The bizarre wing of the Jamaican flightless ibis Xenicibis xympithecus: a unique vertebrate adaptation

Nicholas R. Longrich and Storrs L. Olson

1 Department of Geology and Geophysics, Yale University, PO Box 208109, New Haven, CT 06520, USA
2 Division of Birds, National Museum of Natural History, Smithsonian Institution, PO Box 37012, Washington, DC 20013-7012, USA

Birds have frequently evolved to exploit insular environments by becoming adapted to a terrestrial lifestyle and losing the ability to fly, usually via reducing the wings and pectoral girdle. The enigmatic flightless ibis Xenicibis xympithecus (Threskiornithidae) from the Quaternary of Jamaica provides a rare example of flight loss in ibises. We report on previously undescribed fossils of Xenicibis, and show that the wing differed radically from that of all other birds, flightless or volant. The metacarpus is elongate, grotesquely inflated and has extremely thick walls; phalanges are short and block-like; the radius is distally expanded; and the humerus is elongate. The furcula, coracoid and sternum are all well developed. We propose that the elongate forelimb and massive hand functioned in combat as a jointed club or flail. This hypothesis is supported by the morphology of the carpometacarpus, by features permitting rapid extension of the wing and by the presence of fractures in wing bones. Although other birds use the wings as weapons, none resemble Xenicibis, which represents a unique and extraordinary morphological solution to this functional problem. Xenicibis strikingly illustrates how similar selective pressures, acting on a similar starting point, can result in novel outcomes.

Keywords: Threskiornithidae; flightlessness; Jamaica; Quaternary

1. INTRODUCTION

Birds have repeatedly evolved flightlessness to exploit insular environments where mammalian predators and competitors are absent, and flightlessness is typically associated with reduction of the forelimbs and pectoral girdle [1,2]. Flightlessness has evolved dozens of times in island habitats, and in many taxa, including waterfowl, megapodes, rails, pigeons, parrots [2] and ibises [3,4].

Ibises (Threskiornithidae) are a small, nearly cosmopolitan family of long-billed, long-legged ‘wading’ birds that inhabit wetlands, forests and plains [5,6]. All extant species are volant, but two extinct species are flightless. These are the kiwi-like Apteribis [4,7], from the Hawaiian Islands, and the peculiar Xenicibis xympithecus, described from fragmentary remains from the Quaternary of Jamaica [3]. Xenicibis was a relatively large ibis; a maximum femur diameter of 8.7 mm predicts that it weighed approximately 2 kg [8], roughly the size of a domestic fowl. It was considered possibly flightless based on an incomplete coracoid, a supposition confirmed by the discovery of a complete humerus [9].

Later, a partial skeleton prepared from a block of cave breccia (USNM 460349) included the radius, ulna and a carpometacarpus so utterly strange in morphology that it appeared to represent some inexplicable pathology. However, subsequent discoveries of additional material from numerous additional individuals, including almost all of the skeleton (figure 1), show that the bizarre morphology of the wing represents an adaptation unprecedented among the vertebrates, which we here describe and attempt to interpret.

2. DESCRIPTION AND COMPARISONS

The highly modified manus is unlike that of any other bird, flightless or volant (figure 2a–d). The major metacarpal is massive, inflated, strongly bowed and expanded distally. Its diameter is up to 12.8 mm dorsoventrally and 9.9 mm anteroposteriorly, exceeding the diameter of the femur. The bone is hollow, but the anterior wall is broad and thickened (figure 2e), being up to 3 mm thick in this area, whereas the cortex of the femur is under 2 mm thick.

The alular metacarpal has a reduced extensor process. The shaft of the minor metacarpal has a thick cortex and a subtriangular section, unlike the strap-like form seen in other birds, and is unusual in being shifted dorsally to lie directly behind the major metacarpal.

The carpal trochlea has a reduced ventral ridge and the articulation for the radiale is symmetrical, pulley-shaped and extended anteriorly. This joint allowed the wrist to swing forward in the plane of the antebrachium, without the complex pronation and supination that occurs in the wing of volant birds [10], while the anterior extension of the carpal trochlea permitted hyperextension of the manus.

The proximal phalanx of the major digit is a stubby and block-like element (figure 2h). It has a subtriangular section and weakly developed articular surfaces.

The radius (figure 2h) is expanded distally to give it a club shape, and it is unlike typical birds in that its diameter exceeds that of the ulna. Unusually, the ulna is
slender and nearly straight (figure 2h). Its proximal articular surface is on the proximal end of the bone such that the elbow can be fully extended, placing the ulna’s long axis in line with the humerus. Distally, the shaft is dorsoven-trally flattened and the articulation for the ulnare is reduced.

The humerus (figure 2h) is typically of flightless birds [9] except that the shaft is elongate and bowed dorsally. The shaft is slender proximally but expanded distally. The distal end is twisted by approximately 30° such that the articular facets are directed ventrally.

Unlike other flightless birds, particularly Apteribis, the pectoral girdle is relatively well developed. The coracoids (figure 3e) and furcula (figure 3f) are large and robust. The sternal carina (figure 3g), while reduced compared with volant ibises, is large when compared with that of Apteribis or other flightless birds.

Other skeletal elements show modification, albeit less extreme. As in other ibises, the beak is long and decurved (figure 3a,b), but the tip is knob-like, as in Apteribis, rather than spatulate. The parietals and frontals (figure 3d) are thickened by a honeycomb of cancellous bone. The vertebræ and notarium are robust, but otherwise unremarkable. The hindlimb (figure 3h–j) resembles that of Apteribis in being massive, with a shortened tibia and tarsometatarsus. The anterior portion of the ilium is dorsally expanded to form a tall crest and the synsacrum is robust (figure 3k,l), again resembling Apteribis.

