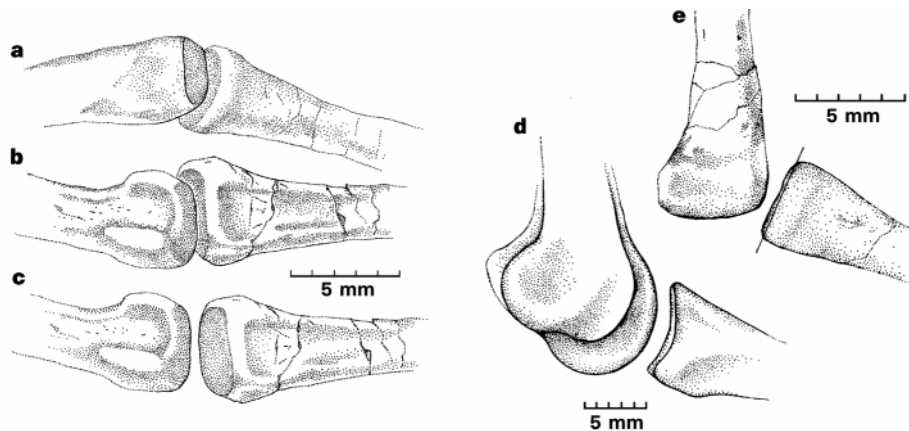


Figure 3 Metatarsal-phalangeal (MP) joints of *D. weintraubi* and a bird. **a–c**, MP joints of *D. weintraubi*. **a**, Digit II in dorsal view; **b**, digit III in ventral view; **c**, reconstruction of digit III in ventral view when separated. **d**, Distal end of tarsometatarsus and proximal end of proximal phalanx of digit III when hyperextended in a bird (albatross), showing the rounded trochlea extending onto the tarsometatarsal shaft and the concave proximal end of the phalanx.

e, Reconstruction of a similarly hyperextended articulation of metatarsal and proximal phalanx of digit III of *D. weintraubi*, separated slightly, showing consequent disarticulation of most joint surfaces dorsal and ventral to the small area of contact. The line through the phalanx shows the deepest extent of the articulating surface.

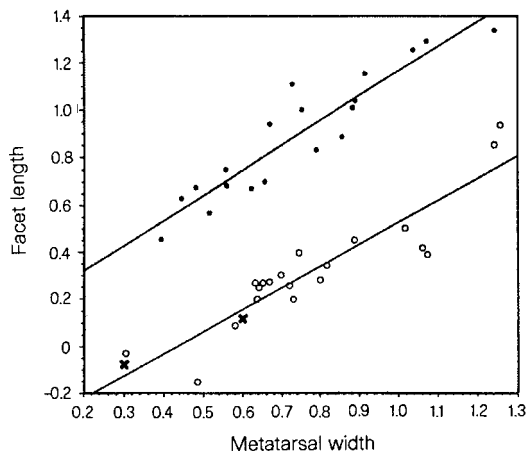


Figure 4 Length of the articulation surface on the distal end of the metatarsus in avian and non-avian reptiles, illustrating the greater extent of this surface in birds. The graph plots the log of the length of the distal articulation facet on the dorsal surface of metatarsal III (y-axis), measured parallel to the shaft from the distal end of the bone to the proximodorsal end of the articulation surface, against the log of the distal width of metatarsal III as a measure of size (x-axis). The short dorsal articular surface in both *D. weintraubi* and *D. macronyx* is comparable to that in reptiles that do not hyperextend their toes and are plantigrade rather than digitigrade as birds are. Filled circles, birds; open circles, lizards, crocodylians, and turtles; crosses, *D. macronyx* (left) and *D. weintraubi* (right). For reptiles, $(\log y) = 0.93(\log x) - 0.406$, $r^2 = 0.827$; for birds, $(\log y) = 1.056(\log x) + 0.111$, $r^2 = 0.865$.

