

Pterodactyl habits — real and radio-controlled

SIR—Following in part new work by others^{1,2}, Unwin³ has suggested that the pterosaur's ability to move on the ground was very limited. This contradicts arguments that pterosaurs were terrestrial, erect-limbed bipeds⁴. Pterosaur anatomy and lifestyles show a diverse pattern of running and climbing adaptations.

It has recently been shown that in some pterosaurs the lower hip elements were splayed apart, and that the acetabulum faced to the side or a little up⁵. Unwin believes this means that they had sprawling, "clumsy" legs. But sprawling lizards and certain bats are quite agile, and erect birds also have widely separated lower hip elements and side-facing hip sockets. The sharply inturned, bird-like femoral head of the early pterosaur *Dimorphodon* worked in an erect plane, with the knee only moderately bowed out. In more advanced pterosaurs less offset, more spherical femoral heads indicate that they had reverted to more supple, semi-erect legs. Trackway gauge probably remained narrow because the knee was sharply flexed postero-medially. It is emphasized that the pterosaur's avian-style knee, shank and ankle were too stiff to follow the twisting motions of a truly sprawling gait. Nor did any pterosaur have reduced swift- or frigate bird-like legs that would have made them incompetent on the ground.

Quetzalcoatlus firmly establishes that pterosaurs were fast and agile on the ground. This giant lived on a flat floodplain 400 km from the palaeocoastline⁶. Restorations I helped draw up for a scale flapping flight model⁶ indicate that *Quetzalcoatlus* was 10 feet tall and massed perhaps 250 pounds; too large to roost in trees, pursue aerial prey, or to snap up fish from its habitat's limited watercourses while on the wing. Carcass scavenging was not possible either because the crane-like beak was much too weak, and even Marabou storks use their much stouter beaks only to pick up scraps dropped by vultures⁷. Instead, *Quetzalcoatlus* probably picked up fish, frogs, turtles and so on from the shallows. On windless days it had to

take off with an $\sim 30 \text{ km h}^{-1}$ run. The dense bristle-toothed jaws of smaller filter feeders such as *Pterodaustro* could also only be swished through the water as they waded.

As for how pterosaurs walked, flexing the elbow 90° downwards allowed their arms to work in a narrow gauge mode. Long-tailed rhamphorhynchoids could have been both two and four legged, except for *Dimorphodon* whose upper arm and hand were too short relative to the hindlimb for quadrupedalism. I agree with Pennycuik² that the tailless pterydactyls lacked the adaptations for full bipedalism found in tailless birds — they were more quadrupedal.

Impressions show that the wing membrane's trailing edge attached to the body⁴, or to the thigh¹, although these may be partly folded membranes overlapping the thighs. The rhamphorhynchoid's long, rudder-tipped tail acted as an auxiliary control surface. Tailless pterodactyls may have evolved their more supple legs in order to manipulate a hip-to-ankle membrane. Folded for streamlining during cruising flight, it could have deployed into an inverted-V shaped tail surface for landings, for instance. Traces of such a uropatigium appear to be preserved in two *Pterodactylus* specimens^{1,8}, despite Wellnhofer's arguments to the contrary.

As shown by squirrels, cats, and many birds, running and climbing are not mutually exclusive adaptations. Small pterosaurs were probably good at both, and the long, divergent outer toe of rhamphorhynchoids may have enhanced the grasping ability of their feet. However, the rhamphorhynchoid's long, ossified-rod stiffened tails could not fold tightly enough to be out of harm's way if their owners hung from branches by their hindfeet³.

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Of fast teeth and big heads

SIR—Beynon and Wood interpret their important data on early hominid molar growth¹ to suggest that hominid growth two million years ago was 'more rapid' than that for modern teeth: "The absolutely shorter growing period of these larger molar crowns suggests that there was strong selection to form teeth quickly and have them erupted into the mouth early in development." There is a confounding problem of anthropocentrism here — and a common fallacy of adaptationist thinking in cases of pleiotropy.

Comparisons of the duration of life span phases in primates suggest that developmental rates have been slowed between monkey and ape, and slowed again between ape and modern humans; it is probably not a matter of 'why they were fast' but of 'why we are so slow'.

For our slowing, a proximate cause is not hard to find, given a tendency toward juvenilization (besides the flatter faces of later adult hominids, the progressively-reduced crown surface area of mandibular cheek teeth² is also consistent with retention of juvenile features). Precocious puberty does make heads relatively larger, compared to pelvic outlets, causing problems in subsequent generations. Given that a fetus with a big head kills not only itself but its mother and thereby other siblings, it is hard to imagine a more serious 'genetic disease' than big heads; the resulting selection against average and faster-than-average developmental rate variants must have been severe, with only slower-than-average variants surviving to raise children³.

Although the selection pressures on slowing might have been solely associated with slowed fetal development to hold down head size until the end of standard gestation, slower somatic development probably carried over to later life as well, since later developmental landmarks also suggest slowing⁴. Such 'birth canal bottleneck' selection favouring slowed development is far removed from 'strong selection to form teeth quickly'. Where there is pleiotropy — overall developmental rates are a prime example of diverse body features controlled by a common set of genes — cause and effect are sometimes linked by long indirect paths that confound straightforward adaptationist reasoning.

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The half-scale, radio-controlled flapping model of the pterosaur *Quetzalcoatlus* in flight over Death Valley. Wingspan of the model was 11 m. Courtesy AeroVironment Inc.