Adaptation for a terrestrial, flightless lifestyle is correlated with hypertrophy of the hindlimbs and pelvis, and reduction of the forelimbs and pectoral girdle [1,2]. In this context, the long forelimbs and well-developed pectoral girdle of Xenicibis suggest that the wings were not functionless vestiges. The twisted humerus, short antebra-chium and massive, bowed metacarpus make it extremely unlikely that its wing could have functioned in flight; but the extreme modification of the forelimb argues that the wings had been adapted to function in some capacity.

3. FUNCTIONAL IMPLICATIONS
Attempts to identify avian analogues are complicated by the unique morphology of Xenicibis. The distally expanded radius does find parallels among steamer ducks (Tachyeres spp.; N. R. Longrich 2010, personal observation) and the extinct Rodriguez Island Solitaire (Pezophaps solitaria, Columbidae [11]). In those species, the wings are (or were) used to deliver hammering blows to conspecifics [11,12], suggesting that the wing of Xenicibis may have functioned as a weapon. Perhaps a better analogue is to be found among some of the mantis shrimps (Stomatopoda: Gonodactylidae); these have a club-like, distally inflated dactyl that is used to strike prey and conspecifics [13], again hinting that Xenicibis may have used the club-shaped hands to deliver blows.

We therefore propose that the wing of Xenicibis functioned as a club or flail. Several features of the limb would have facilitated this function. Kinetic energy is the product of mass and velocity squared; accordingly, weapons such as clubs and flails have a long handle to increase the angular velocity of the club, and are heavily weighted to increase the mass accelerated by the swing, and the centre of mass is near the end of the club, where the angular velocity is highest. Precisely this design is seen in the hand of Xenicibis, where the end of the wing is massive, and the proximal metacarpus and long forelimb could act as a handle. The comparatively weak wrist joint does not preclude such a function, because during impact a club acts as a free body [14]; the hollow metacarpal also allows the hand to achieve greater strength for a given amount of material, much like an aluminium baseball bat [14].

Several morphological adaptations would have further increased the wing’s effectiveness as a weapon. Reduction of the extensor process and elongation of the manus would decrease the mechanical advantage of the wing extensors, producing a more rapid wing extension. The retention of long wing bones allows the forelimb to be swung rapidly, while the ability to hyperextend at the elbow and wrist increase the wing’s effective length, and therefore its angular velocity when swung.

This hypothesis can be tested by looking for direct evidence of agonistic behaviour in the form of traumatic injuries sustained from delivering or receiving blows. Fractures are common in pugnacious birds such as the steamer ducks and solitaire [11,12], and are therefore predicted to occur in Xenicibis. Two bones of Xenicibis show evidence of healed fractures. The first is a humerus that was broken in two (figure 4a); a fracture callus indicates healing although the bones failed to knit. The second specimen (USNM 460349) is a carpometacarpus (figure 4b) with a massive callus overgrowing the anterior surface of the major metacarpal and extending inside the bone as well; the hand apparently suffered an impact that fractured the anterior wall of the metacarpal.

4. DISCUSSION AND CONCLUSIONS
A number of birds use the wing as a weapon, although none resemble Xenicibis. Some employ sharp spurs,
including screamers (Anhimidae), some jacobas (Jacana, Hydrophasianus), the spur-winged goose (Plectropterus), the torrent duck (Merganetta) and nine species of lapwing (Vanellus) [5,15,16]. Other birds bear a bony knob on the alular metacarpal that is used to punch and hammer opponents. These include steamer ducks (Tachyeres),
of Falconiformes, including hawks, kites, falcons and ibises are monogamous [5], and there is no evidence that the club is dimorphic. It is therefore likely that intraspecific combat would have focused on securing territory, rather than mates. Given this, the need for Xenicibis to defend its nest and young may have been greater than in other insular birds. It should be kept in mind, however, that the hypotheses of intraspecific combat and defence are not mutually exclusive.

Discussions of evolution often focus on the importance of adaptive determinism, where similar selective pressures tend to produce similar results [23], versus contingency, where chance events cause similar starting points to lead to different outcomes [24]. Although many birds have co-opted the wing to serve as a weapon, in the case of Xenicibis, adaptation of the wing as a potent weapon has produced a design that is not only unique among the thousands of species of extant and fossil birds, but also unique among vertebrates. Although the appendages of vertebrates have repeatedly become specialized for walking, running, swimming, burrowing and flying [25], Xenicibis is unique in having modified its pectoral appendage into a jointed club that can be swung to increase the speed and energy of the blow. Xenicibis therefore strikingly illustrates how evolution can produce radically different outcomes, even as similar selective pressures act on similar morphologies.

We thank Ross MacPhee for the opportunity to study the Red Hills fossils. Discussions with Helen F. James and Richard L. Zusi and guidance from B. Rosemary Grant were helpful in developing this project. N.R.L. received support from an NSF Graduate Research Fellowship, an Alberta Ingenuity Graduate Studentship and the Yale Institute for Biospheric Studies. Finally, we thank the reviewers for their helpful reviews of this paper. Fossil specimens are deposited in the Department of Paleobiology, National Museum of Natural History (USNM), Smithsonian Institution, Washington, DC.

**REFERENCES**