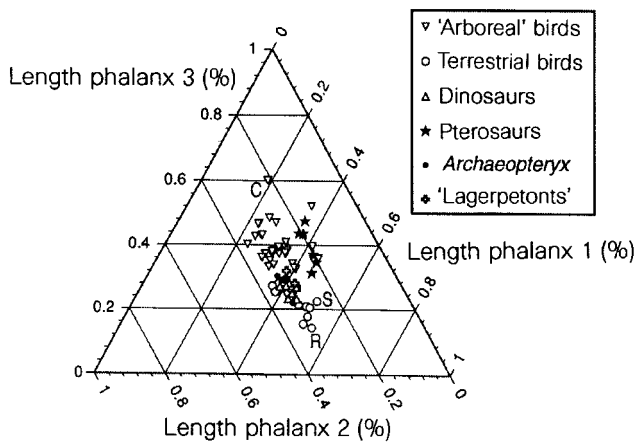


Figure 5 Ternary diagram showing relative lengths of the three non-ungual phalanges of pedal digit III in living birds and fossil archosaurs expressed as a percentage of the summed lengths of the three phalanges. For example, the phalangeal proportions of the grasping digit III of a swift (*Chaetura cinereiventris*), represented by the inverted triangle (identified as C) closest to the apex of the diagram, are, from first to third phalanges: 19, 21, and 60%. Conversely, the phalangeal proportions of the fully terrestrial, and highly cursorial, rhea (*Rhea americana*), represented by the open circle closest to the base of the diagram (R), are 54, 32, and 14%. We include data from studies of 32 climbing, perching, or raptorial birds (3 woodpeckers, a toucan, a colie, 4 parrots, 2 cuckoos, a hoatzin, 4 owls, 6 falconiforms, an oilbird, a hornbill, a swift, and 7 perching passeriforms), all of which possess grasping feet. Data from studies of 22 terrestrial birds (4 raites, a tinamou, 3 penguins, 4 galliforms, 2 herons, a stork, an ibis, 3 charadriiforms, a sand grouse, a cuckoo (*Geococcyx californicus*, the roadrunner), and a falconiform (*Sagittarius serpentarius*, the secretary bird labelled S) are included. Ten theropods and one ornithomimid are the dinosaurs included. Two specimens of the early fossil bird *Archaeopteryx* are represented by filled circles and two primitive dinosauriforms are represented by open crosses (*Marasuchus*, upper left, and *Lagerpeton*). The lower cluster of three pterosaurs (stars) includes (lowest to highest stars) *D. macronyx*, *D. weintraubi*, and *Peteinosaurus zambellii*; the upper cluster includes (left to right) *Rhamphorhynchus muensteri*, *R. longicauda*, and *Anurognathus ammoni*. The pterosaur points lie on or close to a cluster of five non-terrestrial falconiforms (the most dorsal, above *A. ammoni*, being the osprey, *Pandion haliaetus*).

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Explaining the geographic distributions of sexual and asexual populations

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Examination of the geographic distributions of sexual organisms and their asexual, or parthenogenetic, competitors reveals certain consistent patterns. These patterns are called geographic parthenogenesis^{1–8}. For example, if we compare sexual organisms with closely related asexuals, we find that, in the Northern Hemisphere, there is a strong tendency for the asexuals to occur further to the north. One researcher to document this pattern is Bierzychudek, who examined 43 cases (drawn from 10 genera) where the geographic distributions of a sexual plant and a closely related asexual are known⁴. In 76% of these cases, the asexual plant's range was more northerly than the range of the sexual. Some of the remaining cases probably fit with this pattern, but more data must be obtained before this suggestion can be confirmed. Asexuals also tend to occur at high altitudes, and in marginal, resource-poor environments^{1–8}. We have constructed a mathematical model of a habitat that stretches from south to north in the Northern Hemisphere. Our computer simulations based on this model support the idea that a single basic process may account for much of what is known about geographic parthenogenesis. This process involves the movement of individuals from areas in which they are well adapted to areas where they are poorly adapted.

Details of our model are given in Box 1. We assume that the hypothetical organisms living in the habitat are obligately sexual hermaphrodites. Each adult produces a large number of offspring through 'female effort' (for example, by producing seeds or eggs), and mating is random within local areas. We also assume that the growing season is longer as one moves further south, and so, over the course of a generation, adults in southern regions produce more offspring through female effort than do adults in northern regions. Within a local area, the expected number of offspring produced by female effort is the same for all adults.

After the production of offspring the adults die, and the juveniles are subject to viability selection. A given juvenile's chance of surviving this stage depends on its phenotype, and on the local environment within which it is born. The optimal phenotype varies from one location to another. We assume that phenotype is entirely determined by genotype. Offspring phenotypes are normally distributed around the mean of the phenotypes of their parents (this is the 'infinitesimal model'⁹).

After viability selection, some juveniles migrate to other regions.